

Is the socio-spatial distribution of mound-building mice, *Mus spicilegus*, compatible with a monogamous mating system ?

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SUMMARY

We tested whether the socio-spatial distribution of mound-building mice, *Mus spicilegus*, could be compatible with a monogamous mating system as suggested by several behavioural laboratory studies. A five day trapping session took place in an agricultural field in the Gyöngyös region (Hungary) at the end of April 2000. The species was identified through genetic techniques based on the microsatellite locus *Musmcka*. In total 43 animals were captured, and recapture rate was high (6/10 for males, 17/33 for females). Out of the 33 captured females, 17 were pregnant. Animals were generally recaptured in the same trap. Spatial associations (animals captured in the same trap) were observed between a male and a female (six cases) but also between females (six pairs and two trios) with or without a male. Based on these results we questioned the occurrence of monogamy and we proposed that polygyny could occur at least during the beginning of the reproductive season and in this studied population. Female biased sex-ratio and high population density may have favoured polygyny. However, associations between females could have resulted from the development of strong social bounds during the six months spent together during winter inside the mound. A possible consequence is that polygyny might be restricted to the over-wintering generation.

KEY WORDS :

Mound-building mice,
Mus spicilegus, CMR,
monogamy, socio-spatial
organization.

RÉSUMÉ

Le but de ce travail était de vérifier sur le terrain si la distribution socio-spatiale de la souris glaneuse, *Mus spicilegus*, pouvait être compatible avec la monogamie suggérée par plusieurs études comportementales menées en laboratoire. Nous avons réalisé une session de piégeage sur cinq jours consécutifs à la fin du mois d'avril 2000, dans la région de Gyöngyös (Hongrie). L'espèce est déterminée à l'aide d'un marqueur génétique (Musmcka). Quarante-trois animaux ont été capturés, et le taux de recapture était élevé (6/10 pour les mâles, 17/33 pour les femelles). Dix-sept des 33 femelles capturées étaient gravides. Les animaux ont généralement été recapturés dans les mêmes pièges. Des associations spatiales (animaux capturés dans le même piège) ont été observées entre un mâle et une femelle (six cas), entre plusieurs femelles (six paires et deux trios) accompagnées ou non d'un mâle. Ces résultats nous amènent à remettre en question la monogamie et à proposer l'existence possible d'un système polygyne, du moins au début de la période de reproduction et pour la population étudiée. Le biais du sex-ratio observé en faveur des femelles, ainsi que la forte densité de population pourraient avoir favorisé une polygynie locale. Plus encore, les associations entre femelles pourraient découler de liens sociaux forts s'établissant pendant les six mois d'hivernage commun au sein des tumulus. La polygynie serait alors réservée à cette génération d'animaux hivernants.

INTRODUCTION

Monogamy occurs in only 3 to 5 % of all mammal species (Kleiman 1977 ; Mock et Fujioka 1990). More recent studies suggested a higher incidence of monogamy, especially in nocturnal mammals (see review in Fietz *et al.* 2000), but the proportion remains low compared to birds. According to Trivers (1972) monogamy is common in birds because parental care can be shared by male and female, on the contrary polygyny is most likely to occur in mammals because parental care is mainly borne by females. Males, less implicated in parental care, are able to invest more time and more energy in search of additional matings. Following this assumption, monogamy would have evolved in mammalian species only when paternal care is of a paramount importance for the survival of the young (Fietz 1999). Other authors have proposed monogamy in mammals to be a consequence of the spatial and

temporal distribution of females. Monogamy is imposed on males by sufficiently wide dispersion of females coupled with the synchrony of oestrus (Imms 1988 ; Östfeld 1990). Paternal care may then be considered a possible consequence of a monogamous mating system through promotion of contact between father and offspring (Dunbar 1995 ; Komers et Brotherton 1997).

The mound-building mouse, *Mus spicilegus*, is an outdoor species. Contrary to the well-known polygynous house mouse, *Mus musculus domesticus* (Crowcroft and Rowe 1963 ; Reimer and Petras 1967 ; Lidicker 1976 ; Bronson 1979 ; Gerlach 1990), the mound-building mouse was considered to be a monogamous species. Indeed, studies held on captive animals in laboratory conditions showed that this species displayed several behavioural features characteristic of monogamous species. Females develop a strong social bond with their familiar male following copulation and display a low level of tolerance towards unfamiliar males (Patris and Baudoin

1998). The establishment of a strong social bond following copulation has been shown to characterize monogamous species in voles (Insel *et al.* 1995). Moreover, male and female mound-building mice cooperate in parental care (Patris and Baudoin 2000), and females are very aggressive towards unfamiliar females (Suchomelová *et al.* 1998 ; Patris *et al.* 2002). This social intolerance between females may result in a wide dispersion of females. Nevertheless, no field data gives clear indication as to the mating system of the species. Simeonovska-Nikolova and Gerasimov (2000) realized five-day trapping sessions in an alfalfa field in northern Bulgaria at four periods of the year (April-May, June-July, September and November). Spatial distribution of the mice was documented only for the June-July session, and females appeared to be spatially isolated which may correspond to the intolerance observed in captivity (Suchomelová *et al.* 1998 ; Patris *et al.* 2002). Nevertheless, only a few captured mice (11/147) were identified as *Mus spicilegus* according to craniometrical studies (Gerasimov *et al.* 1990). As the field site was located in a region where *M. spicilegus* and *M. musculus musculus* were sympatric, confusion between the two species remained possible (cf Orsini *et al.* 1983).

The aim of this work was to assess the spatial distribution of mound-building mice, at the beginning of the reproductive period, in order to see whether it was compatible with a monogamous mating system. In other terms, we expected to find exclusive spatial associations between a male and a female, and a wide dispersion of females.

MATERIAL AND METHODS

Animals

The geographical range of mound-building mice extends from south-eastern Austria to Romania and North into Ukraine (Orsini *et al.* 1983 ; Bonhomme 1992 ; Sage *et al.* 1993 ; Sokolov *et al.* 1998). This species is thought to have occupied steppe grassland habitats originally, but due to the extension of farming, mound-building mice are mainly found in agricultural fields (Unterholzner and Willenig 2000). The main

characteristic of the species is its ability to build complex mounds at the beginning of autumn. Several mice born in late summer join together to build a mound, a voluminous heap of seeds and other vegetal materials covered with earth, where they over-winter but do not breed. From genetic analysis of four autosomal and four X-linked microsatellite loci, Garza *et al.* (1997) concluded that individuals in a mound were generally issued from at least two parental pairs which could be consistent with monogamy. The parental pairs were composed of related females and their unrelated mates which suggested females to be more philopatric than males. In spring, mice of six months of age leave the mound and reproduce (Naumov 1940 ; Pisareva 1948 ; Murariu 1981 ; Orsini *et al.* 1983 ; Duryadi 1993 ; Milishnikov *et al.* 1998).

Study site

The site was located in the Gyöngyös region (Hungary), 5 km east of Karácsond in an agricultural area mainly devoted to wine-growing. The exact position of the field site, determined by GPS, was 47° 44.133' N and 19° 58.204' E. The field, almost flat (altitude 165 m), encompassed a sunflower field (100 m × 493 m) surrounded by vineyards. There was a homogeneous clayey soil in the entire study area.

Trapping session

A square grid of 100 traps (traps every 10 meters, trap lines every 10 meters) was disposed, partly in the sunflower field (five lines of ten traps) and partly in a young vineyard (five lines of ten traps). The trap lines were parallel to the vineyard rows. Both fields remained unploughed since the previous summer. The trapping zone encompassed 26 mouse mounds (Figure 1).

A five day trapping session took place between the 24th and 28th of April 2000. The traps (single door and single capture trap, 16 cm × 5 cm × 5 cm, baited with mice pellets UAR type AO4) were opened between 17h00 and 19h00. Traps were checked twice per night. Evening check began between 21h00 and 21h20, approximately an hour after sunset (air temperature : 14.4 °C to 21.4 °C), and ended between 22h00 and 23h00

depending of the number of animals captured. The morning checking began at 6h20 (air temperature : 12.7 °C to 16.5 °C) and ended between 8h20 and 9h45 (air temperature : 20 °C to 25 °C). The traps remained closed during daytime to avoid capture and subsequent overheating of diurnal species such as voles (*Microtus sp.*) in this period, when air temperature reached 28 °C.

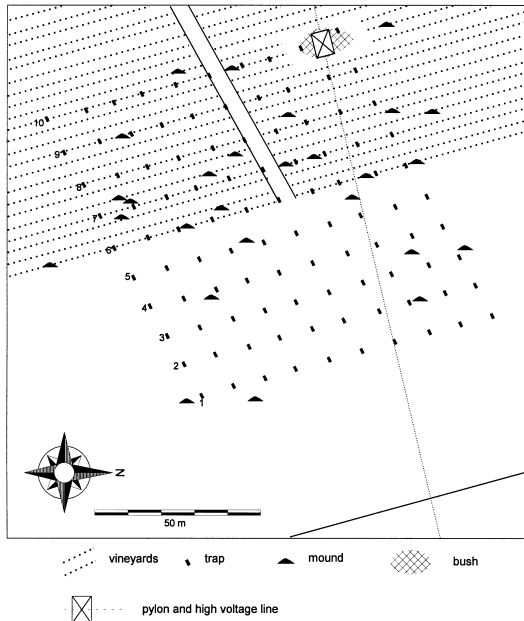


Fig. 1. – Map of the study site showing the trap lines, and the distribution of mounds included in the trapping zone.

Individual marking

Captured animals were sexed, weighted (Pesola spring-scales, precision 0.5 g), and marked for identification. Individual identification was realized by cutting a small piece of the ear (three positions on each ear), which also served for genetic analyses aimed at species identification.

The reproductive state of females (gestation or lactation) was checked. Unpublished laboratory studies showed that the duration of gestation was 21d in the mound-building mouse, like is in house mice (Green 1966), and that visual detection of pregnancy becomes secure only during the last week of gestation. A biometric study

involving 119 mice of 6 months of age born in captivity, which were offspring of animals captured in the Gyöngyös region, showed that males were heavier than females (mean weight \pm s.e. for males and females respectively : 14.5 \pm 0.23 g, N = 60 and 12.5 \pm 0.23 g, N = 59 ; Student's $t = 6.03$, $p < 0.001$) (Gouat and Féron unpublished data). According to these data, we decided to declare that a female was in gestation when pregnancy was clearly observed or when its body weight exceeded the body weight of the heaviest male captured (Figure 2).

After measurements and identification in the field, animals were released at their site of capture and were observed until they disappeared into a burrow. The burrow was then labelled according to the number given to the animal.

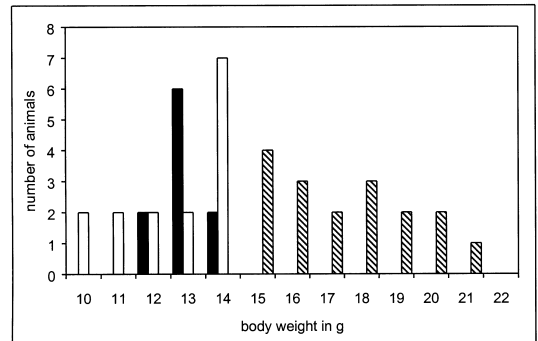


Fig. 2. – Body weight of males (black bars) and females (open and hatched bars) caught in the study site. Females with a body weight exceeding 15 g (hatched bars) were considered to be pregnant.

Species identification

Due to important similarities in their morphology, *Mus spicilegus* and *Mus musculus musculus* are difficult to discriminate in the field. Moreover, preliminary observations performed in the same region during the previous summer have shown that the two species could be captured in the same field. In order to avoid confusion, a genetic identification was performed, based on the microsatellite locus Musmcka showed to be fixed for alternative alleles in *Mus spicilegus* and *Mus musculus* (Duryadi 1993). Total DNA was extracted by Qiamp minikit (Qiagen) from a piece of ear. PCR amplification was performed

according to a standard protocol (Dallas 1992). PCR products were electrophoresed on denaturing gel and polymorphism revealed after autoradiography. All the captured mice were identified as belonging to *Mus spicilegus*.

RESULTS

Evaluation of number of animals present in the study site

A total of 43 mice, 33 females and 10 males, were captured. The number of animals captured per night fluctuated during the trapping session, but the female biased sex-ratio was constant (mean ± SE = 0.77 ± 0.05).

Recapture ratio was 52 % in females, and 60 % in males. Animals were generally recaptured in the following night, and in the same trap (Table 1). When released, mice entered burrows close to the trap (mean distance from the trap ± s.e. = 3.0 ± 0.4 m, n = 38). On two occasions, a mouse made a large circle (> 10 m) around us before entering a hole near the trap. We observed that a mouse may enter a burrow previously used by another mouse.

On the last night of trapping we continued to capture new animals (Figure 3). An evaluation of population size was obtained using the multiple Petersen-Lincoln estimate (Begon 1979) (Table 2). According to this evaluation, 84 % of females and 75 % of males present in the trapping site were captured.

TABLE 1. – Recapture parameters in males and females. Latency is expressed in nights (a value of 1 corresponds to a recapture in the night following the first capture), distance of recapture is expressed in number of intervals between traps (0 means that the animal was recaptured in the same trap, 1 that the animal was recaptured in one of the four nearest traps).

	median latency of first recapture (min-max)	recapture rate number / total number	median distance of recapture (min-max)	median number of recaptures (min-max)
males	1.5 (1-4)	6/10	0.58 (0-2)	1 (1-3)
females	1 (1-4)	17/23	0 (0-3)	1.5 (1-3)

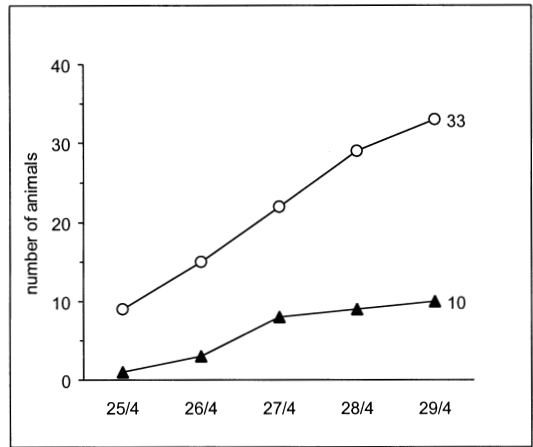


Fig. 3. – Cumulative curve of the number of new males (black triangles) and females (open dots) captured every trapping night.

TABLE 2. – Estimation of population size based on recapture rates observed during the different nights of the trapping session (multiple Petersen-Lincoln estimate). For each trapping night are given the number of animals captured and, between brackets, the number of animals recaptured.

	night 1	night 2	night 3	night 4	night 5	Estimated population size ± s.d.
females	9 (-)	10 (4)	11 (4)	15 (8)	14 (1)	39 ± 7.67
males	1 (-)	2 (0)	6 (1)	3 (2)	8 (7)	13 ± 3.98
total	10 (-)	12 (4)	18 (6)	18 (10)	22 (17)	50 ± 6.43

Distribution of animals

The 80 captures occurred in only 33 of the 100 traps used. This distribution differed significantly from a uniform distribution (one capture per trap and 80 successful traps, $\chi^2 \leq 138.1$, ddl = 1, $p < 0.0001$).

In order to test for the influence of the habitat on the capture rates, we split up the 100 traps into three groups (Table 3). The first group encompassed the five lines of ten traps located in the sunflower field. The second group, labelled border, corresponded to the line of traps located near the first row of vineyards. The last group included the four lines of traps located in the vineyard. Nonparametric ANOVAs on general

scores were performed on the three capture rates (i.e. number of animals captured per trap for males, females and the number of captures per trap), using the exact procedure. When the results were significant, the ANOVAs were followed by pair comparisons using permutation tests and exact procedure (StatXact-3). The border line of traps was more successful than the two other groups. The differences were significant in the male capture rate (ANOVA : $p = 0.005$; permutation tests : border vs. vineyard $p = 0.020$, border vs. sunflower $p = 0.016$) and in the female capture rate (ANOVA : $p = 0.025$; permutation tests : border vs. vineyard $p = 0.006$, border vs. sunflower $p = 0.116$). Nevertheless, the high rates of capture characterizing the border line of traps did not differ significantly from the captures rates of the line of traps with the highest scores for both vineyard and sunflower field (permutation tests : $p > 0.25$) (Table 3).

The presence of a mound within 10 m of a trap did not affect significantly the number of captures nor the number of males captured (Table 4). However, more females were captured in traps with no mound in the immediate vicinity (Table 4). To study the possible interaction between the presence of a mound and the habitat (i.e. vineyards, border, sunflower field), we compared capture rates (mean number of males, females and captures per trap) between traps with and without mound in the vicinity, through a permutation test and a stratification (StatXact-3) according to the type of habitat. None of the comparisons was significant (respectively $p = 0.35$, $p = 0.97$ and $p = 0.97$ for the mean number of male, female and number of capture per trap). In one case, a male mouse was captured four times in the same trap near a mound. When released, the male climbed on the mound to dig out some material and to eat. On one occasion, this mouse entered into a hole in the mound. At the end of the trapping session we dug out several mounds in the vicinity of the trapping zone. Mounds were full of seeds, but no mouse was found inside.

Male and female spatial associations

As the animals appeared to be mostly sedentary and recaptured in the same trap, our defini-

TABLE 3. – Trapping success as a function of the habitat. The mean \pm s.e. number of animals caught (nb males, nb females) and of capture per trap are given for each type of habitat. The best trapping success per line of traps is reported, in italics, for both vineyards and sunflower field. N : number of traps per sample. * : number of females captured in line 7.

	nb males	nb females	nb captures	N
Vineyards	0.10 \pm 0.05	0.28 \pm 0.08	0.50 \pm 0.16	40
<i>Vineyards lines 7* or 9</i>	<i>0.20 \pm 0.13</i>	<i>0.50 \pm 0.22*</i>	<i>0.80 \pm 0.55</i>	<i>10</i>
Border	0.50 \pm 0.17	1.0 \pm 0.26	1.70 \pm 0.42	10
Sunflower	0.10 \pm 0.04	0.42 \pm 0.12	1.86 \pm 0.30	50
<i>Sunflower line 1</i>	<i>0.30 \pm 0.15</i>	<i>1.20 \pm 0.44</i>	<i>3.10 \pm 1.23</i>	<i>10</i>

TABLE 4. – Number of captures and of animals caught (females, males) as a function of the presence of a mound within the 10 m surrounding the trap. The number of traps of each type is indicated in the first line. The statistical results of comparisons between the proportions of captures in the two types of traps are indicated (Pearson's Chi-square statistic, and exact p value) ; * : One female was captured in both type of traps.

	mound		χ^2	p
	present	absent		
nb of traps	58	42		
nb of captures	48	32	0.07	0.88
nb of females *	12	22	5.24	0.03
nb of males	4	6	0.20	0.33

tion of spatial association was restrictive. Only animals captured in the same trap were considered to be spatially associated. Following this operational definition, 15 females were found to be solitary or associated with a single male, and 18 females were included in spatial associations between females (two or three) and between single males and two or three females (Table 5). Associations between females were still observed when only recaptured animals were considered.

No lactating females were captured, and visual diagnosis of gestation was clearly established in only 7 females (body weight 17.5 g to 21.5 g). Females weighing 15 g or more were considered to be pregnant (Figure 2). Following these criteria, spatial associations included several pregnant females (Table 5). However, whenever an association between two females was observed, only one of the two was clearly pregnant.

TABLE 5. – Spatial associations observed during the trapping session for all captured and recaptured animals. The number of females (F) and males (M) is given in the first column. The number of pregnant females is indicated between brackets. In one case (*), a male was associated with two different females, each in a different trap.

	all animals			recaptured animals		
	nb of observations	nb of females	nb of males	nb of observations	nb of females	nb of males
M	2	0	2	1	0	1
F	9	9 (2)	0	7	7 (3)	0
FM	6	6 (5)	5 *	2	2 (1)	2
FF	4	8 (4)	0	1	2 (2)	0
FFF	1	3 (3)	0	1	3 (3)	0
FFM	2	4 (2)	2	1	2 (1)	1
FFFM	1	3 (2)	1	0	0	0
total	25	33 (17)	10	13	16 (10)	4

DISCUSSION

At the time of our trapping session mound-building mice had left the mounds and reproduction had started. The animals appeared to be sedentary. However, the trapping period was too short to determine whether mice might remain sedentary over a long period of time.

The mice were patchily distributed, as revealed by the concentration of captures in only 33 of the 100 traps. Neither the presence of mounds, nor the type of farming (i.e. sun-flower field vs. young vineyard) appeared to influence drastically the spatial distribution of the animals. However, heterogeneous spatial distribution of mice featured by high densities of captures observed at the edge between the two fields suggested an ecotone effect (e.g. Drickamer 1990 ; Koehler and Stanley 1991). Nevertheless, the first line of traps located in the sunflower field had similar or more important capture rates than the border line of traps (Table 3). Hence, heterogeneity in spatial distribution may not be related to habitat heterogeneity but rather to socially-induced spatial associations between animals. In half of the traps where captures had occurred (17/33), two or more animals were captured in the same trap. Solitary females and male-female pairs were observed, which could be compatible with a monogamous mating system. Nevertheless, 55 % of the captured females formed spatial associations

with two to three females, with or without a male. Such associations between females would rather elicit a polygamous mating system (Imms 1988 ; Ostfeld 1990). Moreover, we never captured two males in a given trap which suggested that males avoided each other. Exclusion between males, spatial association between females and a general tendency to be sedentary, strongly suggest a territorial polygynous mating system (Wittenberger 1979).

This conclusion differs from the assumption of monogamy issued from laboratory studies (Patris and Baudoin 1998, 2000 ; Patris *et al.* 2002), from genetic studies on relatedness of animals inside the mounds (Garza *et al.* 1997), and from female dispersion observed in summer in Bulgaria (Simeonovska-Nikolova and Gerasimov 2000). Differences in socio-spatial distribution may be caused by differences in population parameters and affect the mating system in mammals at least at a local level. High densities, which correspond to favourable bioclimatic conditions, may elicit the disappearance of territoriality in favour of hierarchical relationships (e.g. Ferron, 1991). Such a phenomenon could have induced the formation of female associations and favoured a polygynous mating system. In fact the density observed in the present study (52 animals/ha) is high when compared with data reported in the literature (Sokolov *et al.* 1998), but numerous potential sites were left vacant inside the trapping zone, as was shown by the 67 % of traps left

without any capture. Polygyny may also be favoured by a female biased sex-ratio (see Andersson 1994 for review). Such a bias in sex-ratio is not exceptional and has already been reported in several populations of mound-building mice during the reproductive period (Milishnikov *et al.* 1998). The female bias in sex ratio does not appear to have been caused by a sex difference in trapability as male and female recapture rates were similar. Nevertheless we need to replicate this study in other populations before our result could be generalized.

Associations between females implicate a high level of tolerance as observed in the house mouse (e.g. König 1993). However tolerance between females may be affected by reproduction, and intolerance may increase drastically during gestation as shown in solitary ground-squirrel species (Mandier and Gouat 1996). In the present study, none of the captured females were lactating, but several females were gestating. It is therefore possible that intolerance between females may develop only after parturition. Nevertheless, laboratory studies showed that intolerance between female mound-building mice occurred in non-gestating females (Suchomelová *et al.* 1998, Patris *et al.* 2002). Familiarity plays a major role in tolerance (e.g. Bekoff 1981), and intolerance between female mice was demonstrated between unfamiliar animals (Patris *et al.* 2002). In the field, mice spent six months inside the mounds during which cohabitation might elicit the establishment of social bounds between females, strong enough to maintain female association in spite of the advent of reproduction. The philopatry of females, suggested by the data of Garza *et al.* (1997), could reinforce this effect. The next generation will not have the opportunity to develop such social bonds, and intolerance between females may become the rule. We clearly need new data to confirm this assumption, both in the field to check the lack of female association during summer, and in the laboratory to test the relationship between familiarity and tolerance in females.

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