AN ABSTRACT OF THE THESIS OF

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Abstract approved: _____

Jerry O. Wolff

Numerous laboratory studies with at least 12 species of rodents have reported that exposure of females to strange males results in pregnancy disruption or infanticide. The proximate causes and ultimate benefits of these behaviors have been proposed from an evolutionary perspective. To determine if exposure to strange males or females caused pregnancy disruption and (or) infanticide in a resident gray-tailed vole (*Microtus canicaudus*) population, pregnancy rate and juvenile recruitment were monitored in populations of 12 female and 12 male voles following introduction of unfamiliar adults. These experiments were conducted in 12 0.2 ha enclosures using three treatments and a control. Every 10 days 12 males, six males, or six females were removed and replaced in the three treatments, respectively, or the populations were left unmanipulated in the control (3 replicates/treatment). The time to first parturition, time between parturitions, number of juveniles recruited/parturition, and percent of births followed by lactation did not vary among the controls

and three treatments. The only observable effects of treatment were a slight non-significant delay in time to first birth in the 12-male treatment and a slightly significant difference in the number of pregnancies per female. These results do not support previous laboratory studies indicating that exposure to strangers causes pregnancy disruption and (or) infanticide at high rates. Therefore, in field conditions, little evidence was found indicating that female gray-tailed voles' reproductive fitness declines after exposure to strangers. I propose that results from laboratory studies on behavioral aspects of mammals should be validated with field data prior to being extrapolated to natural populations and applied to evolutionary paradigms.

Exposure to Strangers Does Not Cause Pregnancy Disruption or Infanticide in the Gray-tailed Vole

by

Helen M. de la Maza

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

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Helen M. de la Maza, Author

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DEDICATION

This thesis is dedicated to Luis and Maria de la Maza, my parents, who faithfully supported me emotionally, academically, and financially throughout my education.

EXPOSURE TO STRANGERS DOES NOT CAUSE PREGNANCY DISRUPTION OR INFANTICIDE IN THE GRAY-TAILED VOLE

INTRODUCTION

Natural selection theory proposes that individuals should have evolved reproductive strategies that allow them to maximize their reproductive success (Darwin, 1859; Dawkins, 1976). The strategy that is most adaptive to one gender may not be adaptive for the other and consequently evolution may favor behaviors in one sex that are counter-strategies for behaviors of the other sex (Wasser and Barash, 1983). Two behaviors in mammals that possibly have these characteristics are pregnancy disruption (Bruce, 1959) and infanticide (Hrdy, 1979). Pregnancy disruption, in which implantation is blocked or embryos are resorbed or aborted, may be caused by a number of factors. The Bruce Effect (Bruce, 1959), which is the most common form of pregnancy disruption, is thought to be caused by exposure to strange males. Infanticide, the killing of young, committed by males and females has been observed in the laboratory and in the wild in numerous species of mammals (Hausfater and Hrdy, 1984; Parmigiani and vom Saal, 1994). The roles these behaviors play in the evolution of specific reproductive strategies for each sex are paramount to the understanding of mammalian behavioral systems (Wolff, 1997).

Pregnancy Disruption

Pregnancy disruption may have evolved in females as a counter-strategy to infanticide by males (vom Saal and Howard, 1982; Wasser and Barash, 1983). If a male kills a female's young, the female terminates lactation and comes into estrus, thereby giving the male access to a reproductive female (discussed below). Females that are exposed to possibly infanticidal strange males may terminate their current pregnancy to conserve reproductive effort (Hrdy, 1979; Labov, 1980, 1981; Wasser and Barash, 1983; Labov et al., 1985; Storey, 1990, 1994). Termination of pregnancy following exposure to a strange male was originally described by H. M. Bruce in 1959 and has since been known as the "Bruce Effect." This type of pregnancy disruption describes the situation in which a recently inseminated female is exposed to an unfamiliar non-sire male, or his scent, and implantation is blocked or embryos are resorbed. The Bruce Effect has been reported in the laboratory for at least 12 species of rodents, eight of which are Arvicolines (e.g. *Mus musculus*, Bruce, 1959, 1960; Bruce and Parkes, 1961; Drickamer, 1982; *Peromyscus maniculatus*, Bronson et al., 1969; *Microtus agrestis*, Clulow and Clarke, 1968; Milligan, 1976; *M. pennsylvanicus*, Clulow and Langford, 1971; Mallory and Clulow, 1977; Kenney et al., 1977; Storey, 1994; Storey and Snow, 1987, 1990; Storey and Joyce, 1995; *M. ochrogaster*, Stehn and Richmond, 1975; Kenney et al., 1977;

M. montanus, Stehn and Jannett, 1981; *M. pinetorum*, Schadler, 1981; Stehn and Jannett, 1981; *M. californicus*, Heske and Nelson, 1984; Heske, 1987; *Microtus brandti*, Stubbe and Janke, 1994; *Clethrionomys gapperi*, Clulow et al., 1982; *C. glareolus*, Clarke and Clulow, 1973; and *Dicrostonyx groenlandicus*, Mallory and Brooks, 1980; see Appendix F for a sample of laboratory results). In *Microtus*, studies have indicated that monogamous species such as prairie (Stehn and Richmond, 1975) and pine (Schadler, 1981) voles may be more susceptible to pregnancy disruption than polygamous species such as meadow (Storey, 1986) and field voles (Milligan, 1976). Laboratory studies also indicate that nulliparous female voles may be more susceptible to pregnancy disruption than parous females (Stehn and Jannett, 1981; Clulow et al., 1982). If laboratory results are representative of what occurs in the wild, then exposure to strange males should cause pregnancy disruption in a field population. Therefore, the introduction of strange males should cause a decrease in the number of completed pregnancies as well as longer intervals between successful reproductive events in the resident female population (Stehn and Richmond, 1975).

All experimental studies (e.g. Bruce, 1959, 1960; Chipman and Fox, 1966; Clulow and Clarke, 1968; Clulow and Langford, 1971; Stehn and Richmond, 1975; Milligan, 1976; Kenney et al., 1977;

Schadler, 1981; Storey, 1986), except for two (Heske and Nelson, 1984; Heske, 1987), that examined the Bruce effect have been conducted in laboratory conditions. Therefore, whether this form of pregnancy disruption occurs in wild populations or is a laboratory artifact of the forced proximity of the strange male (or his odor) and the pregnant female is not known. Heske and Nelson (1984) and Heske (1987) used semi-natural conditions to study the Bruce effect on *Microtus ochrogaster* and *M. californicus*, respectively, and had similar results to other laboratory studies. The enclosures used by Heske and Nelson were very small (1.25 x 3 m) compared to typical (200 m^2 Heske and Nelson, 1984) home ranges of *M. ochrogaster*. In addition, the small confining enclosures used in 1984 did not allow for dispersal by the defeated strange males (Heske, 1987).

Little is known about the effect of strange females on pregnancy disruption in rodents. Bruce (1960) found that females did not cause pregnancy disruption as did males. However, Huck et al. (1988) found that in hamsters, in which the female is larger and more aggressive than the male, strange males do not induce pregnancy blocking whereas strange females do. No other known studies have been conducted to determine the influence of strange females on pregnancy disruption; therefore, the general effect of introduction of strangers versus specifically the introduction of males on pregnancy disruption has not been addressed. Reproductive female rodents tend to have

exclusive home ranges (Wolff, 1985b) and therefore spatial overlap and persistent exposure to one another is rare. Pregnancy disruption potentially would not have the same fitness benefit for a female perpetrator than it would for a male. Embryo resorption should not occur after the exposure to an unfamiliar female because neither the pregnant female nor the perpetrator would gain reproductive benefit.

Infanticide

Infanticide has been well-studied in numerous mammal species and usually involves strange males killing unrelated offspring. Infanticide committed by males has been observed in the laboratory (Mallory and Brooks, 1978, 1980; Huck et al., 1982; Brooks and Schwarzkopf, 1983; Wolff, 1985a; Mennella and Moltz, 1988; Perrigo et al., 1992; Wilson et al., 1993) and in the field (Hrdy, 1977; Sherman, 1981; Packer and Pusey, 1983; Wolff and Cicirello, 1989). Strange females may also kill offspring of unrelated females in the laboratory (Mallory and Brooks, 1980; Wolff, 1985a; Wilson et al., 1993) and in the wild (Hoogland, 1985; Corbett, 1988; Wolff, 1986; Trulio et al., 1986; Wolff and Cicirello, 1989; Künkele, 1992). Infanticide may be a relatively common adaptive behavior that may occur primarily under three conditions (Hrdy, 1979): (1) females kill young as a form of resource competition for breeding

sites; (2) young are killed by strange males, which in turn gives males access to a reproductive female; and (3) both males and females kill young and eat them as a food source. Each of these functions for infanticide may be an adaptive evolved strategy (Hrdy, 1979; vom Saal and Howard, 1982; Hoogland, 1985) and occurs in many species (Hausfater and Hrdy, 1984; Parmigiani and vom Saal, 1994; and refs. above). The frequency with which these conditions occur should be positively dependent, in part, on the frequency with which strange males and females intrude into resident breeding areas (Stehn and Richmond, 1975; Wolff and Cicirello, 1991; Wolff, 1995). If this premise is correct, increased exposure to strangers should decrease the percent of births followed by lactation and also decrease the number of recruits per parturition in a resident population.

Male Benefits: Sexual Selection Hypothesis

The sexual selection hypothesis (Hrdy, 1979) states that males will commit infanticide on unrelated offspring to gain reproductive access to females. Infanticide of unweaned young will bring a female into estrus early (Schwagmeyer, 1979; vom Saal and Howard, 1982; Packer and Pusey, 1983; Elwood et al., 1990) because lactation, which inhibits ovulation in many mammalian species, will terminate. The male can therefore mate with the female sooner when he kills her

young than if the female returns to estrus after completing lactation and weaning the litter. Sexual selection infanticide has been reported for numerous species of mammals (e.g. Mallory and Brooks, 1978; vom Saal and Howard, 1982; Packer and Pusey, 1983; Schadler, 1985; Wolff and Cicirello, 1989).

Sexual selection infanticide, however, may be complicated in species that exhibit post-partum estrus. In these species, females come into estrus and mate within a short period after giving birth. Females are lactating and nursing one litter while the second litter is developing in utero. Thus, killing of young and terminating lactation will not cause the female to become estrous because she is already pregnant with her next litter. The only way for a male to benefit from infanticide in species with post-partum estrus is for the male to also cause pregnancy disruption in the female. Therefore, the introduction of strange males into a resident population should result in fewer recruits per birth as well as a decreased number of completed pregnancies. The extent to which pregnancy disruption exists in mammals in field situations, especially in combination with infanticide, is not known.

Female Benefits: Resource Competition Hypothesis

The resource competition hypothesis (Hrdy, 1979) states that females will commit infanticide on unrelated offspring to compete with other females for resources such as nests or burrows. Therefore, resource competition infanticide should occur predominantly at high densities when competition for limited resources is most intense. Infanticidal females may gain access to the territory of the resident female (Sherman, 1981; Künkele, 1992) because females which lose their young often abandon their territory (Mallory and Brooks, 1980; Sherman, 1981). Therefore, the introduction of strange females into a resident population should increase the level of infanticide resulting in a decreased percent of births followed by lactation and a decreased number of recruits per parturition.

OBJECTIVES AND HYPOTHESES

The objective of this research was to determine if the introduction of strangers to a resident population of gray-tailed voles (*Microtus canicaudus*) causes pregnancy disruption and infanticide in the field.

To achieve this objective the following hypotheses were tested:

Response to Strange Males

Pregnancy Disruption

Populations in which breeding females are exposed to strange males will exhibit pregnancy disruption. This disruption will result in longer intervals between parturitions and fewer pregnancies that are carried to term in populations exposed to strange males than in control populations not exposed to strange males.

Infanticide

Fewer births will be followed by lactation and juvenile recruitment will be lower in populations that are exposed to strange males than in control populations due to increased rates of infanticide by introduced individuals.

Response to Strange Females

Pregnancy Disruption

Populations in which breeding females are exposed to strange females will not exhibit pregnancy disruption.

Infanticide

Fewer births will be followed by lactation and juvenile recruitment will be lower in populations that are exposed to strange females than in control populations due to increased rates of infanticide by introduced individuals.

MATERIALS AND METHODS

Study Species

To determine if pregnancy rates and juvenile recruitment were negatively affected by the introduction of strange males and females into an established breeding population, the reproductive responses of resident female gray-tailed voles were studied following the introduction of strange males and females. The gray-tailed vole was used as the model species for this experiment because eight of the 12 species used to study pregnancy disruption in the laboratory have been Arvicolines; the gray-tailed vole, also an Arvicoline, is therefore a behaviorally and functionally representative species. The gray-tailed vole is common to the Willamette Valley in Oregon. Breeding occurs between March and December; modal litter size is six; gestation is 21 days; and females can start breeding when they weigh 18 g (Verts and Carraway, 1987; Wolff et al., 1994). Gray-tailed voles have a polygynous/promiscuous mating system and dispersal is male-biased (Wolff et al., 1994). Mean home range sizes for male and female gray-tailed voles are 253 m^2 and 135 m^2, respectively, in wild populations (Wolff et al., 1996), and 94 m^2 and 56 m^2, respectively, in

enclosed populations, (Wolff et al., 1994). Home range size of other Arvicolines, such as *M. ochrogaster,* are typically ~200 m^2 (Heske and Nelson, 1984) and densities range from 50-200 animals/ha (Taitt and Krebs, 1985).

Research Facilities

The study was conducted at a small mammal enclosure facility located at Hyslop Field Laboratory of Oregon State University (Wolff et al., 1994; Edge et al., 1996). The experimental units consisted of 12 0.2 ha (45 x 45 m) enclosures planted with five species of pasture grass and alfalfa (*Medicago sativa*). These enclosures provided an area of suitable habitat that allowed for at least 12 intra-sexually non-overlapping home ranges for a typical wild gray-tailed vole (Wolff et al., 1996). Each enclosure was constructed of galvanized corrugated metal approximately 90 cm high and buried 90 cm deep to prevent escape of, or entry by, burrowing animals (Wolff et al., 1994). Eighty-one Sherman live traps were located in each of the enclosures in a 9 x 9 array with 5 m trap spacing. Each trap was inserted into an aluminum cover to shelter the trap from rain and excessive heat.

Trapping Procedures

The experimental animals were trapped for three consecutive days (=1 trap period) every 10 days from 12 September 1996 through 8 December 1996. The experiment lasted 14 weeks, which allowed the control females to complete at least three reproductive cycles. Traps were propped open and baited with sunflower seeds and oats during non-trapping days to encourage voles to enter the traps. During trap periods, trap doors were set one-half hour before sunrise and data collection began at approximately 1100 hours.

Animals were ear-tagged for individual and permanent identification. The data recorded included: enclosure number, trap location, ear tag number, gender and weight. Reproductive condition of females also was recorded including pregnancy and lactation status, as well as width of pubic symphysis. For females, nipples were noted as either (1) not visible or small, (2) visible or medium sized and possibly scarred, or (3) large and lactating with visible mammary tissue. Parting of the pubic symphysis indicated reproductive state: closed = nulliparous, partly open = parous, but not recently given birth; and wide open = birth within 24 hours. Successful births were determined upon capture by a combination of at least two of these three indicators: (1) weight loss (6-10 g) between trapping periods or trapping days, (2) a wide open pubic symphysis, and (3) a change from absence of mammary tissue (non-lactating) to

presence of mammary tissue (lactating). If a female was found in a Sherman live trap with young, or in a trap cover with a nest and neonates, she was also considered to have had a successful birth. Juvenile date of capture and body mass also were recorded.

Experimental Procedures

Twelve nulliparous females (15-30 g) and 12 adult males (33-52 g) were placed in each of 12 vacant enclosures the first week of September 1996. These densities and a 1:1 sex ratio were within the normal range of wild *Microtus* populations (Taitt and Krebs, 1985; Wolff et al., 1996). The experiment consisted of three treatments and one control, each with three replicates. After the initial introduction of the 24 animals, the control enclosures did not receive any new animals. In one of the experimental treatments (+6 male), six males were removed from each enclosure and replaced with six new adult males (33-52 g) every 10 days throughout the duration of the experiment. The other six males were left in the enclosures. In the second experimental treatment (+12 male), all 12 males were removed from each enclosure and replaced with 12 new adult males (33-52 g) at 10 day intervals throughout the experiment. In the third experimental treatment (+6 female), six males were removed from each enclosure after the first 10 days and replaced with six new adult females (30-45 g) that were not obviously pregnant. In subsequent manipulations, these six new females were removed and replaced every 10 days throughout the duration of the experiment (Fig. 1).

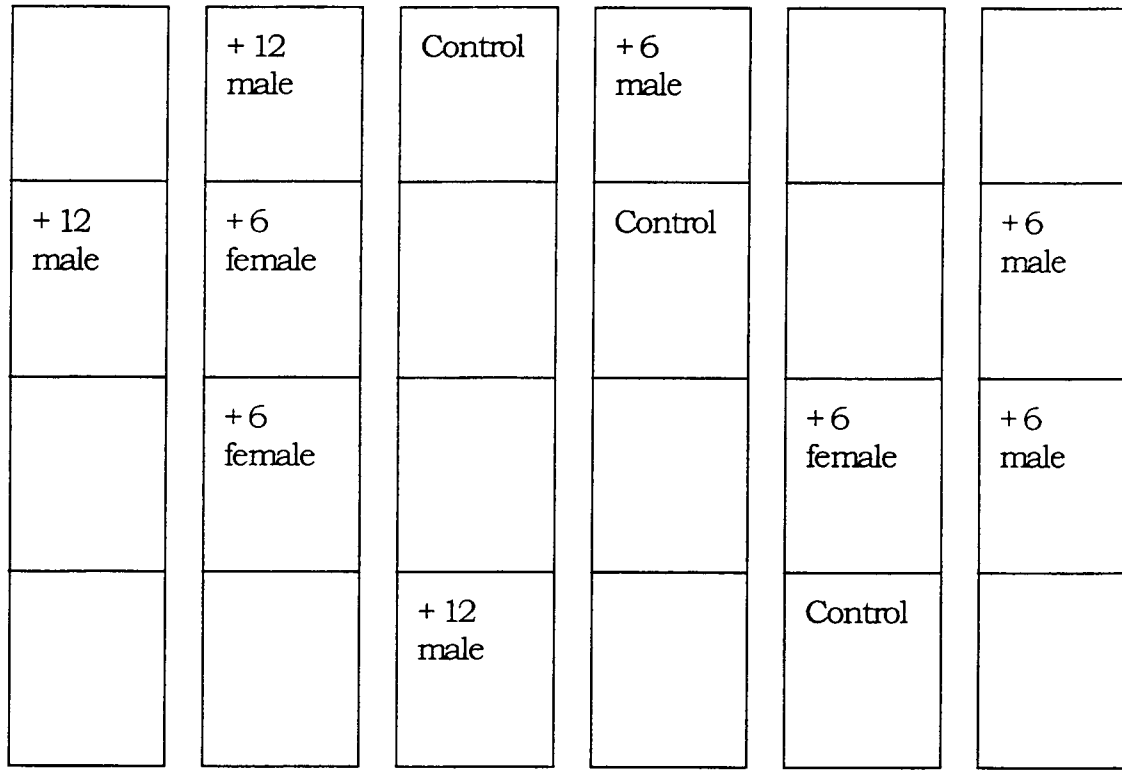

Figure 1. Schematic diagram of the experimental design, including spatial location of control, +6 male, +12 male, and +6 female treatment enclosures, used to study pregnancy disruption and infanticide at Hyslop Field Laboratory, Benton County, OR 1996.

General Protocol

Strangers were introduced into the treatment enclosures in a regular pattern to allow all of the resident females the same chance of being exposed to unfamiliar individuals. To obtain an estimate of exposure of resident females to new males and females in the respective treatments, the space used by introduced males and

females was estimated by plotting their two most distant points of capture. This distance was used as an approximate diameter of a home range and represented a conservative estimate. These home range estimates were mapped on a grid sheet overlapping the home ranges of resident females. Home ranges of resident females were estimated by plotting capture locations on the grid sheet and then connecting the outermost points to form a convex home range area estimate. The mean number of strange males and strange females that had home ranges that overlapped those of resident females was used as an estimate of the minimum number of unfamiliar males and females in the respective treatments to which a resident female was exposed each trap period. Each resident female in the treatment enclosures was exposed to a minimum of one stranger per trapping period.

If a removal animal was not captured during the designated trapping period, it was removed during the next trapping period. However, unfamiliar individuals were introduced regardless of trapping success so resident females were exposed to new individuals every 10 days. Any nests found in or near a trap, or inside a trap cover were noted; if unweaned pups were present, they were counted and then returned to their nest. To maintain stable densities across all of the enclosures, juveniles were removed when they were trapped.

Twenty of the original resident females that were found dead or were not recaptured during the second trapping period were replaced by new virgin females the second or third trapping period. The measurement of days to the first successful parturition for these new females was adjusted by counting from the day of their introduction to the first observed birth to account for their late introductions. Because these females were not present for the duration of the experiment, they were excluded from the analysis of number of pregnancies per female. Females found dead or not recaptured during and after the third trapping period were not replaced to avoid variation throughout the treatments and control.

DATA ANALYSIS

To determine if pregnancy disruption and infanticide were caused by the exposure of females to strangers, several parameters were measured, but not all resident females were included in all of the analyses. Twenty-five females were excluded from the study due to either death or absence of recaptures. Females not captured during three consecutive trapping periods were excluded from certain analyses depending on when the absence occurred. If a female was not trapped for the first few weeks after her introduction and then was lactating when she was first captured, the date of her first parturition could not be determined and therefore she was excluded from the analysis of days to first parturition as well as the analysis that involved determining the days between the first and second parturitions (see Appendix F for complete information on subsamples). Fifty-one and nine females were observed during their third and fourth parturitions, respectively. The small number of observed parturitions near the end of the study may be attributed to the duration of the experiment which may not have been long enough for some females to successfully reproduce three or four times, or, to the absence of females due to their death or nursing of a previous litter.

The date of a parturition was estimated by counting the number of days from the female's introduction into the enclosure to either (1) the exact date of the birth if it occurred during a trapping period, or (2) an estimated date of birth if it occurred between two trapping periods (day four of the seven day non-trapping period). The percent of parturitions followed by lactation was calculated using females in which the parturition date was known and the female was caught at least once during two subsequent trapping periods so her lactation status could be assessed. Only females that were trapped at least once during each of six trap periods were used in the analysis of number of pregnancies per female (see Appendix F). Observable pregnancies during the last trapping period were included in the analysis of total number of pregnancies per female. The number of juveniles recruited per parturition included every neonate and juvenile that was captured during the last 12 weeks of the experiment.

The experiment was conducted using a completely randomized design with fixed effects. One-way analysis of variance F-tests with least significant difference mean separation tests were conducted using Statistical Analysis System (SAS, version 6.11, ©1989-1995) or SYSTAT (version 5.2.1, ©1990-1992). The alpha level was set at 0.05 a-priori. In the analysis of intervals between parturitions the possible correlation associated with repeatedly measuring a subject was

accounted for by including time as a dependent factor. Proportional data, such as that used in the percent of females lactating after parturition, were arc-sine square-root transformed for analysis. The N-value for all analyses was three which was the number of replicate enclosures for each treatment.

RESULTS

If the results obtained from previous laboratory studies (see Appendix G) were indeed correct and observable in the field, then treatment females should have consistently longer intervals between births, fewer successful reproductive events, a lower percent of births followed by lactation, and fewer juveniles recruited per parturition in comparison with resident females in control enclosures. However, the results from this study do not indicate a cause and effect relationship between the introduction of strangers into a resident population and a decrease in reproductive fitness of resident females.

Every 3-day trap period, 65-100% (usually >80%) of the animals were caught. Of the 146 original resident females, 111 (76.0%) survived through the end of the experiment. Female survival rates ranged from 69.4% in the +6 male treatment to 88.9% in the control. Of the 80 original resident males in the control, +6 male and +6 female treatments, 56 (70%) survived through the end of the experiment. Resident male survival rates varied from 30.4% in the +6 male treatment to 76.2% in the +6 female treatment. Animals that were not caught during the last two trapping periods were presumed dead.

Pregnancy Disruption

To determine the average number of days to the first parturition, and between the first and second, second and third, and third and fourth parturitions, 140, 122, 51, and nine females, respectively, were used in the analysis. An analysis of variance (see Appendix A) indicated that the number of days between successive parturition intervals did not vary significantly among the control and three treatments ($F_{3,32} = 0.86$, $P = 0.47$; Fig. 2) However, there was a time by treatment interaction ($F_{9,32} = 2.74$, $P = 0.02$; Fig. 2). The mean number of days to first parturition ranged from 29.53 (S.D.= ± 3.23) in the control to 36.90 (S.D.= ± 4.84) days in the +12 male treatment (Fig. 2). The days between the first and second parturition ranged from 25.7 (S.D.= ± 1.75) in the +6 female treatment to 28.25 (S.D.= ± 3.68) in the +12 male treatment (Fig. 2). The days between the second and third parturition ranged from 21.67 (S.D.= ± 1.15) in the +12 male treatment to 24.02 (S.D.= ± 1.29) in the +6 female treatment (Fig. 2). Only nine females were used to calculate the days between the third and fourth parturition so variation could not be estimated in two of the treatments. The interval ranged from 21.00 in the +6 male and +12 male treatments to 23.50 (S.D.= ± 3.54) days in the control and +6 female treatment (Fig. 2).

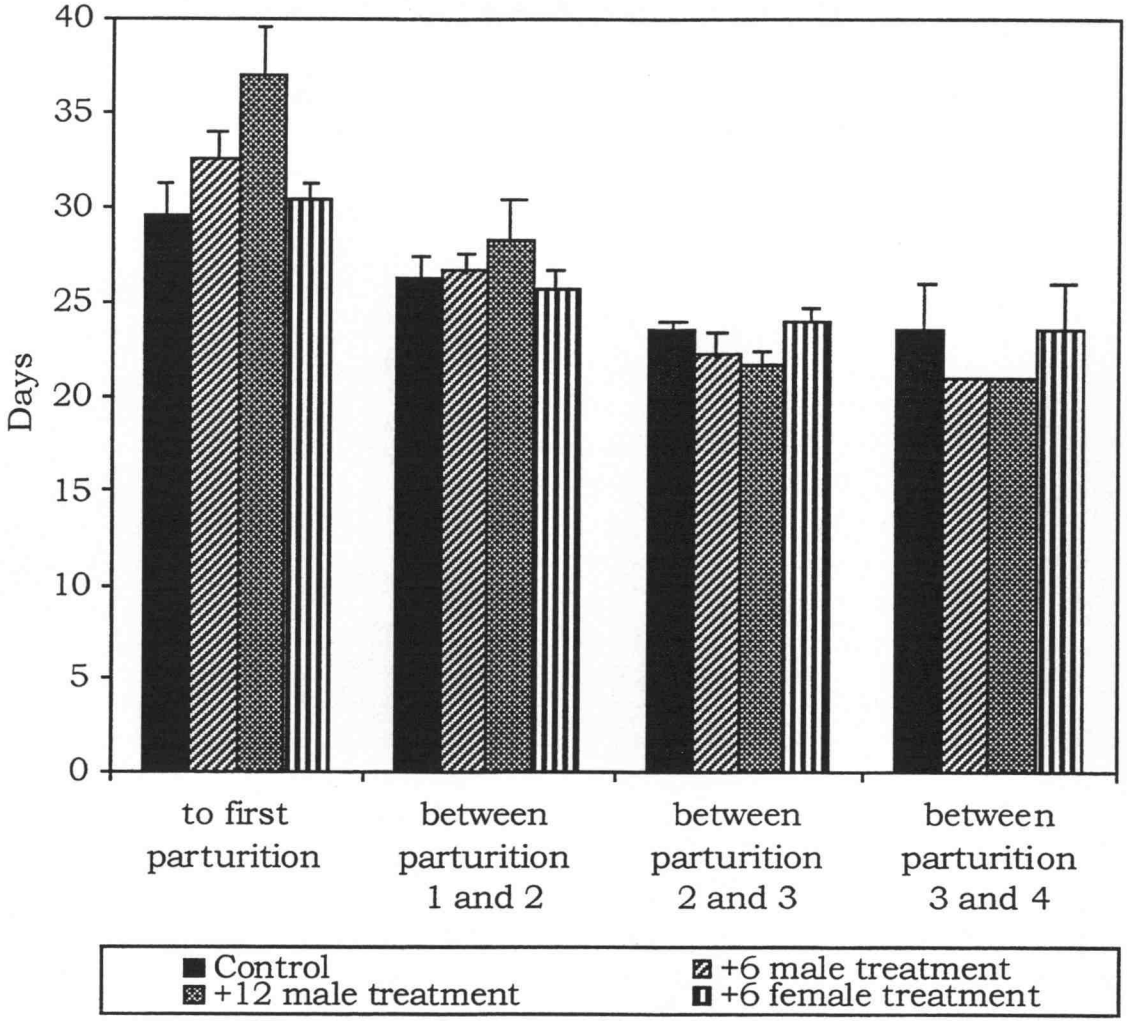

Figure 2. Intervals between parturitions (+1 SE) in resident female gray-tailed voles in control (N = 3), +6 male (N = 3), +12 male (N = 3), and +6 female (N = 3) treatments at Hyslop Field Laboratory, Benton County, OR 1996.

The average number of pregnancies per female was determined for 96 females. The mean number of pregnancies per female ranged from 2.39 (S.D.= ± 0.17) in the +12 male treatment to 3.14 (S.D.= ± 0.14) in the control. The analysis of variance

(see Appendix B) indicated that the number of pregnancies per female varied significantly among the control and three treatments ($F_{3,8} = 4.47$, $P = 0.04$; Fig. 3). The least significant difference mean separation test indicated that the number of pregnancies per female in the +12 male treatment was significantly different from the other two treatments and the control.

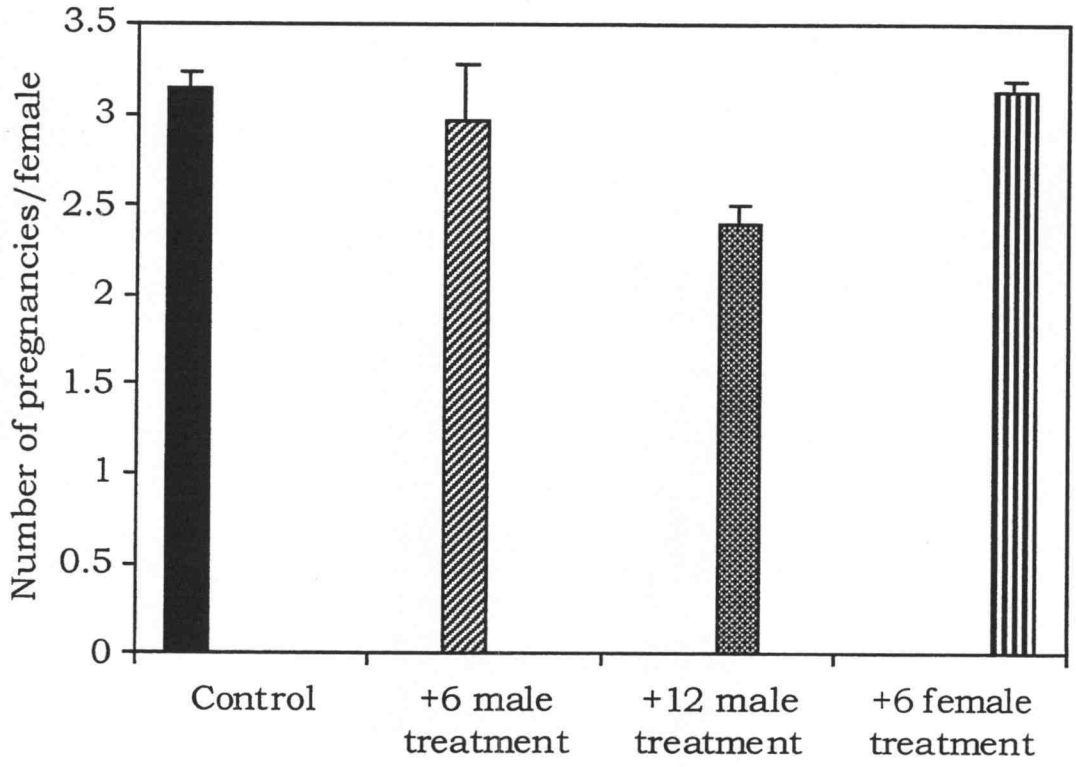

Figure 3. Number of pregnancies (+1 SE) per female in resident female gray-tailed voles in control (N = 3), +6 male (N = 3), +12 male (N = 3), and +6 female (N = 3) treatments at Hyslop Field Laboratory, Benton County, OR 1996.

Infanticide

The average number of births that were followed by lactation was determined for 139 females and 273 births. The mean percent of births followed by lactation ranged from 86.1% (S.D.= ± 0.08) in the +12 male treatment to 93.9% (S.D.= ± 0.05) in the +6 male treatment and did not differ significantly among the treatments and control ($F_{3,8} = 0.55$, $P = 0.66$; Fig. 4; see Appendix C for ANOVA table).

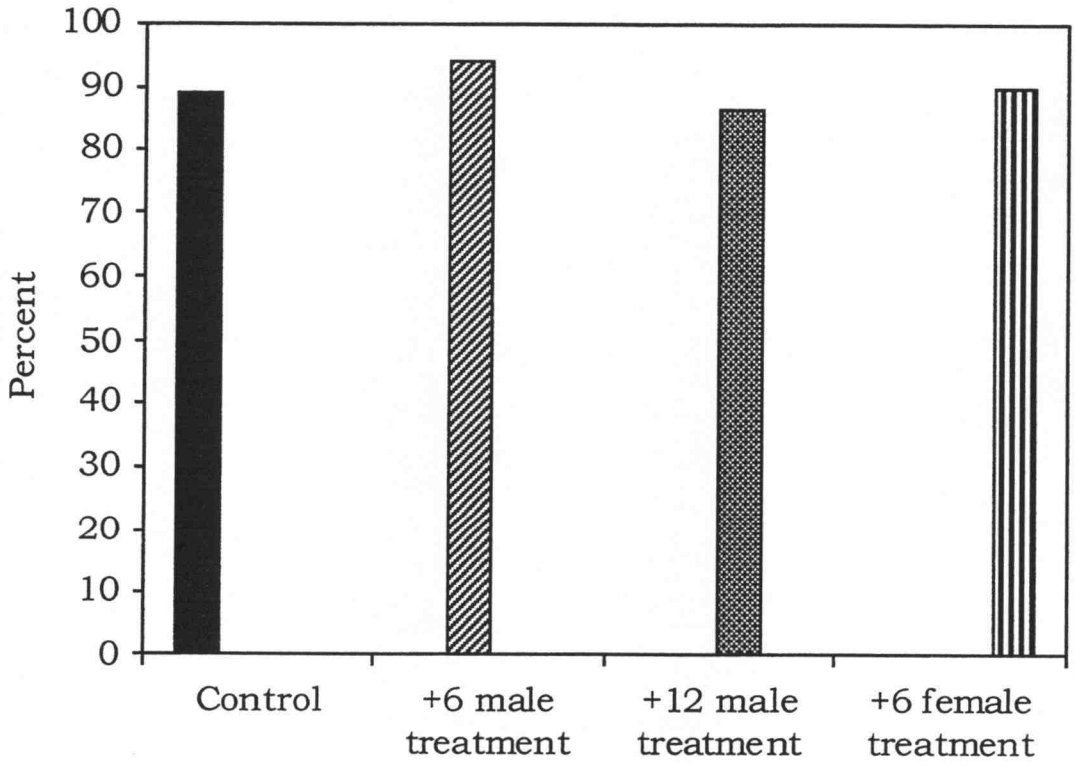

Figure 4. Percent of parturitions followed by lactation in resident female gray-tailed voles in control (N = 3), +6 male (N = 3), +12 male (N = 3), and +6 female (N = 3) treatments at Hyslop Field Laboratory, Benton County, OR 1996.

A total of 973 juveniles were caught from 355 births from 163 females during the 14-week experiment. The mean number of juveniles recruited per parturition ranged from 2.56 (S.D.= ± 0.77) in the control to 3.29 (S.D.= ± 0.39) in the +6 male treatment and did not differ significantly among the treatments and control ($F_{3,8} = 0.94$, $P = 0.46$; Fig. 5; see Appendix D for ANOVA table).

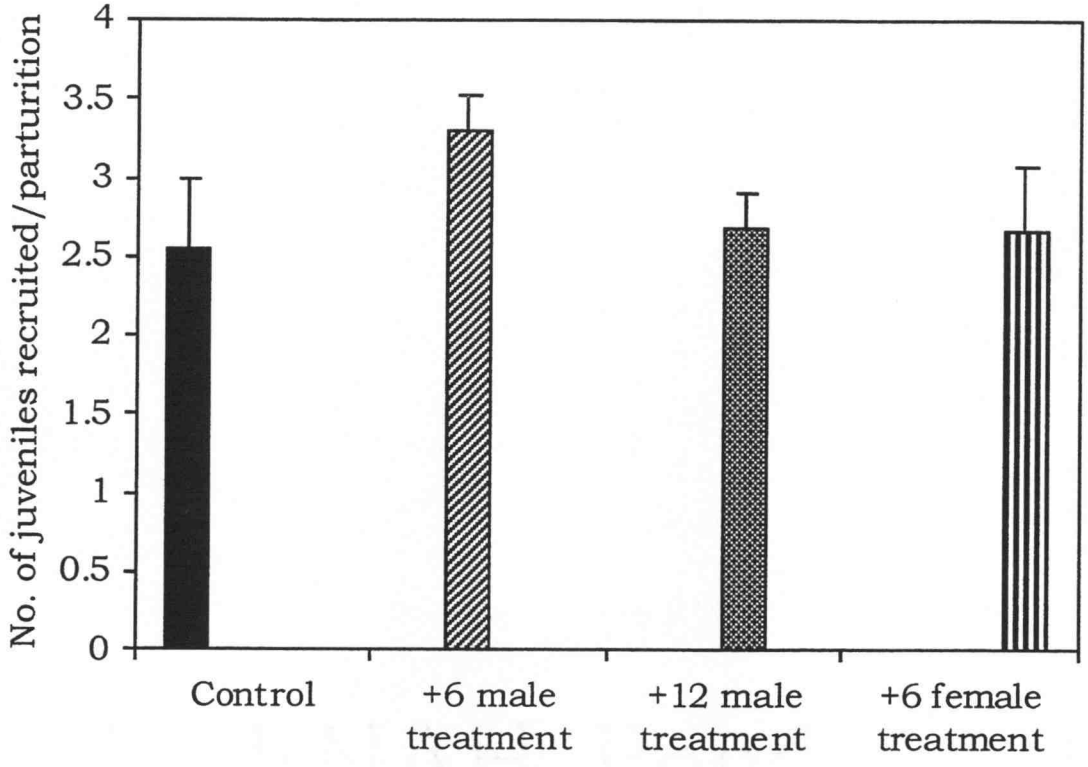

Figure 5. Number of juveniles recruited per parturition (+1 SE) in gray-tailed vole populations in control (N = 3), +6 male (N = 3), +12 male (N = 3), and +6 female (N = 3) treatment conditions at Hyslop Field Laboratory, Benton County, OR 1996.

DISCUSSION

The main objective of this study was to determine if the introduction of strangers into a resident population caused pregnancy disruption and infanticide. Field tests with three treatments involving introduction of strangers at regular intervals analyzed with analysis of variance tests with least significant difference pairwise comparisons indicated that no statistically significant differences existed among the treatments and the control in the mean days to first parturition, intervals between subsequent parturitions, percent of births followed by lactation, and in the number of juveniles recruited per parturition. The mean number of pregnancies per female was the only parameter that was statistically significant.

The variation in survival rates among the control and treatment females may have resulted from the additional disturbance (other than trapping) of removing and replacing individuals from the population. There are two possible explanations for the variation in male survival rates. First, males are more likely than females to lose their ear-tags. Although every effort was made to identify a re-tagged animal, the introduction of six males into the +6 male treatment every 10 days potentially obscured positive identification. Another possible explanation for the decreased survival rate in the treatment

enclosure is that resident males were exposed to competition every 10 days with the introduction of the six new males. Both resident and new males may have been killed in their possibly competitive encounters for access to resources (food and females).

Response to Strange Males

Pregnancy Disruption

If pregnancy disruption had occurred differentially among the treatments and the control in this field experiment, the results should have been similar to previous laboratory findings in which the average rate of pregnancy disruption in nulliparous *Microtus* in 17 experimental treatments was 65% (see Appendix G). The results obtained from the present study, however, contradict the conclusions of numerous laboratory studies (e.g. Chipman and Fox, 1966; Stehn and Richmond, 1975; Heske, 1987) because measured parameters that could have indicated high rates of pregnancy disruption did not show biological significance.

However, the results do indicate two parameters that indicate low rates of pregnancy disruption in the +12 male treatment enclosures. The mean time to first parturition for females in the +12 male treatment was 7 days later than in the control. This difference was due primarily to four of the 38 (11%) females that did not give birth until 56 days after their introduction. In the control enclosures, all females gave birth within 45 days of their introduction. The four females may have skewed the +12 male treatment mean distribution. Similarly, two (6%) other females of the 32 total in the +12 male treatment had a 51 day interval between their first and second

parturitions. These six females may have undergone pregnancy disruption. However, compared to the average Microtus pregnancy disruption rate derived from laboratory studies (65%, see Appendix G), the pregnancy disruption rate (6 of 70 pregnancies = 9%) observed in the +12 male treatment was small. Since the potentially observable effects of stranger introduction are large, within each enclosure that had an average of 12 resident females, there was an 85% chance of observing the pregnancy disruption effect (based on 28% pregnancy disruption rate from Bruce, 1959) (see power analysis (Keppel, 1973; Thomas, 1997) computation in Appendix E). Additionally, if pregnancy disruption were indeed a natural and consistent behavior that females underwent after exposure to strange males, the subsequent intervals between successful reproductive events would have followed a consistent trend throughout the duration of the experiment with the +12 male resident females having long intervals between parturitions, the +6 male treatment females having relatively shorter intervals, and the resident females in the control enclosures having consistent 21-day intervals. The findings from this field experiment do not indicate these results.

Additionally, in natural rodent populations, approximately a 10% turnover occurs every two weeks (Taitt and Krebs, 1985; Stenseth and Lidicker, 1992). Therefore, the +12 male treatment which had 100%

male turnover every 10 days, was an extreme situation which may have led to stress and abnormal physiological processes. Even the +6 male and +6 female treatment enclosures represented high levels of emigration and immigration or (50% male or female/ 10 days).

The mean number of pregnancies per female varied significantly among the control and the treatments. The difference was due to a lower mean of pregnancies per female in the +12 male treatment (2.39) than in the other two treatments or control (2.97-3.14). Two factors could have contributed to this difference. The four females that did not give birth until 56 days after introduction and two females that had an interbirth interval of 51 days between the first and second parturition skewed the +12 male treatment mean toward the lower number. The possibility that these six females exhibited pregnancy disruption cannot be dismissed.

A second factor contributing to the differences in total pregnancies was that the experiment was terminated when many of the females were in the early stages of their third or fourth pregnancy and thus pregnancy could not be detected visually. When analysis was conducted on the mean number of pregnancies for the first 12 weeks of the study, the means ranged from 1.97 in the +12 male treatment to 2.48 in the +6 female treatment and did not vary significantly among the treatments and controls ($F_{3,8} = 2.34$, $P = .15$).

The results from the present field study indicate that the laboratory-derived hypothesis that the introduction of strange males into a resident population causes pregnancy disruption should be questioned for natural populations. A possible explanation for the results indicating that pregnancy disruption does not occur at high rates in a field population of *Microtus* found in this field experiment is that the laboratory environment in previous studies may not have adequately represented natural conditions. As previously noted, all of the aforementioned experiments in which pregnancy disruption was observed in females upon exposure to strange males, except two, were in a laboratory setting. The exceptions took place in "semi-natural" conditions but with limited space (1.25 x 3 m, Heske and Nelson, 1984; Heske, 1987). The laboratory environment is limited in that it fails to simulate natural conditions. Food and shelter are provided ad libitum and animals are housed in small cages. When a pregnant female is confined to a small (e.g. 20 x 40 cm) cage, and a strange male is introduced, neither individual can escape or avoid the other animal. Pregnancy disruption may simply be an artifact of unusual and stressful conditions imposed on the female that would not occur in her natural environment. Chipman and Fox (1966) conducted laboratory experiments with *Mus musculus* in which some pregnant females were exposed to a strange male for five days post-coitum and others were transferred to

clean cages and excited (blown on until they urinated) on day 1 and day 5 post-coitum. Females exposed to strange males experienced an 85% rate of pregnancy disruption and the females that were merely disturbed experienced an 88% rate of pregnancy disruption (see Appendix G for details of study). Therefore the argument that pregnancy disruption in the presence of strange males is an adaptation (Schwagmeyer, 1979; Labov, 1981; Storey, 1994) may be premature and simply a misinterpretation of how selective pressures operate on male and female reproduction.

The experimental environment of this field study was more representative of natural conditions than previous laboratory studies. Food and shelter were not artificially provided. Resident females established their own burrows in the field and had access to resources, such as food and water, within their own home ranges. These experiments were conducted in an area that allowed for approximately 12 intra-sexually non-overlapping home ranges with respect to a typical wild gray-tailed vole home range (135 to 253 m^2, Wolff et al., 1996). This large area allowed animals to move freely throughout their home ranges and burrows and to avoid adverse conditions.

Although pregnancy disruption has not been tested specifically in the gray-tailed vole in laboratory conditions, the study species should not respond differently from the eight other species of

Arvicoline rodents in which pregnancy disruption has been reported (see refs. above and Appendix G). Gray-tailed voles have a promiscuous mating system which may decrease their propensity to experience pregnancy disruption. In the laboratory, polygamous species (Milligan, 1976; Storey, 1986) may show lower rates of pregnancy disruption than monogamous species (Stehn and Richmond, 1975; Schadler, 1981). However, Heske (1987) studied *Microtus californicus*, a polygamous species, and found pregnancy disruption rates as high as 90% (see Appendix G for more results). Therefore, the gray-tailed vole should experience similar rates of pregnancy disruption in the field if the Bruce Effect phenomenon is indeed a natural reproductive behavior. The results from this field study indicate that pregnancy disruption observed in previous studies may be a laboratory artifact that does not occur in field situations. Further field investigations are necessary to validate this hypothesis. Recently, Wolff and Davis-Born (in press) demonstrated that gray-tailed voles do not exhibit risk avoidance behavior in the field as hypothesized based on laboratory studies (Ylönen, 1989, Koskela et al., 1996). Results from the Wolff and Davis-Born study, as well as those from the present study indicate that results derived from laboratory studies may indeed be biased due to artificial laboratory conditions.

Infanticide

If males had committed infanticide to gain access to reproductive females, as has been suggested by previous literature (Hrdy, 1979), then the rates of infanticide should have been comparatively high in the +6 male treatment and even higher in the +12 male treatment. The fact that the mean number of juveniles recruited into the population per birth was 2.69 and 3.29, respectively, compared to 2.80 for the control suggests that infanticide did not occur differentially when females were exposed to strangers as opposed to their sire males. The high proportion (86.1-93.9%) of females lactating after birth also indicates that litters were not being killed by strange males. Thus, using this experimental design, no indication exists that exposure to strange males made neonates more vulnerable to infanticide than those in unmanipulated populations in which dams and sire males were left in place. Two possible explanations for these results are: (1) *Microtus* experience post-partum estrus, and (2) multiple-male mating may result in paternity confusion. Both of these factors may mitigate infanticide.

Gray-tailed voles, as well as many other rodent species (Seabloom, 1985), exhibit post-partum estrus. Thus, a female can breed within 24 hours after giving birth, consequently, infanticide does not necessarily give a male access to a reproductive female

because she can simultaneously lactate and be pregnant. Therefore, infanticide will increase a male's reproductive fitness only if pregnancy disruption occurs in the female in conjunction with the infanticide.

The second possible explanation for the results that indicate no treatment effect for male infanticide is that females may defend against male infanticide by confusing paternity. A female may confuse paternity by mating promiscuously with all the males in her home range to assure that these males have copulated. Several authors (Labov, 1980; vom Saal and Howard, 1982; Mennella and Moltz, 1988; Perrigo et al., 1992; Wilson et al., 1993) found that recent copulatory experience mitigated the tendency for males to commit infanticide. Wolff and Cicirello (1989) found that male infanticide is most common in immigrating males and in resident males that had not sired offspring. If a male has copulated, chances are that his young will be present within his home range; if he disperses elsewhere, however, he will probably not have sired any litters in this area, and therefore infanticide in this new area will not detrimentally affect his own inclusive fitness. Duration of general inhibition of infanticide that results from copulatory experience coincides with when the male's own young would be most vulnerable to infanticide. Inhibition may last between 30 days (Wolff and Cicirello, 1991) and 50-60 days post-coitum (Mennella and Moltz, 1988; Soroker and

Terkel, 1988; Perrigo et al., 1992), which in most rodents coincides with the post-weaning stage when young are no longer vulnerable to infanticide.

If a general inhibition of infanticide results after copulation, then multi-male mating by a female within her home range causes paternity confusion as well as copulatory experience for the males and consequently should decrease their propensity for committing infanticide in that area (Labov et al., 1985; Wolff and Packer, in prep; Agrell et al. in prep). Therefore, the female's association with multiple males in her home range may facilitate the safety of her offspring. Males in promiscuous mating systems copulate throughout the breeding season and therefore infanticide may be effectively eliminated from populations with promiscuous social systems.

Male gray-tailed voles that had cohabited with females, but had not copulated, were observed to commit infanticide in the laboratory (Davis-Born, 1997). Therefore, this species apparently will kill young in some circumstances, however, under the conditions of this field experiment, the results do not indicate that it occurred differentially (if infanticide occurred at all) when pups were exposed to strange males. In that gray-tailed voles are likely promiscuous, as has been shown for many rodents (Fitzgerald and Madison, 1983; Madison, 1980; Jeppson, 1986), introduced males may have had sufficient mating experience to inhibit infanticide even in their new

surroundings (Wolff and Packer, in prep). Therefore, multi-male mating by females may assure mating experience among males and thus reduce the tendency for males to commit infanticide. This hypothesis is consistent with the results from this field study.

Response to Strange Females

Pregnancy Disruption

The studies that have been conducted on pregnancy disruption in the past have been concerned mostly with the effects on a pregnant female of introducing a strange male, but not a strange female. This field study tested the introduction of strange females to a resident population to determine if the Bruce Effect-type pregnancy disruption is specifically caused by strange males or if the introduction of any stranger can cause pregnancy disruption. No significant differences were found between the control and the +6 female treatment in the length of intervals between parturitions and in the number of pregnancies per female. Therefore, the results indicate that pregnancy disruption rates did not increase when strange females were introduced into a resident population. These results are consistent with the hypothesis presented.

Infanticide

Previous literature has indicated that infanticide is a relatively common adaptive behavior in the wild for female mammals (Hausfater and Hrdy, 1984; Parmigiani and vom Saal, 1994). Females may commit infanticide to use the young as a food source or to attain resources being used by a lactating female. The former condition probably does not apply to this experiment because the medium densities (120 voles/ha) maintained in the enclosures assured plenty of food and space for every individual. Also, previous field studies on infanticide in mice and voles rarely have reported associated cannibalism. At the density used in this study, resource competition probably was not a driving force in the animals' behavior. If females had been competing for resources and committing infanticide to gain access to nesting sites, the +6 female treatment would have experienced more infanticide than the control because of its higher female:male ratio (90:30/ha) (Agrell et al., in prep). If the voles had been at higher densities, high rates of infanticide might have become prevalent due to a lower proportion of resources per female. No evidence has been found for density-dependent infanticide in several studies (*Microtus:* Boonstra, 1980; Caley and Boutin, 1985; *Peromyscus:* Wolff and Cicirello, 1991). However, gender-biased density dependence may exist because Wolff and Schauber (1996)

found that at very high densities (>2000 voles/ ha), pregnancy rates (86-98%) did not decline, but juvenile recruitment was inversely related to the number of unrelated females in a patch, but independent of male density. This result suggests that under extreme field conditions, females might commit infanticide more so than males.

Wild populations of gray-tailed voles probably do not experience infanticide due to resource competition unless populations reach unusually high densities (Wolff and Schauber, 1996). Under natural circumstances, however, if females commit infanticide to gain access to resources, and yet resources are rarely scarce, then female infanticide is probably not a persistent pressure to which pregnant females need to adapt. Therefore, low rates of infanticide may also explain why pregnant females exposed to strange females do not undergo pregnancy disruption. If the risk of infanticide is low, then pregnancy disruption upon exposure to a strange female would be reproductively costly and inefficient. Therefore, pregnant females exposed to unfamiliar females should not experience increased rates of pregnancy disruption or infanticide, which is consistent with the results from this study.

Biological Significance

The results from the present study indicate that in a field population of gray-tailed voles, resident females exposed to unfamiliar males and females do not undergo high rates of pregnancy disruption and resident young are not exposed to high rates of infanticide relative to a stable control population in which dams and sire males are retained. Due to the numerous laboratory studies with at least 12 species of rodents that demonstrated pregnancy disruption, hypotheses have been proposed to explain the adaptive significance of this behavior (Schwagmeyer, 1979; Labov, 1981; Storey, 1994). The most prevalent hypothesis is that females supposedly optimize their fitness by aborting a litter during early development if the threat of infanticide by an intruding individual is high enough to decrease the chance of her young surviving once they are born. If, in fact, infanticide were common and pregnancy disruption occurred in the wild as demonstrated in the laboratory, this hypothesis would be feasible and perhaps evolutionarily stable. However, if infanticide commonly occurs in wild populations, females may engage in multi-male mating to confuse paternity and thus reduce the chances of infanticide and losing young. Thus, the behavioral tactics of females may be counter-strategies to those of males.

In the present study, which is the first experimental field study conducted on pregnancy disruption, neither pregnancy disruption nor

infanticide occurred as predicted from laboratory studies. Rodents, such as voles, have relatively short lifespans and if a female were to abort her young every time she met or smelled a strange individual, her reproduction would frequently be disrupted and her fitness would be low. A female vole's reproductive behavior is likely the result of an historical evolutionary risk-assessment and a trade-off in the evolutionary arms race which allows her to assess and respond to her ecological, demographic and behavioral environment.

CONCLUSIONS

Under the conditions of this field study, no biologically significant evidence was found that pregnancy disruption or infanticide occurred differentially among the control and three treatments of gray-tailed vole removal and replacement. The results from this single experimental field study may not be sufficient to negate the results of numerous laboratory studies conducted on the proximate causes of pregnancy disruption and infanticide. However, the results of this study do suggest that the laboratory may not adequately represent a natural environment that would be appropriate for testing hypotheses on reproductive behaviors because of the limited space and artificially high densities common in laboratory conditions.

If laboratory studies are conducted, field tests should be used to assess the validity of the laboratory results prior to establishing hypotheses to explain the adaptive functions of behaviors that may be merely laboratory artifacts. Future research on pregnancy disruption, infanticide, and other reproductive behaviors should simulate natural conditions as closely as possible such that the results can be accurately extrapolated to wild populations.

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APPENDICES

Model: Days = Constant + Treat + Interval + Treat x Interval

Four "Treat" levels.
Four "Interval" levels.

Analysis of Variance

Source	Sum-of-squares	DF	Mean Square	F-Ratio	P
Treat	13.059228	3	4.353076	0.864666	0.469457
Interval	781.15783	3	260.38594	51.721339	0.0000000
Treat x Interval	124.00961	9	13.778845	2.736939	0.017194
Error	161.10082	32	5.034401		

Appendix A. Statistical output from an analysis of variance on the number of days between successive reproductive events in gray-tailed vole populations in control, +6 male, +12 male, and +6 female treatment conditions at Hyslop Field Laboratory, Benton County, OR 1996.

Model: Number of pregnancies/ female = Constant + Treat

Four "Treat" levels

Analysis of Variance

Source	Sum-of-squares	DF	Mean Square	F-Ratio	P
Treat	1.1069689	3	0.3689896	4.47	0.0401
Error	0.6600128	8	0.0825016		
Corrected Total	1.7669817	11			

R-Square: 0.626474
Root MSE: 0.28723091
Number of pregnancies/ female Mean: 2.90618261

T tests (LSD) for variable: NU.PREG

Note: This test controls the type I comparisonwise error rate not the experimentwise error rate.

Alpha = 0.05, df = 8, MSE = 0.082502
Critical Value of T = 2.31; Least Significant Difference = 0.5408

Means with the same letter are not significantly different.

T Grouping	Mean	N	Treat
A	3.1369	3	control
A	3.1250	3	+6 female
A	2.9702	3	+6 male
B	2.3926	3	+12 male

Appendix B. Statistical output from an analysis of variance on the number of pregnancies per female in gray-tailed vole populations in control, +6 male, +12 male, and +6 female treatment conditions at Hyslop Field Laboratory, Benton County, OR 1996.

Model:
Proportion of pregnancies followed by lactation = Constant + Treat

Four "Treat" levels

Analysis of Variance

Source	Sum-of-squares	DF	Mean Square	F-Ratio	P
Treat	0.0094682	3	0.0031561	0.55	.6613
Error	0.0457835	8	0.0057229		
Corrected Total	0.0552517	11			

R-Square: 0.171365
Root MSE: 0.07565008
Proportion of pregnancies followed by lactation Mean: 0.8980798

T tests (LSD) for variable: LACT

Note: This test controls the type I comparisonwise error rate not the experimentwise error rate.

Alpha = 0.05, df = 8, MSE = 0.005723
Critical Value of T = 2.31; Least Significant Difference = 0.1424

Means with the same letter are not significantly different.

T Grouping	Mean	N	Treat
A	0.93939	3	+6 male
A	0.90028	3	+6 female
A	0.89175	3	control
A	0.86061	3	+12 male

Appendix C. Statistical output from an analysis of variance on the proportion of pregnancies followed by lactation in gray-tailed vole populations in control, +6 male, +12 male, and +6 female treatment conditions at Hyslop Field Laboratory, Benton County, OR 1996.

Model: Number of young per parturition = Constant + Treat

Four "Treat" levels

Analysis of Variance

Source	Sum-of-squares	DF	Mean Square	F-Ratio	P
Treat	0.9909417	3	0.3303139	0.94	0.4643
Error	2.8039369	8	0.3504921		
Corrected Total	3.7948786	11			

R-Square: 0.261126
Root MSE: 0.592024
Number of young per parturition Mean: 2.798345

T tests (LSD) for variable: BABIRTH

Note: This test controls the type I comparisonwise error rate not the experimentwise error rate.

Alpha = 0.05, df = 8, MSE = 0.350492
Critical Value of T = 2.31; Least Significant Difference = 1.1147

Means with the same letter are not significantly different.

T Grouping	Mean	N	Treat
A	3.2888	3	+6 male
A	2.6873	3	+12 male
A	2.6611	3	+6 female
A	2.5562	3	control

Appendix D. Statistical output from an analysis of variance on the number of young per parturition in gray-tailed vole populations in control, +6 male, +12 male, and +6 female treatment conditions at Hyslop Field Laboratory, Benton County, OR 1996.

$$\phi^2 = \frac{s' [\Sigma (\mu_i - \mu)^2] / a}{\sigma^2}$$ (after Keppel, 1973)

ϕ = parameter used to determine power on specific table
s = sample size
μ = effect size
a = treatment conditions
σ^2 = variance

Degrees of freedom: Numerator = # of treatment conditions

: Denominator = a (s - 1)

For my study:
s = 12 (average number of females in 1 enclosure)
μ = 28%: low rate of pregnancy disruption observed in a previous (Thomas, 1997) laboratory study (Bruce, 1959).
28% of 12 = 3.36 (raw effect size)
a = 1 (because the effect size represents one 'treatment condition')
o^2 = 23.4256 (square of the standard deviation derived from the days to first parturition for resident females in the +12 male treatment from the present study)
df: Numerator = 1
df: Denominator = 1 (12 - 1) = 11

$$\phi^2 = \frac{12 [(3.36)^2] / 1}{23.4256} = 5.7832115$$

$$\sqrt{\phi^2} = \sqrt{5.7832115}$$

ϕ = 2.4048309 with df = 1,11 at alpha = 0.05

Power is 0.85 (there is an 85% chance that the effect will be observable with this sample size)

If a higher effect is used, such as 50% which is a more typical pregnancy rate in laboratory studies, **power** increases to **0.99**

Appendix E. Calculation of power analysis for the chance that a pregnancy disruption effect is observable in a +12 male treatment condition in a population of gray-tailed voles at Hyslop Field Laboratory, Benton County, OR 1996.

Appendix F. Raw numbers used for measurement parameters in gray-tailed vole populations in control, +6 male, +12 male, and +6 female treatment conditions at Hyslop Field Laboratory, Benton County OR 1996.

Treatment->	Control				+6 Male				+6 Female				+12 Male				Total
Parameters	8	10	13	Total	2	3	9	Total	7	18	19	Total	16	17	23	Total	Grand Total
Days to 1st Parturition (# of females used)	12	10	11	33	12	12	13	37	10	11	11	32	12	16	10	38	140
Days between 1st and 2nd Parturition (# of females used)	9	10	11	30	7	10	10	27	10	13	10	33	8	14	10	32	122
Days between 2nd and 3rd Parturition (# of females used)	4	5	7	16	0	2	4	6	6	9	6	21	2	2	4	8	51
Days between 3rd and 4th Parturition (# of females used)	0	1	2	3	0	2	1	3	1	1	0	2	0	0	1	1	9

Appendix F. Continued

Treatment->	Control				+6 Male				+6 Female				+12 Male				Total
Parameters	8	10	13	Total	2	3	9	Total	7	18	19	Total	16	17	23	Total	Grand Total
No. of pregnancies/ No. of females	23/ 7	27/ 9	25/ 8	75/ 24	19/ 8	23/ 7	26/ 8	68/ 23	25/ 8	26/ 8	15/ 5	66/ 21	20/ 9	24/ 10	23/ 9	67/ 28	276/ 96
No. of females/ No. of pregnancies/ No. followed by lactation	12/ 22/ 20	12/ 25/ 23	12/ 26/ 22	36/ 73/ 65	10/ 15/ 15	12/ 22/ 20	10/ 22/ 20	32/ 59/ 55	10/ 24/ 24	14/ 27/ 21	12/ 26/ 24	36/ 77/ 69	11/ 20/ 18	14/ 22/ 17	10/ 22/ 20	35/ 64/ 55	139/ 273/ 244
No. of births/ No. of juveniles recruited/ No. of females	25/ 86/ 12	35/ 74/ 13	35/ 74/ 14	95/ 234 / 39	21/ 67/ 12	26/ 77/ 12	28/ 104 / 13	75/ 248 / 37	30/ 81/ 13	36/ 69/ 15	30/ 101/ 14	96/ 251 /42	23/ 68/ 13	39/ 111/ 19	27/ 61/ 13	89/ 240 /45	355/ 973/ 163
No. of original females/ No. surviving/ No. found dead	12/ 9/ 0	12/ 12/ 0	12/ 11/ 1	36/ 32/ 1	12/ 10/ 0	12/ 7/ 0	12/ 8/ 1	36/ 25/ 1	13/ 8/ 0	12/ 10/ 0	12/ 8/ 0	37/ 26/ 0	14/ 9/ 0	12/ 10/ 0	11/ 9/ 1	37/ 28/ 1	146/ 111/ 3
No. of original males/ No. surviving/ No. found dead	12/ 10/ 0	12/ 12/ 0	12/ 11/ 0	24/ 33/ 0	8/ 2/ 0	8/ 3/ 0	7/ 2/ 0	23/ 7/ 0	6/ 5/0	8/ 5/ 0	7/ 6/ 0	21/ 16/ 0	NA	NA	NA	NA	80/ 56/ 0.
Females completely excluded from analysis	1	0	1	2	0	1	0	1	5	1	5	11	3	5	3	11	25

Appendix G. Species, author(s), date of publication, methodology, and results from a sample of laboratory studies on pregnancy disruption.

Species, Authors, Date	Methods	Results
Clethrionomys gapperi Clulow, Franchetto, and Langford; 1982	In treatments 1&2, nulliparous females were caged with stud males until coitus occurred. They remained together for 24 hrs., then either (a)the stud male was removed and the female remained undisturbed for 3 wks, (b) the stud male was removed and a strange male was introduced into the cage for 24 hrs., (c) the male and female were transferred to a clean cage, and the male was removed 24 hrs. later, or (d) the female and a strange male were transferred to a clean cage, and the strange male was removed 24 hrs. later. In treatment 3, parous females were caged with stud males until coitus occurred, immediately after either (e) the female and stud male were transferred to a clean cage, and the male was removed 24 hrs. later, or (f) the female and a strange male were transferred to a clean cage, and the male was removed 24 hrs. later.	PD[+] Rates: a) n=20, 30% b) n=20, 85% c) n=20, 80% d) n=20, 90% e) n=18, 67% f) n=19, 58%

[+] PD= pregnancy disruption

Appendix G. Continued.

Lagurus curtatus, *Microtus ochrogaster,* *M. montanus, Pitymys pinetorum* Stehn and Jannett; 1981	Females (age was not controlled for) were housed with a stud male. After coitus occurred, they remained housed together for 12 days. Then the females were exposed to one of 12 treatments. Stud or strange males remained for the rest of the experiment. (1) Nulliparous females that were not concurrently lactating. On Day 12 the stud male was removed and immediately replaced by a strange male. The females were handled every 12 hrs. (2) Same conditions as #1 except the stud male remained with the female. (3) Same conditions as #1 except the female was handled every 48 hrs. (4) Same conditions as #2 except the female was handled every 48 hrs. (5) Parous females that were not concurrently lactating. On Day 12 the stud male was removed and immediately replaced by a strange male. The females were handled every 12 hrs. (6) Same conditions as #5 except the stud male remained with the female. (7) Parous females that were concurrently lactating. On Day 12 the stud male was removed and immediately replaced by a strange male. The females were handled every 12 hrs. (8) Same conditions as #7 except the stud male remained with the female.	PD Rates: *M. ochrogaster* (strain 1): (strain 2) 1) n=48, 90% n=5, 80% 2) n=10, 0% 3) n=13, 69% n=6, 33% 4) n=6, 0% n=4, 0% 5) n=14, 57% 6) n=4, 0% 7) n=14, 64% 8) n=3, 0% *M. montanus* *L. curtatus* 3) n=22, 36% 3) n=8, 25% 4) n=13, 0% 4) n=11, 9% 9) n=12, 8% 9) n=5, 0% 10) n=12, 0% 10) n=2, 0% 11) n=13, 15% 11) n=9, 0% 12) n=2, 0% 12) n=2, 0% *P. pinetorum* 1) n=10, 40% 2) n=4, 0% 3) n=8, 25% 4) n=11, 9% (9) Same conditions as #5 except females were handled every 48 hrs. (10) Same conditions as (6) except females were handled every 48 hrs. (11) Same conditions as (7) except females were handled every 48 hrs. (12) Same conditions as (8) except females were handled every 48 hrs.

Appendix G. Continued.

Mice Gangrade and Dominic; 1984	Post-coitus: (1) an alien male was housed above the female (1 cm. separation between cages) for 3 days; (2) an alien male was housed below the female (1 cm. separation between cages) for 3 days; (3) females were separated from their stud males and left undisturbed in cages; (4) females were separated from their stud males and left undisturbed in corrals (bigger than cages)	PD rates: 1) n=54; 89% 2) n=47; 23% 3) n=25; 8% 4) n=26; 8%
Microtus agrestis Clulow and Clarke; 1968	Post-coitus, females were transferred to (1) a cage with the sire male, or (2) a cage with a strange male, for 24 hrs., and then the female was placed in isolation.	PS* rates: 1) n=20, 80% 2) n=20, 25%
Microtus brandti Stubbe and Janke; 1994	Females were paired with a male and after recognition of pregnancy occurred, females were paired with a strange male.	PD rates: 1) n=12, 50%

* PS= pregnancy success

Appendix G. Continued.

Microtus californicus Heske; 1987	Used "semi-natural" enclosures (1.25x3m) (1) original pair together day 1 through 40 (2) one female paired with one male, on day 10 male was removed, and a strange male was introduced, he was left through day 40; (3) one female paired with one male, on day 10 one strange male was added and left through day 40; (4) original pair together day 1 through 40 in a cage in the enclosure; (5) one female paired with one male in a cage in the enclosure, on day 10 sire male was removed and a strange male was introduced, he was left through day 40; (6) one female paired with one male in 2 enclosures connected by a corridor (to allow for 'dispersal'), on day 10 a strange male was added, day 13 the stranger was removed.	PS rates: 1) n=20; 40% 2) n=20; 10% 3) n=20; 15% 4) n=20; 50% 5) n=20; 10% 6) n=8; 25%
Microtus Ochrogaster Stehn and Richmond; 1975	Females were either (1) paired permanently with a male, or (2) paired with a male that was replaced with a strange male between days 5 through 19.	PD rates: 1) n=26, 15% 2) Strange male introduced between days 3-15 (n=49): 81%. Strange male introduced between days 16-17(n=12): 36%

Appendix G. Continued.

Microtus ochrogaster Heske and Nelson; 1984	Used "semi-natural" enclosures (1.25x3m) (1) original pair together day 1 through 40 (2) one female paired with one male, on day 10 male was removed, and a strange male was introduced, he was left through day 40; (3) one female paired with one male, on day 10 one strange male was added and left through day 40; (4) one female paired with one male in a cage in the enclosure, on day 10 sire male was removed and a strange male was introduced, he was left through day 40.	PS rates: 1) n=9; 89% 2) n=9; 11% 3) n=7; 27% 4) n=12; 0%
Microtus pennsylvanicus Clulow and Langford; 1971	Post-coitus, the female's cage was cleaned and then either (1) the sire male was reintroduced or (2) a strange male was introduced, for 24 hours, and then the female was placed in isolation.	PS rates: 1) n=20, 60% 2) n=20, 20% (but 3 of these mated with the new male)
Microtus pennsylvanicus Storey; 1986	Females were brought into estrus by being exposed to a male through a wire partition for 4 days. The females were either nulliparous or multiparous, and they were exposed to either: (1) female was transferred to a clean cage and the sire male was placed with her until Day 18, (2) female was removed from the original male on Day 4 and she was transferred to a clean cage with a new male, or (3) female was removed from the original male on Day 12 and she was transferred to a clean cage with a new male.	PS rates: Nulliparous: 1) n= 18, 100% 2) n=15, ~5% 3) n=15, ~55% Multiparous: 1) n=15, 100% 2) n=13, ~40% 3) n=12, ~40%

Appendix G. Continued.

Microtus pinetorum Schadler; 1981	Females were impregnated by males. When pregnancy was noted, they were exposed to either: (1) control- original stud male, (2) stud male was removed and an unrelated male was introduced day 10 post-insemination, (3) stud male was removed and an unrelated male was introduced day 15 post-insemination, (4) exposed to stud male for 10 days then female transferred to a clean cage, or (5) exposed to stud male for 10 days then female transferred to a cage soiled by a strange male.	PS rates: 1) n=25, 96% 2) n=33, 12% 3) n=15, 13% 4) n=10, 80% 5) n=30, 7%
Mus domesticus Drickamer; 1989	Post-coitus, the females were transferred to a cage with (1) clean bedding, (2) the sire male's bedding, or (3) a strange male's bedding, for 6 hrs. each of 6 days. Post-coitus, the females were placed into a preference apparatus once every day for 18 days. The choices were: (4) clean-clean bedding (control); (5) stud male vs. clean bedding; or (6) strange male vs. clean bedding.	PS rates 1) n=15, 93% 2) n=15, 87% 3) n=15, 47% Results for 4), 5), and 6) (n=25 for each): In the early stages of the pregnancy, the females prefer stud male vs. clean bedding; and prefer clean vs. strange male bedding. In the middle stages, the preference for stud male bedding decreases. At the end of the pregnancy, the females prefer the clean vs. stud/strange male bedding.

Appendix G. Continued.

Mus musculus Bruce; 1959	Following insemination (by albino males), albino females were isolated for 24 hrs., then exposed to either: (1) strange male or female (albino or wild type) for 24 hrs., or (2) housed in a stock cage on which other mice could climb on the outside of.	PD rates: 1) n=69, 28% (albino) n=35, 71% (wild-type) n=50, 26% (castrated albino) n=48, 0% (female) n=32, 0% (stud male) 2) n=32, 25% (albino males) n=68, 76% (wild-type males) n=49, 0% (females)
Mus musculus Chipman and Fox; 1966	After insemination, females were exposed to one of these treatments: (1) isolation in the stud male's cage days 0 through 7; (2) caged with a strange male days 1 through 5; (3) transferred to a clean cage on days 1 and 5; (4) transferred to a clean cage and 'excited' (blown on until urination) on days 1 and 5; (5) transferred to a clean cage on days 2 and 3 and excited on days 3 and 4; (6) transferred to a clean cage days 1 through 5; (7) cage contents disrupted 2 times/day by rolling cage 360° days 1 through 5.	PS rates: 1) n=50, 76% 2) n=50, 16% 3) n=75, 56% 4) n=25, 12% 5) n=25, 28% 6) n=25, 40% 7) n=25, 36%

Appendix G. Continued.

Mus musculus Bruce and Parkes; 1961	Pregnant lactating females were used after post-partum mating. After a vaginal plug was found, the stud male was removed. 1 day later, females were put into the test situation for 3 days. Females were either housed in a stock box alone (#2, 4, 6, 8) or with strange males (#1, 3, 5, 7). The females had either copious lactation (#1, 2) (nursing 6-8 young) or marginal lactation (#3, 4) (nursing 1-2 young) and the young remained with the female; or, limited suckling (#5, 6) (small litter: young were removed on Day 3 when she was exposed to the males) or, no suckling (#7, 8) (young removed at birth).	PD Rates: 1) n=20, 0% 2) n=17, 0% 3) n=11, 0% 4) n=14, 0% 5) n=19, 32% 6) n=18, 0% 7) n=34, 65% 8) n=34, 29%
Peromyscus maniculatus Bronson, Eleftheriou, and Dezell; 1969	Following insemination, females were exposed to either: (1) sire male removal, or (2) sire male removal and exposure to strange male for 48 hrs. in female's home cage. Female sacrificed 7 days after initial insemination.	Long-term results: Rate of implantation success: PS 1) n=248, 64%; 2) n=275, 24%

Appendix G. Continued.

Peromyscus maniculatus Eleftheriou, Bronson, and Zarrow; 1962	Virgin females were paired with a male. After copulation occurred, the stud male was removed and females were isolated for 24 hrs. in the original cage. The females were then exposed to experimental variables which included: (1) presence (for 24 hrs.) or absence of strange or stud male, (2) freedom or restriction of the male, and (3) size of cage. Females were autopsied 7 days post-insemination.	Treatment — PS rates in cage sizes (n=20 for each) small mdm. large Isolated 90% 60% 30% With stud male 60% 65% 50% W/ strange male 20% 15% 30% W/ empty holding cage 60% Moved to new quarters with empty holding cage 50%