



## Multiple paternity in the bank vole (*Clethrionomys glareolus*): field and experimental data

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### Abstract

The frequency of multiple paternity was estimated in the natural populations of *Clethrionomys glareolus* in northeastern Poland, using enzyme electrophoresis. The percentage of multiply sired litters, those detected and undetected was 35.5 %. A laboratory experiment showed that 30 out of 44 bank vole females mated with two males during one copulatory series (consisting of mounts, intromissions, and ejaculations). Females showed clear preference to finish interrupted copulatory series with the second male, although the interruption of copulatory series did not reduce the chances of pregnancy under laboratory conditions. After the entire copulatory series, all females became non-receptive to any males. We found that under laboratory conditions the number of offspring fathered by the first male did not differ significantly from the number of offspring fathered by the second male. Thus, there are no differences in males' mating success with respect to the mating order in *C. glareolus*. Multiple paternity seems to be a result of social and spatial structure of bank vole populations. It probably evolved as a mechanism to prevent inbreeding.

Key words: *Clethrionomys glareolus*, multiple paternity, mating systems, allozymes

### Introduction

Animal mating systems have been extensively studied for the last few decades (PARKER 1970; SMITH 1984; DAVIES 1991; ARNOLD and DUVAL 1994). Many studies based on protein electrophoresis or DNA fingerprinting showed the occurrence of multiple paternity in a broad variety of animal taxa (SMITH 1984; KAWATA 1988; BURKE 1989; BIRKHEAD and MØLLER 1992; GULLBERG et al. 1997). Multiple paternity can occur when a single female mates with several males within a single estrus period. Such female promiscuity was found in many mammals (SMITH 1984; GINSBERG and HUCK 1989; TEGELSTRÖM et al. 1991; GOMENDIO and ROLDAN 1993; BOELLSTORFF et al. 1994; CLAPHAM and PALSBOELL 1997). Mating systems are regarded as outcomes of the behavior of individuals competing to maximize their reproductive success (EMLEN and ORING 1977). The spatial organization and social behavior of small rodents, as in other mammals, have important consequences for mating systems (IMS 1987; DAVIES 1991).

The bank vole (*Clethrionomys glareolus* Schreber, 1780) is one of the most abundant Palearctic rodent species and its social and spatial structure have been extensively studied (MAZURKIEWICZ 1971, 1983; GLIWICZ and RAJSKA-JURGIEL 1983; BONDRUP-NIELSEN and KARLSSON 1985). Females will not mature unless they occupy an exclusive territory (BUJALSKA 1970). Thus, the mature females of the bank vole have mutually exclusive home

ranges (BUJALSKA 1990; GLIWICZ 1991). Furthermore, the female descendants of one particular female move on to territories as close to the place of birth as possible (VITALA 1977). This results in a kind of family clan system. On the other hand, the spacing systems found in male voles reflect the male reproductive behaviour for obtaining access to the maximum number of fertilizable females (IMS 1987). Home ranges of adult bank vole males are larger than female territories. The degree of home range overlap is high among mature males and male ranges encompass home ranges of several mature females (BUJALSKA 1970; GLIWICZ 1991). Unlike females, only 10% of the male voles settle close to their natal site as reproductive adults (IMS and ANDREASSEN 1991).

There is a clear dominance hierarchy among males in *C. glareolus* (VITALA and HOFFMEYER 1985). Females can discriminate males according to their social rank by odor recognition (HOFFMEYER 1982; ROZENFELD and RASMONT 1991). HORNE and YLÖNEN (1996) showed that postpartum estrus females strongly preferred dominant males for mating, when the female encountered two males: the dominant and the subdominant. However, the authors found that, when the two males were equal in their social status, the females did not show any clear preference for either of the males. Thus, the bank vole females were not simply inclined to mate with a single male, but could be behaviorally receptive to at least two males simultaneously (HORNE and YLÖNEN 1996). Such mating behavior of bank vole females reflects a promiscuous mating system (GLIWICZ 1988) and may imply multiple paternity in this species.

KAWATA (1988) found multiple paternity in *Clethrionomys rufocanus*, a behaviorally similar species to *C. glareolus*. SIKORSKI and WÓJCIK (1990) did not find multiple paternity in a natural population of the bank vole, but they were not able to rule it out. Thus, we decided to re-examine the occurrence of multiple paternity in this species. Firstly, we evaluated the observed frequency of multiple paternity and the paternal exclusion probability in natural populations of the bank vole. Secondly, we estimated males' mating success with respect to the mating order and the frequency of females' multiple matings under laboratory conditions. It is not possible to observe all behavioral events of voles in the wild. Thus, observations of single and multiple matings in the laboratory may allow some conclusions concerning the circumstances of multiple matings under natural conditions.

## Material and methods

Bank voles were collected over the years 1996–1997 in four populations in spring and in one population in spring and summer, in northeastern Poland. Trapping was done during two weeks in every population studied. Number of pregnant females caught in a population ranged from 1 to 19. The total sample consisted of 31 pregnant females (27 in spring and 4 in summer) which brought young (31 litters) in the laboratory. Additionally, 50 immature females and 50 males were captured in autumn 1996 and overwintered in separate cages. They were used for the breeding experiment in spring 1997. Dominance hierarchy among males was not established, as every male was kept in its own cage. Individuals were marked by toe-clipping. Toes were immediately frozen at  $-85^{\circ}\text{C}$  and then prepared as homogenates for genotype screening at phosphoglucosyltransferase-3 locus (Pgm-3). This technique allows to investigate individuals' genotypes at Pgm-3 locus without killing the animals. The tissue samples were run on cellulose acetate plates and stained according to SEARLE (1985). PGM-3 migrates to the most cathodal zone of the PGM system (SEARLE 1985). Alleles were designated by letters from A (the slowest migrating band) to F according to the relative mobility of corresponding bands on the gel.

The genotypes at Pgm-3 locus of wild-caught pregnant females and their laboratory-born offspring were analysed for multiple paternity. Multiple paternity was indicated when more than two different paternal alleles were found in one litter. It should be noted, however, that using a single locus with 6 alleles will underestimate the frequency of multiple paternity in the wild. Furthermore, the analysis of wild-captured females' genotypes and their laboratory-born offspring does not give the possibility to establish the genotypes of the fathers. Thus, there is no data concerning the number of young fathers.

ered by the first and second male in the wild. We estimated the observed frequency of multiple paternity in five bank vole populations studied. Next, we corrected the frequencies of detected multiple paternity by the expected paternal exclusion probability (P), i. e. the probability of detecting an incorrectly assigned parent. Probability P was calculated using the method described by BRUFORD et al. (1992). Calculation of probability P was based on frequencies of six alleles at the Pgm-3 locus in the same five bank vole populations (BORKOWSKA 1999). Next, we used the following formulae to estimate the number and percentage of multiply sired litters (MSL, %MSL; those detected and undetected) in each population and over entire sample:  $MSL = D/P$ , and  $\%MSL = MSL/T$ , where D is the number of observed multiply sired litters, P is the paternal exclusion probability and T is the number of litters tested (GOWATY and BRIDGES 1991).

The laboratory experiment was conducted to establish males' mating success with respect to the mating order and to estimate the frequency of multiple matings by females. Matings occurred between 8.00 and 12.00 hrs in wire-topped plastic cages (50×40×30 cm) containing sawdust. Females in natural estrus and adult males were used. Genotypes at Pgm-3 locus of all voles were known and males were characterized by mutually exclusive genotypes.

Firstly, we established under what conditions an estrus female was behaviorally receptive to two different males. A female was introduced into the cage 30 min before the first male. Pairs that mated within 20 minutes of the introduction of the male were observed until the achievement of satiety criterion of 45 minutes without intromissions (MILLIGAN 1979). Then, the first male was removed and the second male was put into the female's cage. Female and second male were observed for copulation. All the females (27) that mated with the first male until the achievement of satiety criterion formed group A of the experiment.

In the second part of the experiment the first mating male was removed from a female's cage after its one ejaculation. MILLIGAN (1979) noted, there were two ejaculations during whole copulatory series in the bank vole. Thus, the first male had to be removed after its one ejaculation to enable the second male to perform an ejaculation. One to five minutes elapsed between the removal of the first male and females' exposure to the second one. Females that did not perform whole copulatory series with the first males and refused to mate with second males (group B 1) were kept with second males in a cage for 24 hours. Females that continued interrupted copulatory series with the second male were assigned as group B 2. All females that mated with one or two males were observed for 21 days for pregnancy and offspring.

The genotypes at the Pgm-3 locus in young were examined to establish the number of offspring fathered by the first and second male. Differences in males' mating success were tested using Mann-Whitney test (STATISTICA StatSoft Inc. 1995). Chi-square test was used to test females' preferences to mate with a single male or two different males. Differences in the number of litters among three groups of females (group A, B 1, B 2) were tested using Fisher exact test (STATISTICA StatSoft Inc. 1995).

## Results

The analysis of Pgm-3 genotypes in 31 wild-captured females of *C. glareolus* and their offspring revealed that multiple paternity had occurred in at least 7 litters (Tab. 1). This was indicated by the presence of more than two different paternal alleles among the offspring. Multiple paternity was found in every population studied: population 1 – in two out of 15 litters in spring and in one of four litters in summer; population 2 – in one of three litters in spring; population 3 and 4 (both) – in one of four litters in spring and population 5 – in one litter studied in spring. The observed average frequency of litters fathered by more than one male in the five populations all together was 22 % (7 out of 31 litters). The percentage of multiply sired litters (%MSL; those detected and undetected) varied from 21.0 % (in population 1) to 33.3 % (in population 2). Percentage of MSL in the full sample was 35.5 % (Tab. 2).

During the first part of the laboratory experiment we found that a whole copulatory series with the first male (consisting of mounts, intromissions, and two ejaculations) lasted about 50 minutes. Thereafter, all the females from group A (n = 27) became non-receptive and they refused to mate with the second male. In the second part of the experiment

**Table 1.** The genotypes of females and their offspring at Pgm-3 locus and paternal alleles found in litters of wild-caught *Clethrionomys glareolus* from NE Poland.

No.	Mother	Offspring								Paternal alleles
		1	2	3	4	5	6	7	8	
1.	DE	BD	BD	CD	CD	DE	CE	CE	CE	B, C; D or E
2.	DD	BD	DD	DD	DD	DD	DD	DE		B, D, E
3.	DE	BE	BE	BD	CE	DD	EE			B, C, D, E
4.	BD	DD	DD	DD	DE	DE	AB			A, D, E
5.	CE	EE	EE	CE	CE	DE	BC			B, D; E or C
6.	DE	EE	EE	BE	BE	CD				B, C, E
7.	EE	EE	EE	EE	BE	DE				B, D, E

**Table 2.** Number and percentage of multiply sired litters (MSL, %MSL) in five populations of the bank vole from NE Poland. T – number of litters tested, D – number of observed detections, P – the probability of detecting an incorrectly assigned parent, \* ‘Full sample’ indicates values computed over the entire sample of five populations.

Population	T	D	P	No. of MSL	%MSL
1	19	3	0.7522	4.0	21.0
2	3	1	0.6972	1.0	33.3
3	4	1	0.7041	1.0	25.0
4	4	1	0.7590	1.0	25.0
5	1	1	0.7657	1.0	–
Full sample*	31	7	0.6125	11.0	35.5

44 estrus females mated with the first male. When the first male was removed after its one ejaculation and the second male was introduced to the female, animals smelled each other for 5–10 minutes. Then, 30 females (group B2) continued the interrupted copulatory series with a new sire. Fourteen females refused to mate with the second male (group B1). Thus, estrus females showed clear preference to finish interrupted copulatory series ( $\chi^2 = 3.94$ ,  $p = 0.047$ ). One of the females which refused copulation (group B1) was killed by the second male overnight.

Seven out of 27 females (26 %) that performed whole copulatory series with a single male bore young. Eleven females (37 %) from the group B2 had offspring and only one out of 13 females (8 %) that had interrupted copulation with first male (group B1) bore young. However, there were no statistically significant differences in the number of litters between females from group A and group B1 (Fisher exact test,  $p = 0.2477$ ) and group A and group B2 (Fisher exact test,  $p = 0.3619$ ). The Fisher exact test did not show any significant difference between groups B1 and B2 in the number of litters ( $p = 0.1188$ ), either.

The analysis of 11 females that mated with two different males and had offspring, revealed that in four litters pups were fathered by two different males. In one case offspring was fathered by the first male only, and in six litters the second-mating male was the father of all the pups (Tab. 3). The number of offspring fathered by the first male did not differ significantly from the number of offspring fathered by the second one ( $U = 32.50$ ,  $p = 0.0628$ , Mann-Whitney test).

**Table 3.** The number of offspring fathered by the first and the second male of *C. glareolus* born during the laboratory experiment.

Litter	First male	Second male
1.	2	4
2.	4	1
3.	3	2
4.	3	1
5.	5	0
6.	0	5
7.	0	5
8.	0	4
9.	0	4
10.	0	4
11.	0	3

### Discussion

Multiple paternity seems to be a common phenomenon in natural populations of the bank vole. Litters fathered by more than one male occurred in all populations studied, both in spring and summer. SIKORSKI and WÓJCIK (1990) did not find multiple paternity in the bank vole because they studied only two loci with two alleles and one locus with three alleles. Six alleles at phosphoglucosmutase-3 locus (Pgm-3) were found in the bank vole populations from NE Poland (BORKOWSKA 1999). It allowed us to prove for the first time the occurrence of multiple paternity in *C. glareolus*. The average frequency of observed multiple paternity was 22% in the bank vole populations studied. A very similar frequency of multiply sired litters (21%) was found using enzyme electrophoresis in an experimental field population of *Clethrionomys rufocanus* (KAWATA 1988). However, multiple paternity may not always be detected in natural populations, even using the highly variable Pgm-3 locus. This occurs when a female mates with two males possessing identical Pgm-3 genotypes, or males have one Pgm-3 allele in common. Thus, the frequency of detected multiple paternity in *C. glareolus* seems to be underestimated. The percentage of multiply sired litters detected and undetected (%MSL = 35.5%) seems to be a more realistic approximation of multiple paternity frequency in natural populations. This means that at least one out of three females successfully mated with more than one male within a single estrus period. More advanced methods of DNA fingerprinting (GOCKEL et al. 1997) would certainly yield the most precise estimate of the proportion of multiply sired litters in the wild. The basic demonstration of multiple paternity for *Clethrionomys glareolus* in natural populations and under laboratory conditions is convincing, in spite of the fact that we used enzyme electrophoresis. Furthermore, we showed that 30 out of 44 bank vole females trapped in nature mated with two males in the laboratory. This gives the 68% frequency of multiple matings. However, the estimation of frequency of multiple matings under laboratory experiment does not take into account factors such as population density or other demographic factors.

The existence of multiple paternity in *C. glareolus* is closely associated with the social and spatial structure of the population. Bank vole females are able to discriminate males according to their social status and strongly prefer dominant males as mating partners (HORNE and YLÖNEN 1996). A dominant male of *C. glareolus* copulates with an estrus female until she becomes non-receptive and then he leaves her to resume searching. According to our study, a female becomes non-receptive after a whole copulatory series and will not mate with another male. We conclude that mate guarding in the bank vole is re-

stricted to the time of copulation only. However, dominant males cannot monopolize all the females within their area. This is caused by the spatial distribution of individuals in the bank vole populations. The home ranges of males overlap extensively and home ranges of adult females may adjoin or overlap, on average with 13.0 males of *C. glareolus* (SIKORSKI and WÓJCIK 1990; GLIWICZ 1991). Thus, a female may copulate with a subordinate male. If such mating is interrupted by the dominant male, a female will probably finish the copulatory series with him. Therefore, multiple paternity occurred when one male could not deter other males from an estrus female.

In our study we showed that interruption of copulatory series did not reduce the chances of pregnancy under laboratory conditions. It means that one ejaculation may guarantee fertilization of the ova. Why did 68 % of bank vole females continue copulatory series with the second male in the experiment? There are a few hypotheses which may explain the evolution of multiple matings by the bank vole females. GINSBERG and HUCK (1989) suggested that golden hamster females mate multiply avoiding the reduction in fecundity as a consequence of mating with recently mated, sperm-depleted males. Moreover, KAWATA (1988) noted that males of *C. rufocanus* could not successfully mate with more than one female within a day. Bank vole females might tend to mate with several males when males are available thus avoiding temporary male sperm depletion.

On the other hand, mixed-female behaviour probably evolved in the bank vole. BROWN (1997) suggested that females may mate with one male first ensuring fertilization and with a subsequent male to improve offspring quality. This will result in genetic diversification of the brood. Bank vole females that occupy adjoining territories are closely related, because mature daughters establish their home ranges in the vicinity of their mother's range (VITALA and YLÖNEN 1993). In such a case, a promiscuous mating system with multiple paternity seems to be an important mechanism to prevent inbreeding. Furthermore, females may benefit directly by multiple matings. Copulation with the second male may be less costly than resisting (REYNOLDS 1996). Females' refusal to mate with the second male may lead to male harassment. Killing of the female by the second male during laboratory experiment indicates that this may also happen in nature. However, male aggression towards females was rare, as it happened in only one out of 14 cases when females refused to mate.

Mating with every estrus female that males meet appears to be advantageous for males, even if they mate as the second. In our laboratory experiment both males had equal chances of siring offspring ( $U = 32.50$ , ns). However, we were not able to ascertain it in natural populations because we did not know the genotypes of putative fathers. In mammals no differences were found in males' mating success in respect to the mating order when two males mated with a single female close in time (GINSBERG and HUCK 1989). In our experiment spermatozoa from both males were potentially capable of fertilizing the ova at the time of ovulation, so that both males could father the offspring. Furthermore, a copulatory plug is an insufficient barrier to prevent further copulation in the bank vole. This is because the copulatory plug from a previous ejaculation was normally lost from the vagina during the initial intromissions of the next ejaculatory series (MILLIGAN 1979). In our study the second mating males fathered all pups in six out of 11 litters. However, the tendency for the second males to father more young than the first one was statistically insignificant. It should be noted, that due to the small sample size and the necessity of using a non-parametric test, our analysis of the laboratory data has quite low statistical power.

We showed that despite the strong female preference to mate with the dominant male (HORNE and YLÖNEN 1996), multiple paternity occurred in natural populations of the bank vole. It seems to be constrained by social and spatial structures of the populations. It would be of interest to discern whether the frequency of multiple paternity in natural populations is related to other ecological factors such as population density, age structure,

and sex ratio. We conclude that multiple paternity may also occur in Microtine rodents, showing spatial and social structure of the populations similar to the bank vole (BONDRUP-NIELSEN and KARLSSON 1985). Our laboratory results suggest that multiple paternity probably evolved to prevent inbreeding in bank vole populations.

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### Zusammenfassung

#### *Multiple Vaterschaften und Fortpflanzungssysteme bei der Rötelmaus (Clethrionomys glareolus)*

Mittels Enzymelektrophorese wurde die Häufigkeit multipler Vaterschaften in natürlichen Populationen der Rötelmaus (*Clethrionomys glareolus*) aus Nordostpolen bestimmt. Der Anteil von Würfen mit mehreren Vätern betrug 35,5%. Ein Laborexperiment zeigte, daß sich während eines Kopulationsablaufes (bestehend aus Auftreten, Eindringen und Ejakulation) 30 von 44 Rötelmausweibchen mit zwei Männchen paarten. Die Weibchen zeigten eine klare Präferenz, unterbrochene Kopulationsabläufe mit dem zweiten Männchen zu Ende zu führen, obwohl unter Laborbedingungen die Störung eines Kopulationsablaufes die Chancen einer Schwangerschaft nicht reduzierte. Nach dem gesamten Kopulationsablauf wurden die Weibchen gegenüber jeglichen anderen Männchen unempfindlich. Unter Laborbedingungen unterschied sich die Zahl der vom ersten Vater stammenden Nachkommen. Somit hat die Reihenfolge der Begattung bei *C. glareolus* keinen nachweisbaren Einfluß auf den Reproduktionserfolg der Männchen. Die Paarung mit mehreren Männchen mag für Weibchen aufgrund der Vermeidung gelegentlicher Spermadefizienzen oder der Vermeidung von Belästigungen durch Männchen nach dem Kopulationsablauf von Vorteil sein. Die Paarung mit dem ersten Männchen stellt für das Weibchen eine Befruchtung sicher, während der Beitrag weiterer Männchen die Fitness der Nachkommenschaft steigern könnte. Das Auftreten mehrfache Vaterschaften scheint eine Folge der sozialen und räumlichen Struktur von Rötelmauspopulationen zu sein und ist vielleicht im Zuge der Etablierung von Mechanismen zur Inzuchtvermeidung entstanden.

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