



Female competition in wild house mice depends upon timing of female/male settlement and kinship between females

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We assessed the effects of different situational or social determinants on the regulation of female–female competition. We carried out a laboratory study to examine aggression and reproductive success of pairs of wild female mice, *Mus musculus domesticus* spp., as a function of the timing of settlement of females relative to that of males and the genetic relatedness and familiarity between females (sibling versus nonsibling females). After a few days of cohabitation with a male, females were highly aggressive towards, and intolerant of, any intruder female, regardless of relatedness and familiarity. In this condition, monogamy was the resulting mating pattern in approximately 80% of cases. Conversely, pairs of females who made contact with each other at the same time, or prior to cohabitation with a male, showed comparatively little aggression and a high degree of reciprocal tolerance. Only in these latter conditions did genetic relatedness and familiarity between females influence their behavioural interactions and reproductive success. Although nonsibling pairs showed higher frequencies of aggressive interactions than siblings, polygyny resulted in 97% of cases. However, in most sibling groups both the females weaned young and had greater reproductive success than nonsiblings. Nonsibling females appeared to compete for reproduction through the inhibition of reproduction or infanticide. These findings suggest that the timing of male/female settlement in a deme determines the level of female competition, which, in turn, affects the resulting mating pattern. Only when females showed social tolerance did genetic relatedness and familiarity influence reproductive success.

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Based mostly on studies on laboratory strains, female house mice, *Mus musculus* spp., used to be considered nonaggressive and passive towards conspecifics, except when engaging in parental care, the so-called maternal aggression (e.g. Moyer 1974; Mackintosh 1981). However, it is now clear that wild female mice are aggressive in a variety of situations. Aggression by females can be important in the regulation of reproductive potential and population dynamics of house mice social units (Yasukawa et al. 1985; Chovnik et al. 1987; Hurst 1987; vom Saal et al. 1995; Palanza et al. 1996). The timing and context of aggression and its targets appear to differ in females and males (Palanza et al. 1996). More specifically, females appear to become aggressive after short periods of cohabitation with a male and direct attacks mostly towards other females, except during lactation when

males are also attacked. This suggests that females compete either for access to males or for reproductive resources such as space, nest sites or food.

It is thus becoming clear that wild female mice compete for reproductive opportunities. The monopolization of breeding in animal groups has been described as reproductive skew; social groups in which only one individual breeds are considered to have high reproductive skew. In groups with low reproductive skew, group members reproduce more or less equally (Keller & Reeve 1994; Clutton-Brock 1998; Gerlach & Bartmann 2002). For example, both adult breeding and nonbreeding females have been reported in social groups of mice. Lidicker (1976) observed that, under seminatural conditions, 68% of 120 females were reproductively inactive. Furthermore, Gerlach (1990, 1996) showed that female wild mice live in an age-dependent reproductive hierarchy within which a maximum of three females were reproductive and an average of eight were nonreproductive. In highly aggressive wild Canadian mice, females in polygynous groups had lower reproductive success than females in monogamous groups

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(vom Saal et al. 1995) and we observed that only one of two females in 14 polygynous groups reproduced successfully in large artificial territories (Palanza et al. 1996). These findings support the theory that female competition and interference may have consequences for the development of mating patterns, by increasing or restricting the possible range of mating patterns in a population (Ahnesjö & Vincent 1992). Based on existing studies, the degree of reproductive skew in female wild mice appears to be variable and affected by genetic relatedness or familiarity between females (Hurst 1990b; König 1994b; vom Saal et al. 1995).

The social organization of female mice appears, however, to be more complex and variable than the clear-cut territorial dominance observed among males (Hurst 1990a, b). Under natural and seminatural conditions, house mice live in small reproductive units (demes, Berry 1981) consisting of a dominant male (who sires virtually all the litters), one or several breeding females with their offspring, and occasionally some subordinate males (Crowcroft & Rowe 1963; Reimer & Petras 1967; Mackintosh 1981). Males that reach puberty are normally expelled from their natal territories by the dominant male, whereas females can either remain in their natal territories or they can emigrate (Bronson 1979; Gerlach 1996). A high degree of relatedness appears to characterize wild populations of mice (Petras 1967; Selander et al. 1969; Pennycuik et al. 1986; Singleton & Hay 1988). Several studies report that females that share the same territory and nest sites are likely to be closely related (Petras 1967; Lidicker 1976; Pennycuik et al. 1986), but previously unfamiliar (and therefore unrelated) females may also form social groups (Crowcroft & Rowe 1963; Baker 1981). However, the social determinants of female social dynamics remain unclear.

Our primary aim was to assess the effects of different situational and social determinants on the regulation of female–female competition. We examined two main factors: (1) the timing of settlement of females relative to that of males and (2) genetic relatedness (associated with familiarity) between females. We assessed the influence of these variables on aggression and reproductive success of pairs of wild female mice. Our objective was to mimic the emigration of females from their natal territories, which is considered a common event in natural populations of house mice (Berry 1981; Gerlach 1990, 1996). Females can immigrate into an established deme or establish a new deme with siblings who might have emigrated with them or with unfamiliar females (Gaines & McClenaghan 1980).

METHODS

Animals and Husbandry

We used laboratory-born second-generation offspring of wild house mice, *M. m. domesticus*, captured with Sherman live traps in different rural habitats near Capalbio, Tuscany, central Italy. Traps were furnished with apple and seeds to provide water and food, and were ventilated, thus

preventing excessive temperature and humidity. They were set after sunset, at 2000 hours, and were checked twice: at midnight and at 0600 hours. All of the 198 mice trapped were found in good health.

The trapped mice were transferred to our laboratory and housed as reproductive pairs in cages (40 × 20 cm and 15 cm high). We decided to use laboratory-born second-generation offspring to ensure similar developmental and environmental rearing conditions for all experimental subjects. After weaning (28–30 days after delivery), mice were housed with same-sex siblings (two to four per cage) in Plexiglas cages (40 × 20 cm and 15 cm high) at 20–22°C on a 12:12 h light:dark cycle with lights on at 0800 hours. Noise in the animal room was minimized and mice were disturbed as little as possible while being cleaned, watered and fed (MIL Morini, rodent chow, Reggio Emilia, Italy). We used 156 virgin females and 78 sexually naïve males (90 days old).

All animals had been marked by ear punch (diameter ≤ 0.1 mm, Kent Scientific Co., Torrington, CT, U.S.A.) and individually housed in a cage measuring 27 × 13 cm and 12 cm high, for the 24 h preceding introduction into the experimental apparatus. In a pilot study we had evaluated identification methods, specifically, fur shaving, nontoxic dyeing of fur and ear punching. Based on subsequent behaviour of marked mice (immobility, self-grooming, jumping, etc.) and duration of the identification procedure, we concluded that ear punching was the least stressful and most reliable for a long-term study (personal observation). None of the mice showed bleeding or infection following this procedure. The mice were isolated for 24 h to allow recovery from handling. In laboratory mice, 24 h of isolation is not a stressful experience, judging by behaviour and corticosteroid levels (Bartolomucci et al. 2003).

Apparatus

Each enclosure consisted of two lateral Plexiglas chambers (each 40 × 20 cm and 15 cm high) and a central cage (27 × 13 cm and 12 cm high) connected by a transparent T tube that could be closed by removable barriers (Fig. 1). Sawdust covered the bottom of every cage. Food (MIL Morini rodent chow, Reggio Emilia, Italy) and water were available ad libitum and placed on the standard wire lids covering both the lateral cages. Straw nesting material was supplied in the central cage. Each lateral chamber contained two polypropylene tubes to provide cover to mice during encounters.

The external side of the lateral cages had an opening, closed by a removable partition, which could be connected to a polypropylene tube, thus facilitating introduction of mice into the territories without handling.

Experimental Procedure

We designed four experimental groups, according to different possible situations in which one male and two females can establish a basic deme, thus mimicking the possible natural establishment of social groups. Each of

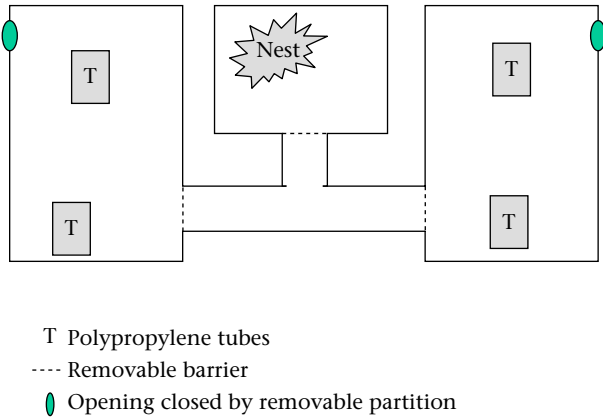


Figure 1. Plan of the layout of the experimental apparatus, consisting of two lateral chambers (each $40 \times 20 \times 15$ cm) and a central cage ($27 \times 13 \times 12$ cm) connected by a transparent T tube. See text for details.

these experimental conditions (Table 1) was further divided into two subgroups based on female genetic relatedness and familiarity. In one subgroup, the two females were genetically related and familiar and had been housed together throughout life. In a second subgroup, the two females were unrelated and unfamiliar; they had been housed apart and were born from parents that had been trapped at different sites.

Condition 1 (C1): a female was paired with an unfamiliar adult male in the apparatus. After 5 days of cohabitation (day 6), each pair met a female intruder that was either a sibling (S) or a nonsibling (NS) of the resident female ($N = 11$ each).

Condition 2 (C2): one unfamiliar adult male mouse was introduced into the apparatus. After 5 days, two females, S or NS ($N = 9$ each), were simultaneously introduced into the apparatus.

Condition 3 (C3): two females, S or NS ($N = 9$ each), and an adult unfamiliar male were simultaneously introduced into the apparatus.

Condition 4 (C4): two females, S or NS ($N = 9$ each), were simultaneously introduced into the apparatus. On day 6, an unfamiliar adult male mouse was introduced.

Female mice are able to recognize their cagemates after 7 days of separation (D'Amato 1997) and in a preliminary test we found that wild female mice were able to discriminate

Table 1. Scheme of the procedure of introduction of a male and two females into the experimental apparatus in relation to the experimental condition (C)

Experimental condition	Introduced on day 1	Introduced on day 6
C1	M+F	F
C2	M	F+F
C3	M+F+F	—
C4	F+F	M

For each experimental condition, half of the females were familiar siblings and half unfamiliar nonsiblings. M = male; F = female.

siblings from nonsiblings after 6 days of separation. We individually housed a female in the experimental cage and introduced an S or NS female into the apparatus on day 6 ($N = 8$ each). Both S and NS females showed little aggression (2/8 S and 3/8 NS) with two to seven attacks during 6 h of observation. Attacks were characterized by light bites without visible signs left on the fur of the attacked animal. Sibling females showed significantly less social investigation than NS females (Mann-Whitney test: $U = 5.00$, $N_1 = 8$, $N_2 = 8$, $P = 0.01$). This finding confirmed that females were able to discriminate siblings from nonsiblings after 6 days of separation. After 6 h, all the females, S and NS, appeared to have socialized and shared the nest, with no further aggression recorded.

All mice were individually identified by an eartag, punched on the day before being introduced into the enclosure. Within each condition, females in each pair were matched for age and weight. Mice were introduced into the apparatus via a polypropylene tube connected to the opening in the lateral cages. When two mice were introduced simultaneously (conditions 2 and 4), they were placed in the lateral chambers (one per cage) while the resident animal was confined in the central cage. In C3, the two females were introduced into the lateral cages and the male into the central one. When only one mouse was introduced, it was placed in a lateral chamber where no other animal was present. After 10 min, barriers were removed allowing the animals to interact. The experiment was performed in two replicates (one in May–July and the other in August–October).

Behavioural Observations

Whenever two females were placed together, we observed them continuously for the first hour and then continued for 6 h afterwards to check whether aggressive interactions occurred (instantaneous sampling every 5 min). Previous experiments indicate that the likelihood of severe and potentially lethal attacks in wild mice is limited to the first few hours after the first social contact (Palanza et al. 1996). For C1, C2 and C3, recording of behaviour started when the two females and the male were caged together; for C4, observations were made both when the two females were placed together in the apparatus and when the male was subsequently introduced.

We recorded the following behaviours: proportion of animals attacking, number of aggressive interactions, frequency of social investigation, submissive postures and tail rattling. Data on females' behaviour are expressed as pair, not individual, scores. The actor of any behaviour was recorded. To avoid exposing females to prolonged chases and aggression episodes (longer than 10 s), even if not severe, an observer was ready to break up prolonged fighting by gently interposing a stick between the animals and allowing the attacked animal to flee (about 15 fights were interrupted this way). We removed mice that were persistently and severely attacked (i.e. when the attacked mouse started showing visible signs of bites). In these

cases we considered the attacked female as nonaccepted and the attacking female as an intolerant dominant. None of the removed mice ($N = 7$, during the first hour; $N = 12$, during the following hours or days) was seriously injured and, after removal, they were returned to their original sibling group in the breeding room.

In the following 9 days, we randomly observed activity in each enclosure for 1 h, four times a day (at 0800, 1200, 1600, 2000 hours). Occurrences of aggressive interactions, tolerance and socialization responses (such as sharing the nest, huddling), were recorded. Dominance in female pairs was assessed on the basis of the higher/lower frequency of aggressive behaviour and/or submissive postures.

From day 10 to the end of the study, cages were examined daily (once every 4 h between 0700 and 2300 hours) for the presence of pregnant or parturient dams and newborn pups. While minimizing disturbance of parturient females, we noted litter size shortly after birth to evaluate survival of young. We considered six indices of reproductive success, namely: proportion of groups in which both the females became pregnant and delivered pups, proportion of pairs in which both females successfully weaned young (i.e. they had at least one pup surviving to postnatal day 18–20), the time until the first litter was born, the time elapsed between first and second female to deliver (in polygynous groups), mean litter size around weaning (18–20 days of age) as calculated both per number of females present and per group, and survival rate of offspring (weaned pups/born pups).

Throughout the study, we tried to minimize disturbance of the mice and interference in their social equilibrium. In all the cases in which two females were left in a group for reproduction, they had ceased any agonistic interactions, showed amicable behaviour and shared the nest. No predictors of possible litter destruction after birth were detected. However, as infanticide of newborn young has been reported when wild female mice are housed together (König 1994a, b; vom Saal et al. 1995; Palanza et al. 1996), we took a series of measures to prevent harm of newborn mice. First, we increased the observations around the expected birth time, when infanticide is most likely to occur (e.g. König 1994a, b; Palanza et al. 1996). Thus, we continuously observed females' behaviour towards pups for at least 6 h after we found pups, and we checked on them every 4 h afterwards from 0700 to 2300 hours. In cases of aggression towards the pups, we interrupted the experiment by separating the females (with their litters) and considered the reproductive output as zero for calculation of survival rate and reproductive success ($N = 10$). Injured pups were immediately euthanized by inhalation of increasing levels of carbon dioxide, while the remaining pups were given to their mothers, which were housed singly. Each reproductive unit was kept until young were 18–20 days old, up to 80 days after male introduction. After the experiment, mice were returned to the breeding colony.

The Italian World Wide Fund for Nature granted permission to trap the mice within the Oasi of Burano (GR, Italy) and the study was conducted under a licence from the Italian Ministry of Health.

Data Analysis

We compared the proportions of animals/groups showing a behaviour (aggressive interactions, tolerance and reproduction) with the Fisher's exact probability test (two tailed) or chi-square test, depending on the sample size. Behavioural interactions between females in C1 were analysed with a two-tailed Mann–Whitney test. As severe attacks resulted in the premature termination of testing by removal of the intruder female, behavioural data were calculated as a proportion of actual observation time and are presented as a rate (frequency/min).

Dependent data (e.g. birth order within female dyads; number of pups weaned by dominant and subordinate females within each group) were analysed with the Wilcoxon paired test (two tailed). Data on the number of offspring weaned and survival rates of offspring were analysed with a two-factor ANOVA (experimental condition and kinship between females; Statview, SAS institute Inc., Cary, NC, U.S.A.). We used a Tukey highly significant difference (HSD) test for binary contrasts.

RESULTS

All scores were pooled, because no significant differences were found between the two test replicates in terms of recorded behavioural responses and reproductive success.

In 57 of the 76 groups the two females tolerated each other, whereas in the remaining 19 groups (mostly C1 groups), the second female was not tolerated. As a result, we obtained 57 polygynous groups (two females and a male) with familiar sisters ($N = 30$) or previously unfamiliar, unrelated females ($N = 27$), and 19 monogamous groups. Litters were born in 73 of the 76 reproductive groups and 114 of the 152 females used in the study (133 females were present for breeding) gave birth, with 83 females successfully weaning young.

Mean litter size at weaning per reproductive group \pm SE was 4.89 ± 0.54 in monogamous groups and 5.94 ± 0.61 in polygynous groups (ANOVA: $F_{1,74} = 0.93$, $P = 0.33$), but in the latter condition sibling females weaned more offspring (8.16 ± 0.79) than nonsiblings (3.48 ± 0.70 ; $F_{1,55} = 19.17$, $P < 0.0001$). Mean litter size \pm SE per female present for breeding was 4.89 ± 0.57 in monogamous groups and 2.97 ± 0.26 in polygynous groups ($F_{1,131} = 7.98$, $P < 0.01$). In polygynous groups, mean litter size for a female cohabiting with a sibling was significantly higher (4.08 ± 0.33) than for nonsiblings (1.74 ± 0.34 ; $F_{1,112} = 24.29$, $P < 0.001$).

Loss of delivered pups was recorded in 31 of the 73 groups in which litters were born. More specifically, loss of pups occurred only in polygynous groups, and mostly in nonsibling female groups (nine cases in S and 22 cases in NS groups; $\chi^2_1 = 9.2$, $P = 0.002$). In two cases, the pups were not cared for by the mother. The mean survival rate of offspring (pups weaned/pups born) \pm SE was 0.94 ± 0.05 in monogamous groups and 0.63 ± 0.05 in polygynous groups (ANOVA: $F_{1,71} = 9.54$, $P < 0.005$). In polygynous groups, survival of offspring was higher for

S ($\bar{X} \pm \text{SE} = 0.81 \pm 0.06$) than NS female pairs (0.38 ± 0.07 ; $F_{1,54} = 20.85$, $P < 0.001$).

Aggression and Socialization

Experimental condition influenced the proportion of female pairs showing aggression during the first hour of observation (Fig. 2a). In C1, a high proportion of female pairs, both sibling and nonsibling, showed aggressive interactions, whereas in the other experimental conditions (C2, C3, C4), no S and few NS pairs showed aggression (C1 versus C2, C3 or C4 for S subgroups, Fisher's exact test: $P = 0.0003$; NS subgroups: $P = 0.0005$).

Table 2 summarizes data on behavioural interactions between females in C1. Although behavioural data are expressed as pair scores, the actor of agonistic behaviours was always and only the resident female. The residents' responses towards S and NS intruder females did not differ for any of the behavioural parameters recorded (i.e. latency to attack, rate of attacks, tail rattling and social

investigation; see Table 2 for statistics). Owing to the very high rate of attacks, in seven groups ($N = 3$ S and 4 NS) we removed the female intruder before the 1-h observation time to avoid the possibility of injuries.

In the following 9 days, sporadic aggressive interactions were recorded between NS females in all the experimental conditions (Fig. 2b). A significant difference (Fisher's exact test) in the occurrence of aggressive interactions between S and NS pairs in C2 ($P = 0.009$), C3 ($P = 0.003$) and C4 ($P = 0.029$) was recorded. Aggressive interactions were seen only during the first 6 days after introduction; after this time, aggressive episodes were not observed.

In C1, the second female was generally removed within a few hours after the intrusion, because she was continuously and vigorously attacked and would probably have been killed (Fig. 3a). As a result, eight S (73%) and nine NS (82%) intruder females were not tolerated.

Conversely, both the females, S and NS, generally shared the enclosure in the other conditions with the exception of one NS female that was not tolerated in C2 and C3 (Fig. 2a). In these conditions, all S females and the majority of the NS females shared the nest in the following days.

We do not report any data on male behaviour, as no difference in male behaviour related to experimental condition or females' genetic relatedness was observed. Males were generally socially and sexually oriented towards both the females.

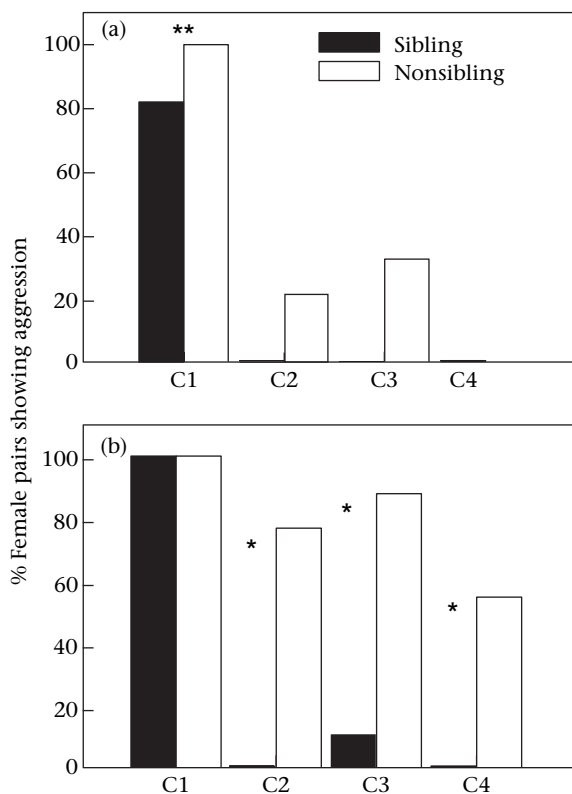


Figure 2. Percentage of female pairs in different experimental conditions (C) showing aggressive interactions: (a) during the first hour of observation; and (b) during the following 7 days of observation (random daily observation). C1: a female cohabited with a male in the territory; the other female was an intruder; C2: two females were simultaneously introduced into a territory already occupied by a male; C3: two females and a male were simultaneously introduced into a territory; C4: two females cohabiting in the territory prior to introduction of the male. In (a) $**P < 0.01$, C1 versus C2, C3 or C4 (sibling and nonsibling females); in (b) $*P < 0.05$, sibling versus nonsibling females in C2 ($P < 0.03$), C3 ($P < 0.005$) and C4 ($P < 0.03$).

Reproductive Success

The dominant female in each pair was considered to be the one that was aggressive towards the other female during the first 10 days of observation. This distinction was possible in all but one of the C1 groups and, in the other experimental conditions, in two out of 27 sibling pairs and in 14 out of 27 nonsibling pairs. In C1 groups (because of the asymmetric contest), the resident female was dominant and reproduced successfully, whereas the intruder female was either not tolerated or did not reproduce. In the other three conditions (polygynous groups), dominance appeared to have no effect on a female's reproductive success ($N = 16$ groups). Mean litter size at weaning for females classed as dominants \pm SE was 2.1 ± 0.57 (total 42 pups) and for subdominants 2.9 ± 0.68 (total 50 pups; Wilcoxon test: $Z = -1.156$, $P < 0.24$). Not taking into account intolerant dominant females, mean reproductive skew (pups weaned by the dominant female minus pups weaned by the subordinate female in each group) \pm SE was -1.0 ± 1 . Table 3 summarizes the data on reproduction relative to each experimental condition, the status of relatedness and social status of the females (intolerant, dominant, subordinate or equal). In polygynous groups, nonsibling females generally established a dominant-subordinate relationship (16 nonsibling groups versus four sibling groups), whereas sibling females typically established egalitarian relationships (26 sibling groups versus 11 nonsibling groups). No difference was found in the time between group formation and pup delivery between

Table 2. Behaviour of pairs of females in C1 (i.e. a female had cohabited with the male for 6 days; the other female was an intruder) during a 1-h observation period

	Latency to attack (s)	Rate of attack (frequency/min)	Rate of tail rattling (frequency/min)	Rate of social investigation (frequency/min)
Siblings ($N=11$ pairs)	720 (1–3600)	0.20 (0–1.5)	0 (0–0.45)	0.05 (0–0.47)
Nonsiblings ($N=11$ pairs)	300 (1–2100)	0.26 (0–1.91)	0.06 (0–0.28)	0.5 (0–0.13)
Mann–Whitney test				
Z	–1.31	–0.95	–0.13	–0.73
P	0.18	0.34	0.89	0.46

Median and range (in parentheses) are given.

dominant ($\bar{X} \pm SE = 25.36 \pm 1.21$ days, $N = 19$) and subordinate (26.83 ± 1.21 days, $N = 12$) females, whereas intolerant females had longer times (32.47 ± 3.36 , $N = 17$) than dominant, subordinate or equal (24.90 ± 0.52 , $N = 64$) females (Tukey HSD test: $P < 0.05$).

In C1, the intruder female was not tolerated in the majority of cases; therefore, only one female in each reproductive group gave birth, regardless of genetic–social relations. In the three S and two NS female groups where the second female was tolerated, both females were pregnant in only one group for each category (Fig. 3b). In the other three conditions, the two females of each group were generally tolerant towards each other and shared the enclosure and the nest. In C3 and C4, both the females, siblings and nonsiblings, became pregnant and delivered pups. Conversely, in C2, there was a higher proportion of S than NS pairs in which both females were pregnant (Fisher's exact probability test, two tailed: $P = 0.049$).

In C1, both females successfully weaned young in only one of 11 sibling groups (Fig. 3c). In both C2 and C3, sibling females were both successful in reproduction (weaned at least one young), whereas in nonsibling pairs only one or none of the two females within each group weaned pups (Fisher's exact test: C2: $P = 0.048$; C3: $P = 0.018$). In C4, where the two females cohabited in the enclosure prior to introduction of the male, no significant difference was found between S and NS females (Fisher's exact test: $P = 0.13$).

Experimental condition, but not kinship between females, significantly affected the time elapsed from pair/group formation until the birth of the first litter in each reproductive group (ANOVA: $F_{3,64} = 7.61$, $P < 0.0002$). Specifically, females in C1 took longer to give birth to the first litter (32.7 ± 3.03 days) than females in C2 (25.52 ± 0.69 days; Tukey HSD test: $P < 0.01$), C3 (22.77 ± 0.37 , $P < 0.001$) and C4 (22.38 ± 0.25 , $P < 0.001$). Females in C2 also showed longer intervals until the first litter was delivered than females in C3 and C4 ($P < 0.005$). In C2, C3 and C4 polygynous groups where both females were pregnant, a significant interaction between experimental condition and kinship was found on the time between the first and the second female to give birth ($F_{2,31} = 3.57$, $P < 0.05$). While sibling females in the three conditions did not differ significantly (C2: 2.7 ± 1.7 ; C3: 2.8 ± 0.95 ; C4 4.5 ± 1.8 days), nonsibling females in C3 showed a longer interval between litters (6.2 ± 1.15 days) than NS females in C4 (2.0 ± 0.59

days; Tukey HSD test: $P < 0.02$; C2 was not considered for comparisons as both NS females were pregnant in only two cases).

The mean number of pups born did not differ between conditions or kinship between females. The mean number of offspring reaching weaning (Fig. 4) was calculated either for each group or for each female present in each group (not taking into account females that were not tolerated; C1: $S = 14$, $NS = 13$; C2: $S = 18$, $NS = 17$; C3: $S = 18$; $NS = 17$; C4: $S = 18$; $NS = 18$) and was analysed by two-factor ANOVA. We observed a significant main effect of kinship between females, but not of experimental condition, on the number of weaned young per reproductive group ($F_{1,68} = 16.53$, $P < 0.001$) or per female within a reproductive group ($F_{1,125} = 13.79$, $P < 0.001$). In this latter case, a nonsignificant tendency for an effect of experimental condition was also found ($F_{3,125} = 2.07$, $P = 0.10$). In both cases, binary comparisons showed a significant difference in the mean litter size between S and NS females in C2 (Tukey HSD test: $P < 0.01$) and C3 ($P < 0.02$), but not in C1 ($P = 0.53$) and C4 ($P = 0.24$). The mean litter size at weaning for each reproductive group (i.e. the male reproductive output) tended to be higher for S females in C3 (Tukey HSD test: $P = 0.056$) and C4 ($P = 0.097$) than in C1, but did not differ in relation to the experimental condition for NS females. The mean litter size at weaning for each female present did not differ in any experimental condition for S females ($0.34 \leq P \leq 0.97$), whereas NS females weaned significantly fewer pups in C2 (Tukey HSD test: $P < 0.02$) and C3 ($P < 0.05$), but not in C4, relative to C1.

Mortality of pups was significantly higher in NS than in S female groups ($\chi^2_1 = 9.2$, $P = 0.002$; Fig. 4). We observed aggressive behaviour of a female towards newborn pups in 10 cases, in which we interrupted the experiment. In these cases, not all of the pups died but they were considered as dead in the data analysis ($N = \text{ca. } 79$). In all remaining cases, we did not observe any direct attack on the pups, but we recorded either the loss of an entire litter at birth or the loss of some pups within litters; we recorded the disappearance of about 85 pups (i.e. over a total of 113 adult females). Loss of pups occurred mainly some days after parturition and we did not detect any predictors of this event.

The survival rate of offspring (pups weaned/pups born) in each group was affected by experimental condition (ANOVA: $F_{3,65} = 3.30$, $P < 0.05$) and kinship ($F_{1,65} = 9.32$,

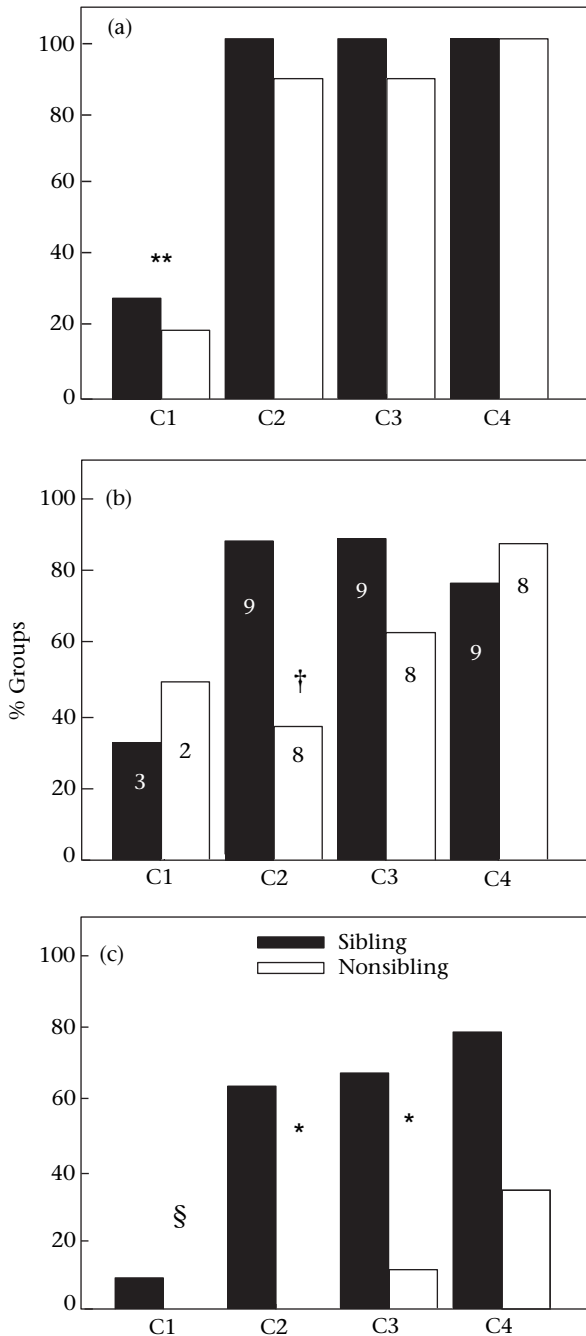


Figure 3. Percentage of groups in which: (a) the two females tolerated each other (i.e. percentage of polygynous groups); (b) both females became pregnant and delivered pups (only polygynous groups were considered; numbers in the bars indicate the number of polygynous groups for each experimental condition); (c) two females reproduced successfully (had at least a pup weaned), as calculated for all the reproductive groups. In (a) $**P < 0.01$, C1 versus C2, C3 or C4 (for sibling and nonsibling females); in (b) $\dagger P = 0.049$, sibling versus nonsibling females in C2; in (c) $*P < 0.05$, sibling versus nonsibling females in C2 and C3; $\S P < 0.05$, C1 versus C2, C3 or C4 (for nonsibling females). See legend to Fig. 2 for explanation of experimental conditions C1–C4.

$P < 0.005$; Fig. 5). While rates of offspring survival did not differ in relation to the experimental condition for S female groups ($0.41 \leq P \leq 0.93$), offspring of NS females had higher survival rates in C1 than in C2 (Tukey HSD test: $P < 0.05$) and C3 ($P < 0.01$), but not in C4 ($P = 0.13$) groups. Survival rates of offspring were higher for S than NS females in C3 ($P < 0.02$) and marginally in C2 ($P = 0.10$), but no significant difference was found between S and NS in C1 ($P = 0.68$) and C4 ($P = 0.12$).

Birth order between the two females in a pair (over those groups where two females were present) affected reproductive success in NS but not in S pairs, independent of experimental conditions. In 24 S pairs where both females gave birth, the mean number of offspring weaned did not differ as a function of birth order ($\bar{X} \pm SE = 4.62 \pm 0.49$ first-born versus 4.50 ± 0.42 second-born offspring; Wilcoxon test: $Z = -0.43$, $P = 0.66$). Conversely, over the 16 NS pairs where both females gave birth, the mean number of pups per first-born offspring weaned was 1.12 ± 0.52 versus 3.37 ± 0.74 in second-born litters (Wilcoxon test: $Z = -2.43$, $P = 0.015$). In the majority of cases, complete or partial loss of the litter of the first female to deliver pups was observed.

Communal nursing

When two nursing litters were present in a polygynous group at the same time, S females always combined their litters in communal nests and both the females were seen nursing the pups at least once. In NS polygynous groups, a high proportion of litters disappeared shortly after birth and thus two nursing litters were seldom present at the same time. Two nursing litters were never simultaneously present in C2; females pooled their litters in communal nests in the only case where two litters were simultaneously present in C3, and in two of four cases in C4. When only one female gave birth or the entire litter of a female was destroyed and thus only one female's litter was present, the two females shared the nest in all but two C2 S polygynous groups, in three of five C4, three of five C4, three of eight C2 and in five of seven C3 NS groups.

DISCUSSION

Our results suggest that the timing of settlement of females, either before, at the same time as, or after male settlement is important in determining a female's behaviour towards other females, as well as in the impact that relatedness (associated with familiarity) between females would have on reproductive success. Furthermore, timing of settlement and relatedness both appear to influence the resulting mating pattern, that is, whether more than one female would reproduce, in other words, whether monogamy or polygyny would occur.

Females that had cohabited with a male for 5 days (and were thus 'resident' in a male's territory) were highly aggressive towards, and intolerant of, other introduced females, either siblings or nonsiblings (C1). In this condition, monogamy was the resulting mating pattern

Table 3. Data on reproduction relative to each experimental condition (C) and status of relatedness (S: sibling; NS: nonsibling) and social status of the females (INT: intolerant; DOM: dominant; SUB: subordinate; EQU: equal)

Kinship (no. of pairs)	Number of females of different social status				Number of females giving birth				Number of pups born/female ($\bar{X} \pm \text{SEM}$)				Number of pups weaned/female ($\bar{X} \pm \text{SEM}$)			
	INT*	DOM†	SUB†	EQU‡	INT	DOM	SUB	EQU	INT	DOM	SUB§	EQU	INT	DOM	SUB§	EQU
C1																
S (11)	8	2	2	2	7	2	1	1	4.8±0.8	5.0±1.0	2.5±2.5	4.0±2.3	4.3±1.0	5.0±1.0	2.5±2.5	4.0±2.3
NS (11)	9	2	2	0	8	2	1	—	5.1±0.8	4.5±0.5	2.0±2.0	—	5.1±0.8	0	1.5±1.5	—
C2																
S (9)	0	0	0	18	—	—	—	17	—	—	—	5.5±1.2	—	—	—	3.6±1.6
NS (9)	1	5	5	6	1	5	2	3	6.0±6.0	4.6±1.3	3.6±1.4	2.8±1.7	6.0±6.0	1.8±1.1	1.2±1.2	0
C3																
S (9)	0	2	2	14	—	2	2	13	—	6.0±1.0	7.5±1.5	5.1±1.3	—	6.0±1.0	6.5±0.5	4.0±1.6
NS (9)	1	5	5	6	1	5	3	5	6.0±6.0	5.4±0.5	2.8±1.3	4.3±1.5	6.0±6.0	0.4±0.4	2.4±1.3	1.0±1.1
C4																
S (9)	0	0	0	18	—	—	—	16	—	—	—	4.7±1.4	—	—	—	4.1±1.5
NS (9)	0	4	4	10	—	4	3	10	—	5.2±0.2	4.7±1.7	5.9±0.9	—	2.2±1.3	4.7±1.7	2.8±1.7

C1: a female cohabited with a male in the territory; the other female was an intruder; C2: two females were simultaneously introduced into a territory already occupied by a male; C3: two females and a male were simultaneously introduced into a territory; C4: two females cohabiting in the territory prior to introduction of the male.

*Number of INT (intolerant) corresponds to the number of monogamous groups.

†Number of DOM (or number of SUB) corresponds to polygynous groups in which a hierarchy was established.

‡Number of EQU/2 corresponds to the number of polygynous groups in which a clear-cut hierarchy was not detected.

§Not including nontolerated subordinates.

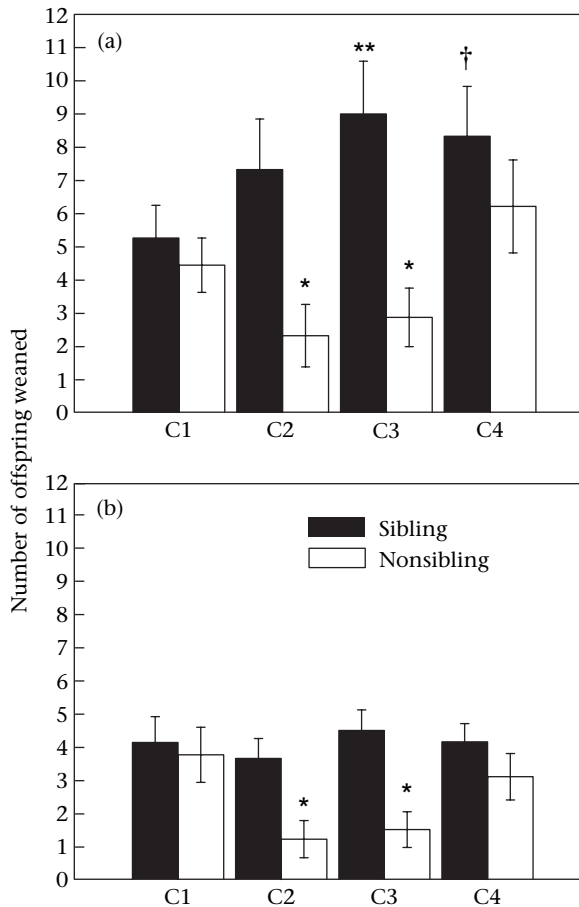


Figure 4. Mean litter size at weaning \pm SE in different experimental conditions C1–C4 (see legend to Fig. 2 for explanation). (a) C1: 11 sibling (S) and 11 nonsibling (NS) groups; C2, C3, C4: 9 S and 9 NS groups; litter size/group. (b) C1: 14 S, 13 NS; C2: 18 S, 17 NS; C3: 18 S, 17 NS; C4: 18 S, 18 NS; litter size/female. * $P < 0.05$, sibling versus nonsibling females in C2 and C3; ** $P = 0.056$, sibling females in C3 versus C1; † $P = 0.097$ sibling females in C4 versus C1.

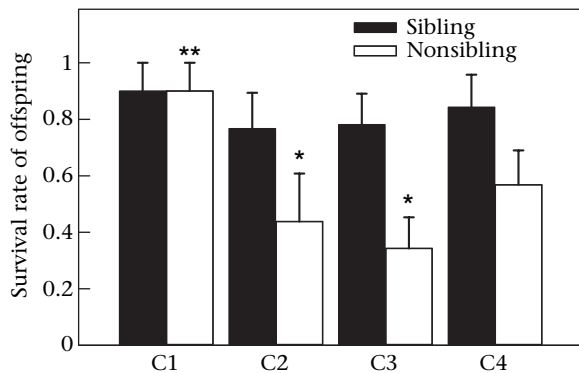


Figure 5. Survival rate of offspring (number of young that survived until postnatal days 18–20/number of pups born) \pm SE for sibling or nonsibling female groups in four experimental conditions (see legend to Fig. 2 for explanation). **Nonsibling females in C1 versus C2 ($P < 0.05$) and C3 ($P < 0.01$); *sibling versus nonsibling females in C2 ($P = 0.10$) and C3 ($P < 0.02$).

in approximately 80% of the cases. Conversely, females that made contact with each other at the same time as (C2 and C3) or before (C4) cohabitation with a male showed comparatively little aggression and a high degree of reciprocal tolerance. Only in these latter conditions did genetic relatedness and familiarity between females influence their behavioural interactions and reproductive success. Although nonsibling pairs showed higher frequencies of aggressive interactions than siblings, polygyny resulted in 97% of cases. However, in most sibling groups both the females successfully weaned young and had greater reproductive success than nonsiblings (measured on the basis of the mean number of weaned pups per female). Nonsibling females appeared to compete for reproduction through the inhibition of reproduction or infanticide. It is possible that in this situation one of the females, the subordinate one, would have left the group under more natural conditions. Gerlach (1996) has shown that female emigration from established demes appears to depend on a female's chances of reproducing.

In polygynous groups, while sibling females established an egalitarian relationship, nonsibling females generally established a dominant–subordinate one, as based on the aggressive/submissive behaviour seen during the first week of cohabitation. Contrary to our expectations and to previous studies (e.g. Palanza et al. 1996), there was no relation between dominance and reproductive success. Possibly, female aggressive behaviour is mainly concerned with the expulsion of same-sex rivals; if the female cannot expel the competitors, her dominance may not be stable. Another hypothesis is that the social relationship between females is not stable because it is modulated by their reproductive state. Although we did not observe aggressive interactions between the females after the first week of cohabitation, episodes of aggression may have occurred anyway before/after delivery or female social relationships may be mediated by other social factors (i.e. pheromones).

In accordance with the game theory model (Maynard Smith 1973, 1982; Maynard Smith & Parker 1976), prior social/sexual experience and possession of a resource can influence the intensity and outcome of competitive interactions. Experimental condition 1 in the present study can be viewed as an asymmetric contest where the two females were not equal in terms of possession of a resource or previous investment in reproduction. In male mice with equal fighting ability, the resident male usually wins encounters against intruders (e.g. Parmigiani et al. 1989). Accordingly, C1 resident females were always dominant and the intensity of aggression was high relative to that in the other conditions (C2, C3 and C4) where the female pairs were tested in a symmetric context (i.e. the two females were equals in terms of prior residence and association with the male). When test females differed in the prior occupancy of space without a male, we observed little aggression and complete tolerance, suggesting that only reproductively active females try to expel other females. Furthermore, females may compete aggressively among themselves not for space (as males do), but for males holding a territory. Because maternal aggression per se cannot prevent infanticide by males in this species (e.g. Maestriperi 1992;

Palanza et al. 1995), the resident male appears to be a necessary defender of the offspring when the intruder is a male (Palanza et al. 1996).

In contrast to kin selection theory and our prediction that a sibling would receive less aggression, resident females in C1 were as aggressive and intolerant of siblings as of nonsiblings, even though they appeared to be recognized, because sibling females showed less investigatory behaviour than unrelated females after 6 days of separation (see also Kareem & Barnard 1982). The finding of very high rates of aggression, even though the intruder females were genetically related and had been reared together, contrasts with the hypothesis that closely related kin should avoid lethal fighting and should cooperate to rear young. Prolonged social familiarity, generally associated with genetic relatedness, is an important variable influencing social interactions in mammals (Fletcher & Mitchener 1987). For instance, male mice are less aggressive and more amicable towards kin than towards unfamiliar unrelated males (Rowe & Redfern 1969; Kareem & Barnard 1982). However, the kin competition hypothesis suggests that aggression towards kin may be adaptive when limited resources are scarce and competition for them severe (Barnard 1989), as confirmed by studies in different social mammal species (Armitage 1989; vom Saal et al. 1995). Our data suggest that when a wild female mouse has established a reproductive unit, and has therefore engaged in reproduction, immigration of any other female is a costly and unsuccessful event and is not influenced by relatedness and familiarity. The resident female strategy seems to be to maximize direct fitness rather than to gain indirect fitness or other secondary benefits, such as increased thermal regulation of nests or protection, as predicted by Armitage (1989). When established, a reproductive unit appears to be substantially closed to immigration of conspecifics, as territorial males in this situation are highly aggressive and intolerant of other males (Palanza et al. 1996). However, König (1989, 1994b) has shown that female mice communally nursing with sisters reared more offspring than a monogamously paired female. In addition, familiarity throughout life with a same-sex partner, irrespective of relatedness, improved reproductive success and led to egalitarian reproduction of females within a social group compared with unrelated unfamiliar females. Accordingly, in our study, lower levels of reproductive competition between females were recorded when two females settled on a territory before a male did (C4).

A number of studies have tried to understand what factors in social groups regulate the reproductive skew, that is, the difference in reproductive success between same-sex members in relation to their social status. Two theoretical models have been proposed (Keller & Reeve 1994; Clutton-Brock 1998; Reeve et al. 1998). The optimal skew model is based on the assumption that dominants can give reproductive incentives to subordinates to keep them as helpers; this model predicts that the subordinate's reproduction should be inversely proportional to its relatedness to the dominant (reproductive skew is low in less related groups; Keller & Reeve 1994). The incomplete control hypothesis assumes that reproduction by subordinates

can result from the relative inability of dominants to control the reproductive ability of subordinates. This model predicts that reproductive skew should decrease, or be insensitive, with increasing genetic relatedness between group members (Clutton-Brock 1998; Reeve et al. 1998; Gerlach & Bartmann 2002). Our results do not appear to support either model, although the incomplete control hypothesis predicts that, at least in conditions C2, C3 and C4, genetic relatedness would lead female pairs to tolerance, an egalitarian relationship and low reproductive skew. However, nonsibling females in polygynous groups showed low reproductive skew, which, in contrast to the sibling conditions, was due to the low number of offspring weaned by both females. In nonsibling female pairs, infanticide by both females within a group was commonly seen, thus decreasing the total reproductive output. Johnstone & Cant (1999) observed that incomplete control of reproduction by the dominants in communal breeders may contribute to the evolution of infanticide. When the dominant cannot entirely prevent subordinates from breeding, it can gain by eliminating unsanctioned young; equally, subordinates can gain by eliminating the offspring of dominants (Johnstone & Cant 1999; Cant 2000). An additional factor that current models of reproductive skew in noneusocial vertebrate groups do not consider is the role of asymmetries in previous investments in determining female behaviour and the resulting group composition and evenness in reproduction. As pointed out by Johnstone & Cant (1998), in many species dominant group members aggressively expel subordinates from the group (see also Gerlach 1990, 1996; Gerlach & Bartmann 2002). In C1 groups, when females showed asymmetries in previous investments (i.e. one had already cohabited with a territorial male, the other was an intruder), the high-investment female generally expelled the intruder female from the group and had higher reproductive output than polygynous groups. Gerlach & Bartmann (2002) concluded that in female wood mice, *Apodemus sylvaticus*, both investment skew and genetic relatedness are important for the regulation of reproductive skew in cooperative breeding.

The present study confirms our previous findings (Palanza et al. 1996) on the coexistence of three possible mechanisms influencing cooperative breeding and reproductive skew in females. However, the present data indicate that the type of competitive strategy adopted by females may be dictated initially by social circumstances (as exemplified by the experimental conditions) rather than by (genotypic) individual variation, and then by genetic relatedness between females. Our findings show that what form female reproductive competition takes depends primarily upon the experimental condition (i.e. situational determinants).

First, one competitive mechanism is intolerance of other females. When a female had cohabited with a male and was thus 'resident' in a territory, she aggressively excluded the other introduced females, either siblings or nonsiblings (C1). Female mice spend a notable part of their adult life pregnant or lactating (Bronson 1979) and these reproductive periods are associated with neuroendocrine changes and significant maternal investment in

the successful rearing of the young. Nine of the 20 attacking resident females were not pregnant when subjected to the intrusion test (as subsequently determined on the basis of the day of delivery) and no significant relation was found between intensity of aggression and pregnancy status. However, these females could have been pregnant at the time of the introduction of the second female and experienced early abortion as a consequence of such intense fighting episodes. The finding that females in C1 took longer to deliver could support this hypothesis. Impregnation and the consequent nursing period may not be the only mechanism by which males can stimulate the aggressive behaviour of female mice, as mere exposure to male urine stimulates aggression between females in this wild stock of mice (Palanza et al. 1994). Increased female aggressiveness in response to a male (or just to male olfactory stimuli) could enhance the probability of a female mating because of subordination (and suppression of reproduction) or dispersal of female rivals. The number of females on a male's territory may thus chiefly be determined by female competition. Furthermore, by expelling female intruders, breeding females can presumably reduce the risk of infanticide.

When the two females were in a symmetric context (C2, C3, C4), reproductive success appeared to be modulated by genetic relatedness and familiarity through two additional mechanisms. One mechanism may involve suppression of reproduction of subdominant females. In C2 groups, where two females were simultaneously introduced into a territory already held by a male, they tolerated each other but only one female became pregnant in nonsibling groups. Thus the modulation of reproductive success by genetic relatedness appears to occur prepartum. Possibly, the two females established a hierarchical polarity and only the dominant female in the pair was able to ovulate and mate. Reproductive suppression of subordinates has been reported in male (Bronson 1979) and female mice (Lidicker 1976), and can be related to social stress (Christian 1970). However, after a few days from introduction into the experimental apparatus, we did not observe further agonistic interactions; females appeared to have socialized and they shared the nest. On the other hand, it is well known that female urine contains olfactory cues that influence the reproductive physiology of other females (Bronson 1979). Reproductive dominance may thus be communicated via pheromones, which can influence reproduction of subadult or subdominant females (Perrigo & Bronson 1982; Vandenberg 1987; Hurst 1990b). In C2 nonsibling groups, the females giving birth did so after a longer interval than C3 and C4 females. This delay in delivering could represent a potential cost related to the reproductive suppression of the other (subordinate) female (Reeve et al. 1998).

An additional mechanism by which females can prevent reproduction of rivals relates to the infanticide of the newborn young. In C3 (two females and a male simultaneously introduced) and C4 (two females cohabiting prior to introduction of the male), loss of pups was recorded more frequently in NS than in S polygynous groups. The modulation of reproductive success by familiarity or relatedness thus appears to occur postpartum. In the

present study, loss of newborn pups from infanticide occurred only when two females were present in the territory. Males are more likely to show infanticide when they are unmated but they become parentally oriented towards pups after mating and cohabitation with the pregnant mate (vom Saal & Howard 1982; Elwood & Ostermayer 1984; Palanza & Parmigiani 1991; Palanza et al. 1996). In the majority of cases, infanticide involved the killing of the first-born litter, possibly by the second female to deliver but before the birth of the second female's own pups. These data agree with previous studies (König 1994a) and confirm suggestions that pregnancy increases the likelihood of infanticide in wild female mice (McCarthy & vom Saal 1985). Because females usually pool litters and share pup caring, younger pups may be at a competitive disadvantage for milk as they have to compete with older pups for access to nipples (Schultz & Lore 1993). Furthermore, if pregnant females kill some of the other females' dependent offspring shortly before they give birth themselves, some of the other female's milk can be redistributed to their own offspring (König 1994a). Exploitation of another female's maternal care may be an important factor modulating competition between females and reproductive skew (König 1994a; Gerlach & Bartmann 2002). In conditions C2, C3 and C4, the occurrence of aggression between females was relatively low in nonsibling females. However, prevention of reproduction, either by inhibition of pregnancy or infanticide, was high between nonsibling females, thus suggesting that females may compete not only for the territorial male but also to exploit maternal behaviour (warmth, milk, retrieving) of the nonreproducing female. Communal nests were present in the majority of cases in sibling female groups, and we have observed both the females on the nest nursing or warming the pups at least once. Nonsibling females showed a more variable pattern of communal nesting. This variability can be related to different factors, such as the occurrence of simultaneous pregnancies or presence of pups.

Our findings indicate that the most successful condition for a female, in terms of litter size at weaning, is nesting alone with her mate or being associated with a genetically related and familiar female. Overall, we did not find an advantage for offspring survival or litter size at weaning as a result of nesting with a sibling female, at least at the level of a single reproductive event. Possibly, other factors (e.g. increased growth rates of litters, nest site protection, nest temperature, predator pressure, etc.) could have further improved breeding success of communally nursing house mice as opposed to singly nesting females. Benefits could become evident over a longer period. In wild mice, pairs of familiar sisters have higher lifetime reproductive success than females living monogamously (König 1994a). In addition, as the number of offspring weaned per female did not differ between singly nesting (i.e. intolerant) females and females breeding cooperatively with a sister, the latter should also gain in terms of inclusive fitness.

For a male, higher reproductive output was recorded in conditions where two related and familiar females nested together. The presence of only one successful reproducing female per group in established male/female pairs or

unrelated female pairs implies that female competition may restrict the range of mating patterns and limit the reproductive output of the dominant male in a deme. Thus, although house mice tend to be polygynous, both the different settlement patterns of females and male, as well as the genetic relationship (and familiarity) between females, may be instrumental in determining the level of competition between females that, in turn, influences the resulting mating pattern.

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