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Exposure to strange adults does not cause pregnancy disruption or infanticide in the gray-tailed vole

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Abstract A widely accepted paradigm in mammalian behavioral biology is that exposure to unfamiliar males causes pregnancy disruption in female rodents (commonly known as the Bruce effect). This behavioral phenomenon has been demonstrated in the laboratory with at least 12 species of rodents, primarily within the genus *Microtus*, and is supposedly an adaptation that provides male perpetrators with reproductive access to females, and functions, for females, as a counterstrategy to infanticide. However, neither the Bruce effect nor its adaptive significance have been tested experimentally in the field. In a controlled field study, we exposed reproducing female gray-tailed voles (*Microtus canicaudus*) to treatments in which males were removed and replaced by either unfamiliar males or females, and found no significant differences in intervals between parturitions, number of pregnancies, and juvenile recruitment among the treatment and control animals. Thus, we conclude that neither the Bruce effect nor infanticide occurred differentially as a consequence of the treatments in gray-tailed voles. Multimale mating to confuse paternity, and postpartum estrus resulting in simultaneous pregnancy and lactation may deter infanticide and functionally negate any benefits of pregnancy disruption in gray-tailed voles and perhaps other murid rodents with similar mating systems. In light of our results, we recommend field verification for other species of murid rodents that exhibit the Bruce effect in the laboratory before the results are applied to evolutionary theory.

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Introduction

Behavioral strategies of males and females have evolved to maximize individual reproductive success (Darwin 1859; Dawkins 1976). The behavioral strategy that is most adaptive to one sex may not be adaptive for the other and consequently a given behavior which might be optimal in one sex might force a less than optimal counterstrategy against that behavior by the other sex (Wasser and Barash 1983). Two behaviors in rodents that purportedly have these characteristics are pregnancy disruption (Bruce 1959, 1960) and infanticide (Hrdy 1979). A form of pregnancy disruption, commonly known as the Bruce effect (Bruce 1960), has been reported in the laboratory for at least 12 species of rodents, including seven of the genus *Microtus* (*M. agrestis*: Clulow and Clarke 1968; Milligan 1976; *M. brandti*: Stubbe and Janke 1994; *M. californicus*: Heske 1987; *M. montanus*: Stehn and Jannett 1981; *M. ochrogaster*: Stehn and Richmond 1975; Kenney et al. 1977; Heske and Nelson 1984; *M. pennsylvanicus*: Clulow and Langford 1971; Storey and Snow 1987, 1990; Storey 1994; *M. pinetorum*: Schadler 1981; Stehn and Jannett 1981). In fact, this form of pregnancy disruption has been demonstrated in all *Microtus* species in which it has been tested. The basic design of these experiments is that a recently inseminated female is exposed directly to an unfamiliar male or indirectly to his odor (urine or bedding), which prevents implantation (e.g., *Mus*) or causes abortion or resorption of the female's embryos (*Microtus*). This response is supposedly adaptive for the male because he can then mate with the female when she returns to estrus. The benefits to the female are less clear, but if the strange male were to kill her offspring after parturition, the female could conserve reproductive effort by aborting her current litter and mating with the new male (Schwagmeyer 1979; Labov 1981; Storey 1994). Thus, the Bruce effect may have evolved in females as a counterstrategy to infanticide by males (Schwagmeyer 1979; Labov 1980, 1981; Huck 1984; Labov et al. 1985).

Most experimental studies that examined the Bruce effect (e.g. Bruce 1959; Chipman and Fox 1966; Clulow and Clarke 1968; Clulow and Langford 1971; Stehn and Richmond 1975; Storey 1986) have been conducted in the laboratory, with two exceptions (Heske and Nelson 1984; Heske 1987). Heske and Nelson (1984) and Heske (1987) used seminatural conditions in small enclosures (1.25 × 3 m) to study the Bruce effect in *M. ochrogaster* and *M. californicus*, respectively, and obtained results similar to those from laboratory studies. However, because the experimental enclosures were smaller than a vole's natural home range (3.75 m^2 compared to ~200 m^2; Heske and Nelson 1984), and because normal movements into and out of these restricted areas were prevented, these studies may not properly simulate natural conditions.

Mallory and Clulow (1977) report observational evidence of pregnancy disruption in the field. However, because their field methods were not experimental and they were not specifically testing the Bruce effect in the field, they were not able to establish a causative explanation for the pregnancy disruption which they found and, in fact, they do not specifically discuss exposure to unfamiliar males as a cause for the disruption. Instead, they hypothesize that pregnancy failure is a result of high density. Therefore, it is still not known whether pregnancy disruption specifically caused by the Bruce effect occurs in wild populations.

Infanticide committed by males has been observed in the laboratory in several species of rodents and provides reproductive opportunities to the perpetrators (e.g., 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). Infanticide of unweaned young will terminate lactation and return the female to estrus (Schwagmeyer 1979; vom Saal and Howard 1982; Packer and Pusey 1983; Elwood et al. 1990). The male can then successfully mate with the female sooner than if he had to wait for her to complete lactation and wean the litter. The role of infanticide in conjunction with pregnancy disruption in natural populations has not been verified or tested experimentally, and yet several authors have suggested that pregnancy disruption may be an evolutionary strategy to prevent infanticide (Schwagmeyer 1979; Labov 1981; Huck 1984).

The objective of our study was to test the hypothesis that exposure of reproducing female voles to unfamiliar males would cause pregnancy disruption thereby increasing the time to and interval between parturitions, and decreasing the number of successful pregnancies as well as the juvenile recruitment rate. We used the gray-tailed vole, *M. canicaudus*, as our behavioral model species to test for the Bruce effect. Gray-tailed voles are genetically similar to *M. montanus* and likely evolved from that species (Hsu and Johnson 1970; Tyser 1975). Gray-tailed voles also are behaviorally and ecologically similar to most other *Microtus* voles (Taitt and Krebs 1985; Tamarin 1985; Wolff 1985b; Tamarin et al. 1990; Wolff et al. 1994, 1996) and thus should respond similarly to other voles with respect to the Bruce effect. Gray-tailed voles occur in grasslands of western Oregon. The breeding season extends from March to December, the modal litter size is six, gestation is 21 days, females can start breeding when they weigh 18 g, and the mating system is polygynous/promiscuous (Verts and Carraway 1987; Wolff et al. 1994).

Methods

Our study was conducted in 12 0.2-ha (45 × 45 m) enclosures constructed of 90-cm-high vole-proof fences and planted with a mixture of pasture grasses similar to natural habitats of gray-tailed voles. The facility provided a simulated natural habitat for voles and has been used for the last 5 years to conduct studies on small-mammal population and behavioral ecology (Wolff et al. 1994; Edge et al. 1996; Schauber et al. 1996). To initiate the study, we placed 13–15 eartagged, nulliparous, 15- to 30-g females, to insure a sample size of approximately 12, and 12 30- to 52-g adult males into each of 12 vacant enclosures in the first week of September 1996. All of the study animals had been living in other enclosures prior to the beginning of the study. A total of 163 females were used to initiate the study. In the data analysis, however, some females were excluded from certain analyses due to lack of sufficient capture data. Therefore, the number of females used in the different analyses varies (Table 1). The 24–27 adults in each enclosure (~135 voles/ha) were representative of medium-density conditions for voles in their natural habitats (Taitt and Krebs 1985; Wolff et al. 1996). All juvenile recruits were counted and then removed to control for density effects.

The voles were trapped for 3 consecutive days (= one trap period) every 10 days for the duration of the study which was 14 weeks. Data collected included trap station location, eartag number, body mass, and reproductive condition including pregnancy and lactation status. Reproductive condition was assessed by a combination of three factors: nipple size and presence/absence of mammary tissue, pubic symphysis width, and change in body mass, both visible and measured (see de la Maza 1997, p. 13). The date of a parturition was estimated by counting the number of days from the female's introduction into the enclosure to either the exact date of the birth, if it occurred during a trapping period, or an estimated date of birth if it occurred between two trapping periods (day 4 of the 7-day nontrapping period; see de la Maza 1997, p. 20). When births occurred between trapping periods, we estimated the date of parturition to be day 4 of the nontrapping period. Because a single average was derived from the respective interbirth intervals of the 12 females in each enclosure, the error introduced by the estimation was mitigated through the averaging process.

The experiment consisted of two male treatments, one female treatment, and one control, each with three replicate enclosures. The male treatments consisted of either removing and replacing all 12 males (+12 male treatment) or 6 of the 12 males (+6 male treatment) with unfamiliar adult males every 10 days. These exposure rates were higher than would occur naturally (~10%; Taitt and Krebs 1985; Edge et al. 1996; Schauber et al. 1996; Wolff et al. 1996), representing 100% and 50% male turnover, respectively, every 10 days. Replacement males came from breeding populations in adjacent enclosures and had likely experienced recent mating activity. The female treatment involved replacing 6 males with 6 unfamiliar females after the first 10 days and then subsequently removing and replacing the six new females with other unfamiliar

Table 1 Sample sizes for the variables and treatments

Treatments	Initial *n* (females)	Sample sizes for birth intervals			Sample sizes for recruitment		
		Days to first parturition	Birth intervals 1–2	Birth intervals 2–3	Females	Births	Pups
Control	39	33	30	16	39	95	234
+ 6 male	37	37	27	6	37	75	248
+ 12 male	45	38	32	10	45	89	240
+ 6 female	42	32	33	21	42	96	251
Total	163	140	122	53	163	355	973

females every 10 days (+ 6 female treatment). Only one study has been conducted on pregnancy disruption using females, and with positive results (Huck et al. 1988). These authors found that exposure to unfamiliar female golden hamsters, *Mesocricetus auratus*, caused pregnancy disruption. Since no similar studies have been conducted with *Microtus*, and no theory applied to pregnancy disruption caused by females, we did not know what to expect, but used females as a control to determine if exposure to any stranger might have a negative effect on reproduction or juvenile recruitment. The removal and replacement of 6 males with 6 unfamiliar females in this treatment altered the sex ratio but not the population density. This difference in the sex ratio may have introduced a confounding variable into the study, but we think its impact on the results, if any, is minimal. The emphasis of the study was on the effects of the introduction of unfamiliar individuals and we felt that it was important to include this + 6 female treatment to control for effects that might have been caused by the introduction of strangers rather than specifically males. Control populations received no manipulations, but animals were trapped and handled at the same rate as the treatment animals. 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. Female gray-tailed voles are territorial and are typically evenly distributed throughout the enclosures (e.g., Wolff et al. 1994; Wolff and Schauber 1996; Bond 1998). Male home ranges are at least twice as large as those of females and on average overlap four to six females (Bond 1998). Therefore, the treatment females in this study were likely exposed to several new males every 10 days.

Data were analyzed by a repeated-measures analysis of variance for the interbirth intervals and a one-way analysis of variance for the other analyses. Enclosures were used as the experimental unit ($n = 3$ for analyses). The raw sample sizes for number of females per treatment, time interval, and other variables are listed in Table 1. A post hoc power analysis using a prespecified effect size and the observed variance (Thomas 1997) was used to insure the study had enough power to detect any significant differences in the Bruce effect among the treatment and control animals.

Results

The difference in the mean number of days to first birth among treatment and control populations approached statistical significance ($F_{3,8} = 3.20$, $P = 0.084$; Fig. 1). A slightly longer time to first birth occurred in the + 12 male treatment; this was because 4 of the 38 females did not give birth until 56 days after their introduction. Similarly, 2 of 32 females in the + 12 male treatment had a 51-day interval between their first and second parturitions. However, birth intervals following the initial pregnancy did not differ significantly among treatment and control populations ($F_{3,8} = 0.80$, $P = 0.527$; Fig. 1). The mean number of pregnancies per female for 96 females for which sufficient data were available ranged from 2.0 to 2.5 and did not differ significantly among the treatments and control ($F_{3,8} = 1.68$, $P = 0.25$; Table 2). The high incidence of pregnancy throughout the duration of the experiment indicates that the resident female voles were reproducing with the strange males that were placed into the treatment enclosures.

The mean percentage of females lactating after giving birth was determined for 273 births by 139 females and ranged from 86.1% to 93.9% and did not differ significantly among the treatments and control ($F_{3,8} = 0.55$, $P = 0.66$; Table 2). These high lactation rates indicate that offspring did not experience differential mortality among the control and treatments. A total of 973 juveniles were caught from 355 births throughout the 14-week experiment. The number of juveniles recruited per birth did not differ significantly among treatments and controls ($F_{3,8} = 0.94$, $P = 0.46$; Table 2). Thus, neither pregnancy disruption nor juvenile mortality occurred differentially among treatment and control groups.

Discussion

The results do not support the hypothesis that introduction of unfamiliar individuals into a resident population of reproducing females causes pregnancy disruption. Field tests with three treatments involving introduction of strangers at 10-day intervals indicated that no biologically meaningful differences occurred among the treatment and control animals with respect to mean days to first parturition, intervals between subsequent parturitions, mean number of pregnancies per female, percentage of births followed by lactation, and number of juveniles recruited per parturition.

We found no indication that exposure to strange females caused pregnancy disruption or infanticide in our field populations. No previous theory has been developed regarding the Bruce effect caused by females (although females did cause pregnancy disruption in one laboratory study with hamsters; Huck et al. 1988). However, female mammals do commit infanticide, apparently as a form of resource competition (e.g., Hrdy 1979; Sherman 1981; Wolff and Cicirello 1991; Wolff 1993; Wolff and Peterson, in press). In our field study, female densities were low

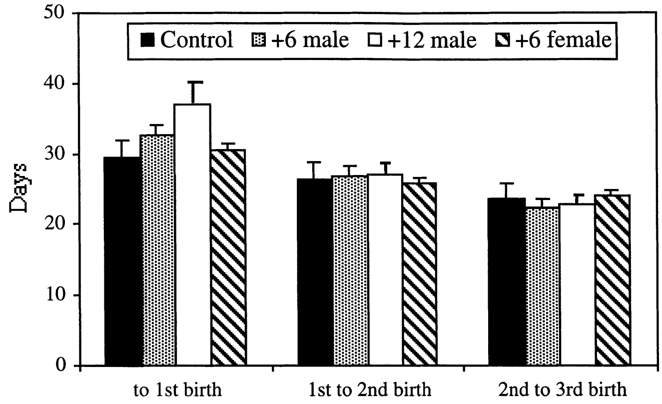

Fig. 1 The mean (+SE) number of days to first birth and for birth intervals for the control and treatment populations of female gray-tailed voles

enough to provide individual, nonoverlapping home ranges. Each female had a home range of ~75–100 m^2 and at least one-third of the available habitat in each enclosure was left unoccupied. Thus, under these conditions, resource competition should be minimal and infanticide committed by females should be uncommon, as our results indicated. The +6 female resident females did not experience higher rates of pregnancy disruption than control females, a result that is evolutionarily reasonable, especially at medium population densities. Successful reproduction is critical for *Microtus* species and therefore pregnancy disruption due to exposure to an unfamiliar female is not an adaptive behavior.

The +6 female treatment functioned as a control for the effects of exposure to unfamiliar individuals rather than specifically unfamiliar males, as in the Bruce effect. We know that the resident females encountered unfamiliar males regularly because in studies under similar conditions in this enclosed system, we found that when males were first placed into our enclosures, they typically wandered considerably and had home ranges of >250 m^2 and overlapped home ranges of four to six females (Wolff et al. 1994; Wolff and Schauber 1996; Bond 1998). In addition, the fact that treatment and control females had similar interbirth intervals indicates that the treatment females were not only exposed to the unfamiliar males but also mated with them. Thus, our results do not provide support for the occurrence of the Bruce effect.

The only indication of the Bruce effect or a delay to first pregnancy was observed 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 4 of the 38 (10.5%) females that did not give birth until 56 days after their introduction. In the control enclosures, all 33 females gave birth within 45 days of their introduction. Similarly, 2 (6%) other females of the 32 in the +12 male treatment had a 51-day interval between their first and second parturitions. These six females may have undergone the Bruce effect. However, the relatively low rate of long birth intervals [6 (8.6%) of 70 pregnancies] observed in the +12 male treatment was small compared to the 77% average Bruce effect rate observed in laboratory studies with other *Microtus* species (Clulow and Clarke 1968; Clulow and Langford 1971; Stehn and Richmond 1975; Schadler 1981; Heske and Nelson 1984; Storey 1986; Heske 1987; Stubbe and Janke 1994). Since the occurrence of the Bruce effect in the laboratory is extensive, within each enclosure that had an average of 12 resident females, there was an 85% chance of observing the Bruce effect in this study [based on a 28% pregnancy disruption rate (Thomas 1997) from Bruce 1959 (see power analysis in de la Maza 1997, Appendix E)]. Also, considering that the exposure rate of 100% male turnover every 10 days is greater than the ~10% which is normally observed in wild populations (Taitt and Krebs 1985; Edge et al. 1996; Schauber et al. 1996; Wolff et al. 1996), our results are rather conservative. Additionally, if pregnancy disruption were a natural and recurrent process that females underwent after exposure to strange males, the interbirth intervals, as well as the time to first parturition, of the treatment females would have been consistently and significantly longer than those of the control females – this did not occur. Similarly, if the Bruce effect were occurring in the treatment animals, the mean number of pregnancies per female would have differed from the control animals, but again, this difference was not observed. Scientists working in the laboratory have found that the Bruce effect may be

Table 2 The mean ± SE number of pregnancies/female at 12 weeks (*in parentheses*: total number of pregnancies, number of females analyzed), percentage of females lactating (*in parentheses*: total number of births per treatment for which adequate data were available, number of females analyzed), and juvenile recruitment per parturition (*in parentheses*: number of juveniles entering the trappable population, number of births per treatment for which adequate data were available) for the control and three treatments (with three replicates per treatment). Probabilities are based on one-way ANOVA

	Control	Treatment			*P*
		+6 male	+12 male	+6 female	
Mean number of pregnancies/female	2.3 ± 0.16 (55, 24)	2.2 ± 0.15 (50, 23)	2.0 ± 0.13 (57, 28)	2.5 ± 0.14 (53, 21)	0.25
Mean percentage of females lactating	89.2 ± 2.30 (73, 36)	93.9 ± 3.03 (59, 32)	86.1 ± 4.40 (64, 35)	90.0 ± 5.62 (77, 36)	0.66
Mean number of juveniles recruited per birth	2.6 ± 0.44 (234, 95)	3.3 ± 0.22 (248, 75)	2.7 ± 0.22 (240, 89)	2.7 ± 0.42 (251, 96)	0.46

more common in first pregnancies (Stehn and Jannett 1981; Storey 1986). In *Mus*, lactation may block the Bruce effect for subsequent pregnancies if females breed during postpartum estrus (Bruce and Parkes 1961); however, this does not seem to be the case for voles (Stehn and Jannett 1981). We started our experiment with all nulliparous females during a peak in the breeding season and still no or minimal pregnancy disruption occurred in first or subsequent pregnancies. This indicates that the Bruce effect was not operating in these voles or that it occurred with such low frequency that it did not have a biologically significant effect on reproduction and recruitment.

The fact that the Bruce effect does not occur at biologically significant levels calls into question the hypothesis that it is a female's evolutionary counterstrategy to infanticide by unfamiliar males (Schwagmeyer 1979; Labov 1981; Huck 1984). In fact, we had no indication that infanticide was occurring differentially in any of the treatments in our field study, although gray-tailed voles that have not copulated will commit infanticide in the laboratory (Davis-Born 1997). The mean numbers of juveniles recruited into the population per birth into the +12 and +6 male treatments were 2.7 and 3.3, respectively, compared to 2.6 for the control, which indicates that infanticide did not occur differentially when juveniles were exposed to strangers as opposed to their fathers. The high proportion (86.1–93.9%) of females lactating after birth also indicates that strange males were not killing entire litters. Thus, using this experimental design, we found no indication that exposure to strange males made young more vulnerable to infanticide than those in unmanipulated populations retaining their dams and sires.

The Bruce effect has not been studied in gray-tailed voles in the laboratory, but in our laboratory breeding colony, pregnancy disruption and/or delays commonly occurred when males were switched among females (R. Bentley and J. Peterson, personal communication). The Bruce effect has been demonstrated in the laboratory (Stehn and Jannett 1981) in the closely related *M. montanus* from which *M. canicaudus* apparently evolved (Hsu and Johnson 1970) and with which it will hybridize (Tyser 1975). *M. canicaudus* is behaviorally and ecologically similar to *M. montanus*, *M. pennsylvanicus*, *M. agrestis*, and *M. californicus* (Jannett 1980; Wolff 1985b; Tamarin et al. 1990 and references cited therein; Boonstra et al. 1993), all of which exhibit the Bruce effect, and thus should be under the same selection pressures for behavioral aspects of reproduction. We think that pregnancy disruption and infanticide are unlikely to occur in natural populations of these *Microtus* for two reasons: postpartum estrus and paternity confusion.

Gray-tailed voles, as well as other *Microtus* and most other murid rodent species exhibit postpartum estrus and can breed within 24 h after giving birth (Seabloom 1985, p. 700). In natural vole populations, postpartum mating is thought to be the most common mode of reproduction (Mcguire et al. 1992). Lactation does not inhibit ovulation and infanticide would not necessarily give a male access to a reproductive female because she can be lactating and already pregnant from a postpartum mating event. Therefore, infanticide will increase a male's reproductive fitness only if pregnancy disruption occurs in conjunction with the infanticide. However, we had no indication that infanticide occurred in the field.

Infanticide may be deterred if males are uncertain about paternity. In that copulation deters infanticide in males and males generally do not recognize their offspring, copulation tends to inhibit infanticide of all young for a given period of time in mice and in the polygamous meadow vole (Labov 1980; Webster et al. 1981; vom Saal and Howard 1982; Cicirello and Wolff 1990; Perrigo et al. 1992; Wilson et al. 1993). As a further insurance against male infanticide, female voles, and females of many other mammal species, may mate with several males in their area to confuse paternity and decrease the chances of infanticide (e.g., Boonstra et al. 1993; Agoramoorthy and Rudran 1995; Cowlishaw and O'Connell 1996; Agrell et al., in press). Because male *Microtus* generally have large home ranges that overlap those of several females, promiscuity is common, copulations and matings are frequent, and females often move their nests and young (e.g., Madison 1980; Wolff 1985b; Tamarin et al. 1990; Boonstra et al. 1993), and thus infanticide by male voles may be mitigated. The males used in this experiment were obtained from breeding populations of voles in adjacent enclosures and had presumably copulated recently. Thus, postpartum estrus resulting in simultaneous pregnancy and lactation, and multimale mating to confuse paternity would not make it adaptive for males to commit infanticide. If infanticide occurs rarely, then it is not a sufficiently selective force to which females need adapt.

We have presented an evolutionary argument for why the Bruce effect should not occur in gray-tailed voles, or perhaps in any other promiscuous rodent that exhibits postpartum estrus. The alternative explanation is that laboratory studies do not adequately simulate or represent natural conditions for these rodents. Chipman and Fox (1966) found that a general disruption of cleaning cages, transferring animals, or blowing on them was sufficient to cause an 88% pregnancy disruption in laboratory mice. Pregnancy disruption may also occur just from changing bedding (Clulow et al. 1982) and handling (Mallory and Brooks 1980). In laboratory studies with gray-tailed voles, we had approximately 80% pregnancy failure for pregnant females brought into the laboratory from the field (H. de la Maza, unpublished data). The artificial conditions of small cages and forced confinement with strange males, no escape routes, and no access to burrows, may create a generally stressful or sufficiently unnatural environment to cause pregnancy disruption that would not occur in natural conditions. 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 reproductive success would be severely compromised. A female vole's reproductive behavior is likely the result of a 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. In light of the results from our field study, we encourage others to conduct experimental field tests of the Bruce effect with other species to determine whether this kind of pregnancy disruption occurs in natural environments, before applying laboratory results to evolutionary theory.

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