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Does mate choice take place in free-living prairie voles *Microtus ochrogaster*? Evidence from field data *

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Abstract We used live-trapping data collected during a long-term study of the social organization of prairie vole *Microtus ochrogaster*, to investigate pair formation and break-up in this species. Most male-female pairs that formed in spring consisted of survivors of communal groups. Whether pairs formed from males and females from the same or different communal groups, the individuals were not family members. When new pairs formed during summer-autumn they typically consisted of unrelated individuals that had been wandering throughout the study site. Thus, our field data indicate that prairie voles avoided pairing with family members. We found no evidence that free-living females based their choice of mate on body mass, or that females preferred sexually experienced to sexually inexperienced males in the field or under semi-natural laboratory conditions. In our study population, pairs that separated were characterized by lower reproductive success, prior to separation, than were pairs that remained together. At any given time, the number of potential mates for males and females was limited. Thus, it seems likely that few individuals had the opportunity to compare simultaneously the characteristics of two or more potential mates. We suggest that pair formation in our study population most likely was opportunistic, with individuals pairing with the first available mate [*Acta Zoologica Sinica* 50 (4): 527-534, 2004].

Key words Prairie voles, *Microtus ochrogaster*, Mate choice

自由生活的橙腹田鼠中是否有配偶选择？来自野外数据的证据 *

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摘要 使用在长期研究橙腹田鼠的社会组织中收集的数据，我们研究了该物种配对的形成和解体。大多数在春季形成的配对包括了各公社群（包括至少两个同性个体的群）过冬后的幸存者。无论雌、雄个体是否来自相同或不同的公社群，配对的个体都不是同一家庭的成员。春秋季形成的新配对，通常包括一直在研究地游荡的无亲缘关系的个体。所以，我们的野外数据表明，橙腹田鼠避免与家庭成员配对；但是没证据表明自由生活的橙腹田鼠以体重为基础来进行配偶选择，也没证据表明在野外或半自然的实验室条件下，雌性个体偏好有性经历的雄性个体。在我们研究的种群中，配对分离的个体都具有一个特征，即分离前的繁殖成功率比未分离的配对个体低。在任何特定的时间内，由于雌、雄性个体的潜在配偶的数量有限，所以，几乎没有个体有机会同时比较两个或更多潜在配偶的特征。结果表明：我们所研究的种群中的配对是机会主义式的，个体与第一个能得到的配偶形成配对关系 [*动物学报* 50 (4): 527-534, 2004]。

关键词 橙腹田鼠 配偶选择

Mating strategy is important to the survival and reproductive success of individuals and, in turn, may

influence population success (i. e., population density) (Fleming, 1979). Reproduction is the great-

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est and population density higher when both males and females have high reproductive potential. Males and females of promiscuous species make a choice each time they mate. Effects of an improper choice at one mating may be compensated for by a proper choice the next time. In monogamous species, however, mate choice has a more lasting effect upon individual reproductive success in that subsequent matings, perhaps through the lifetime of the individuals, will be with the same mate. Thus, the original choice of a mate by a monogamous male and female may have a lasting effect on reproductive success of the pair and on its contribution to population density. Indeed, there may be a general tendency for monogamous species to be more selective in their mate preferences as compared to non-monogamous species (Salo and Dewsbury, 1995).

Origin and history of the two individuals in the pair are important in determining their potential reproductive success and contribution to population density. Are they related, i. e., from the same family group? If related, deleterious genetic effects may reduce reproductive success of the pair (Keane, 1990 a, b; Wolff, 2003). Are they from the same generation, i. e., born in the same season and have experienced the same environmental stresses? Individuals exposed to low temperatures during winter may be in poor physiological condition (Nelson et al., 1989). Reproductive potential of the pair may be least when both have been subjected to winter stresses and greatest when neither has been so stressed. Individuals may use prior exposure to low-temperature stresses as a basis for mate selection. Are either, or both in reproductive condition? If in reproductive condition when they pair, then they may produce young more rapidly and have greater reproductive success than if only one or neither is reproductive at the time of pair formation; rapid production of young may be particularly important for short-lived species. Finally, level of reproductive experience may influence reproductive success of the new pair. For example, increasing parity is associated with increased maternal care and survival of offspring in some species of rodents (Wang and Novak, 1994).

When two individuals mate, presumably they first evaluate each other for specific traits, whether committing to a long-term association (monogamy) or simply to a single mating (promiscuity). Individuals may employ a number of criteria in such an evaluation, and which criteria are most important will likely depend upon the particular species involved. Numerous laboratory studies have examined whether social and mating preferences in voles are influenced by factors such as familiarity (Fadao et al., 2000; Parker et al., 2001; Roberts et al., 1998; Salo

and Dewsbury, 1995; Shapiro et al., 1986; Williams et al., 1992), dominance status (Hoffmeyer, 1982; Horne and Ylonen, 1996; Shapiro and Dewsbury, 1986), body size (Solomon, 1993), mating history (Ferguson et al., 1986; Pierce and Dewsbury, 1991; Pizzuto and Getz, 1998; Salo and Dewsbury, 1995), frequency of scent marking (Mech et al., 2003) or self-grooming (Wolff et al., 2002), and reproductive condition (Webster et al., 1982). Laboratory tests of mate choice, such as those conducted with voles, have been criticized for their typically short duration (often less than 1 hour) (Solomon, 1993; Wolff, 2003) and failure to permit mating with multiple individuals (Wolff, 2003). To our knowledge, there are no data concerning mate choice and pair formation in free-living rodents. Further, although pair separation ("divorce") has been well-studied in birds (Choudhury, 1995; Rowley, 1983), little is known about the phenomenon in mammals.

In this paper we present data relevant to mate choice and the formation and break-up of breeding pairs in a natural population of prairie voles *Microtus ochrogaster*, a species characterized by behavioral monogamy (Getz et al., 1990a, 1993; Carter et al., 1995; Roberts et al., 1998). The data were collected during a long-term study of prairie vole social organization in which we obtained detailed information on the origin, pairing status, and breeding history of most individuals in the population (Getz et al., 1993). Although we have previously described the mating system, social organization and demography of our study population (Getz et al., 1981, 1987a, 1990a, 1993), we have not detailed the history of individuals that form pairs, the likely processes by which they choose mates, or characteristics of pairs that separate. Finally, we also include results from a study of mate choice conducted under semi-natural laboratory conditions and lasting for five days.

1 Materials and methods

1.1 Study areas

The study was conducted in a one hectare *Medicago sativa* (alfalfa) site in the University of Illinois Biological Research Area (Philips Tract), 6 km NE of Urbana, Illinois (40° 15' N, 88° 28' W) from October 1980 through May 1987 (Getz et al., 1993). For a detailed description of the study site, see Getz et al. (1987b).

1.2 Procedures

The *M. ochrogaster* population was monitored twice weekly by live trapping directly at the nests of social groups (Getz et al., 1993). Locations of the nests of all social groups were continuously updated as

part of the study of social organization. Four to five multiple-capture, live-traps were placed next to surface nests or at the entrance of burrows leading to underground nests. The traps were set at the nests at 06:30 h on Monday morning and checked at 3 - 4 h intervals through 24:00 h and again at 06:30 h and 09:30 h on Tuesday morning. This schedule was repeated Thursday morning through Friday morning. The trapped voles were individually marked by toe-clipping and weighed at first capture. Animal identity, sex, and reproductive condition were recorded at each capture; for a 1-year period (May 1986 - May 1987) we recorded body weight at each. For males, testes were recorded as abdominal (non-reproductive) or scrotal (reproductive); females were recorded as vulva closed (non-reproductive) or vulva open, lactating or pregnant (reproductive). We classified animals weighing ≥ 30 g as adults, and those ≤ 20 g when first captured at a nest as offspring of a resident female at that nest.

We considered individuals to be a resident of a particular nest if they were captured primarily at that nest for at least 10 days. Voles that were not residents of a nest were captured at different nests and never met the 10-day residency criterion at any location. In some cases we organized data by the following seasonal categories: winter (December - February), spring (March - May), summer (June - August), and autumn (September - November). We compared reproductive success of pairs that separated with that of pairs that remained together. This was done to determine if reproductive success, or lack thereof, was a factor in the break-up of pairs. We determined reproductive success of pairs by estimating the number of offspring per litter that survived until trappable age, i. e., ≥ 12 days of age (Getz et al., 1993).

We utilized Normal Approximation Binomial, Wilcoxon Paired-Sample, and Chi Square tests (Zar, 1999) where appropriate.

The field protocol was reviewed periodically by the University of Illinois Laboratory Animal Resource Committee throughout the study and approved, based on University and Federal guidelines in effect at the time.

1.3 Social organization and mating system

Three types of social groups are found within our study population: male-female pairs, single females (the majority of which are survivors of male-female pairs that have not formed a new pair), and communal groups (social groups including at least two adults of the same sex) (Getz et al., 1993). All three types of social groups were territorial; spacing between nests was related primarily to population density (McGuire and Getz, 1998). Even at very high

densities, there was essentially no overlap between the territories of adjacent social groups. Getz et al. (1990a, b, 1993), Getz and Carter (1996), and Getz and McGuire (1997) concluded that the fundamental social organization of *M. ochrogaster* consists of communal groups formed from an original male-female pair (46.5%) or single female (23.5%) breeding unit by addition of philopatric offspring and unrelated adults. Philopatric offspring comprise 70% of the additions to the original breeding unit; typically, 68% of male and 73% of female offspring remain at their natal nest until death (McGuire et al., 1993). Offspring that did leave the nest were considered "natal dispersers" for approximately two weeks; thereafter, they were considered to be "wanderers" if they had not settled into a nest. Since the age of dispersal from the natal nest is approximately 45 - 55 days (McGuire et al., 1993), all wanderers were adults. Also, some wanderers may have been adult immigrants from other sites. During the breeding period, approximately 45% of the adult males in the population were not residents of established social groups and were classified as "wanderers" (McGuire and Getz, 1998). At any given time during the breeding period, 24% of the females also were not residents at a nest.

Male-female pairs of *M. ochrogaster* display traits characteristic of behavioral monogamy (Kleiman, 1977), including sharing a common nest and home range (Hofmann et al., 1984, Getz et al., 1993). Paired males display paternal behavior, including grooming, huddling over, and retrieval of young. Paired females preferentially mate with the familiar cohabiting male during postpartum estrus (Getz et al., 1981). Given the opportunity, however, estrous females also will mate with other males.

1.4 Laboratory mate choice trials

One of us (TP) conducted a laboratory study of mate choice based on prior sexual experience of the male (see Pizzuto and Getz, 1998, for a description of the laboratory colony and husbandry procedures). The mate choice tests were conducted under semi-natural conditions in a 1.5 m \times 2.5 m Plexiglas bottomed arena with two 45 cm \times 65 cm compartments at opposite ends of the arena (also described in Pizzuto and Getz, 1998). Three centimeters of sphagnum moss covered the floor of the arena, in which the voles constructed runways that were open to the Plexiglas below. A 20 cm layer of wheat straw covered the sphagnum. Sexually inexperienced males and females were removed from their parents at 21 days of age and maintained in same-sex sibling groups until testing. Sexually experienced males had been paired with a female at 45 days of age and successfully sired

a litter, after which they were removed and maintained in separate cages until testing. All animals were 34 - 86 days of age when tested; experimental animals in each trial were matched for age and body mass.

A sexually experienced male was placed in one compartment, a sexually inexperienced male in the other. Prior to placement in compartments, each male was fitted with a plastic cable-tie collar. The collars allowed males to move freely about their compartments, but prevented them from leaving the compartments. The female was not collared and had free access to both compartments from the arena proper. Location and behavior of the female were recorded by the observer lying below the arena. Electronic timers were used to record the amount of time the female spent in each compartment or outside the compartments in the arena proper. Two 30-min observations were conducted each day, early to mid-morning (08:00 - 11:00) and early to late evening (20:00 - 23:00) for five days. The criteria for the female having made a choice between the two males have been described in Pizzuto and Getz (1998); briefly, the criteria included: (1) moving into a compartment and nesting with the male; (2) spending as much time in the compartment of one male as in the other two areas (arena proper and other compartment) combined; (3) spending at least twice as much time in the compartment of one male as in that of the other male.

2 Results

2.1 Characteristics of individuals that formed pairs

2.1.1 Season of birth and source Because reproduction is very low during most winters (Getz et al., 2004), the majority of male-female pairs that formed in the spring, and for which we have date of birth of the individuals involved, were comprised of adults that were born during preceding seasons, most commonly the preceding autumn (males, $n = 33$: summer, 6.1%, autumn, 78.8%, winter, 12.1%; spring 3.0%; females, $n = 41$: summer, 4.9%, autumn, 53.6%, winter, 34.2%, spring, 7.3%). Thus, the majority of animals forming pairs in spring had experienced winter weather stresses. Only 5.4% of the animals forming spring pairs had not experienced low temperature stresses.

Almost males and females that formed spring pairs were survivors of communal groups. Most pairs were formed from males and females from different communal groups, although nearly one third were formed by individuals from the same communal group (Table 1). None of the individuals from the same or different communal group that formed a pair were

siblings. The wandering males and females that formed pairs most likely were immigrants.

During summer-autumn all but two of the individuals forming the 189 pairs were born during spring-autumn and thus had not experienced low temperature stresses (the exceptions include one male born the previous autumn and one female born the previous winter). Approximately two thirds of the pairs formed during summer-autumn involved wanderer males and females (Table 1). Of the pairs formed by individuals that dispersed from natal nests, none involved male and female siblings, even though in 17 of the 36 instances in which sibling males and females left the nest at the same time, they settled into a nest within 5 m of each other. Similarly, none of the pairs formed from natal dispersers involved individuals from adjacent social groups. Of the 50 pairs forming during the winter, 65.0% were formed by two wanderers (Table 1).

Table 1 Source of individuals (proportions) forming pairs in a free-living population of *Microtus ochrogaster*

Source	Season		
	Spring	Summer-autumn	Winter
Number pairs	91	189	50
Different communal groups	0.639		
Same communal group	0.286		
Both natal dispersers		0.053	0.060
Both wanderers	0.075	0.677	0.650
Natal disperser female, wanderer male		0.090	0.120
Natal disperser male, wanderer female		0.095	0.060
Male pair survivor, wanderer female		0.027	
Female pair survivor, wanderer male		0.058	0.100

2.1.2 Reproductive status In our study population, the proportions of reproductive males and females varied seasonally: spring (94%, males; 81%, females); summer-autumn (98%, males; 91%, females); winter (56%, males; 37%, females). Against this population information, we examined the reproductive condition at time of pairing for pairs forming during these three periods (Table 2). The proportion of males that were reproductive when they formed a pair was significantly lower than that of the general population during both spring and winter ($Z = 2.61$, $P < 0.01$ and $Z = 2.07$, $P = 0.02$, respectively). There was no difference in the proportion of males that were reproductive when forming a pair in respect to that of the general population during summer-autumn, or of females during any season.

Table 2 Reproductive condition of *Microtus ochrogaster* at time of pairing in relation to season (Values represent % reproductive)

Reproductive at pairing	Season		
	Spring (<i>n</i> = 51 pairs)	Summer-autumn (<i>n</i> = 138 pairs)	Winter (<i>n</i> = 50 pairs)
Male and female	58.5	94.2	18.0
Male only	17.7	1.4	18.0
Female only	9.8	4.4	24.0
Neither	13.7	0.0	40.0

2.1.3 Body mass We examined data collected during the period when animals were weighed at each capture (May 1986 - May 1987) to see if females paired with males of larger than average body size. More specifically, we compared the mass of each male that formed a pair with the mean body mass for all adult males in the population the month in which the pairing occurred. Of the 36 males that formed a pair during the 1-year period of frequent weighing, 24 (66.7 %) had a body mass at time of pairing that was lower (on average, 5.4 ± 0.7 g lower) than the mean male body mass for the month in which pairing occurred, 11 (30.5 %) had a body mass that was greater (on average 3.4 ± 0.7 g greater), and one (2.8 %) had a body mass that was the same as the mean male body mass in the month of pairing. Sample sizes were too small for seasonal comparisons for relationships between body mass and reproductive status of males; during summer-autumn, when most of the data were obtained, essentially all the males were reproductive. Although limited, these data suggest that females do not routinely select as mates males of larger than average body size.

2.1.4 Reproductive experience Nine of 12 virgin females tested in the semi-natural environment met the criteria for having formed a pair (Table 3). Four of the nine females paired with an experienced male and five with an inexperienced male. The other three females displayed no preference between sexually experienced and inexperienced males. There was no indication that females made a consistent choice between either an experienced or inexperienced male ($T = 35$, $P > 0.05$).

2.2 Conditions of mate choice

It is difficult to know whether two potential mates of different quality are encountered at the same time in natural populations. Here, we present data on numbers of available males and females in the population, as well as the number and timing of visits to nests of single females to provide some perspective on the likelihood of individuals simultaneously encountering potential mates.

Table 3 Proportion of time sexually inexperienced female *Microtus ochrogaster* spent in chambers of sexually experienced and inexperienced males

Female number	Experienced male	Inexperienced male
1	0.114	0.344
2	0.048	0.362
3	0.822	0.025
4	0.220	0.548
5	0.037	0.625
6	0.096	0.796
7	0.734	0.070
8	0.573	0.051
9	0.489	0.169
10	0.583	0.001
11	0.603	0.001
12	0.094	0.733

Rest of the time the female was in a neutral chamber. See text for observational protocol.

In spring, when most pairs form from survivors of different communal groups, there was an average of 15.8 ± 2.1 adult males/ha in the population and 11.1 ± 1.6 adult females/ha. With 1.4 males for each female and 0.7 females for each male seeking a mate, it seems unlikely that a given individual would have the opportunity to evaluate simultaneously two or more potential mates.

During summer-autumn, when most new pairs formed from wandering females and males, at high population densities ($\geq 150/\text{hm}^2$) there was an average of 72.5 wandering males/ha in the population (range 32 - 119/ hm^2). During the same times, there was an average of 35.0 wandering females/ha (range, 11 - 35/ hm^2), approximately two males per female. There were a total of 258 male visitors to nests of 192 single females. Only one male visitor was recorded at 28.9 % of the single female nests; 71.1 % of single female nests had more than one male visitor. We next looked at the nests with more than one male visitor to determine whether the males were simultaneously present at the nest (captured at the nest the same day). Of 53 instances of two or more males having visited a nest the same day, there were 41 instances of two males at the nest; 11 instances of three males, and one instance of five males present. In contrast, there were 690 records of a male visiting a single female and being the only male visitor that day. The mean interval between all male visitors (males present at the same time were given an interval of zero) was 6.5 ± 0.07 days.

2.3 Reproductive success of pairs

Reproductive success of pairs in which either the male or female left the pair was 0.66 offspring per litter prior to separation ($n = 72$ pairs, with 82 young from 125 litters), while that of pairs that remained together ($n = 217$ pairs, with 404 young from 367 litters) was 1.10 offspring per litter (differences in number of young per litter surviving: $\chi^2 = 18.29$, $df = 1$, $P < 0.01$). Reproductive success of pairs from which the female left ($n = 31$ pairs, with 30 young from 59 litters) was less than that of those in which the male left ($n = 41$ pairs, with 65 young from 52 litters) (0.51 and 0.80 offspring; $\chi^2 = 3.96$, $df = 1$, $P < 0.05$). There was, however, no difference in whether the male or female left in pairs that failed to produce any young (females, 58.1%; males, 58.5%). Significantly more pairs from which either the male or female left the pair produced no young at all when compared to pairs that remained together (58.3% and 31.8%, respectively; $\chi^2 = 16.22$, $df = 1$, $P < 0.01$). Five of the females that left a pair settled into a nest 10 - 12 m from the original nest, while six males settled 10 - 25 m from the original nest. The remainder of the males and females wandered through the site at least one week before disappearing, most likely as a result of mortality.

3 Discussion

Our field data indicate that prairie voles avoid pairing with family members. The majority of the pairs that formed in the spring involved individuals from different communal groups, and when pairs formed between individuals from the same communal group, the individuals were unrelated (i. e., one individual was known to have joined the group as an adult). During summer-autumn, most pairs formed from two adults that had been wandering within the population. Because wandering animals typically are lone survivors of social groups whose other members have disappeared (McGuire and Getz, 1998), it is likely that such individuals were from different family groups. Finally, a small proportion of spring-autumn pairs involved two individuals that had dispersed from natal nests; these pairs never involved siblings or even individuals from adjacent social groups. Our field observations agree with laboratory data indicating the failure of prairie voles to pair and successfully breed with relatives (McGuire and Getz, 1981; Carter et al., 1986; McGuire and Getz, 1991). Two other species of monogamous voles, *Microtus mandarinus* (Fadao et al., 2000) and *M. pinetorum* (Schadler, 1983) exhibit inbreeding avoidance under laboratory conditions, but data are not available regarding their patterns of pair formation in the

field.

We found no evidence that physical condition influenced choice of mate in our study population. Declines in physical condition, measured as reductions in gonadal size, body mass, and brown fat, have been detected in laboratory prairie voles exposed to winter conditions, such as short photoperiods and cold temperatures (Nelson et al., 1989). However, we found no variation among free-living individuals regarding whether they had experienced low temperature stresses. For example, almost all individuals forming pairs during the spring had experienced low temperature stresses, while virtually all individuals forming pairs during summer-autumn had not experienced such stresses. The lack of variation in this characteristic in spring and in summer-autumn made it impossible for animals to use prior exposure to low temperature stress as a basis for mate selection during these seasonal periods. In contrast, adult males in our population clearly varied with respect to body mass (Getz et al., Unpub.). Nevertheless, we found no evidence that females selected males on the basis of body mass. This finding contrasts with laboratory data indicating that male and female prairie voles prefer large individuals of the opposite sex (Solomon, 1993).

Mating and social history have been shown to influence mate choice in voles under laboratory conditions. For example, prairie voles prefer sexually experienced individuals of the opposite sex that have not recently mated to those that have recently mated with another individual (Ferguson et al., 1986; Pierce and Dewsbury, 1991). There is also laboratory evidence that female prairie voles prefer males with which they have just mated or directly cohabited to novel males (Shapiro and Dewsbury, 1986; Williams et al., 1992). Although not strictly comparable to these studies, we found no evidence that female prairie voles select males on the basis of sexual experience when tested under semi-natural laboratory conditions. We also discovered from our field data that individuals need not be reproductive at the time of pairing.

Reproductive success appeared to be a factor in determining whether pairs remained together. Pairs that separated had been less successful in producing young when compared to pairs that stayed together. These findings agree with those from studies of certain bird species in which pairs split to form new alliances in an apparent attempt to increase future reproductive success (Rowley, 1983; Choudhury, 1995).

Laboratory studies of mate choice typically present the test animal with a choice between two individuals of the opposite sex that differ in the specific

trait being studied (Wolff, 2003). While we have some evidence from our study population that two or more males may be present at the nest of a single female at the same time, such situations appear to be relatively rare. Thus, even at times of very high population density it is doubtful that a given female or male would be able to evaluate more than one potential mate at time. When population densities were lower, there would be even fewer opportunities for simultaneous comparisons of two or more mates. An individual conceivably could reject a potential mate that does not have a specific trait, waiting until the "right" individual comes along. We had no evidence of prior visits of another male to a female nest before a pair was formed. There was a male visitor to the nest of a single female approximately once every 6 days. Given the short life span of *M. ochrogaster* (60 days; Getz et al., 1997), it does not seem in the best interest of individuals to wait an unknown time until a more appropriate individual is encountered. We suggest that most mate choices in *M. ochrogaster* are opportunistic with individuals pairing with the first potential mate encountered. Differences between our field results and those of laboratory studies may be attributed to the short duration of the latter observations (Wolff, 2003).

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