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Comparison of the Level of Female Induced Reproductive Inhibition in White-Footed Mice (Peromyscus leucopus noveboracensis) from Michigan and Virginia

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COMPARISON OF THE LEVEL OF FEMALE INDUCED REPRODUCTIVE INHIBITION IN WHITE-FOOTED MICE (PEROMYSCUS LEUCOPUS NOVEBORACENSIS) FROM MICHIGAN AND VIRGINIA

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ABSTRACT

Recent studies of Michigan and Virginia White-footed mice (Peromyscus leucopus noveboracensis) have demonstrated contradictory data regarding the level and presence of female induced reproductive inhibition. These studies have shown that $\leq$3% of young Michigan females reared with an adult bisexual pair reproduced by 150 days of age. On the contrary, 69% of young Virginia females, similarly treated, reproduced by 150 days of age. This phenomenon was reexamined in our laboratory in a comparative study using outbred laboratory colonies developed from mice captured near East Lansing, Michigan and Williamsburg, Virginia. Newly weaned 21 day old females from each breeding colony were raised in the presence of a reproductively proven adult male or a reproductively proven adult bisexual pair.

Results of this comparative study demonstrate that 70% of Michigan and 72% of Virginia P. l. noveboracensis experimental females reared in the presence of a bisexual pair were pregnant or had produced a litter by 150 days of age. The combined 71% reproductive level of young females reared with bisexual pairs was not significantly different from that of young females reared in the presence of an adult male alone. In addition, no significant difference was observed across treatment groups with regard to age of vaginal introitus (38.98 $\pm$ 0.61 days) or age at first parity (91.49 $\pm$ 3.18 days).

These results do not support a proposed high level of adult female induced reproductive inhibition in young female Peromyscus leucopus noveboracensis raised with a bisexual pair. Variations in previously reported data appear not to be due to any intrinsic differences in the Michigan and Virginia animals.

COMPARISON OF THE LEVEL OF FEMALE INDUCED REPRODUCTIVE INHIBITION IN WHITE-FOOTED MICE (*PEROMYSCUS LEUCOPUS NOVEBORACENSIS*) FROM MICHIGAN AND VIRGINIA

INTRODUCTION

Intrinsic population growth control by various cues has been demonstrated in laboratory populations of *Peromyscus*. This control in *P. maniculatus* includes inhibited reproductive maturation and small reproductive organs in freely growing populations (Terman 1965, 1969), sibling pair maturational inhibition (Hill, 1974), adult female induced maturational inhibition of younger females (Lombardi and Whitsett, 1980; Lombardo and Terman, 1980), and maternal or adult female induced reproductive inhibition of younger females (Haigh, 1983a). Inhibited reproduction in freely growing laboratory populations and in females reared with their mothers or unrelated adult females has been demonstrated in *P. eremicus* (Skryja, 1978). Similar findings of inhibited maturation, small reproductive organs, and reproductive failure have been demonstrated in *P. leucopus* (Rogers and Beauchamp, 1976).

A number of recent research efforts have investigated the presence and level of adult female induced reproductive inhibition of young female White-footed mice (*Peromyscus leucopus noveboracensis*). Specifically, a series of papers (Haigh 1983b, 1986, 1987) presented evidence that $\leq$3% of 21 day old newly weaned female *P. l. noveboracensis*, offspring of mice captured near East Lansing, Michigan, reproduced by 150 days of age if in addition to being paired with an adult male, an adult female was present. Inhibited 150 day old experimental females were able to recover and reproduce litters if the adult female was removed. These findings support results reported for P. maniculatus bairdii (Haigh, 1983a) and P. eremicus (Skryja, 1978). Additional work into the mechanism of the inhibition (Haigh et al., 1985; Haigh et al., 1988) demonstrated that the inhibition was not a delay in reproductive maturation but a failure of blastocyst implantation due to a urine borne chemical produced by the adult female.

Because of the relevancy and importance of Haigh's findings to reproductive inhibition as a means of population control in Peromyscus, similar experimental procedures were incorporated to study P. l. noveboracensis captured near the Laboratory of Endocrinology and Population Ecology at the College of William and Mary, Williamsburg, Virginia (Terman, 1992). In this work, contrary to Haigh's results, 69% of young females reproduced by 150 days of age when reared from weaning (21 days) in the presence of a bisexual pair (an adult male and female). In addition, it was found that the rearing of young females from 21 to 90 days of age in the presence of an adult female actually stimulated reproduction compared to rearing in isolation.

The Virginia P. l. noveboracensis results have raised a question about the phenomenon of adult female induced reproductive inhibition in young female White-footed mice. This question was whether the difference in previous results was due to research methodology or to some intrinsic difference between Michigan and Virginia mice. The present comparative study of the Michigan and Virginia P. l. noveboracensis was an effort to examine this phenomenon and answer the following questions: first, whether the presence of an adult female in a bisexual pair situation inhibited reproduction in young females; and second, whether a difference exists in female induced reproductive inhibition between Michigan and Virginia P. l. noveboracensis when studied under the same laboratory conditions.

MATERIALS AND METHODS

The animals used in this study were White-footed mice (Peromyscus leucopus noveboracensis) drawn from outbred (non sib mating) Virginia and Michigan colonies developed and maintained at the Laboratory of Endocrinology and Population Ecology at the College of William and Mary. Data logs of the Virginia, Michigan, and treatment colonies have been placed on file at the Laboratory.

Virginia Research Colony

The Virginia P. l. noveboracensis research colony consisted of animals born to >30 founding pairs established in Fall, 1990 and Spring, 1991. Founding pairs were composed of an animal captured in the wild and one born into an existing laboratory colony maintained as a heterogeneous gene pool by periodic addition of wild caught animals. Wild mice used to found the research colony were captured in the wooded area adjacent to the Laboratory with the assistance of Dr. Richard Terman of the College of William and Mary.

Michigan Research Colony

The Michigan P. l. noveboracensis research colony was founded by mice captured near East Lansing, Michigan in late Summer, 1990 with the assistance of Dr. John A. King of Michigan State University.

<u>General Maintenance</u>

Both the Virginia and Michigan research colonies maintained outbred (non sib mating) conditions. Young were weaned at 21 days of age and maintained with siblings of the same sex until $\geq$60 days of age when they were used to found breeding pairs.

Animals were housed in two compartment opaque plastic cages (each compartment measuring 12.8 by 27.8 by 15 cm). These cages were covered with wire mesh tops with water bottles and incorporated food hoppers. Wood shavings were used as bedding. The bedding and cages were changed every 14 days. Cage tops and water bottles were changed every two months or earlier as needed. Food (Rat, Mouse, and Hamster, Agway 3000) and tap water were provided ad lib.

The Michigan and Virginia research colonies were maintained in different five meter square colony rooms. Experimental animals from both colonies were housed in the same room. Light was provided by four 40 watt fluorescent bulbs (15 ft-candles at the floor) in a 14L:10D cycle from 0700 h to 2100 h. Building construction occurred outside the laboratory complex throughout the treatment period and caused periodic losses in electrical power. These losses in power, while inconvenient, did not seriously alter the light-dark cycle. Room temperature was maintained at 23 $\pm$ 3 °C. A continual temperature record of the experimental room was made using a Seven-day Dickson Minicorder. During the months of May and June, 1991 the Laboratory's air conditioning system suffered numerous failures. Therefore, weekly temperature averages for four weeks during the May-June period exceeded the normal temperature bounds. The research colonies did not show any adverse effects and maintained normal levels of reproduction. A temperature record for the study period can be found in Appendices A and B. Air was exchanged with outside air from five to eight times per hour. Ambient humidity was maintained except during the air conditioning months of May through September when portable dehumidifiers were used to help reduce food mold.

Treatment Design

The experimental animals were selected from the Virginia and Michigan *P. l. noveboracensis* research colonies. Newly weaned 21 day old females were placed with either with a reproductively proven bisexual adult pair or a reproductively proven adult male. An attempt was made to observe at least 30 experimental females in each treatment condition until they produced a litter or had reached 150 days of age. Most experimental animals had at least one parent born in the wild, and all were three or less generations removed from the wild.

Treatment and Observation Criteria

Treatments were begun in April 1991 and observation was completed by February 1992. During this period the following experimental criteria were observed. Experimental females were selected from litters composed of three or more young in which both sexes were represented. These females were not related to the adults with which they were reared. Adults were reproductively proven and adult bisexual pairs had produced their last litter together. Treatment groups were established within eight days of birth of the adult's last litter. All individuals used were toe clipped for identification. Experimental females were examined weekly for evidence of vaginal introitus. All females were visually examined daily for evidence of pregnancy. Young born to adult females during the treatment period were noted and removed on discovery. Treatments were maintained until experimental females had produced a litter or had reached 150 days of age. Treatment groups were terminated and replaced when injury or death prevented individuals from completing the observation period. All experimental females were sacrificed and examined for the presence of uterine scars and or viable pregnancies at treatment termination. Experimental females were preserved for histological study.

Data Recorded

Data recorded for the experimental female were age of vaginal introitus, an approximate indicator of sexual maturation (Clark, 1938; Rogers and Beauchamp, 1974), and age at first parturition. In addition, dates of pregnancy, the number of viable young in utero, and number of young born were recorded for the experimental female. Observations of the adult female when present included number of litters and young per litter.

Statistical Analysis

Measurements of treatment group reproductive level were analyzed by Chi-Square tests of independence. Measurements of vaginal introitus age, first parturition age, and litter size were analyzed by one-way analysis of variance (ANOVA). Statistical comparisons were performed using the SPSSX statistical package. Probability of less than 0.05 was considered significant in all cases.

RESULTS

Data summaries for experimental female age of vaginal introitus, age of first parturition, and litter size across treatments are presented in Appendices C, D, E. and F.

Treatment Losses

All treatment conditions experienced some loss of experimental females either by death or serious injury (Table 1). Typically the experimental female was attacked, injured, and or killed by the adult female, although male aggression, while infrequent, was observed. These losses occurred primarily within the first days of treatment. Analysis showed that a significantly higher number of experimental females were lost when placed with the adult bisexual pair (Michigan 9 lost, Virginia 4 lost) as compared to those placed with the adult male alone (Michigan 1 lost, Virginia 1 lost) ($\underline{X}^2$=8.067, df=1, P=0.005). There was no significant difference in experimental female mortality between Michigan and Virginia bisexual treatments ($\underline{X}^2$=1.923, df=1, P=0.166). The significant higher mortality of young females housed with bisexual pairs should be viewed, however, with caution due to small sample size.

Age of Vaginal Introitus

Of the 121 experimental females followed to treatment termination, all but one exhibited vaginal introitus. A comparison of age of vaginal introitus revealed a range of 26-60 days of age with a mean of 38.70 ± 0.61 (Table 2). This measure was conservative in that experimental females were examined only once each week and only a conclusive vaginal opening was noted. No significant difference in age of vaginal introitus was observed across the four treatment conditions by one-way ANOVA (P=0.4472). There was no evidence that presence of the adult female retarded the occurrence of vaginal introitus in the experimental females.

Age of First Parturition

Seventy-eight of the 121 experimental females produced litters by 150 days of age. A comparison of the age at first parturition revealed a range of 49-149 days of age with a mean of 91.49 ± 3.18 days (Table 3). No significant difference was observed by one-way ANOVA (P=0.8383) across treatments with regards to age at first parturition. The presence of the adult female did not delay the age at first parturition in experimental females.

Reproductive Performance

Seventy percent of Michigan and 72% of Virginia experimental females reared in the presence of a bisexual pair were pregnant or had produced a litter by 150 days of age (Table 4). The reproductive level of Michigan and Virginia experimental females reared with a bisexual pair was not significantly different from that of females reared in the presence of an adult male alone ($\underline{X}^2$=0.012, df=1, P=0.914). No significant difference was noted in any group with regard to numbers of experimental females that were reproductive by 150 days of age ($\underline{X}^2$=2.019, df=3, P=0.5685).

The number of young per litter, while not significantly different across the four treatment groups by one-way ANOVA (P=0.2498), did show a trend to larger litter sizes for Michigan experimental females (Table 5). A test of Michigan versus Virginia experimental female litter size indicated that the trend was significant (one-way ANOVA P=0.0431). Michigan experimental females had a range of 1-6 young per litter with a mean of 4.00 $\pm$ 0.21. Virginia experimental females had a range of 1-5 young per litter with a mean of 3.45 $\pm$ 0.17.

Additional Michigan and Virginia Comparisons

During the later part of this study two pilot projects were undertaken to compare the Michigan and Virginia research colonies. The first involved twelve mixed pairs of Michigan and Virginia animals. These pairs, composed of one Michigan and one Virginia animal, were observed for three months to document reproductive success. Eight out of the 12 mixed pairs, or 75%, produced offspring. Seven first generation (F1) pairs were established and observed. This project was terminated when one F1 generation pair produced a litter within a month of pairing. One F1 generation pair produced a litter within a month of pairing. Michigan and Virginia research animals were apparently able to breed and produce viable offspring.

The second project involved a characterization of mitochondrial DNA restriction endonuclease cleavage sites for mice from the original Michigan and Virginia research colonies. This characterization of three mice from each colony used *Ava*I, *Eco*RI, *Ban*I, and *Hin*DIII restriction endonucleases. No differences in restriction site locations were found between Michigan and Virginia research animals.

TABLE 1. Number of treatments prematurely terminated due to the death or serious injury of experimental females

Experimental Female reared with:	Treatments		
	Established	Terminated*	Completed
Michigan Bisexual Pair	40	9	30[a]
Michigan Male Alone	32	1	31
Virginia Bisexual Pair	33	4	29
Virginia Male Alone	32	1	31
Total	137	15	121

*<u>Significant difference</u> in number of treatments terminated between experimental females reared with bisexual pairs (Michigan 9, Virginia 4) versus those reared with males alone (Michigan 1, Virginia 1): $\underline{X}^2$=8.067, df=1, P=0.005

[a]Total does not include one terminated treatment in which the adult female died due to pregnancy complications

TABLE 2. Age of vaginal introitus for experimental females

Experimental Female reared with:	N	Age (days)* Mean $\pm$ S.E.	Range (days)
Michigan Bisexual Pair	29	38.38 $\pm$ 1.11	29-50
Michigan Male Alone	31	40.64 $\pm$ 1.39	29-60
Virginia Bisexual Pair	29	38.66 $\pm$ 1.22	26-53
Virginia Male Alone	31	38.16 $\pm$ 1.13	28-59
Total	120	38.98 $\pm$ 0.61	26-60

*<u>No significant difference</u> in experimental female age of vaginal introitus across treatments: One-way ANOVA P=0.4472

TABLE 3. Age of first parturition for experimental females by 150 days of age

Experimental Female reared with:	N	Age (days)* Mean ± S.E.	Range (days)
Michigan Bisexual Pair	20	95.75 ± 6.32	49-138
Michigan Male Alone	18	88.50 ± 6.34	55-147
Virginia Bisexual Pair	18	88.67 ± 6.51	57-147
Virginia Male Alone	22	92.26 ± 6.48	53-149
Total	78	91.49 ± 3.18	49-149

*No significant difference in experimental female age of first parturition across treatments: One-way ANOVA P=0.8383

TABLE 4. Experimental females pregnant or parous by 150 days of age

Experimental Female reared with:	N	Reproductive Females*		
		Pregnant	Parous	%
Michigan Bisexual Pair	30	1	20	70%
Michigan Male Alone	31	1	18	61%
Virginia Bisexual Pair	29	3	18	72%
Virginia Male Alone	31	2	22	77%
Total	121	7	78	70%

*<u>No significant difference</u> in experimental female reproductive performance by 150 days of age across treatments: $\underline{X}^2=2.019$, df=3, P=0.5685

TABLE 5. Litter size for experimental females parous by 150 days of age

Experimental Female reared with:	N	Litter Size* Mean ± S.E.	Range
Michigan Bisexual Pair	20	4.05 ± 0.29	1-6
Michigan Male Alone	18	3.94 ± 0.31	1-6
Virginia Bisexual Pair	18	3.44 ± 0.25	2-5
Virginia Male Alone	22	3.45 ± 0.23	1-5
Total	78	3.72 ± 0.14	1-6

*Significant difference in litter size of combined Michigan (4.00 ± 0.21) versus Virginia (3.45 ± 0.17) experimental females: One-way ANOVA P=0.0431

DISCUSSION

The results of the present comparative study of Michigan and Virginia _P_. _leucopus_ _noveboracensis_ indicate that 71% of 21 day old newly weaned females reared in the presence of an adult bisexual pair were pregnant or had produced a litter by 150 days of age (Table 4). These findings are contrary to the $\leq$3% young female reproduction demonstrated by Haigh (1983b, 1986, 1987), but support the work of Terman (1992) in which 69% of Virginia young female _P_. _l_. _noveboracensis_ reproduced.

While the present study does not demonstrate a high level of female reproductive inhibition, a significantly ($P \leq 0.005$) higher number of young females were killed or seriously injured when reared with adult bisexual pairs than those reared by males alone (Table 1). Most of the experimental female injury and mortality appeared to be the result of adult female aggression. This was perhaps due to the condition of the adult females at the time treatments were established in that all adult females had produced a litter within eight days of entering a treatment. The actions of the adult female against the experimental female appear to be a case of postpartum aggression and domination of intruders. This aggression, documented in _P_. _l_.

noveboracensis in other contexts by Wolff (1985, 1986) and by Wolff and Cicirello (1989), has been proposed as a deterrent against infanticidal intruders. While no mention was made of this type or level of aggression in Haigh (1983b, 1986, 1987) and Terman (1992), Skryja (1978) does note that injured young females were removed from experimental treatments.

The age of vaginal introitus was not significantly delayed by the presence of the adult female (Table 2). A combined mean of 38.98 $\pm$ 0.61 days of age for vaginal introitus across treatment groups was noted in this study. This value is consistent with reported values for captive P. leucopus of 38 and 44 days for mice from Campeche, Mexico and Michigan respectively (Lackey, 1978) and 39 days for mice from Pennsylvania (Rogers and Beauchamp, 1974). Haigh et al. (1988) demonstrated that young females reared with only an adult female experienced vaginal introitus at 51 days of age. Young females reared with adult bisexual pairs, however, experienced vaginal introitus at approximately 40 days of age. The adult female induced delay in vaginal introitus was thus reduced by the presence of an adult male. Results of the present study confirm this observation.

The age at first parturition was not significantly delayed by the presence of the adult female (Table 3). An observed mean of 91.49 $\pm$ 3.18 days of age for first parturition across treatment groups was noted. Back-dating

25 days for gestation a mean conception age of 66 days was calculated. This value is consistent with a reported value of 72 days in lab and wild caught P. leucopus from London, Ontario (Millar et al., 1979).

Results of the present study indicate a significantly ($P \leq 0.05$) greater number of young per litter for Michigan experimental females (Table 5). This is consistent with observed geographic trends in litter sizes in which northwestern populations of P. leucopus have larger litter sizes (Millar, 1989).

The aim of this comparative study was to investigate the level of reproductive inhibition in young females reared by adult bisexual pairs and the possibility of intrinsic differences between Michigan and Virginia White-footed mice. No difference between Michigan and Virginia animals in the percent of young females reproducing was observed. Secondly, no difference in reproduction was noted between young females reared with adults males regardless of the presence of an adult female. These data contradict Haigh's (1983b, 1986, 1987) work and require that attention be given to the major procedural differences between Haigh's research and the present study.

While an attempt was made in the design of the present experiment to minimize procedural differences, differences between the studies do exist. The first area is that of environmental, or laboratory conditions such as size and type of cage, temperature, and photoperiod. The present study used opaque cages that were approximately one half the size of Haigh's transparent cages. Temperature was maintained at 23 $\pm$ 3 °C, two degrees higher than Haigh's conditions. Lighting was provided at a 14L:10D cycle while Haigh's provided a 15L:9D cycle. While P. leucopus reproduction has been shown to be influenced by photoperiod (long versus short day) (Johnston and Zucker, 1980; Lynch, 1973) and geographic origin (Lynch et al., 1981) it is doubtful that the minimal environmental differences between Haigh's work and the present study can alone account for the marked difference in reproductive levels.

The second area of difference between Haigh's work and the present study is that of procedure and methodology. Haigh's (1983b) study presented data for young females reared with related adults. Later work presented evidence that there was no significant difference in the reproductive performance of young females reared with related (father-daughter-mother) versus unrelated adults (Haigh, 1986, 1987). The present study maintained strict outbred conditions by not allowing young females to be reared by parents or close relatives. Another possible procedural difference placed experimental females with reproductively proven strange adults whose last litter had been produced and removed within eight days of treatment initiation. These procedural differences between Haigh (1983b) and the present study may have exposed experimental females to different early social experiences. Not only were the adults unrelated to young females in the present study, adult females had produced a litter within eight days of treatment initiation. Moreover, the adult females were typically pregnant at treatment initiation. This pregnancy, however, was less than eight days advanced. These methodological differences, in light of the present study's findings and the recent evidence that changes in social environment are an important stimulus in young female reproduction (Wolff, 1989; Terman, 1992), suggest the need for additional research. This research should include the effect of social environment and adult female reproductive patterns on young female reproduction.

In conclusion, there is no evidence from the present comparative study of Michigan and Virginia Peromyscus leucopus noveboracensis for a proposed high level of adult female induced reproductive inhibition of young females reared with a bisexual adult pair. Further, no intrinsic differences with regard to the level or reproduction or inhibition were noted between Michigan and Virginia White-footed mice. The present findings for P. l. noveboracensis differ with Haigh (1983b, 1986, 1987). In addition the findings differ with evidence for female reproductive inhibition for P. maniculatus (Haigh, 1983a) and P. eremicus (Skryja, 1978). This difference suggests that variations may exist in Peromyscus with regard to the presence, nature, and level of adult female induced reproductive inhibition of young females.

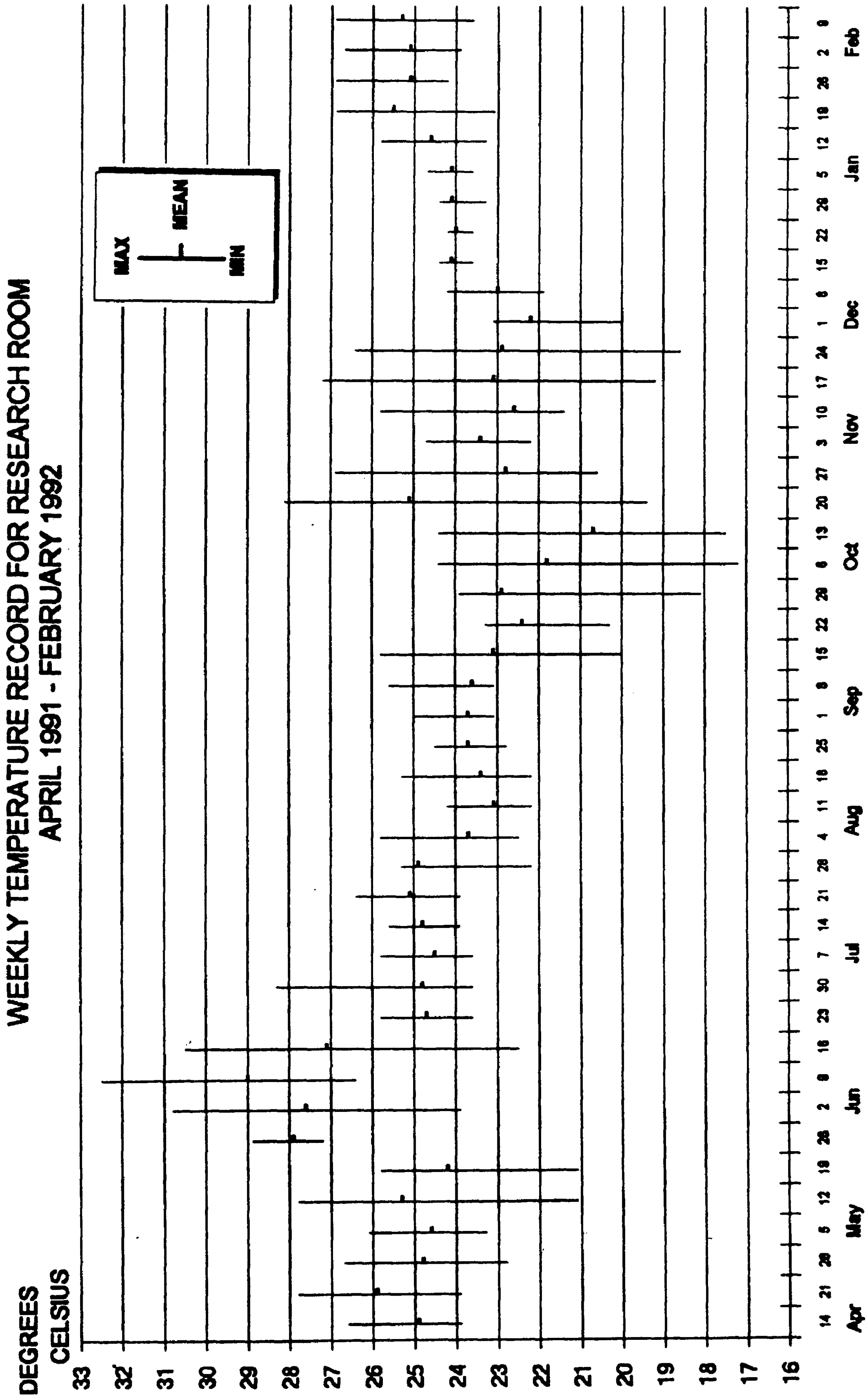
LIST OF APPENDICES

APPENDIX A: Weekly temperature data for research room
April 1991 - February 1992 (Celsius)

WEEK OF	MAXIMUM	WEEKLY AVERAGE	MINIMUM
4/14/91	26.6	24.9	23.9
4/21	27.8	25.9	23.9
4/28	26.7	24.8	22.8
5/05	26.1	24.6	23.3
5/12	27.8	25.3	21.1
5/19	25.8	24.2	21.1
5/26	28.9	27.9	27.2
6/02	30.8	27.6	23.9
6/09	32.5	29.0	26.4
6/16	30.5	27.1	22.5
6/23	25.8	24.7	23.6
6/30	28.3	24.8	23.6
7/07	25.8	24.5	23.6
7/14	25.6	24.8	23.9
7/21	26.4	25.1	23.9
7/28	25.3	24.9	22.2
8/04	25.8	23.7	22.5
8/11	24.2	23.1	22.2
8/18	25.3	23.4	22.2
8/25	24.5	23.7	22.8
9/01	25.0	23.7	23.1
9/08	25.6	23.6	23.1
9/15	25.8	23.1	20.0
9/22	23.3	22.4	20.3
9/29	23.9	22.9	18.1
10/06	24.4	21.8	17.2
10/13	24.4	20.7	17.5
10/20	28.1	25.1	19.4
10/27	26.9	22.8	20.6
11/03	24.7	23.4	22.2
11/10	25.8	22.6	21.4
11/17	27.2	23.1	19.2
11/24	26.4	22.9	18.6
12/01	23.1	22.2	20.0
12/08	24.2	23.0	21.9
12/15	24.4	24.1	23.6
12/22	24.2	24.0	23.6
12/29	24.4	24.1	23.3
1/05/92	24.7	24.1	23.6
1/12	25.8	24.6	23.3
1/19	26.9	25.5	23.1
1/26	26.9	25.1	24.2
2/02	26.7	25.1	23.9
2/09	26.9	25.3	23.6

Temperature record by Seven-day Dickson Minicorder

APPENDIX B: Graph of weekly temperature record for research room April 1991-February 1992



APPENDIX C: Treatment data for Michigan experimental females reared with an adult bisexual pair

Treatment Number	Vaginal Introitus Age (Days)	First Parturition Age (Days)	Litter Size
1	42	66	6
2	34	138	6
3	45	74	3
4	38	-----	-----
5	45	111	3
6	46	-----	-----
7	44	-----	-----
8	30	112	5
9	Terminated, Adult female died		
10	No Vaginal introitus	-----	-----
11	35	65	5
12	Terminated		
13	47	78	4
14	Terminated		
15	42	-----	-----
16	Terminated		
17	29	-----	-----
18	45	121	3
19	Terminated		
20	50	Pregnant at 150 days	
21	Terminated		
22	41	112	4
23	34	----	-----
24	32	134	4
25	45	-----	-----
26	Terminated		
27	33	67	4
28	38	110	4
29	42	131	3
30	34	64	6
31	34	89	5
32	42	123	1
33	Terminated		
34	Terminated		
35	Terminated		
36	35	-----	-----
37	34	115	5
38	29	49	4
39	33	96	4
40	35	60	2
Range	29-50	49-138	1-6
Mean±S.E.	38.38±1.11	95.75±6.32	4.05±0.29

Terminated: seriously injured or killed
-----: no data

APPENDIX D: Treatment data for Michigan experimental females reared with an adult male alone

Treatment Number	Vaginal Introitus Age (Days)	First Parturition Age (Days)	Litter Size
1	42	Pregnant at 150 days	
2	34	64	2
3	39	130	3
4	60	-----	-----
5	45	-----	-----
6	48	-----	-----
7	33	74	5
8	51	-----	-----
9	30	-----	-----
10	48	147	5
11	34	78	1
12	37	90	4
13	48	-----	-----
14	35	110	4
15	42	-----	-----
16	33	133	3
17	36	-----	-----
18	43	-----	-----
19	34	56	5
20	42	-----	-----
21	59	-----	-----
22	50	88	5
23	29	55	6
24	Terminated		
25	42	84	4
26	40	79	4
27	32	75	5
28	38	101	5
29	36	75	4
30	44	96	2
31	40	-----	-----
32	36	58	4
Range	29-60	55-147	1-6
Mean±S.E.	40.64±1.39	88.50±6.34	3.94±0.31

Terminated: seriously injured or killed
-----: no data

APPENDIX E: Treatment data for Virginia experimental females reared with an adult bisexual pair

Treatment Number	Vaginal Introitus Age (Days)	First Parturition Age (Days)	Litter Size
1	38	81	4
2	38	-----	-----
3	49	104	4
4	35	Pregnant at 150 days	
5	35	67	4
6	53	106	3
7	35	76	2
8	33	-----	-----
9	42	-----	-----
10	42	62	3
11	38	-----	-----
12	40	-----	-----
13	42	105	3
14	31	69	4
15	53	123	2
16	42	76	3
17	45	147	5
18	Terminated		
19	34	57	5
20	27	68	4
21	Terminated		
22	Terminated		
23	44	74	3
24	34	Pregnant at 150 days	
25	41	Pregnant at 150 days	
26	34	83	2
27	42	-----	-----
28	40	-----	-----
29	26	147	2
30	41	86	4
31	34	-----	-----
32	Terminated	-----	-----
33	33	65	5
Range	29-53	57-147	2-5
Mean±S.E.	38.66±1.22	88.67±6.51	3.44±0.25

Terminated: seriously injured or killed
-----: no data

APPENDIX F: Treatment data for Virginia experimental females reared with an adult male alone

Treatment Number	Vaginal Introitus Age (Days)	First Parturition Age (Days)	Litter Size
1	28	-----	-----
2	42	Pregnant at 150 days	
3	35	146	2
4	35	108	4
5	36	67	4
6	39	83	4
7	39	97	5
8	33	94	4
9	42	69	3
10	42	132	1
11	59	-----	-----
12	38	-----	-----
13	39	149	3
14	42	-----	-----
15	32	96	4
16	35	134	3
17	31	78	4
18	45	-----	-----
19	41	134	4
20	34	-----	-----
21	44	62	4
22	44	63	3
23	37	70	4
24	34	59	5
25	36	55	5
26	28	84	2
27	43	97	1
28	Terminated		
29	35	102	4
30	34	-----	-----
31	48	Pregnant at 150 days	
32	33	53	4
Range	28-59	53-149	1-6
Mean±S.E.	38.16±1.13	92.26±6.48	3.45±0.23

Terminated: seriously injured or killed
-----: no data

LITERATURE CITED

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

Haigh, G. R. 1983a. The effects of inbreeding and social factors on the reproduction of young female *Peromyscus maniculatus bairdii*. Journal of Mammalogy, 64:48-54.

------. 1983b. Reproductive inhibition and recovery in young females *Peromyscus leucopus*. Journal of Mammalogy, 64:706.

------. 1986. Reproductive inhibition in young female *Peromyscus leucopus*: analysis of mechanisms and effects. Ph.D. dissert., Michigan State University, East Lansing, 89 pp.

------. 1987. Reproductive inhibition of female *Peromyscus leucopus*: female competition and behavioral regulation. American Zoologist, 27:867-878.

Haigh, G. R., D. M. Lounsbury, and T. A. Gordon. 1985. Pheromone-induced reproductive inhibition in young female *Peromyscus leucopus*. Biology of Reproduction, 33:271-276.

Haigh, G. R., B. S. Cushing, and F. H. Bronson. 1988. A novel postcopulatory block of reproduction in white-footed mice. Biology of Reproduction, 38:623-626.

Hill, J. L. 1974. *Peromyscus*: effect of early pairing on reproduction. Science, 186:1042-1044.

Johnston, P. G. and I. Zucker. 1980. Photoperiodic regulation of reproductive development in white-footed mice (*Peromyscus leucopus*). Biology of Reproduction, 22:983-989.

Lackey, J. A. 1978. Reproduction, growth, and development in high-latitude and low-altitude populations of *Peromyscus leucopus* (Rodentia). Journal of Mammalogy, 59:69-83.

Lombardi, J. R. and J. M. Whitsett. 1980. Effects of urine from conspecifics on sexual maturation in female prairie deer mice, Peromyscus maniculatus bairdii. Journal of Mammalogy, 61:766-768.

Lombardo, D. L. and C. R. Terman. 1980. The influence of the social environment on sexual maturation of female deermice (Peromyscus maniculatus bairdii). Researches on Population Ecology, 22:93-100.

Lynch, G. R. 1973. Seasonal changes in thermogenesis, organ weights, and body composition in the white-footed mouse, Peromyscus leucopus. Oecologia, 13:363-376.

Lynch, G. R., H. W. Heath, and C. M. Johnston. 1981. Effect of geographical origin on the photoperiodic control of reproduction in the white-footed mouse, Peromyscus leucopus. Biology of Reproduction, 25:475-480.

Millar, J. S. 1989. Reproduction and development. Pp. 169-232, in Advances in the study of Peromyscus (Rodentia) (G. L. Kirkland, Jr. and J. N. Layne, eds.). Texas Tech University Press, Lubbock, 366 pp.

Millar, J. S., F. B. Wille, and S. L. Iverson. 1979. Breeding by Peromyscus in seasonal environments. Canadian Journal of Zoology, 57:719-727.

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

------. 1976. Influence of stimuli from populations of Peromyscus leucopus on maturation of young. Journal of Mammalogy, 57:320-330.

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

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

------. 1969. Weights of selected organs of deermice (Peromyscus maniculatus bairdii) from asymptotic laboratory populations. Journal of Mammalogy, 50:311-320.

------. 1992. Reproductive inhibition in female white-footed mice from Virginia. Journal of Mammalogy, 73:443-448.

Wolff, J. O. 1985. Maternal aggression as a deterrent to infanticide in Peromyscus leucopus and P. maniculatus. Animal Behaviour, 33:117-123.

------. 1986. Infanticide in white-footed mice, Peromyscus leucopus. Animal Behaviour, 34:1568.

------. 1989. Social behavior. Pp. 271-291, in Advances in the study of Peromyscus (Rodentia) (G. L. Kirkland, Jr. and J. N. Layne, eds.). Texas Tech University Press, Lubbock, 366 pp.

Wolff. J. O. and D. M. Cicirello. 1989. Field evidence for sexual selection and resource competition infanticide in white-footed mice. Animal Behaviour, 38:637-642.

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