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Does time after pair bond disruption affect subsequent reproduction in the socially monogamous woodland vole (*Microtus pinetorum*)?

Caroline A. Renfro, Daniel W. Pesek, Kelly Bobeck, and Nancy G. Solomon

Department of Zoology and Center for Animal Behavior, Miami University, Oxford, OH

Abstract

Disruption of the pair bond between socially monogamous animals leads to changes in behavior, which may have reproductive consequences. There are two alternative hypotheses to explain the effect of the length of time since pair bond disruption on subsequent reproduction. One hypothesis predicts that voles housed immediately with a new opposite-sex conspecific will be as likely to produce litters and will produce them as quickly as voles separated from their initial mate for longer. Alternatively, if attachment between mates is enduring, we expect that more voles separated longer from their previous mates will produce litters and produce them sooner than voles re-paired immediately after separation from their initial mates. Woodland voles, paired with opposite-sex conspecifics, remained together until parturition. Mates were then separated for zero, seven, or fourteen days until re-pairing with an opposite-sex conspecific. Pair bond disruption did not prevent males and females from mating subsequently, which was consistent with data from our breeding colony. In addition, the length of time an individual remained alone after pair bond disruption did not affect the latency to produce a litter. Our results show that having been paired previously does not affect subsequent reproduction in this socially monogamous vole.

Keywords

pair bond; re-mating; re-pairing; rodent; social monogamy; vole

1. Introduction

The occurrence of social monogamy varies extensively among vertebrate taxa (Clutton-Brock, 1989; Ligon, 1999; Bull, 2000; Whiteman and Cote, 2004) but is best studied in birds and some mammals. In these vertebrate classes, social monogamy involves two individuals sharing a territory or nest and living in close proximity to each other (Kleiman, 1977; Wickler and Seibt, 1983; Reichard, 2003). Furthermore, social monogamy implies the formation of an attachment or pair bond between two opposite-sex conspecifics (Wickler and Seibt, 1983; Gubernick, 1994), which is often described as long term i.e., lasting across multiple reproductive bouts (Getz et al., 1987; Moehlman, 1989; Ribble and Salvioni, 1990; Sommer, 2003; Jeschke et al.

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Corresponding author at: Dept. of Zoology, Miami University, Oxford OH, USA, 45056, Phone: 513-529-5454, Fax: 513-529-6900, solomong@muohio.edu (N. G. Solomon).

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2007; Ralls et al., 2007). After forming a pair bond, both males and females often display aggression towards unfamiliar opposite-sex conspecifics (Mason, 1975; Carter et al., 1995; Insel et al., 1995; Hohoff et al., 2002; Thomas and Wolff, 2004). Socially monogamous individuals also prefer to spend more time with their familiar partner than with an unfamiliar, opposite-sex conspecific (Williams et al., 1992; Winslow et al., 1993; Insel et al., 1995).

Most of our knowledge of social monogamy stems from avian studies since monogamy is the most common mating system in this vertebrate class (Black, 1996). Although pair bonds are important in many species of birds, they are occasionally terminated due to death or disappearance by one member of the pair. In some cases, members of the pair may not continue to reproduce with the initial partner, a circumstance which has been termed mate switching or divorce (Rowley, 1983; Dubois et al., 2004). Under these circumstances, the individual(s) from a previous pair can remain unmated or form a new partnership. The avian literature shows that re-pairing occurs fairly often (Ens et al., 1996). Both members of the former partnership may improve their reproductive success by mating with more compatible or higher quality opposite-sex conspecifics (Choudhury, 1995; Ens et al., 1996). Alternatively, only one member may benefit after divorce and the other member of the former pair may suffer a delay in reproduction, because courtship and pair formation may be extended in new pairs (Ens et al., 1996). Finally, it is possible that neither member of the former pair benefits (Jeschke et al. 2007) for reasons such as the costs of finding a new mate. Although the consequences of re-pairing in birds have received some attention (see Choudhury, 1995; Ens et al., 1996; Cézilly et al., 2000; Heg et al., 2003; Jeschke et al. 2007), we know much less about re-pairing in mammals (Svendsen, 1989; Ralls et al., 2007).

The few mammalian studies that exist show that males and females in socially monogamous species usually differ in the specific behavioral changes induced by pair bond disruption (Hendrie and Starkey, 1998; Starkey and Hendrie, 1998; Thomas and Wolff, 2004; Razzoli and Valsecchi, 2006). For example, males are less likely to initiate social contact while females show a decrease in social contact when approached (Starkey and Hendrie, 1998). Physiological effects of pair bond disruption include increased stress (e.g., increased activation of the hypothalamic pituitary- adrenal axis (Adrian et al., 2008) or arousal (increased heart rate, Cubicciotti and Mason, 1975) or a decrease in the size of the ventral gland, suggestive of decreased level of testosterone (Razzoli and Vasecchi, 2006). The length of time alone following pair bond disruption also appears to influence behavioral changes. Few behavioral changes are seen one day after pair bond disruption in males or females but both sexes show indications of increased interest in opposite-sex conspecifics after one week but not one month following pair bond disruption (Hendrie and Starkey, 1998).

Although disruption of the pair bond or time alone after pair bond disruption may affect behavior, a number of females eventually mate after pair bond disruption in laboratory studies (e.g., 71% of female prairie voles, *Microtus ochrogaster*, Thomas and Wolff, 2004). Although females will mate with a new male after pair bond disruption, the interval between previous and subsequent litters for pair bond disrupted females can be longer than for females whose pair bond is not disrupted (e.g., California mice, *Peromyscus californicus*, Ribble, 1992). These results suggest that attachment to the previous mate results in delayed mating.

There are two alternative proximate hypotheses to explain the effect of length of time following pair bond disruption on subsequent reproduction. The first hypothesis is that the pair bond is not enduring (as in Hendrie and Starkie, 1998); therefore, individuals should quickly form new pairs and reproduce. The second hypothesis is that the initial pair bond is enduring, and mating will be delayed or inhibited following the disruption of the initial pair bond (Pizzuto and Getz, 1998). After a longer period of separation from the mate, an individual's reluctance to mate with an unfamiliar opposite-sex conspecific should decrease (Fernandez-Duque et al., 1997).

Additionally, females may be less willing than males to engage in interactions with strangers of the opposite sex shortly after pair bond disruption due to the differences in the costs of reproduction for females versus males (Trivers, 1972; Anzenberger et al., 1986). After being separated from her mate for a longer period, a female may become less reluctant to display affiliative behavior toward an unfamiliar male, while a male's attraction to an unfamiliar female is expected to show less change with longer separation (Fernandez-Duque et al., 1997). To test these alternatives, we conducted an experimental manipulation to determine whether or not males and females would breed with an unfamiliar individual after 'loss' of the former mate and the effect of time from pair bond disruption to re-pairing with a new potential mate on subsequent reproduction in socially monogamous male and female woodland voles, *Microtus pinetorum*.

Woodland voles display traits characteristic of social monogamy, e.g., bi-parental care of young (McGuire and Novak, 1984; Oliveras and Novak, 1986), aggression towards same-sex intruders after formation of the pair bond (Back et al., 2002), and sexual size monomorphism (Gentry, 1968). Based on trapping data collected during the breeding season, 35% of social units in a natural population contain a male-female pair with or without offspring (FitzGerald and Madison, 1983) or appear to be extended families with pups as related as full siblings (Marfori et al., 1997). Females may give birth to multiple litters within a year (Goertz, 1971) but we do not know if they breed with the same male that sired previous litters. We do know that parous female woodland voles will mate with an unrelated, unfamiliar novel male in the laboratory (Solomon et al., 2001) although the effect of the latency from disruption of the pair bond to introduction of a new male and the responses of males to pair bond disruption have not been examined previously.

In this study, voles were isolated from their initial mate and re-paired with a new potential mate after 0, 7, or 14 days. The first hypothesis predicts that there should be no difference in the proportion of individuals that produce litters or in the latency from re-pairing to birth of pups in any treatment if the pair bond is not enduring. The alternative hypothesis predicts that more voles re-paired after fourteen days following separation from their initial mate will produce litters than voles re-paired immediately, and that the time from re-pairing to production of a litter should be shortest in voles that were separated from their previous mates for longest (14 days). Voles separated from their mate for 7 days should be intermediate in terms of latency from re-pairing to production of a litter. Based on existing literature (Trivers, 1972; Anzenberger et al., 1986), we also expected that when there is a short latency between separation from the initial mate and re-pairing with a new opposite-sex conspecific, females would be more reluctant to mate than would males.

2. Materials and methods

2.1 Animal husbandry

The woodland voles used in this experiment were live trapped in Henderson County, North Carolina and housed in the wild animal facility at Miami University in Oxford, Ohio. Voles were housed at 20°C in clear polycarbonate cages (28 × 22 × 15 cm or 38 × 33 × 17cm) with recycled paper bedding (Carefresh; Fangman Industries, Cincinnati, OH, USA) and had cotton Nestlets (Ancare Inc., North Bellmore, New York USA) for nesting material. They were provided with food (PMI Nutrition International's 5013 Rodent Breeder Diet, Brentwood, MO, USA) and water *ad lib*. Their diets were supplemented with rabbit chow (Lab Diet's 5326 High Fiber Rabbit chow, PMI Feeds Inc, St. Louis, MO, USA) weekly. Overhead fluorescent lights provided lighting on a 14:10 photoperiod with lights on at 0600h.

2.2 Examination of colony data

We initially examined records from our breeding colony to determine the percentage of voles that produced litters after being re-paired, the latency from initial pairing to birth of the first litter, and the latency from re-pairing to birth of a subsequent litter. We examined the latency from re-pairing to production of a litter for males and females separately.

Woodland voles were weaned 24 days after birth and housed in sibling groups under conditions described previously. Males and females were considered to be reproductive adults at ≥ 52 and 77 days of age, respectively (Schadler and Butterstein, 1979). When voles reached adulthood, an unrelated male and female were paired in a clear polycarbonate cage ($36 \times 30 \times 12.5$ cm or $38 \times 33 \times 17$ cm) with bedding, a Nestlet and food as described previously. Cages were left undisturbed for 14 days after males and females were paired. Voles were re-paired after the death of their previous mate. Surviving males or females were housed alone at least 14 days before re-pairing.

2.3 Re-pairing experiment

Formation of a pair bond occurs in prairie voles after cohabitation or mating (Williams et al., 1992; Winslow et al., 1993) and we assumed that pair-bond formation also occurs in woodland voles based on laboratory and field evidence of the occurrence of social monogamy in this species (FitzGerald and Madison, 1983; Oliveras and Novak, 1986; Back et al., 2002). Since less is known about pair bond formation in woodland voles, the initial pairs of unrelated, unfamiliar, nulliparous males and females were housed together until they produced a litter or for a maximum of 70 days (greater than two times the length of the gestation period, which is 24 days, Schadler and Butterstein, 1979) to ensure that they had formed a pair bond. Only individuals that produced a litter were used in this study. Based on previous data from the breeding colony, approximately 74.3% of woodland vole pairs produce a litter within this time (Solomon and Vandenbergh, 1994).

Twenty-four days after litters were born, pups were weaned and breeding pairs were separated. Males and females from these pairs were each randomly assigned to one of three treatments: separation from their initial mate for zero, seven, or fourteen days before being paired with a unfamiliar, unrelated, sexually inexperienced opposite-sex conspecific from the vole colony. We selected three time periods (treatments) because we had no apriori knowledge about the length of attachment to a previous mate after separation. We included a 7-day separation period because Hendrie and Starkey (1998) found that gerbils showed increased interest in opposite-sex conspecifics a week after pair bond disruption. The new pair remained together until a litter was produced or for maximum of 70 days. Cages were checked for pups every day starting on the twenty-fourth day after pairing (length of gestation). The latency to deliver a litter (the time from pairing to birth of the new litter) was recorded. We were able to determine which male had sired the litter by the timing of births. Any female that gave birth before 24 days after pairing must have been impregnated by her initial mate and was not included in the data analysis. To further examine any potential problems with subsequent reproduction, we also recorded the number of males and females that died after being paired in each treatment.

2.4 Data analysis

From the colony data, the proportion of voles that produced a litter after being re-paired was examined with a binomial test for males and females separately. To test whether there was a difference between males and females in production of a litter, we used a Chi-square test. A one-way analysis of variance (ANOVA) was used to examine the latency from the initial pairing to production of a litter versus the latency from re-pairing to litter production for males and females. A Student Newman-Keuls test was used if a significant difference was found in

the ANOVA. Latencies were not recorded for all initial litters so sample sizes between initial litters and litters produced after re-pairing may differ.

In the re-pairing experiment, contingency analyses were used to determine if there were treatment differences in the proportion of voles to produce litters. The difference latency from re-pairing to birth of a litter among experimental treatments was analyzed using a two-way ANOVA with treatment and sex as the independent variables. In addition, latency from the initial pairing to birth of pups was also determined using a two-way ANOVA for the initial pairs.

3. Results

3.1 Colony data

Significantly more males from the breeding colony (107/146, 73%) sired litters after re-pairing than expected by chance (Binomial test, $p=0.0007$). The same pattern was found for colony females after re-pairing (44/63, 70%; Binomial test, $p=0.0006$). There was no significant difference between the proportion of males and females that produced litters after re-pairing ($X^2 = 0.261$, $df = 1$, $p > 0.05$).

The latency from pairing to birth of the initial litters in the colony was 35.5 ± 1.4 days ($n = 76$ pairs). The latency to produce a litter in re-paired males (32.2 ± 1.0 days, $n = 101$) was not different from the latency to produce the first litter. When females from the colony were re-paired, the latency from pairing to birth of a litter (29.9 ± 1.1 days, $n = 45$ pairs) was significantly less than the latency to produce the initial litter ($F_{[2,181]} = 3.88$, $p = 0.02$). There were no differences in the latency from re-pairing to birth of a litter in colony males or females.

3.2 Re-pairing experiment

No difference was found in the proportion of re-paired males that sired litters zero ($n=20$), seven ($n=19$), or fourteen ($n=18$) days after re-pairing ($X^2 = 0.261$, $df = 2$, $p = 0.88$; Fig. 1a). The proportion of re-paired females that gave birth also did not differ among treatments ($n = 11, 19$, and 15 , for the zero, seven and fourteen day separation periods; $X^2=0.103$, $df=2$, $p=0.95$; Fig. 1b).

There was no significant difference among treatments in the latencies to produce the initial litter ($F_{[2,72]} = 0.87$, $p = 0.42$; Table 1). There was also no significant difference between males and females in the latency to produce the initial litter ($F_{(1,72)} = 1.14$, $p < 0.29$; Table 1). There was no significant interaction between treatment and sex ($F_{[2,72]} = 0.59$, $p = 0.56$).

There was no difference among treatments in the latencies to produce a litter after being re-paired ($F_{[2,78]} = 0.11$, $p = 0.90$; Table 1). Re-paired females produced litters sooner than re-paired males but the difference was only of borderline significance ($F_{[2,78]} = 3.82$, $p=0.054$; Table 1). There was no significant interaction between treatment and sex in the production of litters after re-pairing ($F_{[2,78]} = 1.00$, $p = 0.91$).

Although there were insufficient data to analyze statistically, there seemed to be no pattern of deaths among treatments or between the sexes. There were only four deaths (4/41, 9.8%) after females were re-paired. Two male partners died: one in the zero-day treatment and one in the fourteen-day treatment. One of the re-paired females died in the fourteen-day treatment and an individual (sex not recorded) died in a seven-day treatment. There were six (6/53, 11.32%) deaths after males were re-paired. Two of the re-paired males died: one from a zero-day and one from a seven-day treatment. One female partner died in a seven-day treatment, two individuals died in the zero-day treatment (sex not recorded) and one individual in the fourteen-day treatment (sex not recorded).

4. Discussion

After disruption of the initial pair bond in animals from our breeding colony and in the experimental manipulation, most male and female woodland voles mated and produced litters within 30 days of re-pairing. About 80% of males and females that were re-paired produced a litter with their new mate. This percentage was not different from the percentage of pairs that produced litters with their initial mate, which suggests that having been paired previously does not affect subsequent reproduction in woodland voles. In addition, data from our breeding colony showed that the latency from re-pairing to birth of a litter in females was shorter than the latency to production of a litter with the initial mate. This result may be due to the fact that sexually experienced females will mate sooner than inexperienced females. The results from the experimental manipulation and data from the breeding colony suggest that woodland voles do not require time alone after loss of the initial mate before mating with a new individual as predicted by the second hypothesis.

Both male and female woodland voles reproduced after loss of mate in a pattern consistent with the prediction from the first hypothesis that there should be no difference in the proportion of pairs to reproduce or in the latency to reproduction in voles re-paired immediately after pair bond disruption versus those separated for 7 or 14 days. Although there may have been behavioral differences among treatments, these did not affect the reproductive outcome after pair bond disruption. Behavioral data were not collected after pair bond disruption as in previous studies (e.g. Hendrie and Starkey, 1998), but the data we do have on vole deaths suggest that no severe aggression, which could have resulted in deaths of opposite-sex conspecifics, occurred. Our results are also consistent with results from previous studies, which showed that parous females, in socially monogamous species, will breed with a new male (woodland voles: Solomon et al., 2001; prairie voles: Wolff et al., 2002; Thomas and Wolff, 2004; beaver, *Castor canadensis*: Svendsen, 1989) although latency from disruption of the pair bond to re-pairing was not investigated in those studies.

We expected that the length of separation would not affect latency to reproduce in males as much as in females. The mean latency between re-pairing and production of a litter was ~34 days for males separated from their initial mates for 1, 7, or 14 days. Thus, there was no effect of the length of separation on the time between re-pairing and production of a litter in males. Although we expected that there would be an inverse relationship between length of separation and latency between re-pairing and production of a litter in females, there was no difference among treatments for females. In addition, re-paired females produced litters sooner on average than re-paired males. The proximate reason for this difference may result from differences in reproductive physiology of females. Although female woodland voles are induced into estrous by exposure to an unfamiliar male (Solomon and Vandenberg, 1994; Solomon et al., 1996), experienced females that were re-paired may have become receptive sooner than inexperienced females, which were paired with males after the males had been separated from their initial mates. Despite the possible reasons, our results are not consistent with the proposed functional hypothesis based on costs of reproduction in males and females (Trivers, 1972).

Although woodland voles are considered socially monogamous, they will mate with other opposite-sex conspecifics if re-paired under laboratory conditions. We do not know as much about the effects of pair bond disruption of woodland voles in nature. Solomon et al. (1998) observed that, in an orchard population, if a female woodland vole is removed from a social unit, another female will move in rapidly and become reproductively active. This result suggests that woodland voles will breed after disruption of the initial pair bond in nature, consistent with the hypothesis that the pair bond is rather weak. Alternatively, reproductive vacancies may represent low cost opportunities for procuring a higher quality mate as suggested by Ens et al. (1993). In addition, since woodland voles are typically short lived due to predation,

there may be a low cost and great benefit of breeding with the remaining opposite-sex conspecific when vacancies from same-sex conspecifics appear (as suggested by Ens et al., 1993). Thus, short-lived mammals like woodland voles may be willing to mate with a new opposite-sex conspecific after loss of the initial mate, to enhance their lifetime reproductive success. This pattern of behavior is also seen in other species of rodents. For example, California mice will mate with unfamiliar individuals subsequent to mate loss (Ribble, 1992). It is not known whether or not females whose mate has disappeared actually form new pair bonds but they do reproduce with other males in the population (see also example of prairie voles, Pizzuto and Getz, 1998).

The results from this study contribute to the growing literature on the behavior of socially monogamous mammals. These results, in conjunction with those from other studies (alpine marmots *Marmota marmota*; Goossens et al., 1998; Ethiopian wolves *Canis simensis*; Sillero-Zubiri et al., 1996; and African wild dogs, *Lycaon pictus*; Girman et al., 1997; fat-tailed dwarf lemurs (*Cheirogaleus medius*, Fietz, 2003) reinforce the idea that the existence of a pair bond in socially monogamous animals does not always prevent them from mating with other opposite-sex conspecifics. Much less is known about mate fidelity and divorce in socially monogamous mammals than is known from previous studies of divorce and mating patterns in birds. Therefore, future studies of socially monogamous mammals living in natural or seminatural populations are required to provide data on the degree of mate fidelity and divorce in as well as the costs and benefits of social and sexual monogamy.

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Fig. 1.

Percentage of re-paired adult A) male and B) female woodland voles that produced a litter after separation from initial mate for 0, 7, or 14 days. Black portion of bar indicates the percentage of woodland voles that produced a litter and the white portion of the bar indicates the percentage of woodland voles that did not produce a litter after being re-paired. Samples sizes are indicated in the white boxes inside the black bars.

Table 1

Mean latencies (days) + 1 SE from pairing to birth of pups in the initial litters and litters born to pairs formed after separation from the initial mate. (n = number of pairs that produced litters in each treatment). Some of the sample sizes for initial litters are smaller because, even though pairs produced litters, the latency from pairing to birth was not recorded.

	Males		Females	
	Initial	Re-paired	Initial	Re-paired
Treatment				
0 days	31.9 ± 1.8 (16)	33.9 ± 2.2 (17)	30.1 ± 1.5 (8)	29.1 ± 1.3 (9)
7 days	31.0 ± 2.0 (13)	34.1 ± 3.0 (15)	28.3 ± 0.5 (16)	31.2 ± 1.8 (16)
14 days	28.7 ± 1.1 (14)	34.2 ± 3.3 (15)	29.2 ± 1.4 (11)	29.3 ± 2.3 (12)