SOCIAL FACTORS CONTRIBUTING TO THE DEPARTURE OF PEROMYSCUS MANICULATUS BAIRDI FROM THEIR NATAL SITE

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Major professor

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ABSTRACT

SOCIAL FACTORS CONTRIBUTING TO THE DEPARTURE OF <u>PEROMYSCUS MANICULATUS BAIRDI</u> FROM THEIR NATAL SITE

By

Irvin Ray Savidge

Parental factors and individual differences contributing to the rate of natal site departure by young *Peromyscus maniculatus bairdi* were studied in the laboratory by using an electric shock barrier of 0.2 milli-amperes between a home cage and another cage. The number of juveniles crossing the barrier each day was recorded from 21 to 48 or 55 days of age. The mice that crossed were returned to the home cage each morning and the shock was turned off one day per week.

The rate of departure increased with age. There was no significant sex difference. The rate of crossing by juveniles was correlated with the father's movements across the shock grid. When the father was restricted to the home cage or to the opposite cage, the rate of crossing was significantly higher in juveniles moving toward their father than in juveniles moving away from him.

Restraining the mother decreased the rate of crossing on non-shock days, whereas the presence of a subsequent litter increased the rate of crossing on non-shock days. The offspring of aggressive mothers with a subsequent litter crossed at a higher rate than the offspring of non-aggressive mothers with a subsequent litter.

Differences between litters were found in juveniles tested as isolates from 21 to 48 days of age. Litters tested together frequently crossed as groups rather than independently.

Parental factors and individual differences contribute to the rate of natal site departure of young deermice. The presence of an aggressive mother with a subsequent litter increases the rate of departure and the presence of sibs or a non-aggressive parent decreases the rate of departure.

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By

Irvin Ray Savidge

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Gary R. Connor designed and aided in the construction of the electrical components of the experimental apparatus.

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INTRODUCTION

The biology of dispersal includes generalities regarding gene flow and population regulation that vary little across widely divergent taxa. Simultaneously it includes details of behavior and ecology that may differ between species or subspecies.

Dispersal may be defined as the movement of an animal from its natal point of origin to its permanent homesite. The dispersal movement may be either a long or a short distance (such as those to an adjacent home range) (Howard, 1960). Whether the dispersal movement is long or short, it consists of three phases: 1) leaving the natal site, 2) crossing a barrier (which may be only distance or may include physical and biological obstacles), and 3) settling in a new area.

Social behavior probably mediates many of the factors influencing the initiation of dispersal, specifically the leaving of the natal site. The social interactions contributing to the departure of juveniles from their natal site have only been postulated. Individual differences observed among juveniles leaving their natal sites may reflect differences in social stimuli or differences in their sensitivities to these stimuli.

Peromyscus maniculatus bairdi was chosen as the experimental species because 1) it is organized as family groups, 2) it is adaptable to the laboratory, and 3) a relatively large amount of information is available on its movements in the field (Dice and Howard, 1951; Stickel, 1968) and on its population dynamics (Terman, 1968). The hypothesis tested is: Social factors and individual differences determine the rate of natal site departure of young *Peromyscus maniculatus bairdi*. To control for environmental variables such as weather, light cycle, habitat, and physical barriers, a laboratory situation was used. A shock grid served as a barrier between two identical cages, thus maintaining constancy in the resistance to the juveniles' leaving their natal site.

LITERATURE REVIEW

Social behavior probably mediates many of the factors influencing small mammals to leave their natal site. For example, in house mice (*Mus musculus*) limited food resources presumably increased dispersal via the social system before the food supply was depleted (Strecker, 1954). The dispersal movements of deermice (*P. m. bairdi*) just prior to sexual maturity also suggest a social factor (Howard, 1949); as does the emigration of different age classes of muskrats (*Ondatra zibethica*) during drought (Errington, 1963). The stimuli from other members of the family may be either attractive or repulsive as in the occasional dispersal of littermates of *P. polionotus* together (Smith, 1968).

The action of the social hierarchy tends to disperse *Mus musculus* upon the attainment of sexual maturity (Brown, 1953). In an expanding colony of *Rattus norvegicus*, conflicts split it into family subgroups (Barnett, 1958). Resident adults of *P. m. austerus* are antagonistic toward intruding juveniles in a laboratory maze and removal of adults in the field improved juvenile survival (Sadlier, 1965).

One of the factors involved in the settling of dispersant rodents (Mus musculus (Delong, 1967), Peromyscus maniculatus austerus (Healey, 1967), and Ondatra zibethica (Errington, 1963)) is the presence of residents in the new area. The removal of residents, however, did not increase the rate of settling by migrant Apodemus (Andrzejewski and Wroclawek, 1962). The social behavior (antagonism toward the immigrants) and not the absolute population density is probably responsible for the failure of immigrants to establish residence in favorable habitat.

The aggressiveness of female Peromyscus in defense of their nest against conspecifics varies with the species (reviewed by Layne, 1968). In some species the young may continue to associate with the mother after weaning. In a few cases both litters may continue nursing for a few days.

Brown (1966) views the social organization of small mammals as consisting of a dominant male who travels freely throughout a neighborhood consisting of the home ranges of the subordinate males and females. He (Brown, op. cit.) suggests replacing the concept of home ranges of individual mice with the concept of each individual fitting into a social pattern. Information on social interactions within natural populations is essential for the understanding of their dynamics (Terman, 1968). Lidicker (1962) argues that emigrants may be those individuals most sensitive to density but not less poorly adapted than non-emigrants. The young animals are most affected by population pressures (Terman, 1968).

In addition to the environmental factors which can initiate dispersal, Howard (1960) postulated an "innate" dispersal mechanism. "Environmental dispersal is a density dependent factor, whereas innate dispersal is independent of density, but both are presumed to be inherited traits" (Howard, 1960, p. 152). Blair (1953) also postulated "an inherent tendency to disperse, stimulated by physiological changes as the animal becomes sexually active." Howard (1949, 1960) considers the animals dispersing short distances (such as to a nearby home range) to be "environmental dispersants" and those dispersing long distances to be "innate dispersants." This view confounds the factors determining whether or not an animal will leave its natal site with the factors determining how far it will travel before settling permanently.

The spread of an introduced allele through a population of house mice has been studied by Anderson, Dunn, and Beasley (1964). They introduced a _t_-allele onto Gull Island by releasing male mice that were heterozygous to this locus. The slow spread of the allele was attributed to the closed social system of this species. Many species probably have a social system intermediate between the closed structure examplified by _Mus_ and the open system envisioned by most genetic models. Such intermediate systems will be difficult to distinguish from open systems in which the demes are isolated by distance. The discovery by Rasmussen (1964) of a shortage of heterozygotes for the blood group polymorphisms of *P. m. gracilis* within a large continuous population in northern Michigan suggests such an intermediate system for *Peromyscus*. Although territoriality has not been demonstrated in this genus, the large volume of literature on spatial distributions in the field (Stickel, 1968) indicates a behavioral mechanism is preventing panmixia.

METHODS AND RESULTS

Several decades of field work on Peromyscus have contributed almost nothing to our knowledge of the behavioral interaction between family members. The utilization of a laboratory design permitted controlling environmental variables such as weather, food supply, and light cycle. Preliminary studies indicated that the size of the cages was not a significant factor in determining if the juvenile leaves the home cage. Several types of barriers (water, maze, and shock) were considered. Shock permitted the best control of the intensity of the barrier and was most effective. The shock level to be used was determined by placing mice on the shock grid and observing their reaction to the shock. It was also found that mice would not cross the shock barrier if no opportunity for exploration of the apparatus was provided.

Subjects. The mice used in these experiments were descendents of Peromyscus maniculatus bairdi trapped in Central Michigan and had been in the colony for less than four generations. Bisexual pairs of adults were housed in 5" x 11" x 6" deep plastic cages and maintained in the laboratory colony prior to the experiment. Each cage contained wood shavings, cotton, and ad libitum food (Purina Mouse Chow), and water. The shavings and cotton were changed on alternate weeks. Large litters were reduced to five mice shortly after birth and litters with less than four mice were not used.

Apparatus. The apparatus was designed to reduce the frequency of crossing a barrier between the home cage and another identical cage. A 3" x 2.5" high passageway with an 18" grid electrified with a 0.2 milliamperes shock connected two 16" x 20" x 8.5" deep plastic cages with wire mesh lids (Figure 1). The electric grid acted as a barrier to the free passage of mice from one cage to another. Each cage contained wood shavings, cotton, and ad libitum food and water. The shavings and cotton were not changed during the experiment. In some experiments, adults were restricted to one cage by an additional barrier of 1/2" wire mesh through which juveniles could pass onto the grid and to the other cage. The adults were too large to squeeze through the 1/2" wire mesh. The light cycle was 8 hours dark and 16 hours light.

General Procedure. Parents with their litter were placed in the test apparatus before the litter reached 14 days of age, and the locations of the mice were checked and recorded each morning. Those found in the opposite cage were returned to the home cage. The mean numbers of crossings per litter were used to test for treatment effects.

Figure 1. **Experimental Apparatus.**

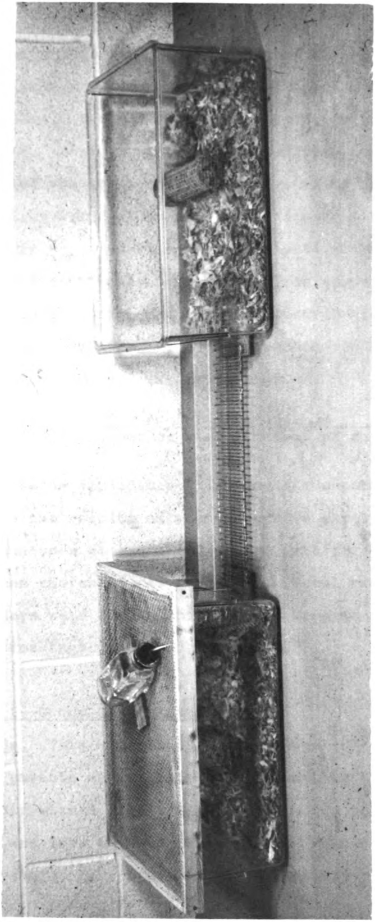


Figure 1

Weeks are numbered by the age of the juvenile at the beginning of the week. One day per week the shock was disconnected to allow the mice to explore the entire apparatus.

Analysis. Analysis of variance was used to determine the effects of the treatments. Juvenile males and females within families were paired and sex differences of the juveniles were examined with paired t-tests within treatment groups. The distribution of crossings was compared to an expected calculated from the binomial distribution with a Chi square test. The expected was based on the sum across families of the binomial expansion where

$$p = \frac{\text{number of crossings}}{\text{number of mice x number of days}} .$$

Other comparisons applicable to a specific experiment are discussed in the results of the respective experiments. The above analyses were applied to the data for the six days per week when the shock was turned on. Total crossings on non-shock days were also compared among treatments when the number of crossings justified analysis.

Experiment I--Group Composition

Methods. This experiment was designed to test the influence of parents on the rate of dispersal of the juveniles. An adult pair with a litter was placed in the apparatus when the litter was less than 14 days of age. When the juveniles were 20 days old, four types of group combinations were produced: 1) parents with litter (no adults removed), 2) adult male with litter (female removed), 3) adult female with litter (male removed), and 4) litter only (both adults removed). Eight replicates of each group were tested until the juveniles were 55 days old. The adults were not restrained and could move across the grid.

Results. The presence of one or both parents did not affect rate of leaving the home cage of the juveniles (Figure 2, Tables 7 and 8) but all treatments exhibited a highly significant increase in rate of leaving the home cage with age of the litter. Interaction between group composition and age was not significant. No effect of the treatments was found on the non-shock days. Sex of the juveniles did not affect the rate of crossing (Table 1). The distribution of crossings for the first four weeks was significantly different from the expected binomial distribution with too few nights having one crossing and too many having none or more than two crossings (Table 2). This unified action among litter mates indicates that individuals of a litter may not have acted independently and there may have been an attraction between them. The number of times juveniles were found in the opposite cage was correlated with the crossings of the adult male but not with the adult female (Figure 3, Table 4).

Figure 2. Experiment I--Group Composition. Crossings per juvenile by week. Shock days only.

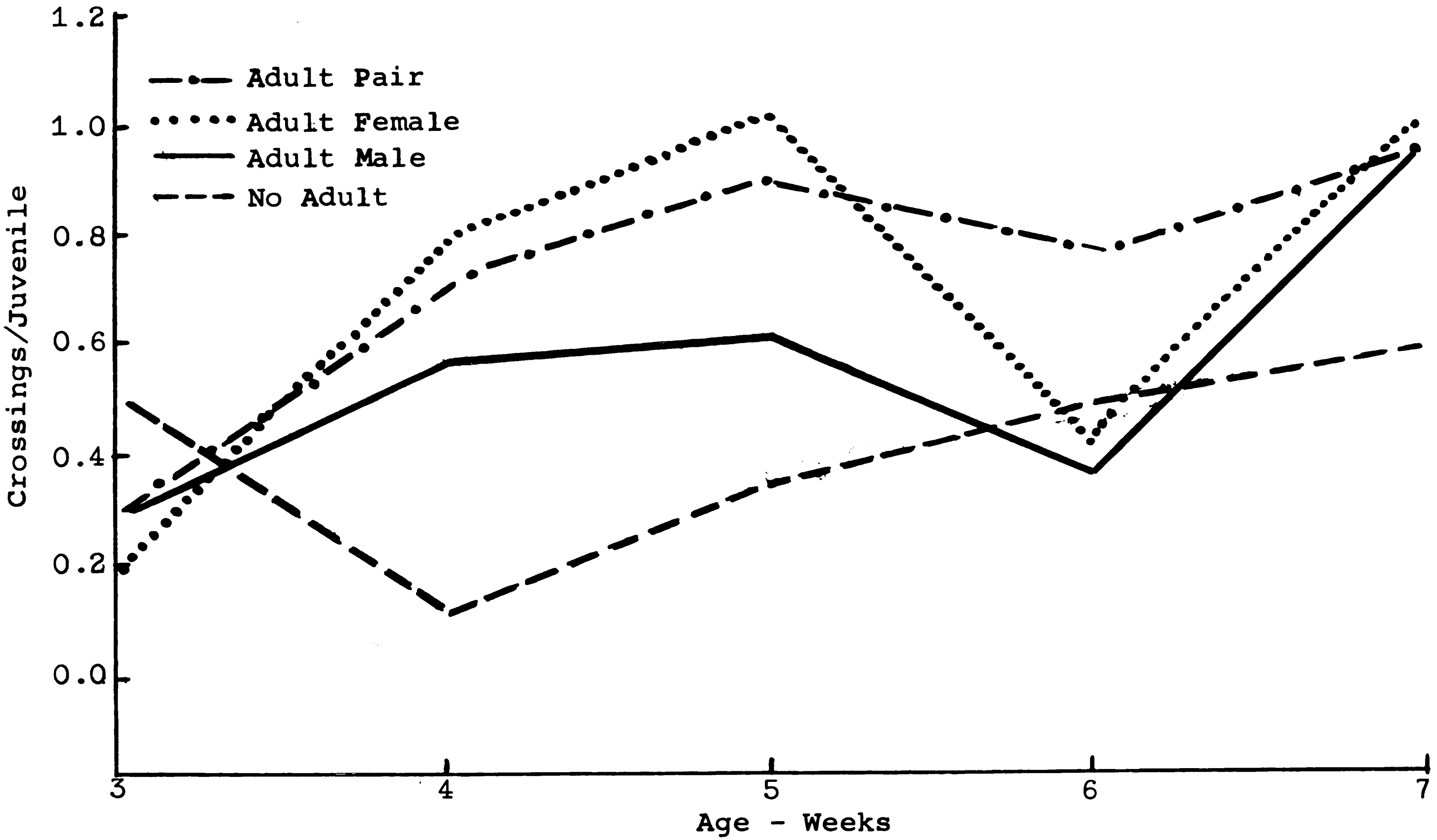

Adult Pair
Adult Female
Adult Male
No Adult
Crossings/Juvenile
1.2
1.0
0.8
0.6
0.4
0.2
0.0
3
4
5
6
7
Age - Weeks

Figure 2

Figure 3. Experiment I--Group Composition. Correlation of crossings of juveniles with crossings of the adults.

A (J:A): Adult male present; crossing of juveniles correlated with crossings of father.

A (J:A): Adult female present; crossings of juveniles correlated with crossings of mother.

A Pr (J:A): Adult pair present; crossings of juveniles correlated with crossings of father.

A Pr (J:A): Adult pair present; crossings of juveniles correlated with crossings of mother.

CORRELATION OF CROSSING

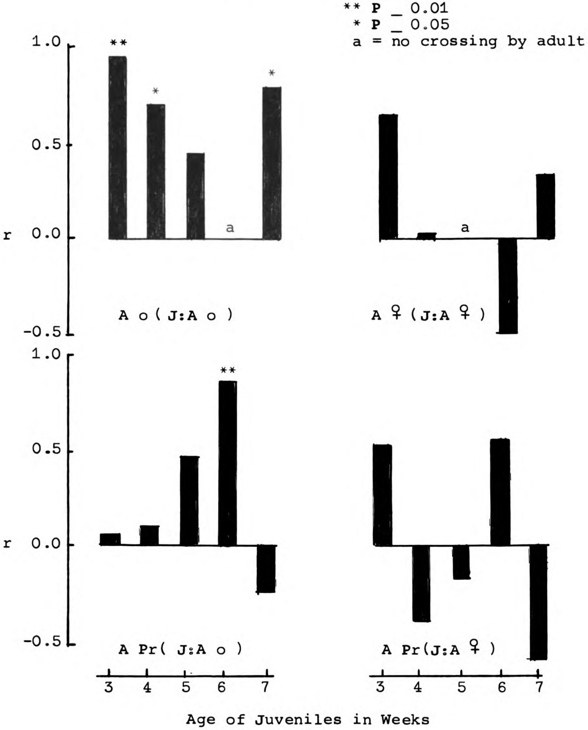


Figure 3

Table 1. Sex differences in rate of crossing barrier. Crossings per female juvenile subtracted from crossings per male juvenile within each family.

	$\bar{d}$	Paired t	df	P
Experiment I				
Adult Pair	-0.86	1.70	7	N.S.
Adult Male	0.81	1.43	7	N.S.
Adult Female	0.58	0.60	7	N.S.
Litter Only	0.35	0.64	7	N.S.
Experiment II				
Male Across	0.24	0.33	5	N.S.
Male Home	0.70	1.02	4	N.S.
Experiment III				
Restrained female with subsequent litter	-0.58	0.67	4	N.S.
Non-restrained female with subsequent litter	-0.33	0.98	4	N.S.
Restrained female without subsequent litter	-0.10	0.60	4	N.S.
Non-restrained female without subsequent litter	0.07	0.16	4	N.S.
Experiment IV				
Aggressive Female	-0.01	0.02	5	N.S.
Non-aggressive Female	-0.63	2.57	4	N.S.

Table 2. Distribution of crossings of juveniles within the family group compared to binomial expectation (weeks 3 to 6). Significance suggests juveniles may be crossing together rather than independently.

	X^2	df	P
Experiment I			
Adult Pair	45.48	3	0.001
Adult Male	10.85	2	0.01
Adult Female	20.34	2	0.001
Litter Only	10.12	2	0.01
Experiment II			
Male Across	8.97	3	0.05
Male Home	1.14	1	N.S.
Experiment III			
Restrained female with subsequent litter	5.57	2	N.S.
Non-restrained female with subsequent litter	12.23	2	0.01
Restrained female without subsequent litter	0.01	1	N.S.
Non-restrained female without subsequent litter	3.66	2	N.S.
Experiment IV			
Aggressive Female	18.43	2	0.001
Non-aggressive Female	2.54	1	N.S.

Table 3. Differences between families within treatments from analysis of variance.

	F	df	P
Experiment I			
Adult Pair	2.42	7,31	0.05
Adult Male	2.20	7,31	N.S.
Adult Female	7.33	7,27	0.005
Litter Only	4.69	7,31	0.005
Experiment II			
Male Across	4.18	5,22	0.01
Male Home	3.39	5,19	0.025
Experiment III			
Restrained female with subsequent litter	3.45	5,22	0.025
Non-restrained female with subsequent litter	8.42	5,22	0.005
Restrained female without subsequent litter	7.57	5,21	0.005
Non-restrained female without subsequent litter	14.31	5,23	0.005
Experiment IV			
Aggressive Female (1+x transformation)	1.51	5,20	N.S.
Non-aggressive Female	1.28	5,21	N.S.

Table 4. Experiment I--Group Composition. Correlation of Total Crossings for the Five Week Period (day 21 to day 55). N=8

Treatment	Combination	Shock	r	P
Adult Pair	J:A♂	on	0.43	N.S.
Adult Pair	J:A♂	off	0.32	N.S.
Adult Pair	J:A♀	on	0.15	N.S.
Adult Pair	J:A♀	off	0.51	N.S.
Adult Pair	A♂:A♀	on	0.78	0.05
Adult Pair	A♂:A♀	off	0.32	N.S.
Adult Male	J:A♂	on	0.76	0.05
Adult Male	J:A♂	off	0.62	N.S.
Adult Female	J:A♀	on	-0.40	N.S.
Adult Female	J:A♀	off	0.56	N.S.

Experiment II--Adult Male

Methods. Since the number of crossings of the juveniles in Experiment I was correlated with the number of crossings of the adult male, an experiment was designed to test whether the adult male attracted the juveniles. An adult pair with their litter were placed in the apparatus with the adults restricted to the home cage. When the juveniles were 20 days old, the adult female was removed. In group 1 the adult male was restrained in the opposite cage, while in group 2 the adult male was restrained in the home cage with the litter. Each group had six replicates. The number of crossings of the juveniles was recorded from 21 to 48 days of age.

The data of weeks 3 and 4 and weeks 5 and 6 were combined to reduce the proportion of zero scores and the data were then transformed by adding 1.0 and taking the square root to attain homogeniety of variance before testing for main effects.

Results. The juveniles crossed the grid at a significantly higher rate to move toward the adult male than to move away from the adult male on both shock and no shock days (Figure 4, Tables 9 and 10). No effect of age was found and no interaction between age and treatment. No sex difference was found (Table 1). The distribution of crossings toward the father indicated the juveniles may have crossed as groups. The number of crossings in the group with the father at home was too small to test with a Chi square. The families within

Figure 4. Experiment II--Adult Male. Means and standard errors of crossings per juvenile by week.

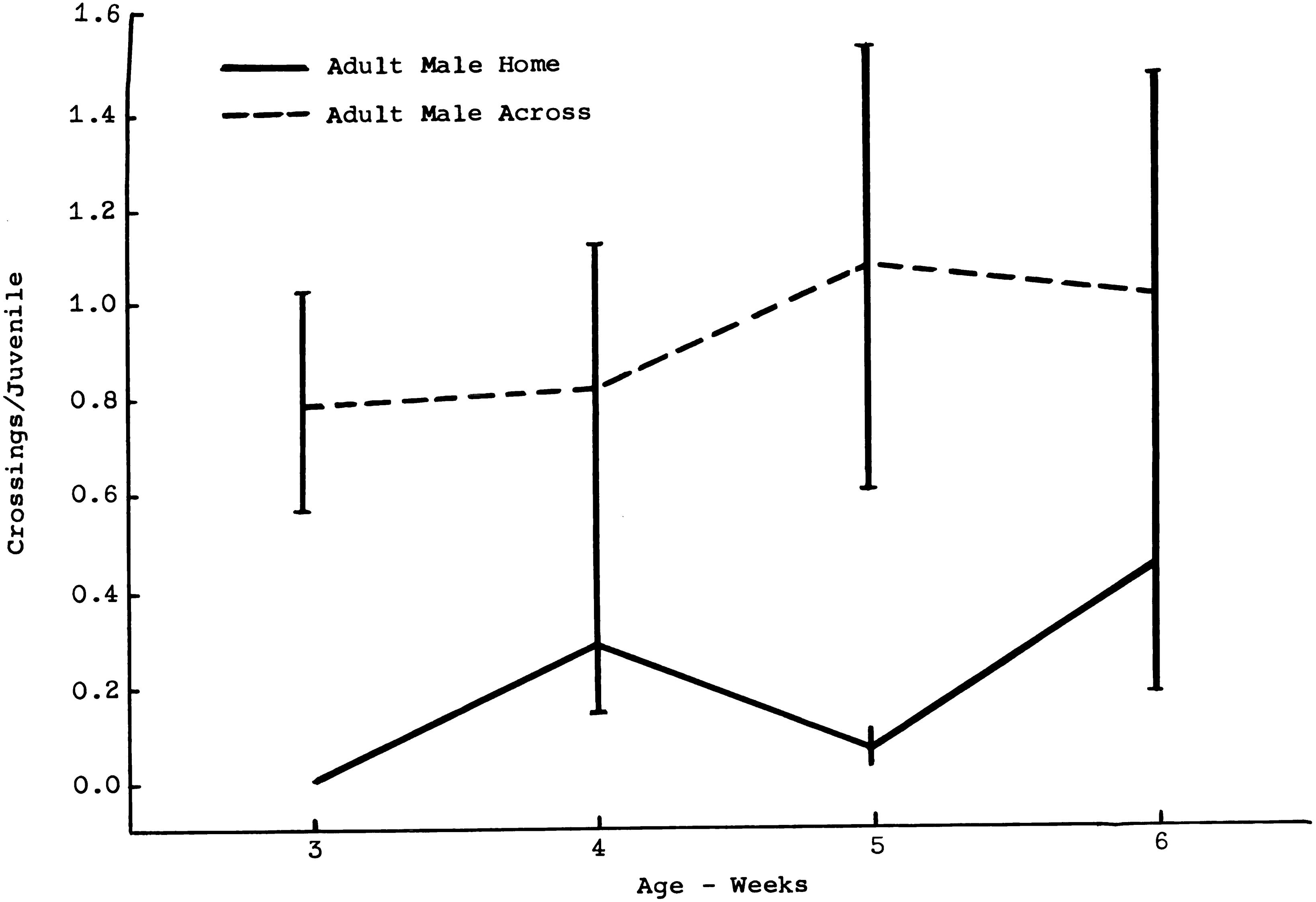

Adult Male Home
Adult Male Across
Crossings/Juvenile
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
3
4
5
6
Age - Weeks

Figure 4

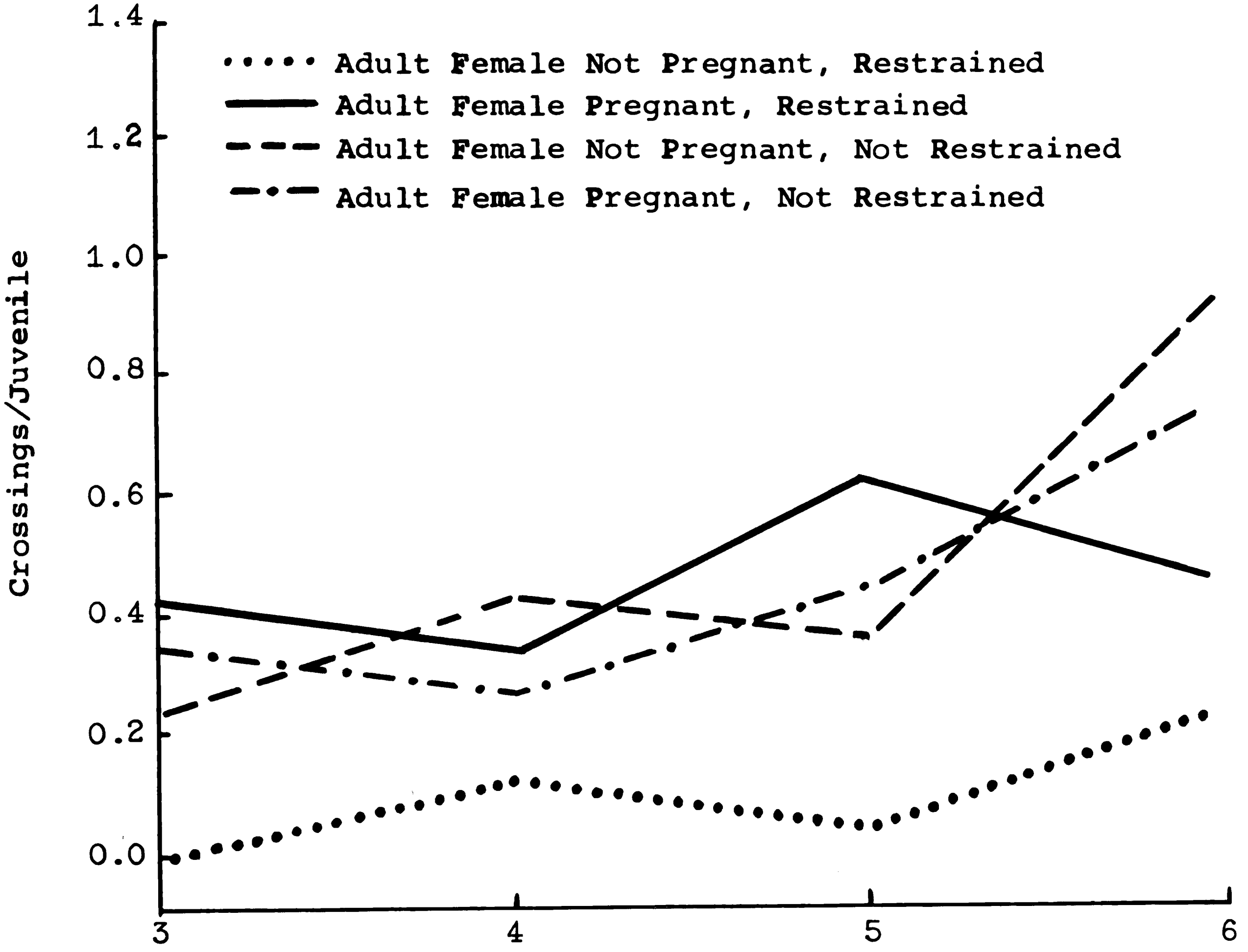
each treatment group appear to be different from each other, but the individual juveniles may not have acted independently which would invalidate this comparison.

Experiment III--Subsequent Litter and Restriction of Adult Female

Methods. Since family differences were found in Experiment I when the adult female was present, the following experiment was designed to test two features of the female which may influence the rate of crossing of the juveniles. The effect of a second litter and the restraint of the mother on grid crossing by juveniles was examined in a cross-classified design with six replicates in each of the following groups: A pregnant female with a litter was placed 1) in a test apparatus with the restraining barrier present and 2) without the restraining barrier. A non-pregnant female with a litter was placed, 3) in a test apparatus with the restraining barrier and 4) without the restraining barrier. The number of crossings made by the juveniles were recorded from 21 days of age to 48 days of age. Weeks 3 and 4 and weeks 5 and 6 were combined to reduce the proportion of zero scores before analysis.

Results. Neither a subsequent litter nor restraint of the adult female had a significant effect on crossings during the shock days. Increased age of the juveniles increased the rate of leaving the home cage, but none of the possible interactions were significant (Figure 5, Tables 11 and 12).

Figure 5. Experiment III--Subsequent Litter and Restriction of Adult Female. Mean number of crossings per juvenile by week. Shock days only.



1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
Crossings/Juvenile
•••• Adult Female Not Pregnant, Restrained
▬ Adult Female Pregnant, Restrained
– – – Adult Female Not Pregnant, Not Restrained
–•– Adult Female Pregnant, Not Restrained
3
4
5
6
Age - Weeks

Figure 5

On non-shock days, however, a subsequent litter increased dispersal and restraining of the mother decreased dispersal, but there was no interaction between the subsequent litter and the restraining. No sex differences were found (Table 1). Groups 1 and 4 had a distribution of crossings not significantly different from the expected binomial. Group 2 had a distribution of crossings that was significantly different from the binomial expectation with too many days with no crossings, too many days with two or more crossings and too few with one crossing. Group 3 had too few crossings to allow comparison (Table 2). (The expected value of days with two or more crossings was too small to validly use Chi square.) Since the distribution of crossings in group 1 and 4 did not differ from random, the individual juveniles of these groups can be assumed to be acting independently. The individuals were then treated as samples to compare the families within a treatment. All four treatment groups had significant differences between families indicating the population of adult females, from which the sample was drawn, was not homogeneous with respect to an unknown trait influencing dispersal (Table 3).

Experiment IV--Aggressiveness of the Adult Female

Methods. Incidental observations in the previous experiments suggested that some parent females attacked their young when the young were returned from the opposite cage whereas others did not. To test whether this difference in aggressiveness could explain the heterogenity of results obtained within previous groups, female mice with litters were divided into two groups according to whether or not they attacked a strange weanling mouse introduced into their cage. The test for aggressiveness consisted of: 1) probing the female with a forceps, 2) removing the litter for one minute and returning it to the female, and 3) introducing a strange juvenile to the female's cage for 1 minute. Since the responses of the female to the first two tests were not distinct, the behavior toward the strange juveniles was used to separate the aggressive and non-aggressive females (Table 5).

Two groups of six replicates each were established: 1) aggressive females and 2) non-aggressive females. A pregnant female with her litter was placed in each apparatus with the restraining barrier present. The number of crossings of the first litter were recorded from 21 to 48 days of age. Weeks 3 and 4 and weeks 5 and 6 were combined before analysis to reduce the proportion of zero scores.

Results. The juveniles in the "aggressive" group crossed the grid at a significantly higher rate than those in the "non-aggressive" group. Age of the juveniles was not significant ($0.10 < p < 0.05$) nor was the treatment age interaction (Table 13, Figure 6). Sex difference of crossings was not significant (Table 1). The distribution of

Table 5. Experiment IV--Aggressiveness of adult female. Test of aggressiveness of the adult females.

Female	Age of litter (days)	Forceps response	Response to juvenile	Sex of juvenile	Juvenile age (days)
1	4	nosing	attack	M	23
2	7	infreq. bite	attack	F	26
3	11	ignored	attack	M	25
4	5	ignored	attack	M	25
5	4	much biting	attack	F	21
6	12	infreq. bite	attack	M	24
7	4	ignored	nosing	F	31
8	8	ignored	nosing	M	26
9	4	ignored	nosing	M	24
10	2	ignored	nosing	M	24
11	7	ignored	nosing	F	23
12	6	ignored	nosing	M	24

Figure 6. **Aggressiveness of the Adult Female. Means and standard errors of the crossings per** juvenile **by week.** Shock **days** only.

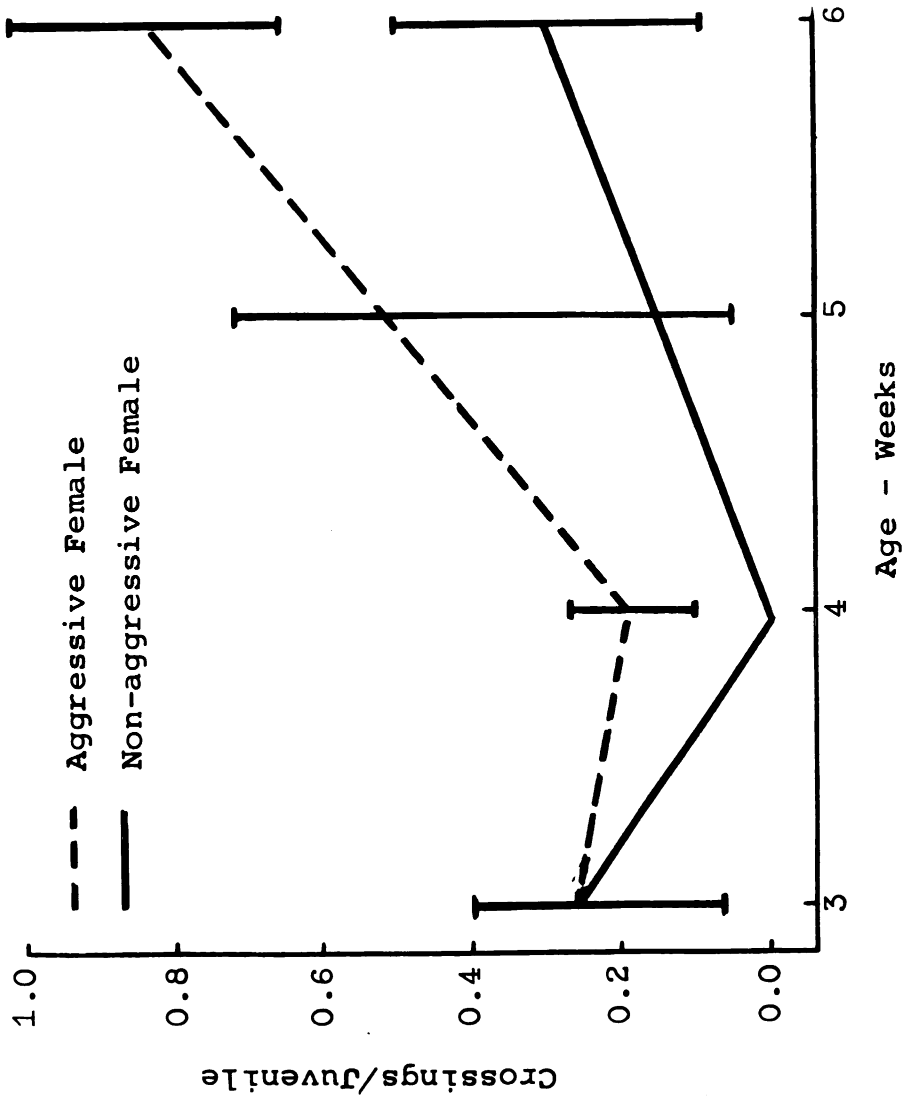

Aggressive Female
Non-aggressive Female
Crossings/Juvenile
1.0
0.8
0.6
0.4
0.2
0.0
3
4
5
6
Age - Weeks

Figure 6

crossings in the "aggressive" treatment was significantly different from the expected binomial (Table 2). The "non-aggressive" grouping had too few crossings to allow comparison. Although the individuals within a family may not have crossed independently of each other, the families within a treatment group were not significantly different from each other. This consistency among families within a treatment was in contrast to the families of the previous experiments, which failed to control for the aggressiveness of the females. There was only one crossing on a non-shock day in the "aggressive" treatment and none in the "non-aggressive" treatment.

Experiment V--Isolated Juveniles

Methods. Since Experiment I indicated significant differences between litters of juveniles with no adult present, this experiment was designed to determine if these results were real or merely an artifact of the juveniles not crossing the grid independently within families. An adult female with a litter consisting of 2 males and 2 females was placed in each of five apparatuses without the restraining barrier. When the juveniles were twenty days old they were placed individually in other apparatuses and their crossings recorded until they were 48 days old. The shock was turned off on the fourth day of each week and any juveniles that crossed the barrier were returned each day to the cage to which they were originally introduced. The analysis was done on the total number of crossings of a mouse over the four week test period.

Results. The differences between litters and the interaction between sex and litter were significant but the sex difference was not (Tables 6 and 15). These results indicate that individuals within a litter act more alike than individuals from different litters when not given the opportunity to respond to each other.

The juveniles in this experiment crossed the grid more frequently than the juveniles tested as litters in experiment I-4 indicating a social attractiveness of littermates (Figure 7).

Table 6. Experiment V--Isolated juveniles. Number of crossings of the individual animals from day 21 to day 48.

	Family					
	1	2	3	4	5	$\bar{x}$
	2	4	3	4	8	3.5
	2	3	0	0	9	
	3	9	3	1	6	5.0
	1	16	3	2	6	
$\bar{x}$	2.0	8.0	2.2	1.8	7.2	

Figure 7. Comparison of juveniles tested individually with juveniles tested as litters.

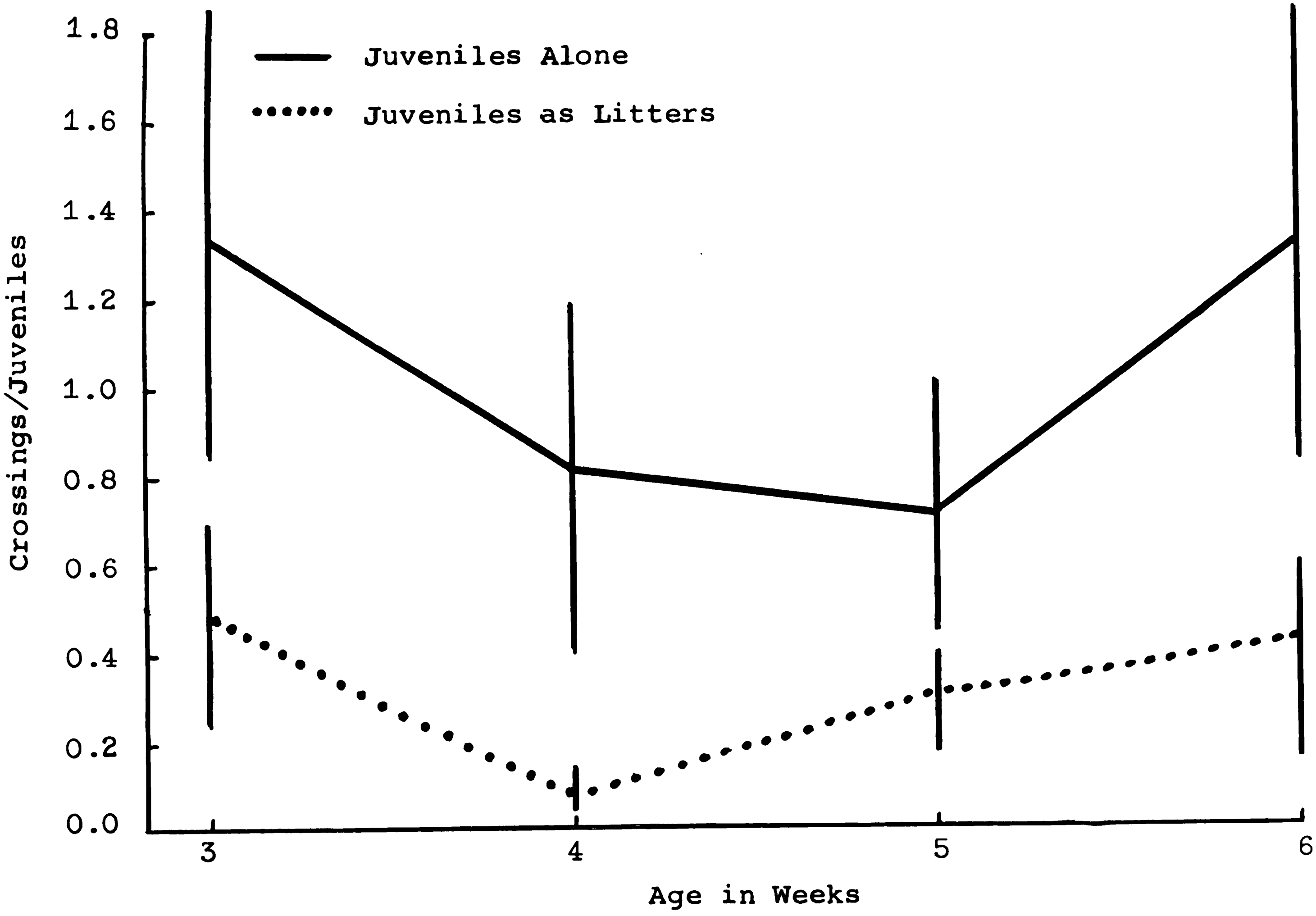

Crossings/Juveniles
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
Juveniles Alone
Juveniles as Litters
3
4
5
6
Age in Weeks

Figure 7

Table 7. Experiment I--Group composition. Mean number of crossings per juvenile and standard errors by week (8 replicate families per group). Shock days only.

	Week					
Treatment	1	2	3	4	5	Total
Adult Pair	0.32±0.10	0.68±0.30	0.89±0.22	0.78±0.22	0.95±0.26	3.63±0.54
Adult Male	0.30±0.14	0.55±0.20	0.60±0.26	0.35±0.10	0.95±0.14	2.76±0.55
Adult Female	0.20±0.20	0.79±0.34	1.02±0.26	0.39±0.10	1.03±0.24	3.44±0.86
Litter Only	0.47±0.24	0.11±0.06	0.33±0.10	0.45±0.20	0.60±0.22	1.96±0.50
$\bar{x}$	0.32±0.09	0.53±0.13	0.71±0.12	0.49±0.09	0.89±0.11	2.95±0.33

Table 8. Analysis of variance for Experiment I--Group Composition.

	df	MS	F	P
	Shock Days			
Source:				
Group Composition	3	0.922	1.40	N.S.
Error between	28	0.659		
Total Between	31			
Weeks	4	1.59	3.57	0.01
Composition x Weeks	12	0.338	0.76	N.S.
Error within	112	0.446		
Total within	128			
Total	159			
	Non-shock Days			
Source:				
Group Composition	3	0.27	0.79	N.S.
Replicates	28	0.34		
Total	31			

Table 9. Analysis of variance for Experiment II--Adult Male

	df	MS	F	P
Shock Days (1+x transformation), by two week period				
Source:				
Location of Male	1	1.428	6.15	0.025
Error between	10	0.232		
Total between	11			
Total week period	1	0.077	1.0	N.S.
Location of male x weeks	1	0.000	1.0	N.S.
Error within	10	0.447		
Total within	12			
Total	23			
Non-shock Days				
Source:				
Location of male	1	2.737	8.04	0.025
Replicates	10	0.341		
Total	11			

Table 10. Experiment II--Adult Male. Means and standard errors of the numbers of crossings per juvenile by week (6 replicate families per group). Shock days only.

	Week				
Treatment	3	4	5	6	Total
Male Home	0.00±0.00	0.23±0.12	0.08±0.05	0.46±0.28	0.78±0.40
Male Across	0.78±0.35	0.85±0.41	1.17±0.49	1.05±0.46	3.85±1.32

Table 11. Analysis of variance for Experiment III--Subsequent litter and restriction of adult female.

	df	MS	F	P
Shock Days (By two week period)				
Source:				
Restraint of Female	1	1.782	1.08	N.S.
Subsequent Litter	1	1.156	1.0	N.S.
Restraint x Subs. litter	1	2.063	1.25	N.S.
Error between	20	1.652		
Total between	23			
Weeks	1	1.980	9.12	0.01
Weeks x restraint	1	0.325	1.5	N.S.
Weeks x subs. litter	1	0.006	1.0	N.S.
Weeks x restraint x subs. litter	1	0.032	1.0	N.S.
Error within	20	0.217		
Total within	24			
Total	47			
Non-shock Days				
Source:				
Restraint of Female	1	0.570	4.57	0.05
Subsequent litter	1	1.215	9.73	0.01
Restraint x subs. litter	1	0.260	2.08	N.S.
Replicates	20	0.125		
Total	23			

Table 12. Experiment III--Subsequent litter and restrictions of adult female. Mean number of crossings per juvenile and standard errors by week (6 replicate families per group). Shock days only.

Treatment	Week 1	2	3	4	Total
Restrained female with subsequent litter	0.43±0.28	0.33±0.15	0.63±0.36	0.45±0.20	1.85±0.83
Non-restrained female with subsequent litter	0.35±0.20	0.28±0.16	0.43±0.15	0.73±0.46	1.79±0.78
Restrained female without subsequent litter	0.00±0.00	0.12±0.05	0.04±0.04	0.24±0.20	0.40±0.27
Non-restrained female without subsequent litter	0.27±0.19	0.43±0.25	0.37±0.19	0.93±0.46	2.00±0.91

Table 13. Analysis of variance for Experiment IV--Aggressiveness of the Adult Female. Shock days only by 2 week period.

	df	MS	F	P
Source:				
Aggressiveness	1	1.245	6.11	0.05
Error between	10	0.204		
Total between	11			
Weeks	1	1.534	4.61	0.1x0.05
Weeks x aggressiveness	1	0.623	1.87	N.S.
Error within	10	0.333		
Total within	12			
Total	23			

Table 14. Experiment IV--Aggressiveness of the adult female. Means and standard errors of the number of crossings per juvenile by week (6 replicate families per group). Shock days only.

Treatment	Week 3	4	5	6	Total
Aggressive	0.23±0.17	0.17±0.08	0.46±0.26	0.73±0.19	1.59±0.33
Non-aggressive	0.22±0.14	0.00±0.00	0.12±0.08	0.28±0.20	0.63±0.16

Table 15. Analysis of variance for Experiment V--Isolated Juveniles. Shock days only.

	df	MS	F	P
Source:				
Litters	4	38.31	9.46	0.005
Sex	1	11.25	1.0	N.S.
Litters x Sex	4	19.69	4.86	0.025
Error	10	4.05		
Total	19			

DISCUSSION

The hypothesis tested in these experiments was: social factors and the individual differences determine the rate that young *Peromyscus maniculatus bairdi* leave their natal site. The following are considered likely factors in the dispersal of *P. m. bairdi*. Both parents and sibs play a role in determining the rate of dispersal of the juveniles. The father and the mother influence the juveniles differently. Individual differences occur both in the behavior of the mother toward her weaned offspring and between members of different litters tested in similar social environments.

Adult Male

In Experiments I and II the juvenile *Peromyscus maniculatus bairdi* were attracted to the father. Several field observations indicate that the father is also attractive in field condition and may aid the juveniles in their initial explorations. A father and his four offspring (*P. m. bairdi*) were captured in the same trap three hundred feet from their home by Howard (1949). Rainey (1955) observed three *P. leucopus* removing chopped grain from a live trap with no indication of competition or hostility.

Adult male P. l. noveboracensis are occasionally found in the nest boxes with females and their litters when the litters were twenty-five days old or older (Nicholson, 1941). On five occasions he found single adult males living with litters after the mother left the nest box, but on nine occasions the adult male did not remain with the litter after weaning by the mother. Young P. m. bairdi follow their parents about in the process of becoming familiar with the parental home range (Howard, 1949).

Survival (disappearance in the field is considered as mortality) of juvenile P. m. austerus is negatively correlated to the aggressiveness of the adult males (Sadlier, 1965; Healey, 1967). In their laboratory studies they used alien juveniles introduced into their apparatus with resident adults and observed aggression. The behavior of an adult male toward strange juveniles is therefore different from his behavior toward his familiar offspring.

The attractiveness of another mouse is, however, not restricted to the adult male. The distribution of crossings within families frequently was non-random (Table 2). Litters crossed the grid in groups more frequently than expected and alone less frequently than expected indicating a social attractiveness among the littermates. Singly tested individuals of a litter also crossed more frequently than littermates tested in groups (Figure 7). In the field littermates of P. polionotus occasionally disperse together

(Smith, 1968). Multiple captures of Peromyscus in single live traps have also been reported (Burt, 1940; Blair, 1942). The tendency of the juvenile to cross as groups was reduced when an adult was restrained to the home cage. This suggests that the attractiveness of the juveniles leaving may be less than the attractiveness of the adults.

Adult Female

The influence of the mother on the juveniles leaving the natal site varies with the circumstances.

Except in the case of an aggressive female with a subsequent litter, the mother attracts the juveniles. In contrast to the father, however, the attraction of the mother decreases as the juveniles become older as indicated by the increased rate of grid crossing of the juveniles with age. Although no correlation of crossings of the juveniles with the mother was found in Experiment I (Figure 3, Table 4), the rate of crossing of juveniles in Experiment III was greater on non-shock days if the mother was not restricted (Table 12). This suggests that the juveniles may have crossed the grid with their mother.

A subsequent litter also increased the rate of grid crossing of the previous litter on non-shock days. The difference is not significant on shock days probably because of the heterogeniety of the females with respect to aggressiveness. Restrained females without a subsequent litter of Experiment II-3 compared with the aggressive and non-aggressive females of Experiment IV suggest that mothers without subsequent litters have the same effect on their juveniles as non-aggressive mothers with a subsequent litter. The effect of a subsequent litter is, therefore, dependent upon the aggressiveness of the female. Since the difference between aggressive and non-aggressive females is seen only in the presence of a subsequent litter, they would all behave as non-aggressive mothers toward the last litter of the season. This, in conjunction with delayed puberty (Howard, 1949), may explain the failure of the last litter of the season to disperse until the following spring.

In the field many females abandon the previous litter or force it out of the nest when the next litter is born. It is not known if there is a correlation between female aggressiveness and whether a female abandons her previous litter or evicts them from the nest in the field situation. Even if a female abandons her litter, her aggressiveness toward the juveniles in the home range may be a factor in the initiation of their dispersal. Burt (1940) reported observing an adult female _P. leucopus_ chasing a young female. He considers old males to be more tolerant than old females toward both young and adults of the same sex.

Individual Differences

In addition to the differences in rate of departure resulting from the individual differences in aggressiveness of the mother, differences between families were found that could not be attributed to the effect of a subsequent litter on the adult female. For example, family differences in the treatment of litters were found in I-4, male across (II-1), male home (II-2), restrained female without subsequent litter (III-3) and non-restrained female without subsequent litter (III-4) (Table 3). The family differences of two of these treatments, litter only (I-4) and male across (II-1) could be explained by the tendency of the juveniles to disperse together (Table 2) as Smith (1968) observed in the field for _P_. _polionotus_.

The results of Experiment V (Isolated Juveniles) suggest an inherent difference between the juveniles of the different families. Maternal influences prior to weaning have not been ruled out since no cross fostering was done. Inherent differences between individuals in the tendency to disperse is strongly championed by Howard (1960).

Overview

The observations of this study viewed in the context of the results of the various field studies allow us to speculate on the dynamics of dispersal in field populations of _Peromyscus maniculatus bairdi_, which is probably similar to other subspecies and species of _Peromyscus_ with minor modification. The initiation of dispersal in widely divergent genera of rodents may also be similar in some aspects.

For example, muskrat mothers also appear to vary in their aggressiveness toward their offspring (Errington, 1963).

The behavioral mechanisms underlying the dispersal of juveniles in the breeding season are more comparable to those studied here than during the non-breeding season. Shortly before weaning, the father often joins the mother and litter (Nicholson, 1941). At that time, or slightly before, the young begin exploring the home range of their parents probably both alone and with the father. The mother may then move to another nest site in the same home range to give birth to her next litter and the juveniles extend their explorations. Some juveniles apparently explore more widely than others. During this time the mother, if she is of the aggressive type may drive the juveniles from her home range. At the onset of sexual maturity, if the young have not previously been driven from their natal home range by their mother, some will make extensive moves to suitable vacant areas perhaps discovered earlier during their explorations. Those driven from their home range prior to puberty probably do not settle down until the onset of sexual maturity and may be driven widely if the neighboring residents are aggressive.

Several aspects of the influence of social behavior on dispersal of mice remain to be studied. For example, the interactions of various family members, such as, the interaction of an aggressive mother in the presence of the father, may be different from either parent alone. Behavioral modifications induced by environmental change may explain seasonal changes and yearly differences in dispersal. The influence of other individuals outside the family is probably different in the different phases of dispersal and the elucidation of these differences will increase our understanding of behavioral population regulatory mechanisms. For example, an adult female may behave differently toward strange juveniles than toward his offspring. Past experiences of the dispersants also undoubtedly influence the observed responses. A description of the interactions and relative influences of social stimuli, previous experience, and individual differences could provide a theoretical framework for interpreting *Peromyscus* population dynamics.

SUMMARY

Social interactions and individual differences in *Peromyscus maniculatus bairdi* influence the rate at which juveniles leave their natal site. In a family group the father is attractive to the juveniles and does not expell them. The social influence of the mother depends upon the presence of a subsequent litter and her aggressiveness in defending her litters. Two types of females were found with respect to aggressiveness. An aggressive mother with a subsequent litter will increase the rate of departure of her previous litter. There is a tendency for littermates to leave together and no sex difference was found. Differences were found between litters when the litter members were tested separately. The social behaviors within family groups of *P. m. bairdi* determine the rate at which juveniles leave their natal site.

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