

AGGRESSION AND FAMILIARITY AS FACTORS IN
MATE SELECTION IN Peromyscus polionotus
AND Peromyscus maniculatus

BY

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To my wife Carole and my daughter Danielle
and to my parents

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Aggressive ability and familiarity were examined as factors in the social preference and mate selection of males and females of the monogamous species P. polionotus, and the polygamous species P. maniculatus. The aggressive behaviors and nesting behavior of P. polionotus were observed in a seminatural apparatus; factors assessed were 1) familiarity based on cohabitation, and 2) aggressive ability as determined through aggressive interactions. Groups observed were composed of either two pairs of familiar opposite-sexed individuals, or two unfamiliar animals of each sex. Preferences of both species were assessed in an automated preference apparatus. In addition to the two factors assessed in the seminatural apparatus, the effects of familiarity based on relatedness were assessed in the preference apparatus. Measures recorded were the number and duration of visits

to stimulus animals. In the seminatural setting P. polionotus of both sexes displayed aggression, and nested more frequently with the more aggressive of two opposite-sexed individuals. Males of this species also exhibited a behavior, aggressive digging, that may signal their aggressive status. Peromyscus polionotus and P. maniculatus of both sexes exhibited evidence of preference for more assertive opposite-sexed individuals (high rather than low tendency to interact) in the preference apparatus. Peromyscus maniculatus of both sexes also displayed preference for individuals of the opposite sex that they had previously been housed with, but such familiarity did not affect preference in P. polionotus. The lack of a significant effect of familiarity on preference in P. polionotus was consistent with the nesting behavior of this species in the seminatural apparatus. Differences in the responses of P. maniculatus and P. polionotus to familiar individuals may be based on differences in the opportunities individuals of these species have to use this factor in mate selection.

Peromyscus polionotus females demonstrated significant preference for siblings over nonsiblings, and males tended to display higher sibling than nonsibling scores. Inbreeding in P. polionotus may permit individuals of this species to found populations in isolated patches of favorable habitat. Lack of significant preference by P. maniculatus for siblings or nonsiblings was interpreted as due to competing preference responses in this species.

SECTION I INTRODUCTION

The success of an organism in leaving a numerous posterity is not measured only by the number of its surviving offspring, but also by the quality or probable success of these offspring. It is therefore a matter of importance which particular individual of those available is to be their other parent. (Fisher, 1958, p. 143)

Few factors are as important to an individual's reproductive success as is the selection of a mate. Mate selection involves more than simply the identification of potential partners as to species and sex. In order for an individual to maximize its future representation in the gene pool it must also select the "best" possible mates on the basis of a variety of other considerations.

There has been much theoretical speculation on the proximate and ultimate bases of mate selection and on the relative importance of mate selection to different mating systems. In the last decade a considerable effort has been made to collect empirical data on mate selection, but large gaps still remain in the existing data which must be filled before many important theoretical problems can be resolved. Particularly lacking are data on male choice and data on mate selection in mammalian species, especially those considered to be monogamous. The lack of data on male choice probably stems in large part from a traditional emphasis on female choice and male-male competition (Bateman, 1948; Daly & Wilson, 1978; Trivers, 1972;

Williams, G. C., 1966) and the belief that male choice was either nonexistent or negligible in the face of this competition. More recently, however, it has been suggested that mate selection should be of some consequence to males as well as females (e.g., Dewsbury, 1982c). The lack of data on monogamous mammalian species may be due in part to two factors that make it somewhat difficult to observe these species: 1) monogamy appears to be uncommon in mammals (Alexander, 1974; Crook, 1977; Kleiman, 1977; Orians, 1969) and 2) most mammals, especially the smaller species, are largely nocturnal (Vaughan, 1978).

Study of the proximate factors involved in mate selection is extremely important to the resolution of issues about the evolution and relative importance of mate selection in various mammalian taxa. Factors that have been proposed to be of major importance to mate selection are of two general types: those related to the genotype of a potential mate, such as genetic quality (Trivers, 1972, 1976; Zahavi, 1975), and relatedness (Maynard Smith, 1956); and those related to resources, such as the ability to accrue resources (Trivers, 1976) and parental investment (Bateman, 1948; Trivers, 1972). The relevance of any particular factors as criteria in mate selection will vary among species, between sexes, and across mating systems, as a function of differences in a group of interrelated variables including ecological factors (Borgia, 1979; Emlen & Oring, 1977; Halliday, 1978). Differences in the degree to which individuals of various species utilize particular factors as criteria in mate selection would be expected to reflect differences in the adaptiveness of those criteria to mate selection in those species. Comparative studies of mate

selection or social preference. In different species, therefore, can provide an empirical basis for evaluation of hypotheses on the importance of various factors to mate selection under different social or mating systems. Such comparisons would be most effective when the species compared were closely related (King, 1970) so that the species do not differ in so many respects as to obscure the relationships of interest.

Two factors of the sort that might be expected to be of broad importance as criteria for mate selection across most species, but may be expected to vary in importance among species, are the aggressive ability of a potential mate, and that animal's degree of familiarity with the individual expressing choice. An individual of high aggressive ability could be defined as one that is highly competent in the performance of aggressive behavior (i.e., displays, threats, and fights). Individuals of high aggressive ability would be expected to perform well in competition for contested resources and defense of mates and/or offspring. Familiarity can be of two types, these are 1) familiarity gained through exposure to other unrelated individuals, and 2) familiarity with kin. In the first sense, familiarity may provide a basis for evaluation of former mates or a means of discriminating between two potential mates. In the second sense, familiarity may provide a basis for avoidance of inbreeding, or as a yardstick for comparison of potential mates (Bateson, 1978, 1980).

This study was designed to provide data on the importance of aggression and familiarity as factors affecting mate preference in males and females of two closely related species of muroid rodents with

different mating systems: the monogamous species Peromyscus polionotus and the polygamous species Peromyscus maniculatus. In light of the relative lack of data on mate selection in monogamous species the major focus of this study is on P. polionotus. The discussions that follow provide a brief review of relevant theoretical factors in mate selection, and a demonstration of the importance of aggression and familiarity as factors in mate selection, with an emphasis on mammalian species.

Aggression as a Factor in Mate Selection

Darwin (1859) recognized that some males could gain a reproductive advantage over other males by defeating them in fights for females. It has been suggested (Bateman, 1948) that the evolution of male-male competition had its basis in differences in male-female strategies of investment in gametes. Males are generally considered to invest little energy in the production of gametes, whereas females invest a great deal (Bateman, 1948; Orians, 1969; Stacey, 1982; Trivers, 1972). Because of their larger investment females are valuable to males, and the probability that females will obtain mates is high, but their reproductive success will be limited by the number of gametes they can produce. Males, however, because they invest little energy in the production of individual gametes, can afford to produce large numbers of gametes--with which they could potentially fertilize large numbers of females. A male's reproductive success, therefore, may be greatly influenced by the number of females he mates with--and males may be expected to compete to fertilize females (see however, Dewsbury, 1982c;

Nakatsuru & Kramer, 1982). This argument was extended by Trivers (1972), who restated it in a more general form based on the overall relative level of parental investment of the two sexes, which he hypothesized to determine the intensity of male-male competition in species as well as the form of the mating system (see however, Kleiman & Malcolm, 1981, p. 371; Wickler & Seibt, 1981). The level of success achieved by a male in competitive mating may often depend upon his ability to dominate other males. This notion has been examined in a wealth of studies, recently reviewed by Dewsbury (1982b), on the relationship between "dominance" and various aspects of reproduction.

A male's ability to conquer other males, however, also provides females with a basis by which to judge him against other males--a basis for "female choice" (Darwin, 1874). Borgia (1979) has suggested that a female's best indication of the relative overall genetic quality of a male is provided through his aggressive interactions with other males. Females choosing aggressive males, or allowing such males to mate with them, may in effect be selecting "good genes" for their offspring (Maynard Smith, 1956; Trivers, 1972). Selection for good genes has also been suggested as a basis for the evolution of extravagant sexually dimorphic characteristics (Fisher, 1930), as a basis for lek behavior (Borgia, 1979), and as a basis for female choice in Drosophila (Partridge, 1980). The major obstacle to the use of heritable factors as a basis for choice is the problem of "using up" the genetic variance for a trait (Krebs & Davies, 1981; Maynard Smith, 1978). Several factors, however, have been suggested to act to maintain genetic variance; these include 1) advantages for

heterozygotes (Borgia, 1979), 2) variation in the optimal genotype in space and time (Krebs & Davies, 1981), 3) factors such as chronic parasitism, that may result in cyclic changes in the optimal genotype (Hamilton & Zuk, 1982), and 4) rate of mutation in polygenic characters (Lande, 1976).

The northern elephant seal (Mirounga angustirostris) provides an example of the importance of male aggressive ability in female choice in a natural setting. During the breeding season males of this species establish dominance hierarchies which are maintained through threat and combat. Dominant males guard groups of females from other males, and account for the majority of first copulations (LeBeauf, 1974; LeBeauf & Peterson, 1969). Females help insure that they will be inseminated by an aggressive dominant male by vocalizing loudly if a subordinate male attempts to mount. The dominant male, alerted by the female, drives off the subordinate male and copulates with the female (Cox & LeBeauf, 1977). The authors note that females of many polygynous species might be expected to incite male-male competition in this manner. Cox (1981) has observed that female elephant seals are less likely to vocalize if the male mounting them has just displayed dominance over another male and suggested that females may thus select for males that frequently display their aggressive ability. Cox hypothesized that in general "in species where social status of males is correlated with their genetic fitness, female choice is likely to be based on social signals which are used in competition between males" (p. 197). Similar hypotheses have been proposed by Borgia (1979) and Alexander (1975). Cox (1981) has provided examples of several species in which females appear to use male's aggressive signals toward each other as a basis for choice. The

list consists of a fairly diverse array of species including territorial birds (Armstrong, 1973; Thorpe, 1961), tree frogs (Whitney & Krebs, 1975a, 1975b), sticklebacks (Tinbergen, 1951), and a lek-forming bird, the ruff Philomachus pugnax (Hogan-Warburg, 1966).

Male aggressive ability need not be heritable or manifest at the time of mating to be an important factor in female choice. Male differences in aggressive ability, for example, will be related to differences in their ability to acquire and hold territories (Brown, J. L., 1964). A female choosing a male with a superior territory is in effect also choosing a male that has been able to first obtain that territory in competition with other males, and further to maintain it in the face of threats from other males.

Female preference for aggressive males has also been demonstrated in laboratory choice tests. Sexually experienced female brown lemmings (Lemmus trimucronatus) in estrus were found, in olfactory choice tests, to prefer dominant over subordinate males (Huck, Banks, & Wang, 1981). Female preference was also predictive of male performance in later dominance tests; estrous females again preferred dominant males while diestrous females preferred subordinate males. The authors found that dominant males had heavier testes and higher testosterone levels than subordinates, and they hypothesized that female choice might be based on differences in androgen dependent male odors. Estrous females were also found to exhibit more copulation with dominant males in tether-choice tests (Huck & Banks, 1982).

Costanzo and Renfrew (1977) studied the preference of sexually experienced and naive female rats for dominant and subordinate male

odors. Ovariectomized sexually naive females displayed no preference in hormonally induced estrus. Ovariectomized sexually experienced females preferred dominant males when not injected with hormones, but subordinate males when in hormonally induced estrus.

As discussed earlier a female may often invest relatively more than a male in offspring, and a female's reproductive success may often be more limited than a male's. Because of these factors females are generally considered to be more choosy than males when selecting mates (Bateman, 1948; Burley, 1977, 1981; Daly & Wilson, 1978; Trivers, 1972; Williams, G. C., 1966) and the majority of studies of social or mate preference have been studies of female choice. Male reproductive success, however, depends on not only the number of mates males acquire but the quality of these mates as well (Wade, 1979). Ralls (1976) has, for example, suggested that larger females may often be better mothers. Factors such as this might be considered trivial if males were capable of inseminating an unlimited number of females. However, although males appear to produce an enormous number of sperm and therefore to be capable of inseminating an enormous number of females, these sperm are emitted as ejaculates--of which a male may produce only limited numbers (Dewsbury, 1982c; Nakatsuru & Kramer, 1982). Mate selection may, therefore, often be of some consequence to males as well as females (Dewsbury, 1982c).

The aggressive ability of females may be an important criterion for male choice. Females with high aggressive ability may be more capable than females with low ability in such behaviors as defense of young or nest sites, or in competition for food items. Males of some species

have also demonstrated an ability to discriminate the aggressive status of other individuals, and therefore the potential to use this factor in mate selection. Male rats, for example, spend more time investigating odor from a dominant male than from a subordinate (Krames, Carr, & Bergman, 1969). Male mice also discriminate between the odors of dominant and subordinate males (Carr, Martorano, & Krames, 1970) and investigate areas marked by dominant males less than those marked by subordinate males (Jones & Nowell, 1973). Both male and female saddle-backed tamarins investigate dominant male scent marks more than those of subordinate males (Epple, 1973, 1974).

Although the majority of preference studies to date have been conducted with polygamous species, there is no reason to believe that members of monogamous species should be any less adept at discriminations based on differences in aggressive status, or that the ability to make such discriminations should be any less useful to members of monogamous species. Aggression serves many of the same functions in monogamous species as in polygamous species. Although male-male competition and aggression near the time of copulation may be less important in monogamous than in many non-monogamous species, aggression serves many functions at other times in an organism's lifetime, and success in these other aggressive encounters will be just as important to monogamous as to polygamous males. For example, defense of resources critical to raising young, and in many cases to initially attracting a mate, is hypothesized by some authors to be universally displayed by males of monogamous species. Kleiman (1977) states that "The male's territorial defense, which prevents the over-

utilization of necessary resources, is practiced by males of all monogamous species" (p. 54). Kleiman (1977) has also indicated that females of monogamous mammalian species may commonly be as involved as males in territorial defense and contrasts this behavior with a lack of territorial defense by non-monogamous females. This hypothesis is similar to one previously proposed by Wilson (1975) as one of the biasing ecological conditions for monogamy - that two adults are required to defend valuable resources contained in the territory. If monogamous females help to acquire and defend resources then monogamous males may do well to choose aggressive females as mates.

An additional consideration, related to the possible function of aggression as a factor in mate selection in monogamous species, is the "early breeding" hypothesis proposed by Darwin (1874). According to this theory the most healthy, more dominant members of a species will come into breeding condition earlier in the season, and establish territories earlier, than the less vigorous subordinate individuals. The more dominant individuals of each sex should then choose each other as the "better" mates in preference to subordinate individuals. Two species whose behavior may support the occurrence of this form of selection are the arctic skua (*Stercorarius parasiticus*) and the mourning dove (*Zenaidura macroura*). Individuals generally pair for life in the arctic skua (O'Donald, 1959). Darker males of this species tend to breed earlier than birds of light or intermediate phenotype, and females breeding for the first time are more successful with dark males. Early breeding and large territory size are both correlated with early hatching, and success of new pairs with dark males may be

related to male ability to hold large territories (Davis & O'Donald, 1976). Dominant male mourning doves prefer dominant females in experiments with penned populations (Goforth & Baskett, 1971). Dominant pairs breed earlier than subordinate pairs, and more offspring of dominant pairs survive.

Based on theoretical considerations, and on the results of research conducted to date, predictions can be made as to the relative importance of aggression as a factor in mate selection in species with polygamous and monogamous mating systems. Males that are above average in their aggressive abilities should generally be preferred as mates by females of monogamous and polygamous species. Females of monogamous species, because they may form long-term pair bonds and consequences of their choice may therefore be more long-term, might be expected to display stronger preference than polygamous females. Males of monogamous species might be expected to display preference for females with higher aggressive ability because, among other considerations, such females may be in breeding condition earlier and might be expected to better share responsibility for territorial defense. Polygamous males might also prefer females with higher aggressive ability because such females may be better able to defend young or resources necessary for raising young, but preference should not be as critical for these males as for monogamous males.

Familiarity as a Factor in Mate Selection

Familiarity could be an important factor in mate selection in several ways. It would be expected, for example, that early familiarity with conspecifics should aid individuals in discriminating

between members of their own and other species. Familiarity could additionally be an important factor in recognition of kin, and therefore a factor of importance in kin-selection and in avoidance of inbreeding. It may also be of importance to animals of many species to be capable of discriminating between unrelated strange and familiar individuals. Two aspects of familiarity, recognition of kin and of familiar others, will be discussed further.

Kin Familiarity

Bateson (1978, 1980) has hypothesized that early experience with kin imprints individuals to aspects of both kin and species, and that such kin familiarity is important to selection of mates of the appropriate species and to avoidance of inbreeding at sexual maturity. Avoidance of inbreeding is an important consideration in mate selection because inbreeding often leads to inbreeding depression--a reduction in the viability of inbred offspring and/or of their ability to reproduce. Inbreeding depression has been documented in a variety of species from ungulates (Ralls, Brugger, & Ballou, 1979) to rodents (Hill, 1974), birds (Bulmer, 1973), and Drosophila (Maynard Smith, 1956). In many mammalian species inbreeding is avoided in part because individuals of one sex emigrate from the natal group before sexual maturity. This type of emigration has been observed in chimpanzees (Pusey, 1980), lions (Bertram 1975, 1976), olive baboons (Packer, 1979), black-tailed prairie dogs (Hoogland, 1982), and a variety of other species. Intergroup transfer of individuals in mammalian species and the significance of this behavior to avoidance of inbreeding have recently been discussed by Packer (1979). Emigration from natal groups

may be mediated by adult aggression in many species (e.g., langurs: Sugiyama, 1965; elephant-shrews: Rathbun, 1979). However, female (and male?) choice has also been suggested as a factor (Hoogland, 1982; Wittenberger, 1981) since individuals should be selected to emigrate from natal groups if 1) relatives refuse to mate with them and 2) alternative mates are not readily available. In at least some rodent species reproductive maturity may be inhibited by pheromones produced by adults (Bediz & Whitsett, 1979; Drickamer, 1979; Lawton & Whitsett, 1979; Lombardi & Whitsett, 1980). For young of such species emigration from the natal group may provide the major opportunity for reproduction.

Although it would appear that avoidance of inbreeding should generally be the rule, certain circumstances may favor inbreeding. If inbreeding were not detrimental, individuals could increase their inclusive fitness through mating with relatives (Bengtsson, 1978; Maynard Smith, 1978). Female control of the sex of offspring in the wasp Euodynerus foraminatus may be used to counterbalance the detrimental effects of inbreeding and allow individuals of this species to take advantage of the increase in relatedness resulting from inbreeding (Cowan, 1979). Bengtsson (1978) hypothesized that it would be adaptive for individuals to inbreed if the costs of inbreeding were lower than the costs that would be incurred in dispersal or in competition for mates in the natal group. Costs incurred through dispersal would include such factors as increased exposure to predators and to unfavorable environmental conditions. Inbreeding may also at times be suited to specialized environmental situations; as noted by

Mayer (1970) "An outbreeder may also be so well buffered that it stagnates evolutionarily. At the other end is the extreme inbreeder which has found a lucky genotypic combination that permits it to flourish in a specialized environmental situation . . . (p. 245). Shields (1982) compared the advantages and disadvantages of outbreeding, inbreeding, and asexual reproduction and concluded that inbreeding is often more advantageous than commonly assumed and should be "expected to be common in organisms produced by stable lineage-environment associations" (p. 274).

Although inbreeding may be adaptive under particular circumstances individuals of most species should, given a choice, prefer to breed with nonsiblings rather than siblings. Some support is lent to this statement by the observation that the initiation of breeding in sibling pairs is often delayed in comparison to the initiation of breeding in nonsibling pairs (Batzli, Getz, & Hurley, 1977; Dewsbury, 1982a; Hill, 1974; McGuire & Getz, 1981). The contribution of preference per se to these findings is, however, difficult to assess. Animals in these studies were not allowed a choice of mates and delayed reproduction, or lack of reproduction, may result from several factors (Dewsbury, 1982a) in addition to preference. It would be expected that reproductively mature males and females of most species should prefer to associate with nonsiblings rather than siblings, and that this preference should be apparent in choice tests.

Familiar Others

Differences in familiarity need not only be defined in terms of differences in relatedness, differences in familiarity may also be

defined in terms of differences in the amount and type of contact an individual has had with others. Familiarity in this sense is an important factor in many aspects of an animal's behavior, including mate choice. Individuals should improve their reproductive success by retaining mates that they have previously bred successfully with and choosing unfamiliar others over mates with which breeding has previously failed. Coulson (1966), for example, found kittiwakes (Rissa tridactyla) were much more likely to change mates if breeding had been unsuccessful; and red-billed gulls (Larus novaehollandiae scopulinus) exhibit similar behavior (Mills, 1973). Although some authors (e.g., Halliday, 1978) have indicated that mate choice based on previous reproductive performance should only be of importance to species which pair bond for more than one season, all that is actually required is an ability to recognize previous mates. This ability has been demonstrated in several species including rats (Carr, Demesquita-Wander, Sachs, & Maconi, 1979; Carr, Hirsch, & Balazs, 1980; Krames, Costanzo, & Carr, 1967), lemmings (Huck & Banks, 1979) and prairie voles (Ward, Baumgardner, & Dewsbury, 1981). The ability to recognize previous mates may also enhance reproduction through allowing earlier breeding. This function of familiarity has generally been stressed for monogamous species (e.g., Daly & Wilson, 1978; Wilson, 1975).

The advantages of familiarity to mate selection, based on reproductive performance or early breeding, are related to an individual's previous breeding experience. Familiarity may, however, also bias selection of mates by sexually inexperienced individuals.

Females may, for example, require a male to exhibit some evidence of "commitment" to forming a pair-bond prior to copulation. The male may fill this requirement by investing a large amount of his time in the relationship, and thus preclude his finding another female (Maynard Smith, 1977), and/or by demonstrating his ability to provide resources (e.g., Nisbet, 1973). Evidence of commitment is likely to be most important to members of monogamous species, especially those in which individuals form prolonged or lifelong bonds, because many individuals of these species may only choose a mate once in their lifetime. Individuals of species that form prolonged pair bonds might also be expected to be more "prepared" (Seligman, 1970) to recognize differences in familiarity, than would be individuals of species that do not pair bond, if familiarity were important to the maintenance of pair bonds.

Many authors have indicated that males of polygamous species should mate with as many different individuals as possible (Adler, 1978; Bateman, 1948; Dawkins, 1976; Williams, G. C., 1966; Zucker & Wade, 1968). Although as noted previously males may have a limited capacity to mate and should therefore be somewhat selective when allowed a choice of partners (Dewsbury, 1982c; Nakatsuru & Kramer, 1982), it may still often be to a males advantage to obtain additional matings if the opportunity is presented. Familiarity may therefore be of importance (at least to polygamous males) in identification of females a male has already mated with. However, because mate infidelity could have serious consequences for monogamously mated individuals (Grafen & Sibly, 1978; Trivers, 1972),

it is likely that individuals of monogamous species have been selected to detect potential philanderers, and to select against such individuals as mates (e.g., Erickson & Zenone, 1976). It may be expected therefore that polygamous males would be more likely than monogamous males to prefer novel over familiar partners. This prediction is consistent with previous suggestions that males of monogamous species should be less likely than males of polygamous species to exhibit a "Coolidge effect" (Thomas & Birney, 1979; Wilson, Kuehn, & Beach, 1963; but also see Dewsbury, 1981a,b).

As a general set of predictions it might be expected that individuals of monogamous species would display greater preference for familiar individuals than would individuals of polygamous species. Because of differences in the consequences of choice it might also be expected that females would display stronger preference than males (e.g., Burley, 1981). Monogamous females would be expected to display the strongest preference for familiar individuals. Monogamous males should be expected to display some preference for familiar individuals, as might also polygamous females (unless greater benefits result from producing multiply sired litters). Polygamous males, however, due to a greater possibility of increasing their reproductive success through mating with more than one female, may be expected to display some preference for novel individuals of the opposite sex.

SECTION II
GENERAL EXPERIMENTAL CONSIDERATIONS AND METHODOLOGY

The discussions in this section provide a brief rationale for the choice of the particular species and experimental procedures that were followed in this study. This section provides general methodological information common to all experiments in this study, and a description of the apparatus used in these experiments.

Selection of Species

One of the methods that may be particularly suited to exposing and interpreting differences in social behavior among species is the comparative approach (Dewsbury & Rethlingshafer, 1973; King, 1970). Muroid rodents are a group that is particularly suited to the use of the comparative method (Dewsbury, 1974, 1978). The two muroid rodent species that were chosen for comparison in this study, the monogamous Peromyscus polionotus (oldfield mouse) and polygamous Peromyscus maniculatus (deer mouse), are both members of the maniculatus species group of the subgenus Peromyscus. Because the majority of mammalian species are considered to be non-monogamous (Alexander, 1974; Crook, 1977; Kleiman, 1977; Orians, 1969) and relatively little information is available about mate choice in monogamous mammalian species, it was considered to be particularly important that one of the species selected for comparison in the present study be a monogamous species. Although monogamy has been suggested for several rodent species,

"except for P. polionotus, the data are circumstantial" (Foltz, 1981a, p. 665) and are open to more than one interpretation. Data supportive of monogamy in P. polionotus include the consistent finding that the majority of reproductively mature individuals are captured as heterosexual pairs (Blair, 1951; Foltz, 1981a; Rand & Host, 1942; Smith, 1966), and behavioral (Blair, 1951) and electrophoretic (Foltz, 1981a) evidence that pairs form long-term reproductive associations. Information about mate selection in this species was also considered to be of importance, in addition to comparative considerations, because one subspecies, the beach mouse (P. polionotus leucocephalus), is presently considered endangered.

In contrast to P. polionotus, electrophoretic evidence indicates polygamy for P. maniculatus (Birdsall & Nash, 1973; Merritt & Wu, 1975) and females may even, on occasion, raise young communally (Hansen, 1957). Dewsbury (1981c) suggests that maniculatus may be even more promiscuous than indicated by electrophoretic studies because these studies do not consider the effect of factors such as "differential fertilizing capacity" (Lanier, Estep, & Dewsbury, 1979) that may affect estimates of the number of matings that have occurred.

Approaches to the Study of Social Preference

Ideally social behavior and social preference should be studied in natural settings. Although this approach may be utilized successfully with diurnal and highly visible species, it is often an impractical, or nearly impossible, approach for many species. As an alternative investigators have often turned to the study of populations in outdoor (Agren, 1976; Boice, 1977; Boice & Adams, 1980; Gipps & Jewell,

1979; Jannett, 1980; Lidicker, 1980) or indoor (Bowen & Brooks, 1978; Crowcroft & Rowe, 1963; Getz & Carter, 1980; Hill, 1977; Poole & Morgan, 1976; Reimar & Petras, 1967; Thiessen & Maxwell, 1979; Thomas & Birney, 1979) seminatural enclosures. While these enclosures do not replicate natural conditions in many respects, they do allow the investigator to approximate some aspects of the natural setting, and allow a degree of control over experimental variables that is generally not available in nature.

Even in a seminatural apparatus, however, interactions may often be so complex that it is difficult to evaluate the effects of any single variable on a particular behavior such as social preference. This problem has led investigators to the use of even more controlled situations, such as preference apparatus of various types, to evaluate the role of various factors in social preference. In the typical preference paradigm an animal (the "choice" animal) is allowed to express preference by "choosing" between two or more alternative stimuli. Behavioral measures of preference may include factors such as the number of approaches, number of visits, duration of visits, time spent huddling together, mating activity, and a variety of other measures. Use of preference apparatus, in addition to allowing more controlled investigation of particular factors (e.g., familiarity) than may be available in seminatural apparatus, allows the experimenter to control the degree of contact between choice animals and stimulus animals. In a tether preference apparatus, for example, stimulus animals are tethered in a fixed area while the choice animal is allowed free access to the apparatus and may express preference through

proximity or contact behaviors, or under appropriate conditions, mating behavior (Ward et al., 1981; Huck & Banks, 1982; Webster, Williams, & Dewsbury, 1982). An alternative method used in preference tests is to place collars on the stimulus animals, and then place these animals in compartments with doorways of a size large enough to allow access by choice animals, but too small for the collared animals to pass through (Mainardi, Marsan, & Pasquali, 1965; McDonald & Forslund, 1978). Direct contact between choice animals and stimulus animals may also be prevented by simply constructing stimulus compartments or containers so that they are not accessible by the choice animal (Agren & Meyerson, 1977; Carmichael, 1980; Carr, Wyllie, & Loeb, 1970; Murphy, 1977; Webster, Sawrey, Williams, & Dewsbury, 1982). Experimenters have also opted at times to test preference for odors from stimulus animals rather than using the animals themselves (Carr et al., 1980; Fass, Guterman, & Stevens, 1978; Gilder & Slater, 1978; Huck & Banks, 1979, 1980; Krames et al., 1967; Ruddy, 1980), or to restrict choice cues to olfactory cues by using anesthetized stimulus animals (Landauer, Banks, & Carter, 1977; Landauer, Seidenberg, & Santos, 1978; Murphy, 1980).

While preference apparatus offer the opportunity for greater control over variables than do seminatural apparatus, the conditions under which preference is assessed do not approximate natural conditions as closely as do conditions in seminatural apparatus. With preference apparatus, therefore, one may run a greater risk of obtaining results that are misleading in respect to behavior under more natural conditions. Social preferences may, for example, sometimes be

expressed less strongly in preference apparatus than they would be in a more natural context; one might therefore be more likely to falsely reject a factor as unimportant to social preference in these tests. One way to minimize this problem is to first assess a species' social behavior in more natural settings, such as in seminatural apparatus, and select factors for preference experiments on the basis of those results. Alternatively one might use results from seminatural experiments in part as a guide in interpretation of results from preference experiments.

General Experimental Information

This study was designed to provide data on aggression and familiarity as factors in the social preference of monogamous and polygamous species. Partial data are available about the function of these factors in the social preference of the representative species chosen for this study, P. polionotus and P. maniculatus.

Available evidence indicates that aggression may be an important factor in the social behavior of P. maniculatus, that more aggressive males may sire more offspring than less aggressive males, and that differences in male aggressive ability may be important in female choice in this species. In P. maniculatus blandus Blair and Howard (1944) found that, in experimental populations consisting of two individuals of each sex, one male would generally establish dominance over the other. The dominant male generally nested with both females more frequently than did the subordinate, and the authors were able to establish (through coat-color markers) that dominant males sired the

majority (19 of 21) of litters in their study. Dewsbury (1979, 1981c) found that male dominance in P. maniculatus bairdi was positively related to copulatory behavior, and that dominant males not only copulated more than subordinates, but that they also sired a larger number of offspring (Dewsbury, 1981c). Eisenberg (1962) observed that after the formation of dominance relationships between male P. maniculatus gambelli, females of this species that had been paired with subordinate males for two weeks prior to aggression tests generally failed to remain with their subordinate male partners and nested instead with the dominant male.

Blair and Howard (1944) studied two subspecies of P. pollionotus, P. pollionotus albifrons and P. pollionotus leucocephalus, and found little evidence of aggression against conspecifics by individuals of either sex. In addition all four individuals (two males and two females) in a group were frequently found nesting together. From these observations the authors concluded that P. pollionotus were a very social species. Field observations, however, do not support the notion that adult P. pollionotus are highly social. Although P. pollionotus are commonly found in family groups composed of a male, a female, and young (Blair, 1951; Foltz, 1979; Rand & Host, 1942; Smith, 1966; personal observations), sexually mature individuals of the same sex are never (Smith, 1966), or very infrequently (Blair, 1951; Rand & Host, 1942) found together in the same nest. In addition Blair (1951) observed wounding in some transient and immature individuals and also observed, in trap and release experiments, that adult females often chased other females from nests. Smith (1967) has suggested that

females of this species "are normally dominant over their mates and play a major role in the process of pair formation and maintenance of the pair bond" (p. 236). P. polionotus have also been observed to exhibit aggression in some laboratory tests (Garten, 1976; Smith, Garten, & Ramesy, 1975), but the conditions for these tests do not allow evaluation of the function of aggression in a social context, or as a factor in social preference.

Few data are available on the function of aggression and familiarity in the social behavior of P. polionotus, or in the social behavior of monogamous species in general. The first set of experiments in this study was designed to provide such data. These experiments were conducted in a seminatural apparatus that was designed with artificial burrows. This design takes into consideration the semifossorial habits of P. polionotus, and thereby allows an approximation of natural conditions in this species.

The seminatural experiments with P. polionotus were followed by preference experiments on both P. polionotus and P. maniculatus. These experiments allowed preference based on aggressive ability and familiarity to be assessed under the same conditions for both species, and thus allowed a direct comparison of the relative value of these factors in the social preference of these two species. The first set of these experiments examines aggressive ability and familiarity with unrelated individuals (based on previous contact) as factors in social preference; the second experiment examines preference for siblings.

General Methods

Subjects

Subjects for this study were 45 to 65 day old individuals of two species of muroid rodent, Peromyscus polionotus subgriseus and Peromyscus maniculatus baldi. The P. polionotus were laboratory-bred animals one to four generations removed from the wild. The parental stock was obtained from two different subpopulations in the Ocala National Forest in Florida. The first group of these animals was trapped in 1978 from road shoulders along State Road 316 between Salt Springs and Eureka. Additional animals for breeding stock were trapped in 1980 from road shoulders along U.S. Highway 19. These two populations are from the same general area as that listed as population 25 by Selander, Smith, Suh, Johnson, and Gentry (1971). The method of capture was similar to that detailed by Foltz (1979).

It is not possible to determine how many generations removed from the wild the P. maniculatus were. This colony was founded at the University of Florida with animals obtained from near East Lansing, Michigan, in 1970, and additional wild stock has been added on several occasions since.

Animals were housed in clear plastic cages measuring 48 x 27 x 13 cm or 29 x 19 x 13 cm with wood shavings as bedding. Purina laboratory animal chow and water were provided ad lib. Prior to serving as subjects all animals were maintained as litters. Peromyscus polionotus litters were weaned at 22 or 23 days of age, P. maniculatus were weaned at 21 days of age. Animals that exhibited obvious physical

defects, such as extensive tail wounds or missing tails, were not selected for study.

Animals of both species were maintained on a reversed 16L:8D photoperiod. All adaptation and testing were conducted during the dark portion of the photoperiod. With the exception of observations conducted in the seminatural apparatus, which was in a separate room, all studies and adaptation periods were conducted in the P. polionotus colony room. Procedural details specific to particular studies are described in the methods sections of those studies.

Apparatus

Seminatural apparatus

The seminatural apparatus was a large square Plexiglas arena 125 cm on a side and 46 cm deep. The sides of this arena were constructed with 1/4 inch Plexiglas and the floor was constructed with 1/2 inch plywood and painted grey. The arena was partitioned, with four 85 cm lengths of 1/4 inch Plexiglas, into a square central area that measured 85 cm on a side and four right angle triangular corner compartments with sides of 85 cm, 61 cm, and 61 cm (See Figure 1).

Two nest boxes were attached to each corner compartment. Nest boxes were constructed with sides of 1/4 inch Plexiglas and 1/4 inch plywood backs. They measured 10 x 9 x 8 cm and had hinged Plexiglas lids to provide access for removal of animals and cleaning. A 3.2 cm diameter hole cut in the front of each nest box provided access for the animals. In each corner compartment two matching 3.2 cm diameter holes, cut in the sides of the apparatus, 45.5 cm from the corner and 1.5 cm from the floor, provided access to the nest boxes. The front of

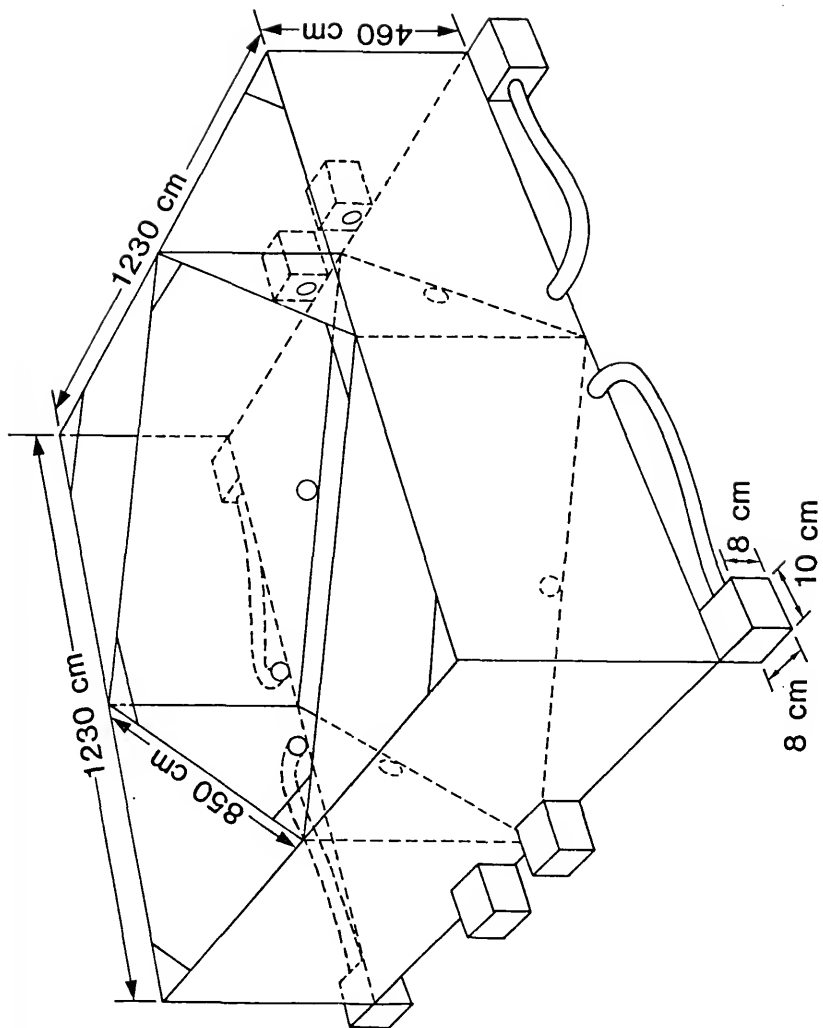


FIGURE 1 Seminatural Apparatus

one of the nest boxes for each corner compartment was connected with silicon cement directly to the side of the apparatus in line with one of these holes. The other nest box in each corner compartment was connected to the second opening by means of a 48 cm length of Tygon polyethylene tubing with an internal diameter of 2.5 cm and an external diameter of 3.2 cm, and thus formed an artificial burrow. Silicon cement was used to attach one side of the nest box to the apparatus and to connect the tubing to the openings for the nest box and the apparatus.

Animals could gain access from the corner compartments to the central area of the apparatus through 3.2 cm diameter holes centered on and 1.5 cm from the bottom of the partition which formed the compartment. A 2.5 cm hole 3 cm from the right angle corner and 2 cm from the floor of the apparatus provided access for the drinking tube of a water bottle.

The seminatural apparatus was in a room separate from the colony room but maintained on a 16L:8D photoperiod identical to that maintained in the colony room. The apparatus was illuminated in the light phase of the photoperiod by four 75-watt incandescent-white bulbs and two 60-watt red bulbs, each suspended three feet above the floor of the apparatus, and during the dark phase of the photoperiod by the two 60-watt red bulbs alone.

Behavioral measures were recorded by means of a 20-channel Esterline-Angus event recorder. The behaviors exhibited by each group of animals, during their four days in the seminatural apparatus, were also recorded on videotape using a Hitachi CCTV low light television

camera, and a Panasonic time lapse VTR video tape recorder set on a 72 hour record mode.

Preference apparatus

The preference apparatus was a three chambered rectangular box with a hinged lid; it was constructed of 1/4 inch Plexiglas and measured 44 x 21.5 x 20 cm (Figure 2). The inside measurements of the two end chambers were 10 x 21.5 x 20 cm. These chambers were open to the central area through a 7 x 7 cm opening. The end chambers were designed to accommodate small removable "choice chambers" which measured 10 x 8 x 6 cm. A "stimulus box" with an inside measurement of 8 x 7 x 8 cm was attached to each end chamber, and was open to it through a 6 x 5 cm opening. When choice chambers were placed in the end chambers, therefore, one end of the choice chamber was accessible from the central area, while the other end was open to the stimulus box. A hardware cloth screen installed in the opening to the stimulus box and a second three-sided piece of hardware cloth which fit the inside of the stimulus box provided a "double screen" between the choice chamber and the stimulus box.

A bank of three red-sensitive photocells (peak response at 735 nm), wired in a series behind each choice chamber, registered entries to the chamber. The light sources for the photocells were 60-watt red light bulbs placed 27 cm in front of the apparatus and directly in front of the bank of photocells. Each photocell was attached to the end of a tubular 4.3 cm piece cut from a 12 x 75 cm disposable plastic culture tube. The outsides of these tubes were painted black; this in effect columnated the light to the photocells. The photocells were

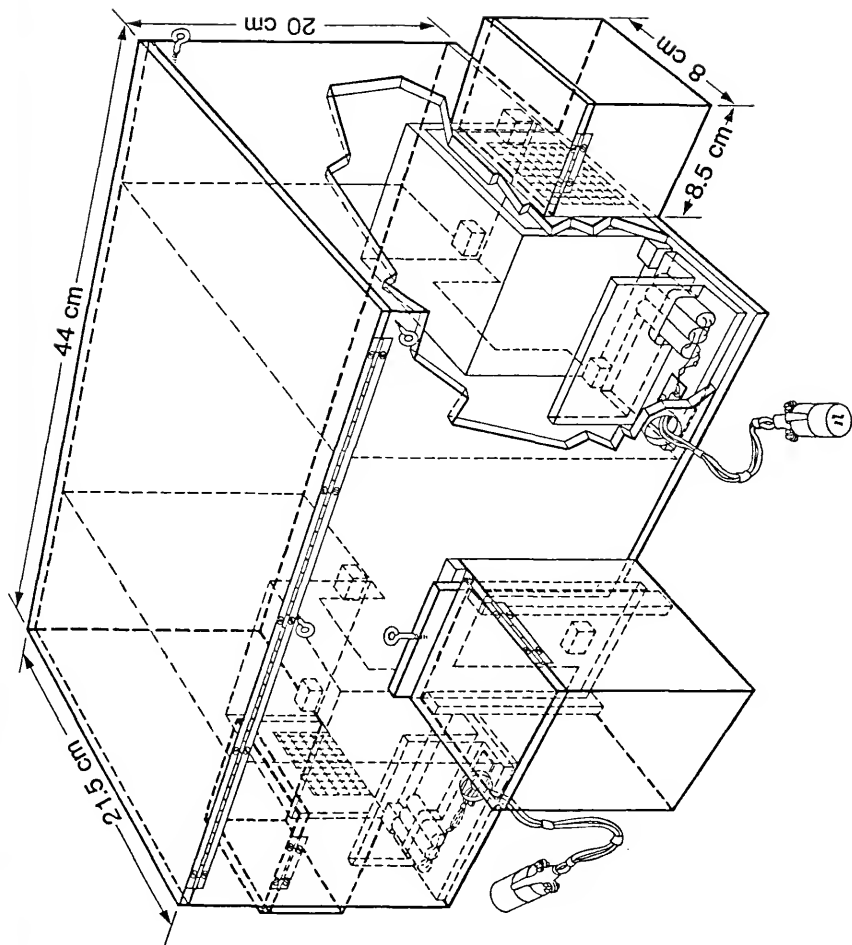


FIGURE 2 Preference Apparatus

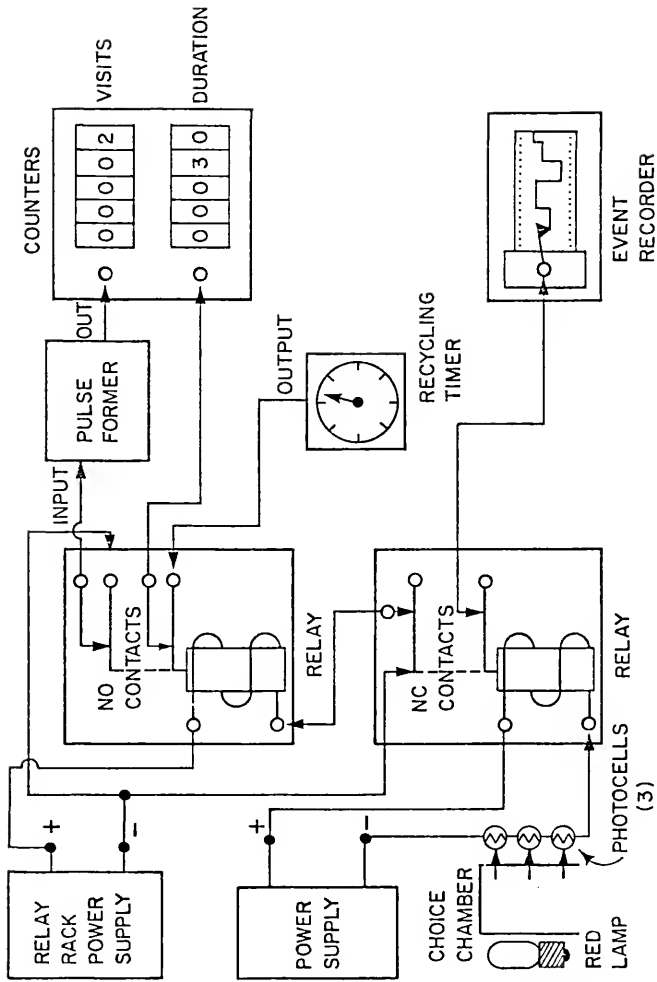


FIGURE 3 Diagram for Preference Apparatus

situated such that in order to register a visit to the choice chamber, an animal had to be completely inside the chamber, and at least partially in the half of the chamber closest to the stimulus animal. Each bank of photocells was wired in a series with the coil circuit of a 10,000 ohm, 24 VDC DPDT relay (see Figure 3). These relays were powered through output from a variable power supply set for a continuous output of 26 volts. One of the normally closed circuits of each of these relays was wired into the pen circuit of an Esterline-Angus event recorder; this provided a permanent record of entries into each choice chamber. Output from another normally closed circuit of these relays was used to control a second set of relays on a relay rack. Two banks of Sodeco counters received input through the normally open contacts of these relays. The first bank of counters was wired in a series to pulse formers and recorded the number of visits to each chamber regardless of visit duration. Input to the second bank of counters was regulated by means of a recycling timer set to produce pulses at 1/3 of a second. These counters recorded the total duration of visits to the nearest 1/3 of a second. Session duration was automatically controlled via another timer (not displayed) which controlled the input to the recycling timer and counters.

Aggression apparatus

The "aggression arena" was constructed from a large 48.5 x 38 x 20 cm plastic cage. Two 3.2 cm diameter holes were cut in the two longer sides of the cage centered 25.5 cm apart and 3.5 cm from the bottom. Silicon cement was used to form a gasket around each hole. Matching holes and gaskets were placed on one side of two 48 x 27 x 13

cm plastic cages. The larger cage and two smaller cages could then be connected by 6.5 cm lengths of Tygon polyethylene tubing (internal diameter of 2.5 cm and external diameter of 3.2 cm) to form the "aggression apparatus" (See Figure 4). During adaptation procedures the aggression arena and smaller cages were connected with unobstructed lengths of tubing; a piece of metal screen in the center of each length of tubing prevented animals from traveling through the tubes during tests. A 1/4 inch 53.5 x 43 cm Plexiglas lid was placed over the large cage, and wire cage lids over the smaller cages, while testing was conducted.

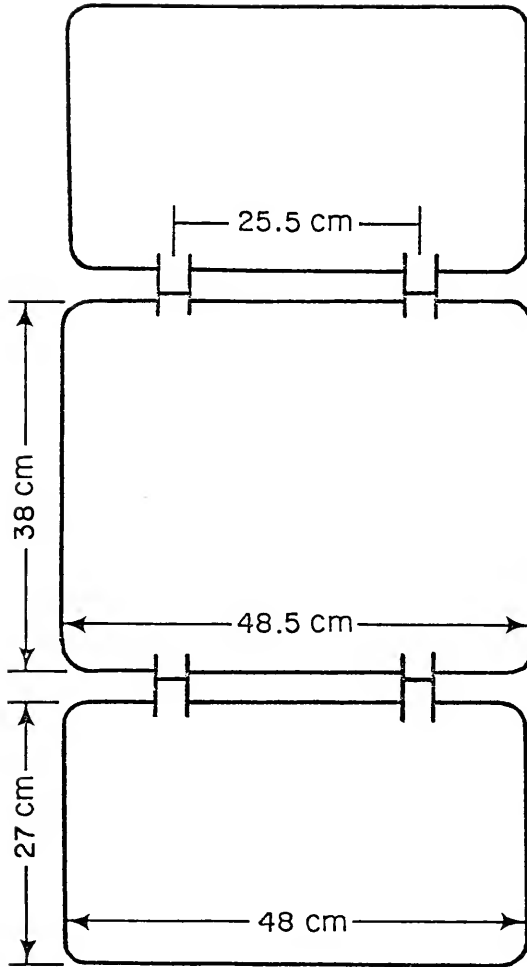


FIGURE 4 Aggression Apparatus

SECTION III EXPERIMENTS

Seminatural Experiments

This section is divided into three major subsections; the three sets of experiments that comprise this study are each described within separate subsections under the headings of Seminatural Experiments, Aggression and Familiarity Preference Tests, and Sibling Preference Tests. Each of these subsections begins with a brief introduction to the experiments in that subsection, and specific information on subjects and procedures for these experiments. This information is followed by the results of these experiments and a brief discussion of the results. The results of all three sets of experiments in this study are discussed together, in the context of the ecology of P. polionotus and P. maniculatus and theoretical considerations, in the General Discussion section.

Introduction

This experiment was designed to provide information on aggression and familiarity as factors in the social behavior and mate selection of P. polionotus. (Similar types of data already exist for P. maniculatus: Blair & Howard, 1944; Dewsbury, 1979, 1981c; Eisenberg, 1962.) Although it is difficult to establish the relevance of factors in social preference per se with seminatural observations, such data can provide an indication of the functions a factor may serve in

nature, and can provide indications of whether a factor may be of importance in social preference.

Subjects

Subjects were 40 male and 40 female P. polionotus. Prior to serving as subjects, animals were maintained as previously described in the section on general methods. Subjects were selected using the criteria described in the general methods, and the additional criterion that the animals within any group had no common grandparents.

Procedure

In order to better separate and evaluate the roles of aggression and familiarity in the social behavior of P. polionotus animals were observed under two different experimental conditions, the "paired" condition and the "single" condition. Twenty animals of each sex were assigned to either the single condition or the paired condition. Animals in each condition were divided into 10 groups; two animals of each sex were assigned to each group. Each of the 10 groups of animals in each condition, single or paired, were treated separately. Animals within each group were lightly anesthetized with ether and shaved in one of the following four patterns: (1) band shaved around the neck; (2) band shaved around the middle; (3) band shaved at the rear; (4) no shaved area. Shaving was performed one day prior to beginning the first experimental manipulation. Approximately equal numbers of males and females received each shave pattern. Subjects under both the single and paired conditions were exposed to a series of three different experimental manipulations. These manipulations, in order,

and their durations were "nest building," 4 days; "seminatural isolation," 3 days; and "seminatural interaction," 4 days.

During the four-day nest building period animals were housed in 48 x 27 x 13 cm plastic cages on San-i-cel bedding. Animals in the single groups were housed individually; animals in the paired groups were housed as two separate pairs of opposite-sexed animals. Three 2-inch square "Nestlets" (Ancare Corp.) were provided as nesting material in each cage. The type of nest built was assessed just prior to the beginning of the dark period on the next 4 consecutive days. Nests were rated as one of three types: (0) no nest; (1) platform nest; (2) covered nest.

The seminatural isolation period began in the first dark phase which followed the nest building period. Animals were transferred from the colony room to the room containing the seminatural apparatus approximately 15 min after the beginning of the dark phase. Animals from single groups were each placed individually in corner compartments, with animals of the same sex in compartments diagonally opposite each other. Animals from paired groups, which had been maintained as pairs during nest building, were transferred to the seminatural apparatus in the same paired relationship. Pairs were placed in corner compartments of the apparatus diagonally opposite each other. The opening from each corner compartment to the central area was closed with a solid black rubber stopper so that animals were restricted to the compartment in which they had been placed. The floor of the central area and of the corner compartments had been covered with San-i-cel to a depth of approximately 1.5 cm; each corner

compartment also contained three Nestlets, and food and water was available ad lib.

Animals were maintained in the corner compartments for 3 days. Activity during this entire period was videotaped. Each pair of animals in the paired groups was also observed for three alternate 10-minute periods during the dark phase on the day the animals were introduced, and on the following two days. On the first day, observation was begun as soon as all animals had been placed in the apparatus. On each of the following 2 days one of the pairs was designated as the first pair to be observed, and the first period of observation was begun when the members of that pair had emerged from their burrow. The behavioral and aggressive measures that were recorded were similar to categories described by Allin and Banks (1968) and Colvin (1973). Measures were recorded by means of a 20-channel Esterline-Angus event recorder. The measures, and definitions of each, were as follows:

- | | |
|----------|---|
| Approach | Scored when an animal came within one and one-half body lengths of another while oriented toward it. |
| Attack | Scored when one animal lunged at or charged another but did not pursue the other or initiate vigorous biting behavior. This behavior could be accompanied by a single bite or attempts to bite. |
| Chase | Scored when one animal pursued another. |

- Fight** Scored when one animal's attack on another escalated to vigorous biting behavior by both individuals. Generally the initiator would knock the other animal over, or roll to one side with the other animal clenched in its jaws while shaking its head, often simultaneously clawing with the rear claws. Fighting often resulted after one animal did not retreat when attacked, but rather attempted to defend itself or at the end of a chase if the pursuing animal caught the other.
- Rough-and Tumble-Fight** A very vigorous form of fighting; rough-and-tumble fights were only scored when both animals were tumbling end over end while attempting to bite and claw each other.
- Displacement** Scored when one animal retreated upon another animals approach.
- Submissive** Scored when one animal, upon approach or attack by another, either rolled over on its back, or reared back upon its hind legs with its nose pointed up, and made no attempt to defend itself. Both approach and submission or attack and submission were scored for each encounter.
- Aggressive Digging** This was a very vigorous form of digging behavior much more intense than the type of digging these animals have been observed to perform in an isolated test (Webster, Williams, Owens, Geiger, and Dewsbury; 1981). Although this behavior was not generally directed toward an opponent, it was very similar to that described by Allin and Banks (1968).

Under both experimental conditions, single and paired, the isolation period was followed by the seminatural interaction period. Ten min prior to the first dark phase in this period the rubber stoppers were removed from the partitions between each corner compartment and the central area. Behavioral and aggressive

interactions between animals, as defined above, were recorded during the first hour of the dark phase for 4 consecutive days. Nesting relationships were recorded each day, for the last 3 of these 4 days, 20 min prior to the beginning of the dark phase. An animal was defined as having nested with another if it was found in the same nest with the other, and videotape records verified that it had not switched nests between the period extending from after the first 1/2 hr of the preceding light phase to 1/2 hr prior to the nest check. Activity during the entire isolation and interaction stages was videotaped.

The seminatural apparatus, including the artificial burrows and nest boxes, was thoroughly cleaned with a solution of Sterigent (a deodorant and disinfectant soap) before each group of animals was introduced to the apparatus. Water bottles were also cleaned and refilled, and fresh San-i-cel, food, and Nestlets were placed in the apparatus.

Results

Peromyscus polionotus appeared to adapt very quickly to the seminatural apparatus in general, and to the artificial burrows in particular. All but five of the 40 individuals in the paired condition entered and explored the artificial burrows within the first hour of observation, and all except two pairs of the 20 pairs observed in the paired condition had constructed at least a rudimentary nest in the burrow by the end of their first day in the apparatus. Individuals in the paired or single groups were only infrequently observed nesting in the alternate nest box, although this box was frequently used for feeding and as an escape when individuals were attacked. Aggressive

relationships between individuals in each group appeared to remain fairly stable over their four days together in the seminatural apparatus. In all 10 single groups, and in seven of the 10 paired groups, the individual with the highest total frequency of aggressive behavior (sum of all attacks, chases, fights, and rough-and-tumble fights) on day one, still exhibited the highest frequency of aggressive behavior on day four. In the other three paired groups the individual that exhibited the highest frequency of aggressive behavior on day two also exhibited the highest frequency on day four.

Each animal in a group could potentially interact with twice as many opposite-sexed individuals as same-sexed individuals. To adjust for this bias, the mean value of any measure of an animal's interaction with both opposite-sexed individuals, rather than the total, was used in analyses involving opposite-sexed individuals.

Several significant differences in aggression were apparent in comparisons between males and females in both the paired and single conditions. Males were more aggressive than females in a statistically significant larger number of groups by all measures except the number of rough-and-tumble fights (designated in tables as r&t fights; see Table 1). Within the single condition males were the more aggressive sex in a significantly larger number of groups by all measures except the number of rough-and-tumble fights and the duration of rough-and-tumble fights. Within the paired condition males were the more aggressive sex in a significantly larger number of groups for the measures of number of attacks, number of fights, duration of fights and number of approaches. There was no measure, for either the paired or

Table 1

Comparison of the Number of Groups in Which
Males or Females Were More Aggressive

Measure	Total (N=20)		Paired (N=10)		Single (N=10)	
	Male	Female	Male	Female	Male	Female
No. of attacks	19	1***	9	1*	10	0**
No. of flights	17	2***	9	1*	8	1*
Duration of flights	18	2***	9	1*	9	1*
No. of chases	17	3**	8	2	8	1*
Duration of chases	17	3**	8	2	9	1*
No. of r&t flights	13	5	6	2	7	3
Duration of r&t flights	15	3**	8	2	7	1
No. of approaches	19	1***	10	0**	9	1*
No. of displacements	15	4*	7	3	8	1*

All durations are in seconds.

Sign test 2-tail * $p < .05$

** $p < .01$

*** $p < .001$

single condition, for which females were more aggressive than males in a larger number of groups.

Males in general also exhibited higher total levels of aggression than females by all measures (see Table 2). Males, in both single and paired groups, exhibited a higher frequency of attacks, fights, chases, displacements and approaches than females. They also exhibited longer durations of chases and fights than females in both types of groups (see Table 3). Although differences in the total amount of submissive behavior exhibited by males and females across both groups were not statistically significant ($t=1.28$, $df=19$, $p>.05$), males had more submissive behavior directed toward them than did females (paired- $t=2.71$, $df=19$, $p<.05$).

Because aggressive digging was not immediately recognized as a possible correlate of aggression, it was not recorded for the three initial paired groups. It was recorded for all subsequent paired and all single groups. No significant differences in the frequency, duration, or mean duration of aggressive digging were apparent in comparisons between paired and single animals. Males displayed higher levels on all of these measures than did females, with the exception of the comparison of the average duration of aggressive digging for single animals. High-aggression males (those in each group with the highest total frequency of aggressive behavior) displayed a higher frequency of aggressive digging than low-aggression males (paired- $t=2.30$, $df=16$, $p<.05$). The difference between high and low-aggression animals in the level of aggressive digging they displayed may be due in part to differences in the response of these two classes of individuals to

Table 2

Comparison of Total Aggression Within Groups by Males
and by Females In Both Paired and Single Conditions

Measure	Male		Female		t
	Mean	(SE)	Mean	(SE)	
No. of attacks	46.30	5.95	10.20	2.41	5.23****
No. of fights	14.55	2.24	3.05	1.07	4.23****
Duration of fights	23.00	3.96	4.60	1.46	4.31****
No. of chases	116.20	12.18	21.85	5.51	5.98****
Duration of chase	679.10	79.01	128.40	32.79	5.59****
No. of r&t fights	5.00	1.44	1.25	.42	2.60*
Duration of r&t fights	10.30	3.04	2.80	1.39	2.35*
No. of approaches	64.10	7.91	23.40	3.61	5.62****
No. of displacements	12.80	2.59	3.40	.90	3.43***

All durations are in seconds.

Paired t-test df=19 2-tail *p<.05 ***p<.01
****p<.001

Table 3
Total Level of Aggression by Males and
Females in Paired and Single Groups

Measure	Total (Paired and Single)				Paired				Single						
	Male		Female		Male		Female		Male		Female				
	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)			
No. of attacks	23.15	4.26	5.10	1.34	13.05****	22.60	6.25	6.15	2.47	5.17*	23.70	5.94	4.05	1.08	8.95***
No. of fights	7.28	1.44	1.53	.56	12.03****	6.55	1.69	1.80	.82	5.79**	8.00	2.36	1.25	.79	6.31**
Total duration of fights	11.50	2.39	2.30	.79	12.20****	11.80	3.14	3.15	1.24	6.31**	11.20	3.67	1.45	.96	5.82**
Mean duration of fights	1.11	.14	.59	.19	5.43*	1.34	.25	.97	.34	.85	.88	.16	.22	.10	11.99****
No. of chases	58.10	10.34	10.93	3.18	15.25****	60.20	16.10	11.75	5.20	6.70**	56.00	13.40	10.10	3.77	8.66****
Total duration of chases	339.55	62.51	64.20	18.90	14.47****	346.35	94.48	65.55	29.32	6.69**	332.75	84.32	62.85	24.64	7.64****
Mean duration of chases	4.31	.41	2.97	.47	4.35*	4.55	.51	2.87	.67	4.06	4.07	.64	3.07	.69	1.02
No. of r&t fights	2.50	.81	.63	.23	4.82*	1.50	.47	.65	.35	1.94	3.50	1.52	.60	.30	3.33
Total duration of r&t fights	5.15	1.69	1.40	.72	4.05*	3.50	1.08	2.10	1.39	.68	6.80	3.20	.70	.39	3.43
Mean duration of r&t fights	1.03	.22	.43	.15	5.16*	1.27	.38	.64	.29	1.78	.79	.22	.22	.10	5.25*
No. of approaches	32.05	4.58	11.70	1.87	16.95****	34.80	6.56	15.35	2.93	7.21**	29.50	6.70	8.05	2.09	9.63****
No. of displacements	6.40	1.53	1.70	.40	8.17****	8.20	2.76	2.60	.63	3.57	4.60	3.67	.80	.41	6.67**
No. of aggressive digs	10.21	2.79	.38	.16	12.00****	9.86	3.29	.07	.07	7.23*	10.47	4.27	.60	.27	5.71*
Total duration of aggressive digging	18.33	5.30	.56	.24	9.24****	15.14	5.92	.14	.14	5.55*	20.68	8.61	.85	.59	4.81*
Mean duration of aggressive digging	.98	.18	.27	.11	9.71****	.87	.19	.14	.14	9.78****	.98	.29	.35	.16	3.14

All durations are in seconds.
Analysis of Variance 2-tail

*p<.05

**p<.02

***p<.01

****p<.001

noises within the apparatus. High-aggression animals often investigated noises made by other individuals in the apparatus. Low-aggression individuals generally ignored these noises or retreated from them. Low-aggression individuals that attempted to dig, therefore, in effect increased the probability of attack by high-aggression individuals, whereas high aggression individuals dug without interference.

Individuals directed more aggression toward same-sex than opposite-sex individuals in both the paired and single conditions (see Tables 4 and 5). Males in both single and paired groups directed more fights and rough-and-tumble fights, and longer durations of these behaviors, against other males than against females. Females in both single and paired groups directed more attacks toward same-sexed than opposite-sexed individuals. Males and females in both types of groups directed more chases toward same-sex than opposite-sex individuals.

Although many of the differences in aggression between sexes were significant, and many significant differences were also found in the level of aggression directed at same versus opposite-sexed individuals, the overall levels of aggression displayed by animals in the single and paired conditions were very similar (means and standard errors were presented in Table 3). Animals in the two conditions displayed significant differences on only two of the aggressive measures: paired animals displayed longer average durations of fights with same-sexed individuals and a greater number of approaches to same-sexed individuals than did animals in the single condition ($t=2.12$, $df=78$, $p<.05$; and $t=2.10$, $df=78$, $p<.05$ respectively).

Table 4
Aggression Against Same-Sex and Opposite-Sex in Paired Groups

Measure	Total				Males				Females						
	Same-Sex		Opposite-Sex		Same-Sex		Opposite-Sex		Same-Sex		Opposite-Sex				
	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)			
No. of attacks	6.63	1.66	3.88	1.04	2.78***	9.75	2.94	6.43	1.81	1.85	3.50	1.27	1.32	.68	2.49*
No. of flights	5.05	.75	1.56	.20	3.62***	4.50	1.21	1.02	.38	3.17***	1.60	.80	.10	.05	1.88
Duration of flights	5.40	1.24	1.04	.43	3.92***	8.05	2.02	1.88	.81	3.46***	2.75	1.24	.20	.11	2.04
Mean duration of flights	1.01	.22	.64	.16	1.60	1.40	.31	.88	.23	2.06	.63	.30	.40	.22	.57
No. of chases	24.80	6.88	5.59	1.52	3.22***	40.60	12.30	9.80	2.68	2.82*	9.00	4.10	1.38	.66	2.12*
Duration of chases	147.30	41.80	29.33	9.74	3.09***	242.35	74.78	52.00	18.00	2.72*	52.25	25.09	6.65	3.33	1.95
Mean duration of chases	3.23	.47	2.67	.44	1.30	3.91	.67	3.70	.52	.34	2.54	.62	1.63	.63	1.53
No. of r&t flights	1.00	.29	.04	.02	3.40***	1.45	.46	.03	.03	3.17***	1.55	.33	.05	.03	1.55
Duration of r&t flights	2.65	.87	.08	.05	2.96***	3.45	1.08	.03	.03	3.19***	1.85	1.37	.13	.09	1.26
Mean duration of r&t flights	.88	.24	.15	.09	2.91**	1.27	.38	.05	.05	3.19***	.49	.26	.25	.18	.18
No. of approaches	6.53	.98	9.28	1.71	1.59	7.40	1.47	13.70	2.98	2.03	5.65	1.31	4.85	1.01	.69
No. of displacements	2.20	.81	1.60	.45	.83	3.30	1.57	2.45	.83	.61	1.10	.36	.75	.24	.85

All durations are in seconds.
Opposite-sex means are mean values per opposite-sex individual.
Paired-t Total df=39 Male and Female df=19 2-tall

*p<.05 **p<.01 ***p<.005 ****p<.001

Table 5
Aggression Against Same-Sex and Opposite-Sex in Single Groups

Measure	Total			Males			Females				
	Same-Sex	Opposite-Sex	†	Same-Sex	Opposite-Sex	†	Same-Sex	Opposite-Sex	†		
	Mean (SE)	Mean (SE)		Mean (SE)	Mean (SE)		Mean (SE)	Mean (SE)			
No. of attacks	5.25	1.23	4.18	1.16	1.60	1.60	2.55	.83	.75	.25	2.23*
No. of flights	3.53	1.12	.55	.21	2.81**	2.81**	5.85	2.00	1.08	.40	2.48*
Duration of flights	4.45	1.55	.94	.41	2.46*	2.46*	7.80	2.84	1.80	.79	2.16*
Mean duration of flights	.49	.10	.42	.12	.74	.74	.78	.16	.68	.18	.58
No. of chases	19.88	4.83	6.59	1.86	3.43****	3.43****	32.00	8.40	12.00	3.31	2.86**
Duration of chases	147.98	37.60	24.91	6.93	3.73****	3.73****	241.55	66.11	45.60	12.20	3.34****
Mean duration of chases	3.45	.66	2.37	.34	1.86	1.86	4.43	1.05	2.88	.46	1.74
No. of r&t flights	1.80	.72	.13	.08	2.44*	2.44*	3.05	1.37	.23	.15	2.16*
Duration of r&t flights	3.15	1.41	.30	.18	2.19*	2.19*	5.65	2.71	.58	.34	2.03
Mean duration of r&t flights	.48	.12	.33	.16	1.30	1.30	.74	.20	.61	.30	.62
No. of approaches	3.70	.92	7.49	1.60	3.06***	3.06***	5.70	1.55	11.80	2.83	2.70*
No. of displacements	.88	.29	.91	.26	.18	.18	1.50	.51	1.55	.46	.15

All durations are in seconds.

Opposite-sex means are mean values per opposite-sex individual.

Paired-t Total df=39

Male and Female df=19

2-tail

*p<.05

**p<.01

***p<.005

****p<.001

Comparisons of aggressive measures between the two conditions within each sex yielded significant differences for females only (means and standard errors were presented in Tables 4 and 5). Paired females exhibited a greater number of approaches to same-sex individuals and a greater number of displacements of same-sex individuals than did single females ($\pm=2.57$, $df=38$, $p<.02$; and $\pm=2.08$, $df=38$, $p<.05$, respectively).

The various measures of aggression recorded tended to be correlated with each other. The total frequency of attacks, chases, fights, and rough-and-tumble fights were correlated within each sex for both paired and single groups, as were the duration of chases, fights, and rough-and-tumble fights. The frequency of approaches was correlated with the number of chases for males and females in both conditions and with the number of attacks for paired males and females and single males (see Table 6). The amount of submissive behavior directed toward single females was correlated with the frequency and duration of fights (Pearson correlation, $r=.724$ and $r=.798$, respectively, $p<.001$) and the frequency and duration of rough-and-tumble fights (Pearson correlation, $r=.704$ and $.800$, respectively, $p<.001$). Submission was also correlated with the total frequency of approaches for paired females and single males (Pearson correlation, $r=.444$ and $r=.515$, respectively, $p<.05$). Frequency of aggressive digging was correlated with the total frequency of aggressive behavior (combined frequencies of attacks, fights, chases, and rough-and-tumble fights) for paired males and females ($r=.638$, $p<.05$, and $r=.845$, $p<.001$ respectively) and single males ($r=.697$, $p<.001$). Duration of

Table 6
 Pearson Product-Moment Correlation of Aggressive
 Measures for Males and Females In Paired and Single Groups

Measure	Paired		Single	
	Male	Female	Male	Female
No. of attacks and chases	.875****	.973****	.889****	.901****
No. of attacks and flights	.570**	.735****	.629***	.714****
No. of attacks and r&t flights	.751****	.765****	.389*	.659****
No. of attacks and approaches	.787****	.564**	.719****	.226
No. of attacks and displacements	.580****	.494*	.797****	.474*
No. of flights and chases	.790****	.842****	.858****	.755****
No. of flights and r&t flights	.686****	.964****	.890****	.898****
No. of flights and approaches	.421	.254	.257	.321
No. of flights and displacements	.843****	.389	.327	.496*
No. of chases and r&t flights	.723****	.856****	.643****	.721****
No. of chases and approaches	.749****	.473*	.609***	.322
No. of chases and displacements	.799****	.471*	.690****	.337
No. of r&t flights and approaches	.469*	.265	.045	.226
No. of r&t flights and displacements	.428	.387	.094	.407
No. of approaches and displacements	.468*	.713****	.898****	.073
Duration of chases and flights	.670****	.865****	.843****	.779****
Duration of chases and r&t flights	.753****	.823****	.689****	.728****
Duration of flights and r&t flights	.750****	.847****	.914****	.933****

All durations are in seconds.
 Correlations based on total frequencies and durations.
 N=20 2-tail test $^*p<.05$ $^{**}p<.01$ $^{***}p<.005$ $^{****}p<.001$

aggressive digging was correlated with total frequency of aggressive behavior for single males ($r=.527$, $p<.05$) and paired females ($r=.845$, $p<.001$). An animal's weight did not appear to be an important factor in aggressive interactions. Only the correlation between weight and the frequency of rough-and-tumble fights in single females was statistically significant ($r=.378$, $p<.05$).

For paired groups comparisons were also made between the level of aggressive behavior that occurred while pairs were confined to the corner compartments and the level after access to the entire apparatus was allowed. Very few aggressive interactions of any type (chases, fights, attacks, rough-and-tumble fights) were observed between pair members during the period pairs were confined to the corner compartments (Mean total frequency of aggressive interaction per paired individual=.20, range = 0 - 4.0). Therefore only the total frequency of aggressive behavior, rather than the frequency of behavior in each category, was used for comparison.

The total frequency of all aggressive interactions (attacks, fights, rough-and-tumble fights, and chases) between pair members while confined to the corner compartments was not useful in predicting frequency of later aggressive interactions with pair members (males: $r=.034$, $p>.05$; females: $r=.087$, $p>.05$) or total frequency of aggressive interactions (males: $r=.015$, $p>.05$; females: $r=.118$, $p>.05$).

Pairing did, however, have some effects on later levels of aggression. Males in paired groups were less aggressive to the females with which they had previously been paired than to females with which

they had not been paired by the measures of frequency and duration of chases (one-tail paired- $t=2.18$ and 2.22 , respectively, $df=19$, $p<.05$). Males also exhibited a higher frequency of approach to females with which they had been paired (one-tail paired- $t=1.78$, $df=19$, $p<.05$). None of these comparisons were significant for females (Number and duration of chases, $t=.38$ and $.76$ respectively, approach; $t=1.08$, $df=19$, $p>.05$).

A problem arises when one attempts to compare different classes of animals as to their levels of aggressive interactions with one another. The problem is that the total amount of contact between different classes of animals may vary. For example, if females tend to avoid other animals, but males do not, individuals would have more opportunities to be aggressive to males than to females. A difference, therefore, in the level of aggression an individual expresses toward individuals of one class versus another may reflect a true difference in the frequency of aggression, or a difference in the frequency of access to individuals of the two classes. One method of gaining a clearer understanding of the level of aggression, and differences in it between classes of individuals, is to construct a scale or index for comparisons which accounts for differences in frequency of contact.

An "aggressive index" was calculated for this study by dividing the total frequency of all aggressive encounters initiated by an animal (frequency of attacks, chases, fights, and rough-and-tumble fights) toward any other class of individuals by the total number of contacts initiated by that animal toward that class of individuals (total aggressive encounters plus the frequency of approaches and

displacements). Although there may be qualitative differences in approaches which elicit displacement or submission and those which do not (for example an aggressive individual may signal its status through adopting a particular posture), no means was available in the present study to detect these cues. Therefore displacements or approaches with submission were classed as contacts without aggression for purposes of constructing the index.

No significant differences were apparent between paired and single groups, or in comparisons between males or females of these groups, in the total frequency of contacts or the frequency of contact with same-sexed or opposite-sexed individuals (see Table 7). Single females did, however, have a significantly higher overall aggressive index (frequency of all aggressive behaviors divided by frequency of all contacts) and a higher aggressive index against opposite-sexed individuals than paired females.

The total frequency of contact was significantly higher for males than for females in the paired and single conditions. Although the overall aggressive index was significantly higher for paired males than paired females, the difference between single males and females was not significant (see Table 8).

Paired males and females and single males all displayed a significantly higher frequency of contact with same-sexed than opposite-sexed individuals. Whereas both paired males and females displayed a significantly higher aggressive index against same-sexed than against opposite-sexed individuals, this comparison was not significant for single males or females (see Table 9). Paired males,

Table 7
 Aggressive Index and Frequency of Contact with
 Same-Sex and Opposite-Sex Animals for
 Paired and Single Conditions

Measure	Total (Males and Females)				Male				Female						
	Paired		Single		Paired		Single		Paired		Single				
	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)			
<u>Aggressive Index</u>															
Total	.39	.05	.57	.06	2.53*	.51	.06	.63	.07	1.33	.27	.06	.51	.09	2.30*
Same-Sex	.49	.06	.51	.07	.27	.61	.08	.57	.09	.40	.36	.08	.45	.10	.71
Opposite-Sex	.30	.04	.47	.06	2.48*	.41	.06	.56	.07	1.60	.18	.05	.38	.08	2.07*
<u>Frequency of Contact</u>															
Total	86.08	17.77	74.98	16.07	.46	133.85	30.67	125.10	27.40	.21	38.30	10.73	24.85	6.76	1.06
Same-Sex	44.20	10.22	35.30	8.03	.68	67.00	17.94	56.60	13.84	.46	21.40	7.21	14.00	5.02	.84
Opposite-Sex	20.94	4.96	19.84	4.62	.18	35.43	6.62	34.25	8.02	.08	8.45	2.24	5.43	1.17	1.20
Paired-t	Total	df=18	Male and Female	df=38	2-tail	*p<.05									

Table 9

Aggressive Index and Frequency of Contact for Males and Females with Same-Sex and Opposite-Sex Individuals

Measure	Total				Male				Female						
	Same-Sex		Opposite-Sex		Same-Sex		Opposite-Sex		Same-Sex		Opposite-Sex				
	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)			
Aggressive Index															
Paired	.49	.04	.30	.06	3.73***	.62	.08	.41	.06	2.69*	.36	.08	.18	.05	2.52*
Single	.51	.07	.47	.06	.56	.57	.09	.56	.07	.08	.45	.10	.38	.08	.68
Frequency of Contact															
Paired	44.20	10.22	20.94	3.99	3.41***	67.00	17.94	33.43	6.62	2.80*	21.40	7.21	8.45	2.24	2.17*
Single	35.30	8.03	19.84	4.62	2.76**	56.60	13.84	34.25	8.02	2.18*	14.00	5.02	5.42	1.17	1.96

Opposite-sex means are mean values per opposite-sex individual.

Paired-t Total df=39 Male and Female df=19 2-tail

*p<.05 **p<.01 ***p<.005 ****p<.001

but not paired females, exhibited a lower aggressive index against pair members than against opposite-sexed non-pair member (two-tail t -test, $df=19$, males and females respectively: $t=2.25$, $p<.05$; $t=1.41$, $p>.05$).

The frequency of nesting arrangements, for days on which complete nest data were available, is presented in Table 10. It is of interest that two animals of the same sex nested together only once without an opposite-sexed animal also present. Animals nested as two opposite-sexed pairs on over 1/3 of the days for which data were available and almost another 1/4 of the nesting arrangements observed included one opposite-sexed pair.

Only data on nesting behavior for days on which nesting relationships were known for all individuals in a group were analyzed statistically. Nest data were available for all but one paired and one single group. Three days of nest data (the total possible) were available for two of these nine paired, and seven of these nine single groups. Two days of data were available for six paired and two single groups, and only one day of data was available for one of the paired groups. The mean number of days of data available for nine paired and nine single groups were 2.11 days and 2.78 days, respectively.

The analyses of nesting behavior presented in the tables are based on the "Wilcoxon-test" (Siegel, 1956). Analysis of nesting behavior by this test in the present study may give more "weight" to observations from groups for which more days of data are available. Significant comparisons in the tables that were not also significant by the "sign-test" (Siegel, 1956) are noted in text. Animals generally nested with opposite-sexed rather than same-sexed animals. Differences in nesting

Table 10
 Frequency of all Possible Nesting Arrangements

	Total	Paired Groups	Single Groups
All four together	4	1	3
Two opposite-sex pairs	15	7	8
Two males, one female	3	3	0
Two females, one male	6	4	2
Two males	0	0	0
Two females	1	1	0
One opposite-sex pair	12	2	10
None together	3	1	2

Only days on which all animals could be accounted for are included
 (Total number of days=44).

Table 11
Nesting Frequency with Same vs. Opposite Sex Individuals

	Total			Male			Female											
	Mean(SE)	Opposite Sex	N	Mean(SE)	Opposite Sex	N	Mean(SE)	Opposite Sex	N									
										Z	Z	Z						
All animals	.54	.10	1.01	.08	.53	4.18***	.39	.10	1.03	.11	23	4.20***	.69	.17	1.00	.10	30	1.86*
Paired animals	.64	.13	.86	.08	24	1.29	.44	.12	.89	.13	8	2.52**	.83	.23	.85	.11	16	.10
Single animals	.44	.15	1.17	.12	29	4.51***	.33	.16	1.17	.19	15	3.41***	.56	.26	1.17	.17	14	2.98***

Same-sex frequency = total nesting frequency with same sex.
Opposite-sex frequency = (total nesting frequency with opposite sex)/2.
N=number of non-tied observations.
Wilcoxon 1-tail *p<.05 **p<.01 ***p<.005 ****p<.001

Table 12
 Nesting Frequency with High-Aggression vs. Low-Aggression Animals of the Opposite Sex

	Total				Male				Female									
	High Aggression		Low Aggression		High Aggression		Low Aggression		High Aggression		Low Aggression							
	Mean (SE)	N	Mean (SE)	N	Mean (SE)	N	Mean (SE)	N	Mean (SE)	N	Mean (SE)	N						
All animals	2.47	.21	1.58	.21	21	3.59***	2.33	.26	1.67	.31	9	2.07*	2.61	.33	1.50	.27	12	2.67***
Paired animals	2.11	.24	1.33	.20	8	2.10*	2.00	.29	1.33	.29	4	1.46	2.22	.40	1.33	.30	4	1.46
Single animals	2.83	.32	1.83	.36	13	2.69***	2.67	.41	2.00	.55	5	1.48	3.00	.50	1.67	.47	8	2.24*

N = number of non-nested observations.

Wilcoxon 1-tail * $p < .05$ *** $p < .005$ **** $p < .001$

frequency with same and opposite-sexed animals were significant for all comparisons except paired animals in general, and paired females (see Table 11). (By the sign test the comparison for all females was also non-significant, $\chi=10$). In general animals also nested with high-aggression rather than low-aggression animals of the opposite sex (see Table 12). This was true for animals in paired groups and single groups, and for males and females. The finding of non-significance for comparisons within paired and single groups, except single females, may be due to the small number of non-tied observations available for comparison. (By the sign test comparisons for paired animals and males in general were also non-significant, $\chi=2$ for both comparisons). Total frequency of aggression was correlated with frequency of nesting with opposite-sexed individuals for paired males and single males (Pearson correlation, $r=.710$, $p<.001$ and $r=.519$, $p<.05$ respectively) but not for paired or single females ($r=.066$ and $r=.219$ respectively, $p>.05$).

Animals did not nest more frequently with familiar individuals. Comparisons based on all paired animals, males, or females were all non-significant (Wilcoxon, N =number of non-tied observations: all animals, $N=24$, $z=1.24$; males, $N=10$, $z=1.22$; females, $N=14$, $z=.60$). Neither the number of days pairs had built nests together during the nest building stage, nor the average type of nest built, was correlated with nesting frequency with pair members (Pearson correlation, nest days, $r=.395$; nest type, $r=.250$).

Discussion

These seminatural observations provide evidence that aggression is likely to be an important factor in social interactions in P.

polionotus. As predicted of the behavior of monogamous species (Kleiman, 1977) frequent aggression was displayed by both males and females, and the majority of aggressive behavior was directed against same-sexed individuals. The suggestion that females of this species are normally dominant over males (Smith, 1967) was not supported by the results of the present study. Males displayed much higher levels of aggression than did females, and females generally exhibited very low levels of aggression toward males. In addition, high-aggression males more frequently performed a behavior, aggressive digging, that could function to display their aggressive status.

Although the frequencies of aggressive behaviors in paired and single groups were very similar, the aggressive index indicated that individuals in paired and single groups behaved differently. Individuals in single groups did not appear to discriminate between the targets of their aggression as well as paired individuals did. Overall, the differences in aggressive behavior between paired and single groups may indicate a tendency for reduced aggression toward opposite-sexed individuals, especially pair members, in paired individuals. This is particularly true of paired males, which displayed both reduced total frequencies of aggression and a lower aggressive index, against females with which they had been paired than against those with which they had not been paired.

Superior aggressive ability would appear to provide some social benefits for individuals, as both males and females nested more frequently with high-aggression rather than low-aggression individuals of the opposite sex. On the other hand familiarity, although it

appeared to reduce aggression between pair members, did not have a significant effect on nesting behavior. It would appear from these observations that, in P. polionotus, aggressive ability may be a more potent factor in social preference than in familiarity. However, because it is unlikely that individuals under the present conditions were always able to control who nested with them, it is probably best to use caution in interpreting these results.

Aggression and Familiarity Preference Tests

Introduction

The results of the seminatural experiments indicated that aggression may be an important factor in social preference in P. polionotus, but cast some doubt on the importance of familiarity in the social preference of this species. This experiment was designed to test preference based on aggression and familiarity in P. polionotus and P. maniculatus in a more controlled manner, through the use of a preference apparatus.

Subjects

Subjects were individuals of two species of murid rodents, P. polionotus and P. maniculatus. A total of 40 animals of each species served as subjects for aggressive tests and aggression preference tests. Prior to serving as subjects, animals were maintained as described in the general methods section. Within each species these animals were each assigned to one of 10 groups, with two animals of each sex per group. In addition to the criteria described in the general methods section, no individual within each group could be

related by more than two common grandparents to any other animal in the group.

Following the aggression tests and aggression preference tests the animals described above also served as "stimulus" animals for familiarity preference tests, while an additional 40 animals, 20 of each sex of each species, served as "choice" animals for these tests.

Procedure

Procedures were identical for each experimental group. Animals for each group were separated from litter mates and individually housed in 48 x 27 x 13 cm clear plastic cages. Peromyscus maniculatus were moved from their colony room to the P. polionotus colony room. On the following day, within the first 1/2 of the dark phase of the photoperiod, animals were lightly anesthetized with ether and marked for identification by shaving them in one of two patterns: either (1) a band was shaved from around the neck area, or (2) a band was shaved from around the middle of the animals. One animal of each sex was shaved in each pattern. Animals were placed in 48 x 27 x 13 cm plastic cages modified (as previously described under aggression apparatus) for aggression testing.

All adaptation and testing were conducted during the dark portion of the photoperiod. Animals were adapted to the preference apparatus on the two days following the marking procedure. On the first of these two days animals were adapted to the procedure that would be used when they served as "choice" animals.

Adaptation to "choice" procedures was as follows: the animal was placed in the start box for 5 min, followed by 1 hour free in the

apparatus without other animals present. Animals that did not exit the start box within 1 1/2 min after the door was lifted were gently prodded with the eraser end of a pencil, often simply lifting the lid of the start box slightly provided sufficient stimulus for the animal to leave the box. The same procedure was followed during tests.

The day following adaptation to choice procedures, animals were adapted to "stimulus" conditions. Adaptation for stimulus animals consisted of being placed in the stimulus boxes at either end of the preference apparatus for 1 hour. Animals which were tested together as stimulus animals for experimental tests were also adapted together. During adaptation of stimulus animals for the aggression preference tests an opposite-sexed "pretest" animal was allowed free in the apparatus and its visits to either chamber recorded. This period was designated as the pretest period. Each pretest choice animal had been adapted to the apparatus previously, and served in several pretests with animals of the opposite sex.

Following adaptation to the preference apparatus animals were adapted to the "aggression apparatus" for 2 hours on each of the next three consecutive days. For these adaptation periods the animals home cage was connected to the aggression arena by means of lengths of Tygon tubing inserted into the holes cut in the sides of the home cage and into the sides of the aggression arena. Animals were restricted to the arena for the first 40 min of the 2 hr period by means of #6 black rubber stoppers inserted in the ends of the connecting tubes. The stoppers were removed for the remainder of the period so that the animal had access to both the arena and its home cage.

Aggression tests were conducted on 3 consecutive days following adaptation to the aggression apparatus. Males and females were observed. Tests were conducted by placing the two shaved animals of the same sex into the aggression arena and observing them for 40 min. Behavior during this period was categorized as approach, displacement, aggressive, or submissive. Frequency of all aggressive behaviors (total of all attacks, chases, and fights) was included under one category because aggressive behaviors other than attacks were extremely infrequent.

Aggressive preference tests were conducted on the 2 days following aggression tests. Two animals of one sex, that had been tested together in the aggression tests, each served once as choice animals. The two animals of the opposite sex, that had been tested together on the aggression test, served as stimulus animals for both tests. Tests were arranged by placing one of the same-sexed pair of stimulus animals in each of the boxes at the ends of the preference apparatus 15 min prior to the beginning of the test, and the choice animal in the start box 10 min later. Tests were initiated by raising the door to the start box, and thereby allowing the choice animal access to the apparatus. Test duration was 1 hr, timed from when the choice animal exited the start box. Order of testing was counterbalanced for sexes across days. Although the stage of estrus was not controlled for in these tests, smears were taken for each female after she had served as a stimulus animal and on the following day.

On the day after the conclusion of aggression tests for a group, the members of the group were each housed in a 29 x 19 x 13 cm plastic

cage with an individual of the opposite sex. These "new" opposite-sexed individuals had been adapted on the previous day to the apparatus under the procedures described for choice animals. These animals each served once as choice animals in the familiarity preference tests that followed. Animals that had been paired for the aggression preference tests also served together as stimulus animals for the familiarity preference tests (The two same-sexed stimulus animals for each of these tests were two individuals that had been partners in tests for aggression). This arrangement produced four tests for each group, two tests for each same-sexed set of stimulus animals.

Smears were obtained from the females of each group prior to the onset of the dark period on the seventh day after animals had been paired. Tests were conducted with stimulus females only when both of these females exhibited smears consisting of at least 75% leucocytes. This type of smear would normally indicate a nonreceptive state. Females that displayed sperm on the smear were tested after they displayed this type of smear. Choice females were tested individually if they displayed smears with at least 75% leucocytes. Test procedures for choice and stimulus animals were as described previously.

Results

Aggression Tests. The level of aggression (attacks, chases, fights, and rough-and-tumble fights) displayed in the aggression tests were very low. No aggressive behaviors were displayed in four of the ten groups by females of either species. Peromyscus polionotus males did not display aggression in two groups, while P. maniculatus males did not display aggression in three groups. The comparison of total

values (for all three tests) for the four behavioral categories recorded are displayed by sex for each species in Table 13. Only the comparison of P. polionotus males and females on frequency of aggressive behavior was significant, with males displaying a higher frequency of aggressive behaviors.

Because the frequency of aggression in these tests was very low it was difficult to determine which animal of a pair was actually the "most aggressive". Instead, the total frequency of approaches and aggressive behaviors was used to provide an indication of which animal of a pair might be more aggressive. This total frequency score, although not an aggression score per se, does allow a comparison of the tendency to initiate interactions or "assertiveness" of the two individuals in a pair. It would seem reasonable to expect that the less timid of two individuals under these test conditions might also be more likely to exhibit more aggression under other conditions. The individual of a pair of animals in aggression tests that displayed the greatest tendency to initiate interactions will be termed the "high-interaction" individual, while the individual that displayed the lower tendency to interact will be termed the "low-interaction" individual.

Aggression Preference. Table 14 presents data on the preferences of animals of each sex for high or low-interaction individuals of the opposite-sex. No preference for high-interaction animals of the opposite sex was displayed by P. polionotus of either sex. Peromyscus maniculatus males, however, did display significantly longer durations of visits with high-interaction females than low-interaction females

Table 13
 Comparison of Mean Total Frequency of Behaviors
 in Aggression Tests by Sex for Each Species

Measure	<i>P. pollionotus</i>				<i>P. maniculatus</i>			
	Male		Female		Male		Female	
	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)
Approach	68.85	12.74	49.45	5.84	34.90	7.29	27.60	6.18
Aggression	3.30	1.35	.20	.12	1.73	.75	1.45	.58
Displacement	5.45	2.80	1.15	.53	1.85	.76	1.15	.68
Submission	4.10	2.21	.25	.14	.05	.05	.05	.05
				t				t
				1.38				.76
				2.29*				.32
				1.51				.68
				1.74				.00

t-test df=38 2-tail *p<.05

Table 14
 Preference by Males and Females for High-Interaction
 and Low-Interaction Animals of the Opposite Sex

Measure	Male				Female				
	High Interaction		Low Interaction		High Interaction		Low Interaction		
	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)	
<i>E. pallionotus</i>									
No. of visits	86.95	14.01	96.65	16.52	54.95	6.54	54.15	7.38	.14
Total duration of visits	616.00	123.49	464.65	109.94	987.10	202.47	769.30	150.96	.76
Mean duration of visits	10.87	2.70	7.39	1.85	28.66	7.78	19.74	5.45	.95
<i>E. maniculatus</i>									
No. of visits	85.40	56.43	25.50	4.08	55.75	18.59	59.80	25.40	.41
Total duration of visits	1220.50	248.61	948.50	163.27	1031.90	275.59	595.43	202.89	1.07
Mean duration of visits	66.59	29.19	27.75	9.85	44.22	14.31	21.81	9.41	1.18

All durations are in seconds.
 Paired-t 1-tail df=19

* $p < .05$

and 16 of 20 males visited high-interaction more frequently than low-interaction females (sign test, $N=20$, $\chi=4$, $p<.01$). High-interaction P. maniculatus females and low-interaction P. maniculatus males both displayed significantly longer durations of visits with high rather than low-interaction animals of the opposite sex (means for high-interaction females with high and low-interaction animals = 1155 sec and 159 sec, one-tail paired-t: $df=8$, $t=2.37$, means for low-interaction males with high-interaction and low-interaction animals = 1559 sec and 468 sec, one-tail paired-t: $df=9$, $t=2.13$; $p<.05$ for both comparisons).

Although the stage of estrus for females in aggression tests was not controlled, data were available for this factor. Comparisons of male preference for high-interaction and low-interaction females were made for these tests in which both stimulus individuals were in diestrus (see Table 15). The only significant finding was a preference by P. maniculatus males for high-interaction females by the measure of duration of visits. This is also the only comparison which had been significant when data from all females was included. Comparisons could not be performed within the non-diestrous condition as there were no cases for P. polionotus in which both stimulus females were non-diestrous, and only two such cases for P. maniculatus females.

Comparisons of male preference for diestrous versus non-diestrous high-interaction females and diestrous versus non-diestrous low-interaction females are presented in Table 16. Peromyscus polionotus males displayed more visits to non-diestrous high-interaction females than to diestrous high-interaction females, and P. maniculatus males

Table 15
 Comparison of Male Preference for
 High-Interaction and Low-Interaction
 Females in Diestrus

Measure	High Interaction		Low Interaction		t
	Mean	(SE)	Mean	(SE)	
<u>P. polionotus</u>					
No. of visits	70.86	11.41	76.00	16.18	.29
Total duration of visits	618.14	152.07	419.60	115.14	1.33
Mean duration of visits	11.22	2.75	8.47	2.54	1.12
<u>P. maniculatus</u>					
No. of visits	217.00	187.73	17.50	3.85	1.07
Total duration of visits	1291.28	510.14	114.94	61.94	2.43*
Mean duration of visits	71.55	48.03	6.32	2.36	1.37

All durations are in seconds.

Paired-t P. polionotus df=13

1-tail *p<.05

P. maniculatus df=5

Table 17
 Preference for High and Low Interaction Males by Diestrous
 or Non-Diestrous P. polionotus and P. maniculatus Females

Measure	<u>P. polionotus</u>					<u>P. maniculatus</u>								
	Diestrus		Non-Diestrus			Diestrus		Non-Diestrus						
	Mean	(N)	SE	Mean	(N)	SE	Mean	(N)	SE	Mean	(N)	SE	t	
No. of visits to high	58.21	(14)	8.02	47.35	(6)	11.62	75	42.18	(11)	13.00	82.57	(7)	49.68	.96
No. of visits to low	54.14	(14)	9.28	54.17	(6)	12.96	.00	40.36	(11)	15.33	97.86	(7)	69.58	.99
Total duration of visits to high	920.19	(14)	224.78	1143.22	(6)	453.60	.49	1344.79	(11)	410.50	779.43	(7)	418.81	.92
Total duration of visits to low	872.55	(14)	211.02	528.39	(6)	44.00	1.05	624.82	(11)	288.52	297.95	(7)	97.68	.87
Mean duration of visits to high	24.30	(14)	8.19	38.82	(6)	18.16	.85	55.86	(11)	18.66	36.92	(7)	28.73	.58
Mean duration of visits to low	22.10	(14)	7.52	14.23	(6)	4.76	.65	21.04	(11)	12.37	8.51	(7)	2.72	.79

All durations are in seconds.

t-test P. polionotus $df=18$

P. maniculatus $df=16$

2-tail

$p > .05$ for all comparisons

visited non-diestrous low-interaction females more frequently than diestrous low-interaction females. All other comparisons of male preference based on stage of estrus were non-significant. The stage of estrus did not significantly affect female preference for high or low-interaction males of either species (see Table 17).

Familiarity Preference. Male and female P. polionotus did not display preference for familiar individuals over unfamiliar individuals of the opposite sex by any measure, although the comparison of the total duration of visits did approach significance for females (one-tail paired-t, $df=19$, $t=1.47$, $p=.054$). Peromyscus maniculatus males and females displayed significantly more visits to familiar than to unfamiliar individuals of the opposite sex. Females also displayed longer durations of visits to familiar males than to unfamiliar males (see Table 18), and a greater number of females exhibited more visits to familiar than to unfamiliar males (one-tail sign test, $N=18$, $\chi=5$, $p<.05$).

Because stimulus animals in familiarity preference tests had previously been evaluated in aggression tests, the "attractiveness" of these animals in familiarity preference tests could also be evaluated on the basis of their tendency to interact with other animals. These comparisons are presented in Table 19. Peromyscus polionotus females displayed significantly more visits to high-interaction than to low-interaction males, and the difference in the number of females that spent longer durations with high-interaction than low-interaction males was also significant (one-tail sign test, $N=20$, $\chi=5$, $p<.05$).

Table 18
 Preference for Familiar and Unfamiliar Animals
 of the Opposite Sex by Males and Females of Each Species

Measure	Male				Female				
	Familiar		Unfamiliar		Familiar		Unfamiliar		
	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)	
<i>P. pollienotus</i>									
No. of visits	128.00	19.65	144.30	22.95	98.15	12.90	91.70	16.47	.48
Total duration of visits	522.22	99.31	539.47	105.04	773.62	155.50	428.88	138.04	1.47
Mean duration of visits	5.87	1.37	6.68	1.96	12.10	3.65	9.63	4.75	.42
									†
<i>P. maniculatus</i>									
No. of visits	46.75	10.22	32.15	4.61	32.15	6.62	18.10	3.31	2.42*
Total duration of visits	978.15	209.73	781.58	215.56	1439.80	295.83	540.90	199.16	2.08*
Mean duration of visits	37.71	10.13	37.88	13.38	183.04	85.88	45.27	27.30	1.46

All durations are in seconds.
 Paired-t $df=19$ 1-tail

* $p < .05$

Table 19
 Preference by Males and Females for High-Interaction and
 Low-Interaction Animals of the Opposite Sex in Familiarity Tests

Measure	Male				Female				
	High Interaction		Low Interaction		High Interaction		Low Interaction		
	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)	
<i>P. polionotus</i>									
No. of visits	136.45	21.92	135.85	20.96	110.95	17.34	81.90	12.94	2.19*
Total duration of visits	440.75	54.31	620.93	130.77	676.00	146.56	526.50	153.96	.61
Mean duration of visits	4.95	.89	7.62	2.19	12.43	4.93	9.29	3.39	.53
<i>P. maniculatus</i>									
No. of visits	40.85	8.14	38.05	8.06	26.40	5.79	23.85	5.13	.39
Total duration of visits	999.02	225.21	760.70	198.13	1032.45	289.93	948.25	253.37	.18
Mean duration of visits	40.21	12.70	35.38	10.95	160.82	85.62	67.50	32.58	.96

All durations are in seconds.

Paired-t $df=19$ 1-tail * $p < .05$

Discussion

Whereas individuals observed in the seminatural apparatus had exhibited appreciable levels of aggressive behavior, levels of aggression displayed by individuals in the aggression apparatus were very low. This finding was somewhat unexpected. The object of the procedures followed in the present study had been to condition individuals to treat the aggression arena as an extension of the home cage. In previous observations individuals housed in cages identical to those used to form the aggression arena had displayed fairly high levels of aggression to intruders after one to two weeks of residency (unpublished observations). In the present study individuals were tested for aggressivity in the arena on the seventh through ninth days of residency in the home cage. Although individuals did not have access to the home cage during aggression tests, they had been allowed to travel freely between the home cage and aggression arena during adaptation. In addition, during aggression tests the home cages and the aggression arena were attached in a manner that allowed a fairly free flow of air between them. Many individuals were observed to spend long periods sniffing and gnawing at the entrances to their home cages. Individuals therefore appeared to recognize their home cage as opposed to a strange cage (unfortunately these observations were not quantified). During aggression testing, however, individuals did not behave as residents in the aggression arena, nor did they defend the entrances to their home cage. Animals in these tests were simultaneously exposed to olfactory cues from both their home cage and that of their opponent. These test conditions may have led to

conflicting "flight" and "flight" responses (See Hinde, 1966), and thereby resulted in low aggression scores.

It is of interest that individuals in the seminatural apparatus displayed high levels of aggression toward one another immediately upon being allowed access to the central arena, even though none of these individuals had previous exposure to this area, and had been in residence in the connected home areas only three days. The observation of higher levels of aggression under the seminatural conditions than under aggression-test conditions may be due in part to the fact that individuals in the seminatural apparatus were exposed to opposite-sexed individuals during tests while individuals in the aggression apparatus were not (Barnett, Evans & Stoddart, 1968; Brain, Benton, & Bolton, 1976; deCantazaro, 1981; Flannelly & Lore, 1977; O'Donnell, Blanchard, & Blanchard, 1981). Exposure to females has been demonstrated to increase male-male aggression in *P. maniculatus bairdi* (Terman, 1982; Dewsbury, Personal communication). Exposure to opposite-sexed individuals was, however, not required to elicit aggression in the previously mentioned tests of resident *P. polionotus* in aggression-arena-sized cages; and males in the seminatural single-housed condition were observed in several tests to initiate high levels of attacks and chases prior to exposure to females.

Preferences for high-interaction (and presumably more aggressive) individuals were not as strong as might have been predicted from the results of the seminatural experiments in the present study, or from the results of previous studies (e.g., Blair & Howard, 1944; Eisenburg, 1962). Although in the majority of comparisons (over 80%)

scores on the measures of preference for high-Interaction individuals were higher than those for low-Interaction individuals, most of the differences displayed between high and low-Interaction individuals were non-significant. This may be a reflection of the low levels of aggression displayed in these tests. Previous Investigators (e.g. Huck et al., 1981) have hypothesized that the differences in odors displayed by dominant and subordinate animals are mediated by differences in the physiological changes induced in these individuals through aggressive encounters. The levels of aggression in the present tests may not have been high enough to fully induce the physiological changes necessary for clear-cut discriminations on the part of choice animals.

Although levels of aggression were low in aggression tests, females of both species, and P. maniculatus males, displayed significant preferences for the more "assertive" individual of the opposite sex under some preference test conditions. Significant preferences were not displayed for low-Interaction individuals of either sex in either species. Under the assumption that individuals that are more assertive would also normally be more aggressive, these findings are consistent with the hypothesis proposed earlier that individuals of these species should prefer aggressive opposite-sexed individuals, and also with the nesting behavior exhibited by P. polionotus in the seminatural apparatus.

In familiarity preference tests P. maniculatus of both sexes displayed preference for familiar individuals of the opposite sex, while P. polionotus did not display such preference. Although the

lack of preference displayed by P. polionotus in the familiarity preference tests is consistent with observations made in the seminatural study, results of the familiarity preference tests are contrary to predictions made earlier as to the behavior of these two species.

Sibling Preference Tests

Introduction

Individuals of most rodent species will be exposed to siblings during development. Such exposure may, of itself or in conjunction with genetic factors, influence mate selection (Grau, 1982; Halpin & Hoffman, 1982; Smith, 1966). The general consensus holds that, except under special circumstances, individuals should prefer to breed with non-relatives (Daly & Wilson, 1978; Dewsbury, 1982a; Krebs & Davies, 1981; Wittenberger, 1981). Rasmussen (1970), however, has suggested that inbreeding may be fairly extensive in some species of Peromyscus, particularly P. maniculatus (Rasmussen, 1964); and Howard (1949) has proposed that inbreeding may account for as much as 10 percent of breeding in P. maniculatus. Smith (1966) has suggested that "a considerable amount of inbreeding" (p. 50) also occurs in P. polionotus.

Not all investigators agree with these proposals however. Selander (1970) has questioned the genetic basis for Rasmussen's (1964) conclusions regarding P. maniculatus, and other investigators (Dewsbury, 1982a; Hill, 1974) have demonstrated suppressed reproduction for sibling matings in this species. Foltz (1981b) has also questioned Smith's (1966) proposal of high levels of inbreeding in

P. polionotus. The present study was designed to evaluate preference for siblings in P. polionotus and P. maniculatus.

Subjects

Both P. polionotus and P. maniculatus served as subjects for sibling preference tests. Subjects were selected from 12 litters of each species that contained at least two animals of each sex. Two animals of each sex were selected from these litters, under criteria in the general methods section, and maintained together throughout the experimental procedure. Litters selected for groups were unrelated by more than one common grandparent. Two litters of each species comprised an experimental group.

Procedure

Individuals were ear-punched for identification, and P. maniculatus litters were moved to the P. polionotus colony room. On the following day animals were adapted to the preference apparatus, without other individuals present, as both stimulus animals and choice animals.

Preference tests were of two types, same-sex tests and opposite-sex tests. In same-sex tests choice animals had a choice between a same-sexed sibling stimulus animal and a same-sexed nonsibling. In opposite-sex tests animals had a choice between two opposite-sexed individuals, one a sibling and one a nonsibling. Each animal in a group served twice as a stimulus animal and once as a choice animal for each type of test. In an opposite-sex test, for example, males 2 and 4 would serve as stimulus animals for choice females 2 (one of the 2 male siblings) and 4 (a 4 male sibling). They would each also serve as

choice animals with stimulus females 1 (a 2 male sibling) and 3 (a 4 male sibling).

Preference tests were conducted on the two days following adaptation. All tests of one type (i.e. opposite-sex tests) and half of the tests of the other type were conducted on the same day. Testing was completed on the second day. The order of test type across days was counterbalanced. The number and duration of visits to each chamber were recorded on each test and for the adaptation period. Vaginal smears were obtained for each female before the beginning of the dark cycle on each test day.

Results

Peromyscus polionotus females demonstrated a preference for siblings over nonsiblings (see Table 20). Sibling males were visited significantly more frequently than nonsibling males, and a significantly larger number of females spent longer durations with sibling rather than nonsibling males (sign test, $N=24$, $\chi=6$, 2-tail $p<.05$). They also spent significantly longer durations with sibling rather than nonsibling females. None of the comparisons for siblings versus nonsiblings were significant for P. polionotus males or for P. maniculatus of either sex (see Tables 20 and 21). It is, however, of interest that scores for P. polionotus males on tests with opposite-sexed animals mirror those of P. polionotus females (higher scores for siblings), while for all but one measure (average duration of visits for females) P. maniculatus display higher scores for opposite-sexed nonsiblings.

Table 20
 Preference by *P. polionotus* Males and Females for
 Siblings and Nonsiblings of the Same-Sex and Opposite-Sex

Measure	Total (Male and Female)				Males				Females						
	Sibling		Nonsibling		Sibling		Nonsibling		Sibling		Nonsibling				
	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)			
Preference for Opposite-Sex															
No. of visits	109.83	13.45	91.65	11.83	1.93	111.42	16.48	107.67	17.66	.35	108.25	21.61	75.62	15.43	2.16*
Total duration of visits	840.42	113.62	592.93	94.51	1.64	701.33	124.02	690.96	145.59	.06	979.50	188.94	494.90	120.30	2.00
Mean duration of visits	22.28	4.85	17.30	4.59	1.32	22.40	7.71	22.25	8.38	.03	22.16	6.05	12.34	3.68	1.61
Preference for Same-Sex															
No. of visits	134.92	20.69	100.48	15.21	2.01*	153.71	29.10	102.46	14.80	1.97	116.13	29.54	98.50	26.95	.79
Total duration of visits	740.85	107.23	516.38	89.11	1.57	622.13	131.40	614.35	164.46	.04	859.58	168.29	418.42	67.62	2.45*
Mean duration of visits	18.20	4.72	28.12	14.07	.69	17.59	7.82	46.87	27.75	1.05	18.62	5.47	9.37	2.82	2.04

All durations are in seconds.
 Paired-t Total df=47 Male and Female df=23 2-tail *p<.05

Table 21
 Preference by *P. maniculatus* Males and Females for
 Siblings and Nonsiblings of the Same-Sex and Opposite-Sex

Measure	Total (Males and Females)				Males				Females						
	Sibling		Nonsibling		Sibling		Nonsibling		Sibling		Nonsibling				
	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)			
Preference for Opposite-Sex															
No. of visits	16.17	2.13	20.81	3.59	1.40	17.17	3.14	17.88	2.37	.34	15.67	2.94	23.75	6.81	1.37
Total duration of visits	837.83	166.46	1412.64	186.58	1.84	885.76	231.94	1542.86	260.28	1.49	789.89	243.40	1282.42	270.29	1.09
Mean duration of visits	127.46	69.27	159.99	43.89	.38	65.42	22.13	157.58	50.86	1.53	189.51	137.06	162.41	72.71	.17
Preference for Same-Sex															
No. of visits	18.73	2.27	17.40	2.09	.69	18.58	3.24	17.58	2.58	.41	18.88	3.24	17.20	3.35	.54
Total duration of visits	1144.24	166.51	1108.87	178.61	.11	1134.33	246.92	1250.43	250.54	.26	1154.15	228.76	967.31	256.64	.43
Mean duration of visits	118.33	34.31	182.54	73.67	.75	124.63	51.15	112.04	33.03	.19	112.03	46.83	253.03	143.72	.38

All durations are in seconds.
 Paired-t Total df=47 Male and Female df=23 2-tail p>.05 for all comparisons

Table 22
 Comparison of Male Preference for
 Sibling and Nonsibling Females in Diestrus

Measure	<u>Sibling</u>		<u>Nonsibling</u>		†
	Mean	(SE)	Mean	(SE)	
<u>P. polionotus</u>					
No. of visits	90.83	24.40	95.33	21.10	.33
Total duration of visits	777.06	173.36	904.81	259.62	.41
Mean duration of visits	28.66	13.16	35.11	15.51	.94
<u>P. maniculatus</u>					
No. of visits	18.21	4.45	14.64	3.22	1.36
Total duration of visits	1048.67	323.90	1448.26	367.33	.64
Mean duration of visits	87.96	35.79	201.42	84.01	1.12

 All durations are in seconds.

†-test P. polionotus df=11

P. maniculatus df=14

2-tail

p>.05 for all comparisons

Table 23

Preference by *P. polionotus* and *P. maniculatus* Males for Sibling and Nonsibling Females in Diestrous and Non-Diestrous Conditions

Measure	<i>P. polionotus</i>				<i>P. maniculatus</i>									
	Diestrus		Non-Diestrus		Diestrus		Non-Diestrus							
	Mean	SE	Mean	SE	Mean	SE	Mean	SE						
No. of visits to siblings	98.06	18	18.04	151.50	6	35.39	1.44	18.78	18	3.80	12.33	6	12.79	.89
No. of visits to nonsiblings	110.61	18	19.90	98.83	6	41.02	.28	16.44	18	2.77	22.17	6	4.55	1.05
Total duration of visits to siblings	731.83	18	141.89	609.83	6	274.82	.42	978.48	18	271.95	607.61	6	463.55	.68
Total duration of visits to nonsiblings	727.02	18	184.01	582.78	6	205.69	.42	1452.89	18	304.40	1872.78	6	521.85	.72
Mean duration of visits to siblings	25.08	18	9.52	14.54	6	12.31	1.79	75.07	18	28.49	36.48	6	22.58	.75
Mean duration of visits to nonsiblings	25.00	18	10.80	14.01	6	9.28	.56	169.53	18	66.48	121.71	6	46.62	.40

All durations are in seconds.

t-test $df=22$ 2-tail $p > .05$ for all comparisons

Table 24

Preference for Sibling and Nonsibling by Diestrous
and Non-Diestrous P. polionotus and P. maniculatus Females

Measure	<u>P. polionotus</u>					<u>P. maniculatus</u>								
	Diestrus		Non-Diestrus		t	Diestrus		Non-Diestrus		t				
	Mean	(N)	SE	Mean		(N)	SE	Mean	(N)		SE			
No. of visits to siblings	116.95	(19)	26.59	75.20	(5)	21.26	14.56	(18)	2.50	17.00	(6)	9.74	.35	
No. of visits to nonsiblings	75.94	(19)	18.96	74.40	(5)	20.57	.04	26.56	(18)	8.65	15.33	(6)	8.46	.71
Total duration of visits to siblings	1048.26	(19)	219.76	718.20	(5)	371.22	.70	850.70	(18)	295.33	607.44	(6)	451.16	.42
Total duration of visits to nonsiblings	554.00	(19)	147.42	270.33	(5)	108.88	.96	956.07	(18)	274.65	2261.44	(6)	564.97	2.27*
Mean duration of visits to siblings	21.94	(19)	6.50	23.00	(5)	16.97	.07	229.15	(18)	181.91	70.63	(6)	65.91	.49
Mean duration of visits to nonsiblings	15.55	(19)	4.43	7.77	(5)	5.65	.63	57.38	(18)	23.00	477.47	(6)	255.73	2.87**

All durations are in seconds.
t-test $\underline{df}=22$ 2-tail * $p<.05$ ** $p<.01$

Table 25

Preference for Sibling and Nonsibling Females by Diestrous and Non-Diestrous P. polionotus and P. maniculatus Females

Measure	<u>P. polionotus</u>					<u>P. maniculatus</u>								
	Diestrus		Non-Diestrus			Diestrus		Non-Diestrus						
	Mean	(N)	SE	Mean	(N)	SE	Mean	(N)	SE	t				
No. of visits to siblings	126.37	(19)	36.57	77.20	(5)	27.08	15.18	(17)	3.18	23.80	(5)	9.28	1.13	
No. of visits to nonsiblings	105.16	(19)	33.63	73.20	(5)	22.66	47	13.06	(17)	2.27	18.00	(5)	7.13	.86
Total duration of visits to siblings	909.35	(19)	203.09	670.47	(5)	255.13	57	940.14	(17)	262.81	1576.80	(5)	598.22	1.10
Total duration of visits to nonsiblings	434.53	(19)	81.01	337.20	(5)	113.08	46	1083.75	(17)	317.14	887.53	(5)	611.42	.29
Mean duration of visits to siblings	21.55	(19)	6.77	8.42	(5)	2.34	.97	123.60	(17)	64.70	96.24	(5)	55.35	.22
Mean duration of visits to nonsiblings	10.54	(19)	3.53	4.93	(5)	.74	.80	306.08	(17)	198.16	172.44	(5)	160.74	.35

All durations are in seconds.

I-test P. polionotus $df=22$ P. maniculatus $df=20$ 2-tail $p > .05$ for all comparisons

As with the aggression preference tests comparisons were made of male preference for siblings and nonsiblings in diestrus and of male preference for diestrous versus non-diestrous siblings and nonsiblings. None of these comparisons were significant for either P. polionotus or P. maniculatus males (see Tables 22 and 23). Comparisons of the preferences of females in different stages of estrus did, however, yield some significant differences. Although P. polionotus females exhibited no significant differences in preferences based on stage of estrus, P. maniculatus females did display significantly greater preference for nonsibling males, by the measures of total and average durations of visits, when in a non-diestrous condition over a diestrous condition (see Tables 24 and 25).

The possibility of litter effects on preference scores was also evaluated by conducting a one-way analysis of variance on the "difference scores" between preference scores for siblings and nonsiblings. Significant litter effects were found for the average duration of visits by P. polionotus males to females ($F(11,12)=3.77$, $p<.05$), and for the total duration of visits by P. polionotus females to males ($F(11,12)=3.08$, $p<.05$).

Discussion

While Peromyscus polionotus males generally displayed higher scores on preference measures for siblings than for nonsiblings, these comparisons were not significant. P. polionotus females, however, did display significant preferences for siblings over nonsiblings. The results of this study, therefore, may offer some support for proposals of high levels of inbreeding in P. polionotus (Smith, 1966). The

observation that scores for preference by P. maniculatus males and females were generally in the opposite direction from those for P. polionotus is of interest. This difference may indicate a greater preference for siblings by P. polionotus than by P. maniculatus. It is also of interest that non-diestrous P. maniculatus females displayed a greater preference than diestrous females for nonsibling males, since females in a non-diestrous condition would be more likely to be receptive. These results are consistent with previous studies demonstrating suppression of reproduction in sibling matings of P. maniculatus (Dewsbury, 1982a; Hill, 1974), and the implicit conclusion from these studies that inbreeding should be avoided by members of this species.

SECTION IV GENERAL DISCUSSION

In the general discussion the observations of the present study are examined in light of previous research, and interpretations are suggested for these observations that are consistent with the ecology and mating systems of P. maniculatus and P. polionotus. The general discussion section is divided into six subsections. The first of these subsections examines aggressive ability as a factor in preference. This subsection begins with a fairly extensive overview of the ecology of P. maniculatus and P. polionotus, and also presents evidence for the role of aggression in the ecology of these two species. The ecological information presented in this subsection serves as a background for discussions which follow in all subsequent subsections. The discussion of the ecology of these species is followed by a discussion of factors that may provide an adaptive basis for selection of aggressive mates in these species.

The second subsection deals with familiarity as a factor in preference and with the effect of prior breeding experience on preference for familiar individuals, and includes a discussion of the opportunities that may be available for P. maniculatus and P. polionotus to utilize familiarity as a basis for mate selection. This subsection is followed by a subsection on the related topic of kinship as a factor in preference. The subsection on kinship discusses

evidence for and against inbreeding in P. maniculatus and P. polionotus, and the ecological and social factors that may affect preference for siblings as mates in these species. This subsection is followed by a subsection on the evolution of monogamy in P. polionotus, and the summary for this study.

Aggressive Ability as a Factor In Preference

Many of the observations in the present study were consistent with the general hypothesis that aggressive ability may be important in the social behavior and mate selection of monogamous and polygamous species. They were also consistent with the specific predictions that aggression should be an important component of the social behavior of P. polionotus, and that P. polionotus and P. maniculatus of both sexes should prefer mates with high aggressive ability. In the seminatural experiments aggression was routinely displayed by both male and female P. polionotus, and both males and females of this species nested more frequently with the more aggressive of the two opposite-sexed individuals. Female P. polionotus also displayed preference for the more assertive of two males in familiarity preference tests; and preference for more assertive individuals was displayed by P. maniculatus males and high-interaction P. maniculatus females in aggression preference tests.

The preferences exhibited by these species may be mediated through advantages in reproduction gained by individuals that choose mates with good aggressive ability over those that choose mates with poor aggressive ability. Some of the possible advantages accrued by individuals that choose mates with high aggressive ability have been

briefly discussed in previous sections. The present discussion will focus on the advantages that might be gained through such choice by individuals of the two species of interest in this study, P. polionotus and P. maniculatus, in the context of the ecology and mating system of these two species.

Ecology, Mating System, and Aggressive Ability

Many ecological variables will play a role in determining to what extent aggression may be adaptive for individuals of any particular species, and thus also the importance of aggressive ability as a quality in mates. The ecology of a species may often be as major a factor as its mating system in determining the importance of aggressive ability to reproductive success in that species. Among the more general ecological problems with which individuals of a species must cope with in order to reproduce successfully, and one that also affects the mating system of a species, is the availability and defensibility of resources necessary to reproduction (Brown, J. L., 1975; Clutton-Brock & Harvey, 1978; Emlen & Oring, 1977; Halliday, 1978; Oring, 1969). Aggressive ability may play an important role in the acquisition and defense of these resources in monogamous and non-monogamous species. Individuals that choose mates high in aggressive ability may be insuring that adequate resources will be available for themselves and their offspring; choosing such mates should therefore be more adaptive than choosing mates with low aggressive ability.

Peromyscus maniculatus

Peromyscus maniculatus occurs in a wide variety of habitats over most of the North American continent (Baker, 1968; Hamilton, 1943; Hooper, 1968). This species will accept a wide variety of food items (Cogshall, 1928; Martell & Macaulay, 1981; Williams O., 1955) and nest sites (Blair, 1940; Hamilton W. J., 1943; Howard, 1949), and the distribution of the various subspecies in the environment may be governed more by different behavioral responses to different habitat types than by any absolute differences in nesting requirements or food preference (Dice, 1922; Harris, 1952; Wecker, 1963). The subspecies of P. maniculatus may for the most part be divided into two general types, those adapted for and occupying openlands such as fields, and those adapted for and occupying woodlands and brushlands (Baker, 1968). Peromyscus maniculatus bairdi, the subspecies observed in the present study, is generally found in "open fields, sand beaches, and arable land of the prairie states..." (Hamilton W. J., 1943, p. 270).

Peromyscus maniculatus bairdi generally live in overlapping home ranges (Blair, 1940). As is typical of other Peromyscus (Stickel, 1968), each home range contains several nests and refuge holes, and mice may change nests frequently (Blair, 1940; Howard, 1949). In addition to utilizing several types of naturally occurring nest sites (Blair, 1940; Howard, 1949) individuals of this subspecies are capable of constructing their own burrows (Houtcooper, 1972). Peromyscus maniculatus bairdi is therefore more likely to be restricted to particular locations within its preferred habitat by considerations such as the availability of sufficient food than by availability of

nest sites. This Interpretation receives support from observations by Howard (1949) which indicate that increasing the number of nests available in an area does not increase the number of resident breeding mice in that area; and by observations which indicate that P. m. bairdi cache food for winter use (Hamilton W. J., 1943; Howard, 1949), and that the availability of food may limit the number of resident breeding adults in other subspecies of P. maniculatus (Fordham, 1972; Gashwiler, 1979; Taitt, 1981).

The habit of caching food and the large winter aggregations observed in this subspecies (Howard, 1949, 1951) are probably adaptations for winter survival. Energy requirements for these mice in the winter months are high (Howard, 1951) and populations in some localities may suffer severe winter mortality (Blair, 1940; Howard, 1949). These mice do exhibit an ability to become torpid at low temperatures. In severely cold weather, however, individual mice may not be able to become torpid without freezing. Utilization of cached food allows individuals to maintain high metabolic rates (and therefore a high body temperature), and huddling in winter aggregations both reduces body heat loss and allows individuals to become torpid (Howard, 1951). Winter aggregations generally appear to consist of a breeding pair and at least one previous litter, additional conspecific adults of both sexes, and sometimes individuals of other species (Howard, 1949). Peromyscus maniculatus bairdi have generally not been observed to breed in the winter (Blair, 1940; Howard, 1949), although a few individuals may sometimes be capable of breeding through the winter in favorable microhabitats (e.g., Cornshocks: Linduska, 1942).

If food availability is the primary factor determining the suitability of a particular area (within the preferred habitat type) for breeding in P. m. bairdi, one might expect that it would also affect the social organization and mating system of this species. Because P. m. bairdi appears to utilize a wide variety of different food items, the importance of which may vary seasonally (Houtcooper, 1978), it is likely that defense of the food supply per se is not economically feasible. Peromyscus maniculatus bairdi appear to have opted instead for a strategy of limiting the number of breeding individuals in or near their home ranges. This is accomplished in part by adults aggressively limiting juvenile settlement in their home range (Ayer & Whitsett, 1980; Enders, 1978; Whitsett, Gray, & Bediz, 1979). In some subspecies of P. maniculatus juvenile settlement appears to be restricted largely as a result of male aggression toward juveniles (Fairbairn, 1977; Healey, 1967; Metzgar, 1979, 1980; Mihok, 1979; Sadleir, 1965); while for other subspecies (including P. m. bairdi) female aggression might be as important as or even more important than, male aggression in limiting juvenile settlement (Ayer & Whitsett, 1980; Enders, 1978; Fordham, 1971; Taitt, 1981; Whitsett et al., 1979). As in other subspecies of P. maniculatus (Fairbairn, 1978; Healey, 1967; Llewellyn, 1980), male aggression in P. m. bairdi appears to be under hormonal control (Whitsett et al., 1979). The level of aggression in male P. m. bairdi may therefore follow a seasonal pattern of changes as described for other subspecies of P. maniculatus (Healey, 1967; Llewellyn, 1980; Metzgar, 1979; Sadleir, 1965).

The general seasonal pattern of changes in the level of aggression for male P. maniculatus, as described by Healey (1967), consists of a spring increase in male aggression (which is correlated with an increase in testicular size) to a peak through the major breeding season, followed by a drop in the level of aggression to negligible levels at the time fall aggregations occur. This seasonal pattern of changes in the level of male aggression is reflected in seasonal changes in social organization. At least some subspecies of P. maniculatus have been observed to form large non-aggressive non-breeding winter aggregations (Dice & Howard, 1951; Howard, 1949, 1951; Metzgar, 1979). Although sufficient observations are not available to permit evaluation of the generality of the tendency of P. maniculatus to form large winter aggregations, most subspecies of P. maniculatus do appear to exhibit a spring dispersal period prior to the major breeding season. The shift in behavior and social organization that occurs at this time have probably been best described by Healey (1967) for P. m. austerus. According to Healey a greater number of mice survive the winter than are compatible on the breeding territories. Animals which were resident in the overwintering areas, and their offspring, are most likely to be dominant in and therefore most likely to settle in these areas, while subordinate animals disperse. Established residents aggressively exclude new settlers, while aggressive interactions between neighboring residents are reduced. In P. m. austerus mutual avoidance between same-sexed resident adults may lead to mutually exclusive home ranges within sexes, but overlapping

home ranges between sexes (Healey, 1967; Sadleir, 1965). Other authors (e.g., Metzgar, 1979), however, have observed a pattern in this subspecies that is exhibited by several other subspecies of P. maniculatus including P. m. bairdi -- same-sexed home ranges may overlap, but appear to overlap much less extensively than home ranges for opposite-sexed individuals (Blair, 1940, 1942, 1943; Howard, 1949; Morris, 1955). The general pattern observed in these studies consists of large resident-male home ranges that overlap each other slightly, while each also extensively overlaps several smaller resident-female home ranges. In at least some subspecies residents may also tolerate same-sexed non-breeding subordinates within their home range (Metzgar, 1979, 1980).

The breeding system of P. maniculatus appears to be somewhat labile. Although males generally appear to form breeding relationships with a few adult females within their home range (Blair, 1958; Howard, 1949; Mihok, 1979; Terman, 1961), adults have been observed in combinations that included more than one breeding individual of either sex (Blair, 1958; Howard, 1949), and members of this species have also been observed to form long lasting and apparently exclusive breeding pairs under some conditions (Blair, 1958; Howard, 1949). Metzgar (1979) has proposed a general system to explain the lability apparent in Peromyscus breeding systems.

In the proposed system, the home ranges of breeding males overlap those of adult females broadly and the two classes occur together far more frequently than by chance alone. Within a sex, breeding adults are evenly dispersed but considerable home range overlap may occur depending on density and home range size. The large home range of a breeding male usually includes all or parts of several adult female home ranges. Female ranges may be overlapped by ranges of several breeding

males, especially when male-male overlap is extensive. However, even with extensive overlap, each breeding male might spend most of his time with a particular female (Garson, 1975). Furthermore, under some conditions (low densities and small home ranges), this generally loose male-female association might be expressed as enduring male-female pairs. (p. 142)

The particular breeding relationships exhibited by a given population of P. maniculatus may be largely determined by food availability, as food availability appears to influence population density and home range overlap in this species, and may also result in an alteration in the sex ratio of the breeding population. A more abundant food supply in an area may result in an increased density of adult mice in that area (Fordham, 1972; Gashwiler, 1979; Taitt, 1981), and a contraction of home range for breeding individuals of both sexes (Taitt, 1981). Although Taitt (1981) noted an increase in the number of both sexes in an area supplied with additional food; Fordham (1972) observed an increase in the number of females and the proportion of females breeding, but no increase in the number of males. A reasonable explanation for this difference was proposed by Taitt (1981) who noted that while she had provided additional food to a winter population, Fordham (1972) had provided additional food during the breeding season. The aggressive resident males in Fordham's study may have prevented recruitment of additional males, but not females. Abundant food in the breeding season may, therefore, result in a female biased breeding population. A skewed sex ratio may in turn have an effect on the breeding associations exhibited by P. m. bairdi. Howard (1949) has noted that "in areas where the sex ratio was not equal, as many as three females lived in the same nest box with one

male, and as many as three males lived in one nest box with one female" (p. 14).

As noted earlier, although P. maniculatus do not appear to defend feeding areas per se, resident animals may prevent over-utilization of food supplies within their home ranges by aggressively limiting the settlement of potential breeders in these areas. The presence of an adequate food supply within a home range may increase the probability of winter survival for residents and their offspring. The observations reviewed in the preceding discussions indicate that the availability and distribution of food items may have major consequences not only on the distribution and survival of these mice, but on the social behavior and breeding relationships exhibited by them as well.

Peromyscus polionotus

In light of several aspects of the ecology of P. polionotus, choosing mates with high aggressive ability may be adaptive for members of this species. One ecological factor of primary importance to this species is the availability of suitable nest sites. Because they construct their own burrows (Hayne, 1936; Smith, 1966; Smith & Criss, 1967) P. polionotus are not restricted by the availability of naturally occurring nests per se. This species does, however, require a fairly narrow range of soil conditions for nest construction, and in habitat undisturbed by man is probably restricted to areas in early successional stages (Golley, Gentry, Caldwell, & Davenport, 1965), and sandy beach areas. According to Smith (1966) abundance of P. polionotus "is correlated with soil type, amount of soil drainage

(Table 2), type and amount of vegetation. All of the habitats occupied by this species are characterized by sparse vegetation and relatively well-drained or recently plowed soils ..." (p. 11). Well-drained fine sand soils were preferred for burrowing, and mice "never constructed burrows in hard soils where digging was difficult, nor in areas where the hardpan was close to the surface of the ground" (p. 13). Few mice were observed in heavily forested areas, or in areas with dense vegetation (Rand & Host, 1942; Smith, 1966; Personal observations), and the number of mice nesting in a given area appeared to be negatively correlated with the density of vegetation (Rand & Host, 1942; Smith, 1966). Individual mice construct several burrows in close proximity (Rand & Host, 1942; Smith, 1966) within a fairly well defined home range (Blair, 1951; Davenport, 1964) and defend these burrows against intruders (Blair, 1951). It is likely that in addition to defending burrows within their home range, individuals also aggressively exclude other potential settlers from suitable nest areas near their burrows. This suggestion is supported by the observation that often the burrows within a given area all appeared to have been constructed by a single individual, or pair of individuals (Rand & Host, 1942; Smith, 1966), and by observations in the present study that animals attacked and chased one another in all areas of the seminatural apparatus, and not just in the area that actually contained their burrow. Although P. polionotus defend burrows within their home range (Blair, 1951), they do not appear to defend their entire home range (Davenport, 1964). The apparent lack of defense of home range by

P. pollonotus may be a reflection of the fact that this species utilizes a wide variety of food items (Gentry & Smith, 1968; Smith, 1966) that are probably not economically defensible.

Although multiple burrows may simply serve a survival function as refuges from predators, the maintenance of several burrows is more likely to act in some manner to maximize reproductive success in P. pollonotus. Blair (1951) and Rand and Host (1942) observed that P. pollonotus change nests frequently; this frequent change of nest site could be a strategy to reduce the level of parasitic infestation of offspring. P. pollonotus have also been observed to utilize unoccupied burrows as food caches (Blair, 1951; Rand & Host, 1942; Smith, 1966). Some evidence exists that populations of this species may at times be food limited (Smith, 1971; Smith & Blessing, 1969); cached food might provide a food reserve that would allow parents and offspring to survive and/or reproduce during such periods. Alternatively cached food could contain nutrients that, although not critical for survival, might be critical for reproduction. Food caches may therefore allow breeding in seasons during which it would not otherwise be adaptive. Evidence supportive of these hypotheses are Smith's (1966) observations that food-deprived individuals of this species become torpid at very cool temperatures while non-food-deprived individuals do not, and observations of improved reproductive performance in pairs fed acorns (a frequently cached food item) parasitized by beetle larvae. Abundant cached food may allow individuals to maintain a level of activity compatible with breeding, even in cooler temperatures, and high-quality food caches (e. g.

acorns containing beetle larvae) may provide nutrients that would otherwise not be available in winter months.

An additional benefit that may derive from the maintenance of multiple burrows has been discussed by Foltz (1979). Upon the birth of a new litter older offspring may move into a nearby burrow with their father. The behavior of moving to nearby burrows may allow offspring to extend the period during which they may take advantage of parental resources and care. Offspring that receive extended care may be better able to compete for food and to establish burrows when they disperse than offspring that do not receive such care. This may be of particular importance in P. polionotus because dispersing individuals appear to suffer very high mortality (Smith, 1966, 1968).

The maintenance of multiple burrows by P. polionotus appears, as a result of the factors discussed, to be a highly adaptive strategy for members of this species. The facts that P. polionotus are restricted to very specific types of habitat, and that individual mice maintain several burrows in an area, probably act as major factors that limit the size of the breeding populations in this species. If nest sites are a limited and critical resource for P. polionotus, one would expect individuals of this species to compete for them, and to defend them from conspecifics.

According to consensus polygyny should be generally be advantageous to males (Brown J. L., 1975; Daly & Wilson, 1978; Dawkins, 1976; Orians, 1969; Verner, 1964), and males should therefore attempt to control limited resources in a manner that allows them to acquire additional mates. Because nest sites appear to be a

limited and defendable resource for P. polionotus, males of this species might be capable of gaining multiple mates by controlling areas suitable for nesting (see Verner & Willson, 1966, p. 145). This species has, however, consistently been found to exhibit a monogamous mating system (Blair, 1951; Foltz, 1979, 1981; Rand & Host, 1942; Smith, 1966).

According to Emlen and Oring (1977) the two preconditions for a species to exhibit a polygamous mating system are that (1) individuals must be potentially capable of economically defending multiple mates, or resources critical to gaining multiple mates, and (2) individuals must be able to utilize that potential. Several factors may prevent P. polionotus males from fulfilling these two preconditions for polygamy. Among the more important of these factors are the distribution of nest sites and food items, and it is likely that monogamy in P. polionotus rests upon considerations related to both of these factors.

Availability of nests. As discussed previously the number of suitable nest sites for P. polionotus in any given area may be very limited. It is possible that nest sites for this species may be so limited as to impose monogamy because two adults are required for their defense (See Wilson, 1975, p. 330). Alternatively a male may be capable of defending a sufficient number of burrows to maintain a single female and her litter, but nest sites may be too dispersed for a male to defend a sufficient number of burrows to maintain two females. Although the maintenance of multiple burrows appears to be important in terms of the ecology of P. polionotus, in light of the available data

It is difficult to evaluate how many burrows a pair might actually require to maximize its reproductive success. While the availability or distribution of nest sites alone might explain monogamy in P. polionotus, it is most likely to be of importance in conjunction with other factors. One might expect for example that if food items were abundant year-round, burrows would not be used as food caches, and males might be more capable of acquiring additional females.

Availability of food items. If suitable habitat for burrowing was abundant a male might be capable of defending enough burrows to maintain several females. However, even if burrows were abundant, females themselves may be too widely dispersed to defend if food items are sparse (Clutton-Brock & Harvey, 1977, 1978; Eisenberg, 1977), or if food items are so widely dispersed around nest areas as to make it highly unlikely that a female could raise a litter without assistance. Under these conditions females may require males to display some evidence of commitment (Maynard Smith, 1977) prior to mating with them, or may impose monogamy on males by aggressively preventing other females access to their mate (Wittenberger, 1979, 1981; Wittenberger & Tilson, 1980).

Aggression and Mate Selection

Intraspecific aggression

Peromyscus maniculatus. As discussed in preceding sections aggression is an important component of the social behavior of Peromyscus maniculatus, and an individual's aggressive ability probably plays a major role in determining if that individual will be capable of establishing and maintaining itself as a breeding member of the

population. In laboratory studies dominant males of this species have been found to be more successful than subordinate males in nesting with females (Blair & Howard, 1944; Eisenberg, 1962), copulating with females (Dewsbury, 1979; 1981c), and siring offspring (Blair & Howard, 1944; Dewsbury, 1981c). Dewsbury (1981c) has also observed that females tend to approach and solicit dominant males more frequently than subordinate males. Although female approaches were confounded with copulatory behavior and male availability because females "tended to approach and solicit males with which they were copulating and which were nearby" and "this was generally the dominant male" (Dewsbury, 1981, p. 892); these observations may indicate female preference for dominant males in this species. The observation in the present study, of a preference by males and females for the more assertive of two opposite-sexed individuals, is consistent with the hypothesis that individuals of this species may prefer aggressive individuals as mates.

Peromyscus polionotus. Although some investigators (e.g. Blair & Howard, 1944) have observed only very low levels of aggression in P. polionotus, other investigators (Garten, 1976; Smith, Garten & Ramsey, 1975) have observed higher levels; and these investigators have proposed that aggression in P. polionotus is genetically based, and that it may play an important role in both the social behavior and social organization of this species. Information presented in the preceding discussions suggested that aggressive ability may serve important functions in intraspecific competition in P. polionotus, and may therefore be an important factor in mate selection in this species. The results of the present study support the hypotheses that aggressive

ability may be important in the social behavior and mate preferences exhibited by this species. In the seminatural experiments individuals of both sexes displayed aggressive behavior, the majority of which was directed against same-sexed individuals. This is consistent with the type of behavior Kleiman (1977) has proposed as indicative of monogamy. In addition members of both sexes nested more frequently with the more aggressive of two opposite-sexed individuals, and members of both sexes displayed significant preference for more assertive individuals of the opposite sex in preference tests.

Interspecific aggression

Because individuals of most species appear to compete with members of other species for at least some resources, aggressive ability could function in interspecific as well as intraspecific interactions. Peromyscus maniculatus appears to compete with other species in many parts of its range (Drickamer, 1978; Holbrook, 1978; Kritzman, 1974; Redfield, Krebs, & Taitt, 1977), and P. polionotus often appears to compete with Mus musculus for food (Briese & Smith, 1973; Caldwell & Gentry, 1966a). Aggressive competition for resources is also common in Microtus; for example: M. agrestes appears to compete with M. arvalis for resources (Dienske, 1979), while both of these species may at times be in competition with Clethrionomys glareolus (DeJonge, 1979); M. longicaudus appears to be excluded from its preferred habitat by M. montanus in some localities (Randall, 1978); and M. pennsylvanicus and M. ochrogaster may also compete in some areas (Miller, 1969). Individuals in most rodent populations are probably exposed to at least a moderate level of interspecific competition for

resources, and individuals with high aggressive ability would be expected to fare better in this competition than individuals of low aggressive ability, and thus to be preferred as mates. Interspecific competition could, therefore, function to maintain choice for aggressive mates in many species--including those that may not exhibit high levels of intraspecific aggression.

Early breeding

Earlier breeding (Darwin, 1874) is probably not a consideration in the preference displayed for aggressive mates by P. polionotus, but may be of some importance to P. maniculatus. It is unlikely that early breeding is an important factor to P. polionotus. Although P. polionotus display breeding peaks and declines they do not appear to be seasonal breeders (Davenport, 1964; Smith, 1966). Therefore, although some seasons may be better for breeding than others (Smith & McGinnis, 1968), an individual can not really get an "earlier start" in breeding than others in the population.

Peromyscus maniculatus on the other hand do appear to be seasonal breeders, and also form large winter aggregations that may contain unrelated adults (Howard, 1949). More-aggressive individuals might be capable of initiating breeding earlier than less-aggressive individuals after dispersal from winter aggregations when competition for resources is likely to be intense (Healey, 1967; Taitt, 1981).

Bruce effect

Exposure of females to unfamiliar males may result in pregnancy blockage (Bruce, 1959; 1960). This phenomenon is known as the "Bruce

effect", and several explanations have been offered for it. Many of these hypotheses have been reviewed by Schwagmeyer (1979), who has proposed that "females are, in effect, selecting one mate in preference to another when pregnancy blockage occurs. One would therefore predict that the Bruce effect would be limited to circumstances in which the benefits from mating with the new male outweigh any cost of the delay in parturition or physiological effects involved" (p. 934).

This argument has recently been extended by Huck, Soltis, and Coopersmith (1982). These investigators observed that dominant male house mice (Mus musculus) significantly reduced the survival of strange pups, whereas subordinate males did not, and that dominant males would copulate with a female after killing her litter. Previous investigators (Hrdy, 1979; Labov, 1980; Mallory & Brooks, 1980) had suggested that, in species in which males committed infanticide, it would be less costly for females to block pregnancy and mate with a strange male than to lose the litter later through infanticide. Following these suggestions, their own observations, and the observation by Huck (1982) that dominant males are more effective in initiating pregnancy blockage; Huck et al. (1982) proposed that it is most advantageous for females to display pregnancy blocks when confronted with dominant rather than subordinate males because they face the greatest risk of infanticide by these males. As stated by Schwagmeyer (1979), by displaying pregnancy blocks females are in effect displaying a preference to mate with aggressive males; and the Bruce effect would be adaptive in this context as long as the costs of postponing the current litter were outweighed by the benefits derived

from mating with a male of high aggressive ability. The Bruce effect, like the inciting behavior of female elephant seals (Cox, 1981; Cox & LeBeouf, 1977), may be a means by which a female ensures that she mates with males with high aggressive ability.

Heritable aggressive ability

The benefits of selecting mates with high aggressive ability that have been discussed to this point are not dependent upon any component of an animal's aggressive behavior being heritable. The expression of many of the components of aggressive behavior has, however, been demonstrated to be at least partially under genetic control (Scott, 1966; Scott & Frederickson, 1951; Simon, 1979). The components of aggression may be divided into two major categories: components related to the tendency for an animal to display aggression, or its "aggressiveness", and components related to the ability of an animal to effectively perform aggressive behaviors. The validity of this division is supported by research reviewed and discussed by Scott (1966), and by Scott and Frederickson (1951). As stated by Scott (1966) "Heredity produces important differences in fighting behavior between mouse strains, some being more easily excited to fight than others and some strains being more capable of winning than others" (p. 691).

Although an animal's tendency toward aggression and its ability to perform aggressive behavior effectively may be separable, they would be expected to be highly positively correlated. One would expect that it would not be adaptive for an animal to be highly prone to engage in aggressive encounters if it stood little chance of winning those

encounters; nor on the other hand would it be expected to be adaptive for an animal to be completely unprovokable if it had high aggressive ability. Because fights involve potential costs as well as potential benefits (Maynard Smith, 1976; Maynard Smith & Price, 1973), individuals should assess opponents carefully, and fight only when they have a reasonable expectation of winning (Clutton-Brock & Albon, 1979; Clutton-Brock, Albon, Gibson & Guinness, 1979). Individuals that most frequently display aggressive behavior, therefore, should normally also be those individuals that have the highest aggressive ability. If the display of aggression is an indication of an individual's aggressive ability, then these displays may be used to evaluate that individual's potential as a mate (Cox, 1981; Cox & LeBeouf, 1977). While, as previously noted, many of the benefits that may accrue to individuals that choose mates with high aggressive ability do not depend on that ability being heritable, choosing aggressive mates should be even more adaptive if any of the components of aggressive ability are heritable. Individuals selecting aggressive mates would gain not only immediate benefits, such as better territory or defense of nest site, but "good genes" (Maynard Smith, 1956; Trivers, 1972) as well. (However see, Krebs & Davies, 1981; Maynard Smith, 1978, p. 170, 171; Parker, 1979, p. 146; for limits on the use of heritable factors as a basis for choice). Selection of mates with high aggressive ability may be adaptive even when such individuals do not hold the best available resources, if these individuals are more attractive as mates, and aggressive ability is heritable. This combination of conditions has

been suggested to act to lower the polygyny threshold in species (the "sexy son" hypothesis: Helsler, 1981; Weatherhead & Robertson, 1979).

Some observations of Peromyscus maniculatus bairdi and P. polionotus suggest that the display of aggression, or displays related to aggressive ability, may provide a basis for mate selection in these species. Dewsbury's (1981b) observation that P. maniculatus females approach and solicit dominant males more frequently than subordinates in two-male copulatory tests, although open to other interpretations, is also consistent with this suggestion. In the present study high-aggression P. polionotus males displayed aggressive digging more frequently than low-aggression males, and may act to prevent the display of this behavior by low-aggression males. The areas around nest sites of this species often exhibit evidence of frequent digging behavior. Although members of this species do not appear to exhibit territorial behavior (Davenport, 1964) they do defend nest burrows (Blair, 1951), and most likely also some of the area around burrows. The "incipient burrows" and other evidence of digging near nest burrows may provide an indication to individuals that an area is occupied; and aggressive digging may be a means of displaying an ability to construct and defend burrows.

Familiarity as a Factor in Preference

The results of the present study were not consistent with the hypothesis that members of monogamous species should display greater preference for familiar than unfamiliar individuals, nor with the hypothesis that the effects of familiarity on the choice of members of polygamous species should be negligible. In familiarity preference

tests individuals of both sexes of the polygamous species Peromyscus maniculatus displayed preference for familiar individuals of the opposite sex, while individuals of the monogamous species Peromyscus polionotus did not display preference. In addition, P. polionotus did not display preference for nesting with familiar individuals of the opposite sex in the seminatural experiments. Two types of factors may have influenced the behavior of P. maniculatus and P. polionotus in familiarity preference tests; these are 1) factors related to the prior history of the animals tested and 2) factors related to the ecology and social system of these particular species.

Prior History

The ability to recognize differences in the familiarity of individual odors has been demonstrated in a wide variety of mammalian (Brown, R.E., 1979; Halpin, 1980) and non-mammalian (Halpin, 1980) species; and evidence exists that individuals of many rodent species may exhibit preferences based on this ability (Brown, R.E., 1979). Of particular relevance to the present discussion are observations suggesting that an individual's preference for familiar or unfamiliar conspecifics may be determined in part by whether that individual previously received monogamous or polygamous mating experience. While monogamously mated female rats appear to prefer the odor of a familiar over a novel male, polygamously mated females display no preference, polygamously mated males prefer novel females, and monogamously mated males may either display no preference or preference for novel females depending on test conditions (Carr, Krames, & Costanzo, 1970; Carr et al., 1979; Carr et al., 1980; Krames et al., 1967). The general

tendency in these studies appears to be greater preference for familiar individuals after monogamous mating experience and greater preference for novel individuals after polygamous mating experience. Dewsbury (1979) has also observed a higher probability of mating in P. m. bairdi in tests in which individuals were familiar (had previous monogamous mating experience) than in tests in which mates were unfamiliar.

Prior to familiarity preference tests animals in the present study were housed with a single opposite-sexed conspecific and therefore, outside the possibility of having mated with siblings, would have had only monogamous mating opportunities prior to these tests. While pretest housing conditions may in part explain the preference for familiar individuals displayed by P. maniculatus, they can not explain the lack of preference displayed by P. polionotus. The lack of preference displayed by P. polionotus in the familiarity preference tests, although consistent with observations of the nesting behavior of this species in the seminatural study, is inconsistent with predictions based on the mating system of this species. These differences in the preference of P. maniculatus and P. polionotus may be explained by differences in the ecology and social organization of these two species.

Ecology and Social System

Peromyscus maniculatus

As noted previously breeding P. m. bairdi appear to maintain overlapping home ranges (Blair, 1940). Although breeding adults appear to aggressively limit settlement of strange juveniles in their home

range (Ayer & Whitsett, 1980; Enders, 1978, Whitsett et al., 1979) little overt aggression appears to occur between members of established populations (Hill, 1977; Terman, 1961, 1974). Lack of aggression between established residents in a population is not uncommon, and may be a result of the "dear enemy" phenomenon as described by Wilson (1975): "A territorial neighbor is not ordinarily a threat. It should pay to recognize him as an individual, to agree mutually upon the joint boundary, and to waste as little energy as possible in hostile exchanges thereafter" (p. 273). This effect appears to occur in at least some (Healey, 1967), but not all (Vestal & Hellack, 1978) subspecies of P. maniculatus.

The dear enemy phenomenon may be a factor in juvenile dispersal and settlement in P. maniculatus. Blair (1958) observed that the majority of juveniles in a population of P. maniculatus in Texas dispersed either very short distances from the natal site or not at all; and 38 percent of the females and 28 percent of the males in a population of P. m. bairdi in Michigan did not disperse from their natal home range to breed (Dice & Howard, 1951). Healey (1967) has suggested that for P. maniculatus "an animal's chances of breeding are severely limited when it moves any distance from its birth place" (p. 388). These observations suggest that a juvenile has the greatest probability of breeding successfully if it remains on or near the parental home range. In light of the aggression directed toward unfamiliar juveniles by adults (Ayer & Whitsett, 1980; Enders, 1978; Healey, 1967; Sadleir, 1965) one of the more successful strategies for

juvenile P. maniculatus may be to breed with its neighbors rather than to attempt to disperse and breed with unfamiliar conspecifics.

Early breeding may be an additional factor acting to increase the adaptive value of selecting familiar mates in this species. As is typical of other Peromyscus (Terman, 1968), P. maniculatus tends to remain in a particular area once it has established itself as a breeding resident of that area. The apparent sedentary nature of residents, and the overlapping home ranges they exhibit (Blair, 1940; Howard, 1949; Mihok, 1979; Morris, 1955), probably result in each resident breeding within a fairly well defined group of familiar conspecifics. Individuals within an area aggregate in the winter and disperse from these aggregations to breed in the spring (Howard, 1949; Metzgar, 1979). Individuals that have become familiar in overwintering aggregations or through prior breeding may be able to pair more quickly, and establish themselves as breeders earlier in the spring than unfamiliar individuals.

Peromyscus polionotus

Peromyscus polionotus are sedentary once they become resident in an area (Blair, 1951; Smith, 1966, 1968), are not seasonal breeders (Davenport, 1964; Smith, 1966; Smith & McGinnis, 1968), and exhibit a monogamous mating system in which they form long-term reproductive pairs (Blair, 1951; Foltz, 1979, 1981). In addition, members of this species are generally fairly short lived (Dapson, 1972). As a result of these factors the opportunities for members of this species to utilize familiarity as a factor in mate selection during its lifetime may be somewhat limited. Two situations that could occur in which

familiarity may be a factor in mate selection in this species would be in the initial selection of a mate upon attaining reproductive maturity, or in the selection of a new mate upon the death or incapacitation of the current mate. These possibilities will be examined in the following discussion.

As in P. maniculatus, P. polionotus exhibit overlapping home ranges that do not appear to be defended against breeding adult conspecifics (Davenport, 1965). It is likely that the majority of aggressive interactions in P. polionotus, other than possibly aggression incidental to foraging, are centered around the defense of nest sites (Blair, 1951). In light of the specific nesting requirements of this species, nest site defense would probably effectively limit juvenile recruitment into the resident breeding population since it is unlikely that a juvenile could obtain nest sites in competition with adult conspecifics. A juvenile could breed near the natal home range if it were able to attract a neighboring resident animal as a mate. Opportunities for a juvenile to enter a breeding relationship with a familiar resident are, however, likely to be very limited. Established residents may be exposed to the choice of juvenile mates only in the event of the reproductive failure or death of their existing mates. Juveniles, however, would generally be expected to perform more poorly in competition with residents than would an adult mate. In addition a juvenile's reproductive performance is unproven, and at least for females generally below that of adults (Caldwell & Gentry, 1965b; Smith, 1966; Williams, Golley, & Carmon, 1965). The best choice for a resident adult after the loss of a mate,

therefore, would probably be to mate with a neighboring resident rather than a juvenile; or barring the availability of a neighboring resident to mate with a transient adult.

Although small groups of young sexually immature *P. polionotus* have been observed in the winter (Smith, 1966), it is unlikely that familiarity from relationships in these groups has a general effect on mate selection in this species. These groups comprised less than three percent of the social groups observed by Smith (1966), and such groups were never observed by Rand and Host (1942). Smith (1968) has suggested that these groups are composed of litter mates that are overwintering in parental burrows. Several observations lend support to this suggestion. First, adult defense of burrows (Blair, 1951) makes it unlikely that unrelated individuals would be tolerated in burrows. In addition, evidence reviewed by Foltz (1979) suggests that parental males may move with litters to burrows near the natal burrow. Finally, the largest of these groups observed by Smith (1966) was composed of six individuals, which is within the range of litter sizes reported for *P. polionotus* (Laffoday, 1957; Smith, 1966; Williams, Golley & Carmon, 1965).

Kinship as a Factor in Preference

Although inbreeding may be advantageous under certain conditions (Bengtsson, 1978; Cowan, 1979; Maynard Smith, 1978), the generally detrimental effects of inbreeding, such as inbreeding depression, have likely led to the evolution of mechanisms to avoid inbreeding in most species (Bixler, 1981). Evidence available for the two species of interest in the present study, *P. maniculatus* and *P. polionotus*,

suggests both high and low levels of inbreeding for these species. In the following discussion evidence for and against inbreeding in these two species, and the relevant observations from the present study, will be discussed in the context of the ecology and social behavior of these species.

Inbreeding in *Peromyscus maniculatus*

Evidence for and against inbreeding

Howard (1949) noted that in the population of *P. m. bairdi* he studied "There seemed to be no bar to the mating of close relatives, and parent-offspring matings and pairing between sibs occurred when conditions were such that these related mice happened to be together at the time when they became sexually active" (p. 15). Howard (1949) estimated that up to 10 percent of the matings in the population he observed were inbred. Rasmussen (1964) has also suggested a high level of inbreeding for *P. m. gracilis* based on the observation of a shortage of heterozygotes in the population he observed. Foltz (1979, 1981b) has, however, criticized both the Howard (1949) and Rasmussen (1964) studies on the basis of methodological flaws. This criticism seems well founded on the basis of evidence cited by Foltz (1979), and by observations that reproductive performance in sibling matings in this species is below that for nonsibling matings (Dewsbury, 1982; Hill, 1974). Although differences in the preference of *P. maniculatus* for siblings and nonsiblings in the present study were statistically non-significant, scores in the majority of comparisons were higher for nonsiblings than for siblings; and *P. maniculatus* females that were not in diestrus displayed significantly greater preference for

nonsibling males than did females in diestrus. These observations are consistent with the hypothesis that P. maniculatus should prefer nonsiblings as mates over siblings.

Ecological and social factors

Because P. m. bairdi may exhibit inbreeding depression (Dewsbury, 1982a; Hill, 1974) individuals of this species would be expected to display stronger preference for nonsiblings than was exhibited in the present study. The small differences in preference exhibited in the present study might be explained if P. m. bairdi, although attracted to nonsiblings as mates, are also attracted to siblings on other bases.

It might be adaptive for siblings to be attracted to one another if by remaining together they were able to increase direct benefits to themselves (e. g., through increased survival), or if such behavior resulted in an increase in their inclusive fitness (Hamilton, W. D., 1964, a, b). At least two factors in the behavior of P. m. bairdi make it probable that they will maintain extensive contact with relatives, including siblings, and thereby provide opportunities for kin selected behavior in this species. First, P. m. bairdi tend to disperse short distances from their birthplace before establishing a home range (Dice & Howard, 1951; Howard, 1949). It is likely therefore that many of the residents in a population will have settled near relatives. In addition, because winter aggregations may include nearby residents (Howard, 1949), it is likely that at least some of these relatives are likely to overwinter together.

Participation in winter aggregations may greatly increase an individual's probability of surviving until the spring breeding season

(Howard, 1951). The ability to remain in aggregations through the winter appears to depend largely on the availability of adequate food to maintain the aggregated mice (Howard, 1951). Although mice could venture out of aggregations to forage, this behavior would be somewhat self-defeating. Food items will likely be scarce in winter months and difficult to find, and increased exposure to cold during foraging will result in increased heat loss, making it necessary to forage even more intensely to gather sufficient food to maintain body temperature at an adequate level. The amount of food cached near an aggregation of P. m. bairdi may therefore determine how successfully members of that aggregation survive the winter.

Although information is not available as to what factors determine where aggregations are formed, the nucleus of these aggregations is generally a parental pair and one of their litters (Howard, 1949). It is likely that parents cache food near the time of the birth of their last fall litter, and that the combination of this small aggregation and food cache may often attract additional neighboring individuals. Because many of these individuals may be related to the family group, inclusive fitness may be increased by allowing them to join the aggregation and utilize the food cache. Two additional factors, however, may be of importance in this context. First, at least up to a point, increasing the size of an aggregation may benefit all of its members because a larger group can more easily maintain a higher temperature. This may in part explain the observation that individuals of other species are sometimes allowed in aggregations (Howard, 1949). Second, laboratory observations (Rice, 1972; Terman, 1974) suggest

that an existing food cache may act as a stimulus for hoarding behavior in *P. m. bairdi*. If individuals joining an aggregation also add to the food cache they may in effect "pay their own way" as members of the aggregation. The behaviors exhibited by at least some of the individuals in aggregations, therefore, may be mutualistic.

Whether the behavior of an individual in an aggregation is viewed as mutualistic, or kin selected (or both), will depend on the costs of that behavior to the individual, and upon who receives the benefits of that behavior. The behavior of individuals of other species in aggregations of *P. maniculatus*, for example, may be mutualistic. The costs and benefits to the resident parental pair, however, are much more complex. Costs incurred by these animals in caching food include expenditure of time and energy, and possibly increased exposure to predators. An additional possible cost of aggregation is related to the fact that abundant food in the spring may allow pairs to breed early (Gashwiler, 1979; Taitt, 1981). If food caches are severely depleted during winter aggregation, spring breeding may be delayed for the parental pair. In return for these costs the parental pair provide benefits to themselves, their offspring, and possibly neighboring siblings. Kin selection may therefore act as one of the factors that maintain winter aggregations in *P. m. bairdi*, and may therefore be one of the factors that act to maintain attraction to siblings outside of a breeding context. Although this hypothesis is untested, the relatedness of individuals within aggregations could be assessed through electrophoretic and trap-retrap studies.

The tendency toward philopatry in P. maniculatus may also lead to opportunities to increase inclusive fitness through cooperative breeding. Communal litters, and apparently cooperative care of these litters, have been observed in populations of P. maniculatus in Texas (Blair, 1958), Colorado (Hansen, 1957), and Michigan (P. m. bairdi; Howard, 1949). Many of the hypotheses on the effects of ecological and kinship factors on cooperative breeding have recently been reviewed (Koenig & Pitelka, 1981) and will not be discussed in detail here. The generally accepted hypothesis is "that habitat saturation provides the primary impetus for philopatry, and through it for evolution of group territoriality and cooperative breeding. . ." (Emlen, 1982, p.32). As described by Emlen (1982) "As population numbers increase, suitable habitat becomes filled or 'saturated'. Unoccupied territories are rare, and territory turnovers are few. As the intensity of competition for space increases, fewer and fewer individuals are able to establish themselves on quality territories. The option of breeding independently becomes increasingly limited" (p. 32). An additional factor that may mediate the occurrence of cooperative breeding in P. maniculatus is the sex ratio. Howard (1949) has noted that breeding combinations with more than one individual of either sex occur in areas where the sex ratio is not equal. The relatedness of the individuals in these breeding groups is unknown. A reasonable hypothesis, in light of the social organization and behavior of this species, is that under conditions of high population density and unequal sex ration, same-sexed siblings of the "surplus" sex may find it more adaptive to establish

themselves in breeding groups with a member of the opposite sex than to attempt to gain resident breeding status on their own.

Inbreeding in *Peromyscus Polionotus*

Evidence for and against inbreeding

Smith (1966) and Smith, Carmon, and Gentry (1972) have presented evidence that *P. polionotus* may be highly inbred. This finding appears to be at odds with evidence that reproductive performance in *P. polionotus* is positively correlated with genic heterozygosity (Smith et al., 1975). Smith et al. (1975) have suggested that the level of inbreeding in this species is linked in an adaptive manner to population density, level of aggression, and dispersal. These investigators suggest that at low and increasing population densities levels of aggression and dispersion will also be low, while levels of inbreeding will be high. When population density rises individuals will begin to outbreed more, and produce more-aggressive heterozygous offspring that are better suited to competition in the population or during dispersal. Smith (1968) has also suggested that opposite-sexed siblings display a tendency to disperse together, and has observed that the females in these sibling pairs may often be pregnant.

Foltz (1979, 1981) has suggested alternative interpretations for many of the observations presented by these investigators as evidence of inbreeding in *P. polionotus*. These interpretations are however only presented as alternatives, and Foltz (1979, 1981) was not able to exclude the possibility of high levels of inbreeding in this species. In light of Smith's (1966) observation of a preference by *P. polionotus* females for sibling males over nonsibling males Foltz (1981)

suggested a need for additional research on the mating preferences of P. polionotus. The present study indicates that females P. polionotus, as suggested by Smith (1966), display a preference for siblings. Males of this species also tend to display higher sibling than nonsibling scores on preference measures, although their comparisons were nonsignificant.

Ecological and social factors

The apparent tendency toward inbreeding in P. polionotus (Smith, 1966, 1968; Smith, Carmon & Gentry, 1972) may be mediated by the very specific habitat requirements of this species, and the probability that individuals must disperse long distances to find new patches of favorable environment. Shields (1982) has suggested that "if conditions existed that favored relatively faithful transmission of parental genomes, then inbreeding could be favored over both asexuality and outbreeding (p. 264)... Owing to its flexibility and capacity to transmit successful parental genomes with maximum fidelity, inbreeding is expected to be common in organisms produced by stable lineage-environment associations" (p. 274). The very specific habitat requirements of P. polionotus may result in such a stable lineage-environment association in this species. Because habitat requirements for this species are so specific (Rand & Host, 1942; Smith, 1966, 1968), offspring are likely to be most successful if they breed in areas in which conditions vary little from those of their birth place.

The patchiness of suitable environment for P. polionotus may also predispose this species to inbreeding through selective pressures similar to those that have been proposed to operate on Microtus pennsylvanicus (Batzli et al., 1977; Getz, 1978). In reference to the breeding habits of M. pennsylvanicus Batzli et al. (1977) note that "Microtus pennsylvanicus . . . occupies smaller patches of moist meadow or marsh. Under these circumstances, strange mates may not always be available, and it would be disadvantageous if siblings could not breed with one another. . . . If M. pennsylvanicus must continually locate and repopulate isolated patches, the offspring of the founder(s) must mate in order to assure success." (p. 590)

Similarly, for P. polionotus, Smith (1968) noted that

these mice are found characteristically in habitats of early stages of primary or secondary succession (Golley et al., 1965). For this reason it is likely that large distances between suitable habitat exist, and with time succession makes the habitat unsuitable for the mice. The pine forest habitats which they are associated with on the mainland are fire subclimaxes (Laessle 1958a, 1958b; Smith, 1966) and utilization of available habitat might require certain individuals to disperse long distances to find recently burned areas. (p. 49)

Smith (1968), as noted previously in this discussion, has also observed a tendency for opposite-sexed sibling pairs of P. polionotus in breeding condition to disperse together.

Bateson (1978, 1979) has suggested that animals learn characteristics of parents and siblings, and then use this information to choose individuals that are only slightly different from kin as mates. Gilder and Slater (1978) have observed behavior in mice that appears to conform to this rule, and a similar rule of thumb may provide a basis for the apparently cyclic preference for siblings

observed by Smith et al. (1972). The cyclic changes in sibling preference that may occur in this species could be generated by the rule "choose siblings as mates if they are not too similar". For P. polionotus this may mean "prefer siblings as mates as long as your parents were not the product of a sibling mating".

Garten (1976) has observed a positive correlation between aggression and genic heterozygosity in P. polionotus, and (Garten, 1977) between genic heterozygosity and exploratory behavior. As offspring from nonsibling matings are more heterozygous than offspring from sibling matings, offspring from nonsibling matings should be more likely to disperse. In light of the previous discussion on the patchiness of the environment for this species, it may be adaptive for them to disperse to new breeding habitat as sibling pairs (as observed by Smith, 1966) and for offspring of these pairs to breed with siblings. Smith et al. (1975) have observed low levels of heterozygosity in P. polionotus populations at low and early stages of increase in population density, which may indicate that individuals at this stage of population growth may in fact be inbreeding. The offspring of the second generation in the new habitat, however, being the offspring of inbred parents, would be expected to choose nonsiblings as mates. As the population density peaked many of the offspring from these outbred matings would be expected to disperse with siblings and renew the cycle. At the stages of late population rise and early decline then, the level of heterozygosity in the population would be expected to be relatively high, as observed by Smith et al. (1975).

Evolution of Monoqamy In Peromyscus Polionotus

Peromyscus polionotus is morphologically more similar to the "prairie forms" of P. maniculatus (e.g. P. m. bairdi or P. m. pallescens) than to the "forest forms" of this species (Hooper, 1968), and most likely originated from one of the prairie forms of P. maniculatus during the Pleistocene interglacial stages (Blair, 1950). As discussed previously, although P. polionotus and P. maniculatus are closely related, and display similarities in a number of aspects ranging from habitat preference and morphology to behavior, they exhibit large differences in social organization and mating system. The evolutionary divergence in the social behavior and mating systems of P. polionotus and the prairie forms of P. maniculatus, such as P. m. bairdi, may be explained through examination of the differences in the amount of and distribution of suitable habitat for these taxa, and differences in climate in the present day distribution of these taxa. Blair (1950) and Smith (1966) have described the factors that apparently have led to the existing distribution of P. polionotus, and its separation from the parental species P. maniculatus.

The present geographic relationships of these two species can be explained if we assume continuous distribution of maniculatus across the coastal plain in Pleistocene time. This distribution possibly, but not necessarily, might have been only in a narrow strip along the Gulf beaches. With encroachment of the Gulf on the land during Pleistocene inter-glacial stages, there was the opportunity for a part of this population to be isolated in Florida, for parts of Florida projected as islands during these periods (see Cooke, 1939). The postulated coastal-plain population of maniculatus disappeared eastward of Texas, effectively isolating the Florida population. (Blair, 1950, p. 266)

Certain soil characteristics appeared to be important in limiting the distribution of mice. In relatively undisturbed habitats, the mice occurred primarily on fine sand.... Deposits of sorted sands have been laid down in several ways in Florida (Laessle, 1958b). Wind was an important agent along the beach dunes. The action of water was important along the flood plains of large rivers, the shorelines of lakes and islands, and submerged offshore bars. All areas above the current water level were at one time part of the Florida shoreline. As the water level fell during glacial periods, numerous deposits of fine textured sand were gradually exposed. Their continuity was later destroyed by erosion (Alt and Brooks, 1965). These deposits and their associated vegetation are frequently widely spaced with the intervening habitat unsuitable for the old-field mouse. These interrupted sand deposits are ecological islands for this species. (Smith, 1966, p. 13-15)

The climate in Florida would have been much cooler during the Pleistocene glaciations than at present, and may have been at least somewhat similar to conditions under which *P. m. bairdi* exists presently. Assuming that the Pleistocene prairie forms of *P. maniculatus* would share many characteristics with present day prairie forms of *P. maniculatus*, one may hypothesize that many of the characteristics of the species ancestral to *P. polionotus* may presently be exhibited by *P. m. bairdi*. Among these characteristics would be the ability to construct shallow burrows (Houtcooper, 1972), tendency to form winter aggregations (Howard, 1949) and to cache food for winter use (Hamilton, W. J., 1943; Howard, 1949), and possibly a predisposition under some conditions to form exclusive reproductive pairs (Howard, 1949).

Food caches and winter aggregations may have been as adaptive for the ancestral stock *P. polionotus* was derived from as they appear to be for *P. m. bairdi* today (Howard, 1951). As the glaciers

retreated and the climate warmed, however, the function of these habits may have changed. The loose sand soils available may have allowed the ancestral P. polionotus to construct deeper burrows than its predecessors. This factor, and a warmer climate, would have allowed the ancestral species to maintain a favorable temperature in nest burrows year-round, and would probably have resulted in lower mortality. The advent of more constant nest conditions would have in turn reduced the necessity for large winter aggregations as it would be more likely that a family unit (parents and offspring) could maintain an adequate nest temperature alone. More constant nest burrow conditions and warmer climate would also act to reduce the need for large food caches for winter survival. Food caches may, however, also serve another function. Peromyscus maniculatus, although normally a seasonal breeder, is capable of breeding through the winter if adequate food is available (Linduska, 1942; Taitt, 1981). Conditions of more moderate and stable temperature, along with an increased probability of an adequate winter food supply, are likely to have increased the possibility for successful year-round breeding in P. polionotus. The capacity of winter breeding would further act to limit winter aggregations to immediate family, because it would be more adaptive to use food caches to produce additional offspring, than to use these resources to increase inclusive fitness through supporting more distant relatives.

The possibility of breeding continuously, in conjunction with ecological factors, may have provided a basis for the establishment of monogamy as the predominant mating behavior in P. polionotus. The

major ecological factors of importance to monogamy in this species, as discussed previously, appear to be the availability and distribution of nest sites and food items. Constructing deep nest burrows limits choice of breeding areas; and caching of food suggests that food may be only seasonally abundant, with more food available than necessary for survival and breeding in warmer months, and a reduced food supply in winter months. Distribution and availability of nest sites and food items may act, as discussed earlier, to limit possibilities for polygamous matings by males. Constructing deep nest burrows and provisioning food caches, however, provide a stable breeding environment for P. polionotus. A longer breeding season would allow females to produce more offspring. Through investment in burrows and food caches, males may have been able to increase the number of offspring they produced by pairing with a single female, to above that they would have expected by mating polygamously. Although this shift in the behavior of ancestral P. polionotus males could be interpreted as "investment in offspring" in a very broad sense, these behaviors do not really go beyond those presently practiced by polygamous P. m. bairdi males, who also maintain nests and cache food that may be used by mates and offspring. The major shift that occurred in individuals of the ancestral species may rather be interpreted as a shift in emphasis from behavior resulting in increased inclusive fitness through benefits to distant relatives, to a limitation of these same benefits to offspring and to increased productivity by male-female pairs. This, of course, does not preclude the possibility that improved male care of offspring could have been a factor that added to the adaptive value of

exclusive breeding relationships in P. polionotus, but suggests that such behavior may not have been necessary for the evolution of monogamy in this species.

Summary

The present study is consistent with the hypothesis that aggressive ability may serve as a basis in mate selection for both sexes in monogamous as well as non-monogamous species. In a seminatural setting aggressive interactions occurred frequently between members of both sexes of the monogamous species P. polionotus, and individuals within groups appeared to form stable aggressive relationships. Males of this species exhibited a behavior, aggressive digging, that may function to signal their aggressive status to females. Individuals of this species of both sexes nested more frequently with opposite-sexed individuals that exhibited high rather than low aggressive ability. Male and female P. polionotus, and male and female P. maniculatus, also exhibited evidence of preference for more assertive opposite-sexed individuals (high rather than low tendency to interact) when tested in a preference apparatus.

Preference for individuals of high aggressive ability appears to be adaptive in terms of the ecology and social system of these two species. In P. polionotus high aggressive ability may insure that an individual is able to obtain limited nest sites and food and defend them against conspecifics. Female aggression could also be a factor acting to maintain monogamy in this species (see: Kleiman, 1977; Whittenberger, 1979, 1981; Whittenberger & Tilson, 1980). Females of this species, however, do not appear to be dominant over males (see

Smith, 1966). Peromyscus maniculatus of both sexes appear to utilize aggressive ability to limit settlement of juveniles on their home range (Ayer & Whitsett, 1980; Enders, 1978; Fordham, 1971; Taitt, 1981; Whitsett et al., 1979). Aggressive ability is also important in male-male competition in P. maniculatus (Blair & Howard, 1944; Dewsbury, 1981c). Although in order for it to be adaptive to choose mates with high aggressive ability it is not necessary for aggressive ability to be heritable, the adaptiveness of such choice would be expected to increase if components of this ability were heritable.

In preference tests familiarity appeared to be an important factor to individuals of both sexes of the polygamous species P. maniculatus, but of little consequence to individuals of either sex of the monogamous P. polionotus. The lack of significant preference for familiar individuals by P. polionotus in preference tests was consistent with observations of the nesting behavior of this species in the seminatural apparatus. Although the preferences displayed by P. maniculatus could be a result of housing conditions prior to familiarity tests (Carr, Krames & Costanzo, 1970; Carr et al., 1979; Carr et al., 1980; Krames et al., 1967), these conditions do not appear to provide an explanation for the lack of preference displayed by P. polionotus. Differences in the responses of P. maniculatus and P. polionotus to familiar individuals in preference tests may be based on differences in the opportunities individuals of these two species have to make use of this factor in mate selection. As a result of factors of ecology, social behavior, and breeding system, these opportunities may be much more limited for P. polionotus than for P.

maniculatus. Familiarity may, however, aid in maintaining pair bonds in P. polionotus through reducing aggression, as familiarity did appear to reduce aggression between familiar opposite-sexed individuals in seminatural experiments.

Although only P. polionotus females demonstrated a significant preference for siblings over nonsiblings, males of this species also tended to display higher sibling than nonsibling scores in preference tests. This finding is consistent with the observation by Smith (1966) that female P. polionotus appear to prefer siblings as mates over nonsiblings. Peromyscus maniculatus of both sexes displayed only nonsignificantly higher scores for nonsiblings than for siblings in preference tests.

Inbreeding in P. polionotus may be an adaptive strategy that permits individuals of this species to found populations in isolated patches of favorable habitat. A similar strategy has previously been proposed for Microtus pennsylvanicus (Batzli et al., 1977; Getz, 1978). The lack of significant preference for nonsiblings demonstrated by P. maniculatus, a polygamous species, may be due to competing preference responses in this species. Although P. maniculatus appear to avoid breeding with siblings (Hill, 1974; Dewsbury, 1982a), individuals may also be attracted to relatives through a preference for mating on or near their natal home range, and through opportunities to increase their inclusive fitness through interactions with relatives.

The shift from polygamy to monogamy in ancestral P. polionotus may have occurred as a result of a shift from an emphasis on aggressively limiting settlement on home ranges to defense of the nest site, concomitant with a shift away from increasing inclusive

fitness through aid to distant relatives to increasing personal fitness through limiting aid to a single mate.

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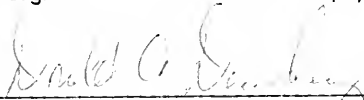
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BIOGRAPHICAL SKETCH

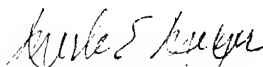
I was a member of the "baby boom," born to George E. and Mary L. Webster on May 5, 1948. I started my life in Oshkosh, Wisconsin. Three moves later the family was settled in my parents present home in Rothschild, Wisconsin. I completed high school in neighboring Schofield at D. C. Everest (home of the "Evergreens") in 1966, and continued my education for another two years at the Marathon Campus of the University of Wisconsin, in Wausau, Wisconsin. Toward the end of 1968 I met Carole . . . and followed her south to New Orleans, where we were married in July of 1969. In August of 1969 I became a member of the U. S. Air Force and served four years as an oral surgery technician at Keesler A.F.B., Biloxi, Mississippi. Our daughter, Danielle, was born in 1972 just prior to our leaving the service and rejoining the student population. I completed the requirements for my B.S. at the University of Wisconsin in Madison, Wisconsin, in 1976, and we headed back south to the University of Florida where I completed the requirements for the M.S. in 1979.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.



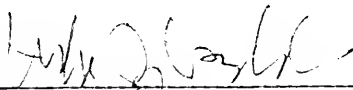
Dr. Donald A. Dewsbury, Chairman
Professor of Psychology

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Dr. Merle E. Meyer
Professor of Psychology

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Dr. Wilse B. Webb
Graduate Research Professor of Psychology

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Carol Van Hartesveldt

Dr. Carol Van Hartesveldt
Associate Professor of Psychology

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H. Jane Brockmann

Dr. H. Jane Brockmann
Associate Professor of Zoology

This dissertation was submitted to the Graduate Faculty of the Department of Psychology in the College of Liberal Arts and Sciences and to the Graduate Council, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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Dean for Graduate Studies
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