

Deficit in reproduction in polygynously mated females of the monogamous mound-building mouse *Mus spicilegus*

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Abstract. In monogamous mound-building mice *Mus spicilegus*, facultative polygyny was observed in April, at the beginning of the reproductive season. In order to evaluate the cost of polygyny, we compared, under laboratory conditions, the reproductive success of trios and pairs composed of sister females mated with unrelated brother males. Females in trios were able to tolerate each other during the reproductive period and to reproduce with the same male under spatial constraints. Nevertheless, polygyny had a strong negative effect on the reproductive success of the females. The average number of young per litter was smaller in trio females than in paired females, whereas the interval between two successive litters was higher. As a result, the number of litters and the number of young per time unit were smaller in each of the trio females compared with paired females. Agonistic behaviour being absent in trios, our results strongly suggest that living in trios led to pheromonal production that affected the female physiological state and reproduction. Males of trios did not obtain a better reproductive success than males in pairs.

Introduction

Facultative polygyny may occur in monogamous species when some males succeed in monopolising several females (Møller 1986). Polygynous males generally increase their reproductive success compared with monogamous males, whereas females suffer a cost of polygyny (Searcy and Yasukawa 1989; Davies 1993). The decrease of reproductive success in females is considered to be the consequence of a lack of paternal behaviour (brooding, care of young, defence against predators, defence of territory) and of a competition with other females for territory resources (food restriction, nest sites). Previous studies have been performed mainly in birds, where monogamy is common, but other studies encompassed insects (Schlyter and Zhang 1996) and fish (Kokita and Nakazono 2001). Studies in mammals are scarce (Zabel and Taggart 1989; Dietz and Baker 1993; Bouteiller and Perrin 2000; Dobson and Baudoin 2002; Hodges *et al.* 2002), mainly because monogamy occurs in only 3–5% of all mammal species (Kleiman 1977; Mock and Fujioka 1990).

Monogamous mound-building mice provide the opportunity to investigate the effect of polygynous mating on reproductive success. Polygyny was observed in 30% of breeding units, in April, at the beginning of the reproductive season (Gouat *et al.* 2003b). The mound-building mouse *Mus spicilegus* is an outdoor species living in agricultural fields in the steppe zone of central and eastern Europe (Orsini *et al.* 1983; Sokolov *et al.* 1998; Unterholzner *et al.* 2000). Reproduction occurs from March to September. In early autumn,

juveniles from different litters (Garza *et al.* 1997) join to build voluminous mounds composed of seeds, stalks and other vegetal material and covered with earth (Sokolov *et al.* 1998; Unterholzner *et al.* 2000). Beneath the mounds, mice dig tunnels and nest chambers where they overwinter without reproducing (Gouat *et al.* 2003a). At the beginning of spring, mice leave the mounds, disperse and reproduction begins. According to genetic data, males appear to disperse more than females (Garza *et al.* 1997). Facultative polygyny was observed during this period of the biological cycle in a population with a skewed sex ratio exceeding three females for one male (Gouat *et al.* 2003b). Spatial groups of two or three females were trapped and genetic data revealed that sisters or non-sister mice composed these groups (C. Poteaux *et al.*, unpublished data). During the rest of the reproductive season, females are distant from each other (Simeonovska-Nikolova and Gerasimov 2000). Laboratory studies have shown that unfamiliar adult females are very intolerant towards each other (Suchomelová *et al.* 1998; Patris *et al.* 2002). Gouat *et al.* (2003b) suggested that the association between females was made possible by the development of strong social bonds during the 6 months spent together inside the mound. After pair formation, females develop strong and exclusive social bonds with their mates (Patris and Baudoin 1998). Laboratory studies revealed that, compared with house mouse males, mound-building mouse males present an efficient paternal behaviour. Males alternated their presence in the nest with females and, as a result, the young remain less frequently

alone than observed for house mice (Patris and Baudoin 2000). In house mice, common nesting was observed both under natural conditions (Bronson 1979) and in outdoor enclosures (Manning *et al.* 1995; Dobson *et al.* 2000) and common nesting often increased the reproductive success of females (König 1993, 1994a, 1994b).

The aim of the present study was twofold. First, we wanted to test whether familiar and related females were able to share a male and to reproduce as observed in the field. Second, we wanted to evaluate whether females engaged in polygyny have a reproductive success lower than that of monogamous females. Evaluation of the cost of polygyny is not easy under natural conditions because other confounding variables, such as female quality (Grønsetøl *et al.* 2003) or territory quality (Pribil and Picman 1996), are difficult to control (Davies 1993). In order to test whether polygyny is costly for female mound-building mice, we compared, under laboratory conditions, the reproductive success of trios and pairs composed of sister females mated with unrelated males that were brothers.

Materials and methods

The experiments comply with the current laws of France (authorisation 93-006 for PG; authorisation 006399 for CF, Laboratory approval from the Prefecture of Seine Saint Denis, prefectorial decree 02-2651).

Animals and breeding conditions

Experimental animals were derived from a stock of 80 wild mound-building mice caught in three areas in the Gyöngyös region (Hungaria) in October 1999 and bred to the F₂ generation under laboratory conditions (20 ± 1°C and 14 : 10-h reversed light-dark cycle). Food (mice pellets type M20; Special Diet Services, Witham, Essex, UK) and water were provided *ad libitum*. Bedding was composed of sawdust and cotton was provided for nesting material. Mice were weaned at 28 days of age and housed in same-sex sibling groups from 35 days of age.

Formation of reproductive units

Two types of reproductive units were formed: (1) pairs composed of one female and one unrelated male; and (2) trios composed of two sister females and one unrelated male. Before the formation of the reproductive units, animals were isolated (all males and females for pairs) or grouped by two (dyads, females for trios) for a 1 week period, called thereafter the isolation period. The isolation period started at 85 days of age (mean (± s.e.m.) age of males: 84.7 ± 1.2 days (*n* = 48); mean age of females: 85.3 ± 0.7 days (*n* = 72)). On the day of pairing, animals were placed, during the light period, in a polycarbonate cage (43 × 27 × 20 cm) with fresh bedding and cotton. Food and water were provided *ad libitum*. Animals were kept under observation for at least 1 h after pairing and observations were made at various stages during the following dark period.

Females of a given litter were assigned randomly to a pair and a trio, limiting as far as possible the differences in female quality. For similar reasons, males matched with these females were brothers. According to the availability of animals, 24 trios and 24 pairs were set in two successive series, the first one (14 trios and 14 pairs) began between 13 and 27 February and the second began between 21 May and 17 June (10 trios and 10 pairs). Animals used in the two series were all different. Reproductive units were kept under observation over a period of 70 days after pairing and until 15 October if reproduction occurred.

Data analysis

Animals were weighed and checked for sexual state on the day of isolation and on the day of pairing. The sexual state of males was evaluated independently by two experimenters while the male was placed in a transparent box. Testis position was classified as abdominal, scrotal or scrotal plus. In the scrotal plus position, two clearly oval masses were observable, whereas in the scrotal position, the scrotum appeared as a unique mass (Gouat *et al.* 2003a). In adult female mound-building mice, vaginal closure is interrupted by short periods of opening and sexual receptivity (Féron and Gheusi 2003). The vaginal aperture in females was checked while females were held in the hand.

Breeding units were checked daily for reproduction. A non-intrusive inspection was held during the light period and birth was detected by the vocalisations of pups and by looking inside the nest through the bottom of the cage. Every week, nests were opened and the general state of animals was observed in order to detect gestation. The increase in body mass of females became conspicuous in the last week of gestation and the shape of the body was clearly modified. Consequently, we assumed that all gestations reaching the last week were detected and that no spontaneous abortion or cannibalism of new-born could have been missed. The date of birth and the number of pups were recorded. In trios, young were attributed to one or the other female according to suckling marks. When the two females of a trio gave birth simultaneously (24 h interval), half the total number of pups was arbitrarily attributed to each female (six cases in two trios). Young were weaned at 28 days of age. Until weaning, and even after, the mortality rate of the young was very low (<1%) and data at weaning did not reveal any more information. Therefore, in the present study, we only report the number of young at birth.

In order to compare reproduction between trios and pairs, two types of comparisons were made. The first type of comparison tested whether the reproductive success of females was altered by living in trios. We compared reproductive results between females in pairs and the average female in trios. Only reproducing females were considered. The average value of females in trios corresponded to the mean value of the two reproducing females or to the value of the only reproducing female. In the second type of comparison, we tested whether the reproductive success of males increased when mated with two sister females. Therefore, comparisons were made between the two types of reproductive units considered as a whole.

The proportion of successful units (i.e. units where reproduction occurred at least once) was compared between pairs and trios using the Pearson's Chi-squared test and the Exact procedure on StatXact-3 (Cytel Software, Cambridge, MA, USA).

Different reproductive parameters were calculated from the data collected on successful reproductive units. The latency of the first litter corresponded to the delay, in days, between pairing and the first litter. The inter-litter interval was calculated for each female and, in trios, for the entire reproductive unit. The number of young per litter was expressed, for each female, by the number of young in the first litter, the average number and the maximum and minimum number of young at birth. The average number of young per litter was calculated on all litters produced by a female during the period of observation with the exception of the first litter. We excluded the first litter because the number of litters produced differed between the two types of females and the number of young tend to increase between the first litter and following litters.

To evaluate the reproductive success of females, we calculated two ratios: (1) the number of litters per time unit; and (2) the number of young per time unit. The unit of time was 28 days because this is the usual inter-litter interval observed in our breeding stock (P. Gouat and C. Féron, unpublished data).

Comparisons of reproductive parameters and reproductive success between pairs and trios were conducted through permutation tests with the series (i.e. first or second) used as a stratum (StatXact-3; Cytel Software). Permutation tests give the exact probability of occurrence

of such or more extreme distributions than the observed distribution (Mundry and Fischer 1998). Because data of body mass were normally distributed, comparisons were made using the parametric Student's *t*-test in Statistica 5.1 (StatSoft, Tulsa, OK, USA). Data are given as the mean \pm s.e.m.

Results

Isolation period

Most males displayed an abdominal position of the testes on the first day of the isolation period (30/48) and on the last day (25/48). Males tended to gain approximately 10% body mass during the week (13.6 ± 0.4 v. 14.8 ± 0.3 g for first and last days respectively). Most females displayed a closed vagina on both the first day and the last day of the isolation period. The number of females with an opened vagina increased from one to five in isolated females ($n = 24$) and from three to seven in females in dyads ($n = 48$). For a similar body mass at the beginning of the isolation period (mean for each group 12.0 ± 0.4 g), isolated females gained more weight than females in dyads (1.2 ± 0.2 v. 0.7 ± 0.1 g, respectively; $t = 2.28$, $P = 0.03$).

Proportion of successful reproductive units and females

No animal was injured in any of the reproductive units. Animals cohabitated very peacefully and, in the days following pairing, animals built a nest shared by all members of the reproductive unit. Some pairs and trios were kept for more than 6 months without any problem and continued to reproduce.

The proportion of successful reproductive units was higher in pairs (75%; 18/24) than in trios (54%; 13/24), but the difference was not significant ($\chi^2 = 2.28$; d.f. = 1; $P = 0.114$). In the majority of successful trios (85%; 11/13), both females reproduced. However, the proportion of reproductive females was significantly higher in pairs (75%; 18/24) compared with trios (50%; 24/48; $\chi^2 = 14.98$; d.f. = 1; $P = 0.0001$).

Reproductive parameters

Reproductive females of a trio were rarely synchronised (two trios of 11 in which both females reproduced) and first litters may be separated by up to 81 days (mean 22.9 ± 7.8 days).

Compared with the average female in trio (Table 1), females in pairs had their first litter earlier ($P = 0.0007$) and the inter-litter duration was shorter ($P = 0.0453$). The number of young in the first litter and the maximum number of young per litter did not differ significantly ($P > 0.20$), whereas the mean number and the minimum number of young per litter were greater for females in pairs ($P = 0.0451$ and $P = 0.0318$ respectively). The two females of a trio did not differ significantly in their reproductive parameters (data not shown; $P > 0.28$, permutation tests for paired samples) with the exception of the inter-litter interval, which was smaller for the second female, but the difference was not statistically

Table 1. Comparisons between pairs and trios of reproductive parameters

Comparisons were made between females in pairs ($n = 18$) and females in trios (Average; $n = 13$; average of the two reproductive females of each trio or data of the only reproductive female), or the complete trio unit (Total unit; $n = 13$). Data are the mean \pm s.e.m. The average number of young per litter was calculated for all litters produced except the first litter

Parameter	Pairs	Trios	
		Average	Total unit
Latency of first litter (days)	28.44 ± 1.29	41.69 ± 4.82^A	32.00 ± 4.44
Inter-litter duration (days)	27.77 ± 0.43	30.94 ± 2.00^A	18.77 ± 1.46^A
No. young per litter			
First litter	6.39 ± 0.20	6.15 ± 0.45	5.85 ± 0.66
Average	7.72 ± 0.20	6.77 ± 0.50^A	6.76 ± 0.48^A
Minimum	5.83 ± 0.26	4.77 ± 0.53^A	4.08 ± 0.64^A
Maximum	8.61 ± 0.23	7.77 ± 0.56	8.54 ± 0.53

^ADiffers significantly ($P < 0.05$) from Pair data (permutation test with stratification for the period, exact procedure).

significant (34.6 ± 8.3 v. 30.3 ± 7.5 days for the first and second females, respectively; $n = 9$; $P = 0.078$, permutation test for paired samples).

When reproductive units were considered rather than females (Table 1), the latency of the first litter did not differ between pairs and trios ($P = 0.49$) and the inter-litter duration was shorter in trios than in pairs ($P < 0.0001$). The mean number and the minimum number of young per litter were higher in pairs than in trios ($P = 0.0389$ and $P = 0.0059$ respectively). The number of young in the first litter and the maximum number of young per litter did not differ significantly ($P > 0.57$).

Reproductive success

Reproductive success, evaluated through the number of litters per 28 days (Fig. 1) and the number of young per 28 days (Fig. 2), was significantly higher in paired females than for the average females in trios ($P = 0.0033$ and $P = 0.0005$ respectively). Females in trios did not differ significantly between each other (number of litters per 28 days 0.63 ± 0.08 and 0.57 ± 0.05 for first and second females, respectively ($P = 0.445$); number of young per 28 days 3.92 ± 0.65 and 3.68 ± 0.45 for first and second females, respectively ($P = 0.715$); $n = 11$; permutation tests for paired samples).

When the trios were considered as reproductive units (i.e. reproductive successes of both females were added), reproductive success was higher in trios than in pairs, but the difference was significant only in the number of litters per 28 days ($P = 0.0176$; Fig. 1) and not in the number of young per 28 days ($P = 0.2829$; Fig. 2).

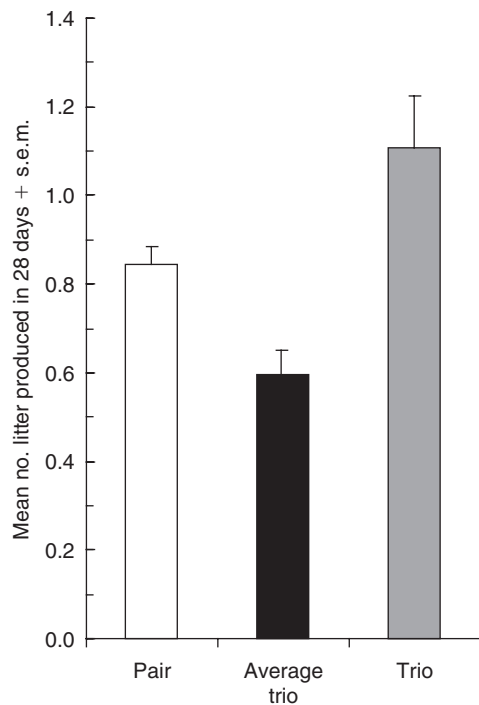


Fig. 1. Comparisons of the reproductive success between pairs and trios, expressed as the number of litters per 28 days. Comparisons were made between females in pairs (Pair) and the average female in trios (Average trio) or the complete trio unit (Trio).

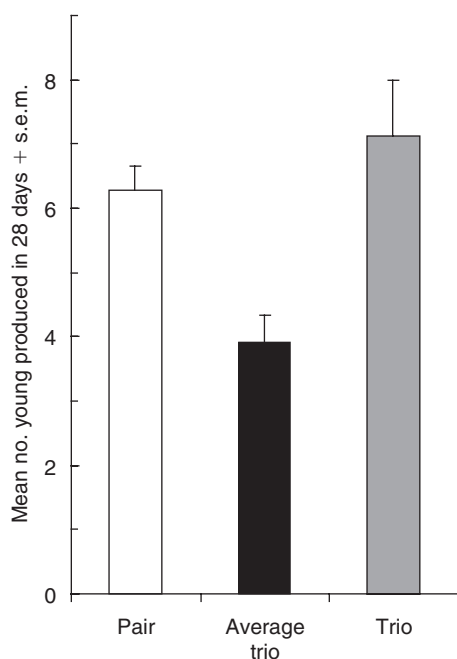


Fig. 2. Comparisons of the reproductive success between pairs and trios, expressed as the number of young produced per 28 days. Comparisons were made between females in pairs (Pair) and the average female in trios (Average trio) or the complete trio unit (Trio).

Discussion

Our data confirmed that two familiar sister females were able to tolerate each other during the reproductive period, as has been observed in the field (Gouat *et al.* 2003b), and that they were able to reproduce with the same male under spatial constraints. This result clearly differed from the intolerance observed between unfamiliar females during dyadic encounters (Suchomelová *et al.* 1998; Patris *et al.* 2002). Familiarity, then, appears to be a key factor in increasing the level of tolerance between females. In a study held in outdoor enclosures (8.8 m²) containing several shelters, females did not associate, whatever their degree of familiarity and relatedness (Dobson and Baudoin 2002). Experiments took place in summer and experimental groups were composed of two or three females (familiar sisters or unfamiliar females) and two or three males (unfamiliar and unrelated). In most of these experimental groups, mortality was high for both males and females and generally only one pair succeeded in reproducing. The main differences compared with the protocol of the present study were the presence of more than one male and the available space. In BALB/c mice, it was shown that aggression was higher in groups of eight males than in groups of three males and that aggression tended to increase slightly with the space available (Van Loo *et al.* 2001). In mound-building mice, unfamiliar males are intolerant of each other, as shown by dyadic encounter experiments (Patris *et al.* 2002). Males are never associated in the field (Simeonovska-Nikolova and Gerasimov 2000; Gouat *et al.* 2003b). Conflict between males may have caused this lack of association between females. However, in a sister experiment performed on house mice under similar conditions (Dobson *et al.* 2000; Dobson and Baudoin 2002), males also excluded each other, but this did not prevent female association and common nesting. Another possible explanation is that with more males and space available, several pairs may have formed in each group, as suggested by Dobson and Baudoin (2002), and that exclusion occurred more between pairs than between females. Solicitations by different males could inform females on the abundance of potential mates and may affect the social relationships of grouped females. New data are needed to test these hypotheses.

In monogamous mammals, intolerance between females and the exclusive use of space during the reproductive season are the rule (Dunbar 1995; Komers and Brotherton 1997). In experimental trios of the monogamous prairie vole *Microtus ochrogaster*, composed of two females and one male, only one female succeeded in breeding. The remaining female was excluded, or even killed (Hodges *et al.* 2002). In golden lion tamarins, associations between females include a female and her daughter. The cost of polygyny is then compensated by an increase in inclusive fitness (Dietz and Baker 1993). In the present experiments, familiarity and relatedness were linked. This is a common situation both in overwintering

groups and in reproducing groups of females (Garza *et al.* 1997; C. Poteaux *et al.*, unpublished data). The respective influence of these two factors on social tolerance between females remains to be evaluated.

In the present study, polygyny had a strong negative effect on the reproductive success of females. The average number of young per litter was smaller in trio females than in paired females, whereas the interval between two successive litters was higher. As a result, the number of litters and the number of young per time unit was smaller in females in trios compared with females in pairs. Both females of trios suffered this loss of reproductive success equally. The proximal factors are not known, but food restriction and stress may be discarded because food was provided *ad libitum*, animals were never injured or in bad shape and some trios continued reproducing after 6 months of common life. In many rodent species, grouping affects reproduction through the increase of agonistic interactions and the pheromonal productions affecting the physiology of individuals (Marchlewska-Koj 1997). Agonistic behaviour was absent in trios and our results suggest that living in trios led to pheromonal productions affecting the physiological state and reproduction of *M. spicilegus*. In house mice, an adrenal-mediated urinary pheromone that inhibits the oestrous cycle under grouping conditions has been characterised (Ma *et al.* 1998). The oestrous cycle of females placed in groups of four to six individuals was significantly perturbed, whereas the oestrous cycle was only slightly affected in pairs of females (Champlin 1971). Female mound-building mice appeared to be more sensitive to female presence than female house mice. As observed in house mice, grouping three or four unfamiliar *M. spicilegus* females spaced out periods of sexual receptivity; furthermore, grouping induced long-lasting vaginal closure and, consequently, a lack of sexual receptivity (Féron and Gheusi 2003). Very sensitive to female closeness, *M. spicilegus* in trios may have reproductive disruption when they cohabit. Because trios and pairs did not differ in the characteristics of first litters (latency and number of young), but in the following litters, we can also hypothesise that pregnancy of the first female temporarily affected the sexual receptivity and pregnancy of the second female. Field data seem to confirm this hypothesis; gestation was detected in only one of the two females in trios during the trapping session (Gouat *et al.* 2003b). Inhibition of pregnancy by other pregnant females has already been described in golden hamsters (Huck *et al.* 1983) and rats (Gudermuth *et al.* 1984). In golden hamsters, inhibition is mainly provoked by the subordinated–dominant relationship (Huck *et al.* 1983). In the rat, there was no physiological indication that females had been under stress. These results suggest that a suppression pheromone was emitted by the first female to become pregnant, causing disruption of reproduction in the other female (Gudermuth *et al.* 1984). A similar phenomenon may be suggested in *M. spicilegus* females placed in trios. Daily investigation of the vaginal

state and collection of vaginal smears could have shed more clear information on these issues, but these procedures may have caused disruption of reproduction. Thus, mechanisms involved in the reproductive impairment in trio females have to be investigated, but their action may promote monogamy in mound-building mice.

One may have thought that mating with two females would significantly increase the reproductive success of males. In fact, under the present experimental conditions, males of trios did not obtain a better reproductive success than males in pairs. In the field, living in trios may have a different effect on the reproductive success of males. Studies in birds have shown that polygynous males may suffer an increase of cuckoldry because of the inefficiency in guarding two distant females (Dunn and Robertson 1993; Freeland *et al.* 1995; Freeman-Gallant 1997; Johnson *et al.* 2002; Pilastro *et al.* 2002; Cordero *et al.* 2003). In mound-building mice, the effect of polygyny on cuckoldry may be cut down. Males acquired females simultaneously and females were able to share a common nest. Moreover, mated females tend to repel unfamiliar males, even during post partum oestrus (Patris and Baudoin 1998). Conversely, living in trios may also have positive effects on the survival rate of the young, as observed for house mice (König 1993, 1994a, 1994b). The mortality of small rodents is high in the field. The death of a female may be compensated, even partially, by the presence of the other female. However, the benefit of the presence of a surrogate mother may be limited, because females of a given trio were seldom in synchrony. Even if common nesting was the rule, the two females were not always lactating during the same period. Parental care displayed by the surrogate mother may then be reduced to a kind of paternal care. Male mound-building mice cooperate efficiently with females. Compared with pairs of house mice, where the male usually followed the female in or outside the nest, male and female mound-building mice tended to alternate their presence with the pups (Patris and Baudoin 2000). As a result, the young were left alone less often, thereby preventing hypothermia, infanticide and predation. The presence of a third adult may increase the efficiency of parental care. Nevertheless, this hypothetical gain of reproductive success must compensate the cost of the presence of supplementary females. Abundant food resources may reduce this cost and, conversely, scarcity of food resources may prevent facultative polygyny, as shown for red foxes (Zabel and Taggart 1989). Cooperation in parental care in trios remains to be studied in order to evaluate its effect on the survival of young under natural conditions.

The cost of polygyny was high for females in trios. Field data show that facultative polygyny occurs in a population with a skewed sex ratio, with three females for one male (Gouat *et al.* 2003b). One may hypothesise facultative polygyny to be a response to the shortage of males: females were making the best of a bad situation. Nevertheless, only 55% of the trapped females were grouped, 27% of females were

solitary and 18% were associated with a male (Gouat *et al.* 2003b). We clearly need more information on the formation of reproductive units to gain an insight into the emergence of facultative polygyny in mound-building mice.

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