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Nest Defense and Survival of Offspring in Highly Aggressive Wild Canadian Female House Mice

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VOM SAAL, F. S., P. FRANKS, M. BOECHLER, P. PALANZA AND S. PARMIGIANI. *Nest defense and survival of offspring in highly aggressive wild Canadian female house mice.* PHYSIOL BEHAV **58**(4) 669–678, 1995.—Nest defense behavior was examined in wild female house mice (*Mus domesticus*) that were derived from a stock initially trapped in Alberta, Canada. The first objective was to determine whether behavior toward pups prior to mating was related to the intensity of postpartum aggression in a variety of social situations. Therefore, prior to the experiments we screened virgin females for their behavior toward a newborn pup [60% of the females exhibited infanticide and 40% were noninfanticidal: 7% were parental (retrieved and hovered over the pup) and 33% ignored the pup]. Infanticidal and noninfanticidal females were then mated with males and used in four experiments. In Experiment 1 the females were housed individually prior to delivery, while in Experiment 2 the females were allowed to remain with their mates; in both situations all females successfully reared litters of similar sizes. Male and female intruders (that had all exhibited infanticide when previously tested with a pup) were placed separately into a test cage containing a lactating female during the first four days after delivery. Regardless of the presence of the stud male, previously infanticidal females were more aggressive (exhibited more attacks per min) toward both male and female intruders than were previously noninfanticidal females; infanticidal females also exhibited more of both forms of attack (offensive and defensive) and also attacked with greater intensity than did noninfanticidal females. The number of attacks toward intruders of both sexes increased for both infanticidal and noninfanticidal females between Day 1–4 postpartum, but very high rates of attack were observed on all days by the lactating females, including the day of delivery. In Experiments 3 and 4 only the most aggressive (previously infanticidal) females were tested. In Experiment 3, two unrelated, unfamiliar females were mated separately and then were housed together just prior to delivery, which was planned to occur 3–4 days apart. In 5 of the 15 cages, all pups disappeared on the day of delivery of the second female to deliver her litter. In the remaining 10 cages, it appeared that none of the pups produced by the 20 females were killed. Thus, in this experiment, 66% of pups survived to Day 4 postpartum. In Experiment 4, two previously infanticidal female siblings, which had been housed together since birth, were placed together with a stud male. In all 9 cages only one female became pregnant and delivered pups, but only 3 litters survived to Day 4 (no litters were observed being attacked during intruder tests). In contrast to kin-selection theory and our expectation that a sibling would contribute to communal rearing and nest defense, housing siblings together thus resulted in the lowest overall reproductive success (3/18; 17% of the females produced litters that survived to Day 4 postpartum) of any of the social conditions examined. We discuss the implications for social structure and population dynamics of the extremely high aggressiveness and infanticidal tendency, regardless of kinship, of females from this stock of wild mice.

Defense   Nesting   Postpartum aggression   Infanticide   *Mus domesticus*

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INTRODUCTION

HOUSE mice living commensally with man often form social units termed demes, which are typically composed of a single dominant male, a few subordinate males, and several females occupying contiguous nests (6). When females emigrate from their natal territory, which is a common event around puberty in house mice, they may build a nest by themselves or establish a new deme with an individual male. Alternatively, females might enter an established deme and thus share a nest area with unfamiliar females, although it remains to be determined whether immigration into established demes by migrating females is common (14,15,35,42). There is also evidence that in mouse demes, inbreeding occurs among animals that do not disperse. Nursing females may be found in nests containing young of assorted ages, suggesting that communal nesting sometimes occurs, and it is considered likely that communally nesting females are siblings that remained within their natal deme (3,14,46).

Dispersal and the possibility of immigration of mice into a deme containing unrelated mice is important in the socioecology of mice in that both male and female mice kill the infants of other conspecifics, and it is generally assumed that familiarity and/or relatedness influence the likelihood of infanticide. More specifically, infanticide by males and females varies dramatically between laboratory stocks of mice (29,31,34,44). While the majority of virgin females do not exhibit infanticide in laboratory stocks of mice (17,39), in wild stocks most virgin females exhibit infanticide, and when pregnant, virtually all females exhibit infanticide (12,17). Thus, both female and male wild mice [other than the stud (18,34,43,45)] present in and around the nest area when a female delivers pups can influence whether the pups survive. This raises an important question concerning the effect on fitness of communal nesting with siblings (or other genetically related females) vs. unrelated females (1,2,11,14).

During late pregnancy and postpartum, female mice are highly aggressive toward intruders into the nest area (38). Postpartum aggression by wild female mice may serve to protect infants from infanticide by conspecifics of both sexes. In a study of postpartum aggression in a laboratory stock of Swiss mice, there was a different type of attack exhibited by lactating females toward male intruders (defensive attack, characterized by bites directed toward vulnerable body regions, such as the head and ventral surface) and female intruders (offensive attack, characterized by bites directed toward nonvulnerable body regions, such as the rump and tail). These different types of attack may be related to the fact that sexually naive intruder males are more likely to kill the female's pups than are intruder females in this stock, and intruder males thus elicit defensive, also referred to as protective, aggression (26). However, similar to females from other wild stocks of mice, a majority of virgin females from the stock used in the experiments described here exhibit infanticide (most sexually naive males also exhibit infanticide), which suggests that a difference based on sex of intruder in the type of attack exhibited by lactating females might not occur in wild mice.

There were a number of objectives of the experiments described here. Our first objective was to determine whether there was a relationship between the likelihood of success in defending pups against intruders and the intensity of postpartum aggression by lactating female mice as a function of their prior behavior toward pups. We thus categorized virgin females as being infanticidal or noninfanticidal toward a newborn pup and then compared these two groups of females for postpartum aggressiveness toward both male and female intruders during the first 4 days after parturition. In a comparison of mice from different genetic stocks, there was a correlation between the likelihood of infanticidal behavior prior to mating and the intensity of postpartum aggression by females (27)

Second, since there is less intense postpartum aggression toward previously noninfanticidal intruders relative to previously infanticidal intruders (10,32), we only tested lactating females for postpartum aggressiveness toward intruder males and females that had previously shown infanticidal behavior toward a newborn pup. Our objective was to control for the behavior of the intruder and to create a situation in which the intruder was a threat to the litter and would thus be most likely to elicit attack by the lactating females. Third, to simulate burrows of mice inhabiting fields and to provide animals with a defensible nest area typical of a mouse burrow, in all of the experiments lactating females were provided with a nest box and that could only be entered by a small tunnel.

A fourth objective was to determine whether there was a relationship between the tendency to exhibit infanticide prior to pregnancy and the form of postpartum aggression (offensive vs. defensive) exhibited toward adult, conspecific intruders during the early postpartum period. Variability in different forms of intraspecific aggression is related to social structure in house mice (29). A fifth objective addressed in Experiments 1 and 2 concerned the role of the stud male in shared nest defense and the protection of pups, particularly against male intruders. Postpartum aggression toward both male and female intruders was thus examined in lactating female mice when they were housed by alone (Experiment 1) or allowed to remain with their mate (Experiment 2). We predicted that the presence of the stud male would result in an increase in the overall level of aggression toward male intruders, due to attacks by both the resident stud male and lactating female. In contrast, the stud male was expected to show little aggression toward female intruders.

In experiment 3 and experiment 4 we investigated reproductive success in female mice when housed with another female (unrelated in experiment 3 and related in experiment 4) but without the stud male being present. In Experiment 3 we housed unfamiliar, nonsibling females together after they had been mated with different males about 4 days apart. We mated these pairs of unrelated females at different times to determine whether asynchronous production of litters (which would be expected in a mouse deme) would lead to the loss of litters; the prediction was that the female which was still pregnant at the time that the unrelated cage mate delivered might attack the pups as they were delivered, based on the prior observation that virtually all pregnant females exhibit infanticide (17). In Experiment 4 we examined the possibility of shared nest defense in female siblings that had remained together since birth (they were not separated while allowed to mate with the same male). We thus placed a stud male with a pair of sibling females with the expectation that, in the majority of pairs, both females would ovulate and mate [as a result of male-induced, synchronous ovulation (6)], deliver litters at the same time, and then share in the defense of the litters against infanticidal male and female intruders. We predicted on the basis of kin-selection theory that shared nest defense against intruders might be one benefit of communal nesting with a female sibling (14).

In the four experiments described below, aggression toward intruders and success at protecting their young was thus examined in lactating female mice when they were maintained in four different social situations: (i) housed singly; (ii) housed with only their mate; (iii) housed with an unfamiliar; nonsibling female; and (iv) housed with a familiar, sibling female.

GENERAL METHODS

Animals and Housing

The animals used in these experiments were the descendants of mice (*Mus domesticus*) trapped near Calgary, Alberta, Canada in 1979. The mice were maintained as an outbred stock at the University of Texas at Austin until 1987, when a colony was established at the University of Missouri with 45 randomly selected breeding pairs. The animals were then maintained as an outbred stock in standard polypropylene mouse cages on Aspen bedding in rooms maintained at 23oC on a 12:12 light:dark cycle, with lights on at 0700 h. Water and food (Purina 5001) were available ad lib. After weaning at 23 days of age, animals were maintained in same-sex groups (3–5 per cage) with their siblings.

Preliminary Test for Behavior toward Young

At 60 days of age all animals were housed individually, and 24 h later they were tested for their behavior toward a single 1–3-day-old pup. This test consisted of placing one pup into a corner of each animal's cage with a minimum of disturbance. The animals were observed for a maximum of 30 min. If the pup was attacked, which typically occurred within 1 min, the test was immediately terminated, and the pup was removed from the cage and killed painlessly by CO_2 asphyxiation and cervical dislocation. These animals were labelled as spontaneously infanticidal. If the test animal responded to the pup by retrieving the pup to the nest and then grooming and incubating (hovering over) the pup, the animal was labelled as parental. If the pup was not attacked or retrieved to the nest within the 30-min test period, the test animal was recorded as having left the pup unhandled. The females that did not attack the pup, whether the pup was parented or left unhandled, were categorized as noninfanticidal.

Males remained individually housed after this test for infanticide. For these experiments, both infanticidal and noninfanticidal females were provided with the opportunity to mate with males and become pregnant. The conditions of housing differed for the females used in each of the experiments, and detailed methods are described below.

Testing Chamber for Nest Defense

A few days prior to delivering their young, the females were housed in 43 × 23 × 13 cm polyethylene cages on Aspen bedding. A nest box (10 × 7.5 × 7 cm) constructed of polyethylene was provided. The nest box did not have a bottom and rested on the Aspen bedding. Nesting material was provided (one Nestlet, Amcare, Manhasset, NY). An important aspect of the nest box was that it could only be entered via a 5-cm diameter tunnel which was 7-cm long. The nest box and tunnel were provided to simulate burrows of mice inhabiting fields and to provide animals with a defensible nest area. The cages were covered by a stainless steel lid on which food and a water bottle were placed.

Postpartum Aggression Test and Measure of Reproductive Success

Beginning with the day on which pups were first observed (Postpartum Day 1), each female was tested for postpartum aggression toward an intruder two times per day at 1000 h and 1600 h on consecutive days. Each day both a male and a female intruder were introduced into the test chamber. The order of introduction of the male (M) and female (F) intruders was MF, FM, MF, FM, etc., for one-half of the females in each group, while the opposite sequence was used for the remaining animals in each group to control for order of presentation. Only infanticidal males and females were used as intruders, since Parmigiani et al. (32) have reported that in Swiss mice, nursing females differ in their behavior toward infanticidal and parental males. No male or female intruder was used more than one time in an experiment.

The intruder was left in the test chamber for a maximum of 3 min. Preliminary tests had indicated that a longer test period resulted in the likelihood of the intruder being severely wounded. Due to the very high aggressiveness of many individuals in this stock of mice and the desire to reduce injury to the intruder, the intruder was removed prior to 3 min if the number of attacks exceeded 20 during the first one-min period or the intruder entered the nest area and initiated an attack toward a pup in the litter. The purpose of this latter procedure was that in previous studies using a domestic stock of Swiss mice, a nursing female was always unable to protect her pups against infanticide by a male intruder and the entire litter was always lost once the intruder male counter attacked, subdued the lactating female, and then attacked a pup in the litter (28).

Two measures of aggression were used to assess nest defense: rate of attack (number of attacks per minute) and intensity of attack; we used rate of attack rather than total number of attacks since, as described above, the total duration of testing was not always 3 min. The intensity of attack measure was based on the number of visible wounds received by the intruder during a test, which was determined by careful examination of the pelage after removal of the intruder. Bite-target analysis (5,26) was used to categorize wounds as resulting from biting directed toward the nonvulnerable body regions (flanks, back, rump and tail), referred to as offensive or competitive attack, and the vulnerable body regions (the head as well as the entire ventral surface), particularly the inguinal and genital areas, referred to as defensive or protective attack.

As a measure of reproductive success we counted the number of pups that were alive at the end of the experiments (on the afternoon of Day 4 postpartum). We did not attempt to determine the number of surviving pups prior to the end of the experiment, since this would have required removing the nest box and handling the pups. Unlike many laboratory stocks of mice, these animals are difficult to handle and become highly aroused when disturbed. Disturbing a wild female mouse by handling her pups shortly after delivery results in some females killing their litters after they are placed back into the nest (17).

Statistical Analysis

Parametric data, such as number of attacks per minute, were analyzed by ANOVA using the multi-factor, repeated-measures analysis available on the Statistical Analysis System (SAS), and planned comparisons were made using the LS-means test. Prior to conducting ANOVAS in each of the experiments, Chi Square analysis was conducted to compare the proportion of animals which exhibited or did not exhibit a behavior. ANOVAS were conducted and means were computed based only on the data from animals which showed the behavior, and zeros based on animals not showing a behavior were not included in the ANOVAS and calculation of the means. The null hypothesis was rejected at the 95% confidence level.

EXPERIMENTAL PROCEDURES AND RESULTS

Preliminary Test for Behavior toward Newborn Young

Adult virgin males ($n = 165$) and females ($n = 148$) were screened for their behavior toward a single 1–3-day-old pup. For females, 60% were infanticidal and 40% were noninfanticidal (7% were parental and 33% did not handle the pup). For males, 72% were infanticidal, 10% were parental and 18% left the pup unhandled [in subsequent studies, a slightly higher percentage (about 85%) of males in this stock have typically exhibited infanticide, while the percentage of females exhibiting infanticide has been similar to that reported here (23)].

NEST DEFENSE BY PREVIOUSLY INFANTICIDAL AND NONINFANTICIDAL FEMALES HOUSED INDIVIDUALLY AFTER MATING

The objective of this experiment was to compare nest defense behavior in response to male and female intruders of previously infanticidal and noninfanticidal females during the first 4 days postpartum when they were housed individually.

Methods.

After the preliminary test to assess each animal's behavior toward young, 10-infanticidal and 10-non-infanticidal females were paired with a male. When the females were visibly pregnant, they were placed by themselves in the test chamber described above. Beginning at 1000 h on the day on which pups were first observed, intruders were introduced into the test chamber as described above.

Results

In all of the cages pups survived to Day 4 after delivery (mean ± SEM: 6.6 ± 0.7 live pups). The mean number of pups for females in this study did not differ from the number of live pups found on the day of birth for females of the same stock in our breeding colony ($n = 50$ breeding pairs; 6.4 ± 0.4 live pups). There was also no difference in surviving pups when compared to the number of live pups delivered by cesarean section (just prior to normal parturition) from 100 primiparous females (7.1 ± 0.3 live pups) for use in other experiments. This finding shows that the number of live pups found in utero at the end of pregnancy is very similar to the number of pups surviving after birth in this stock of mice and also shows that disturbance due to the test procedures did not result in the loss of pups.

In contrast to some commonly used laboratory stocks of mice [for example, Rockland-Swiss (39)], most of the experimental females exhibited aggression toward intruders on the day of delivery. Figure 1 shows that the rate of attack increased significantly between Day 1 and Day 3 postpartum for both infanticidal and parental females ($p < 0.001$), while there was no difference between Day 3 and Day 4. Ignoring sex of intruder, infanticidal females were more aggressive toward intruders than were parental females on test Day 1, 2, and 3 ($p < 0.05$), but not on Day 4 ($p > 0.1$).

Neither infanticidal nor noninfanticidal females differed in their rate of attack toward the male vs. female intruders. However, the results in Fig. 2 show that there was a marked difference between infanticidal and noninfanticidal females in the rate of attack toward the female intruder ($p < 0.001$), while the difference between infanticidal and noninfanticidal females in the rate of attack toward the male intruder also tended to differ ($p = 0.057$); these p values are based on planned comparisons after conducting the multi-factor, repeated-measures ANOVA.

Disregarding sex of the intruder, significantly more infanticidal females (53%) than noninfanticidal females (11%) inflicted visible wounds on the intruder (χ^2; $p <$ 001). This subset of infanticidal females attacked with a greater intensity (1.14 ± 0.15 visible wounds) than did the noninfanticidal females who

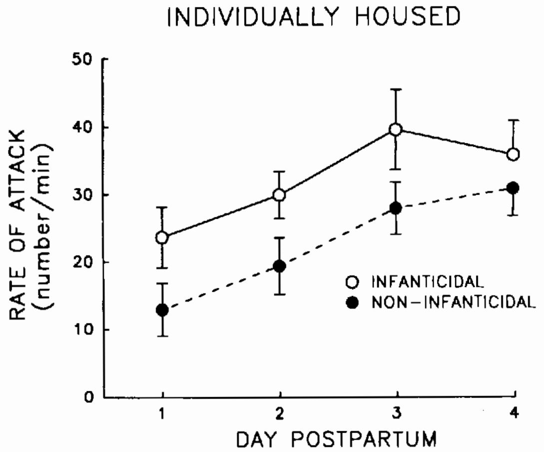

FIG. 1. Mean (±SEM) rate of attack toward intruders (both male and female combined) by individually housed females during the first four days postpartum in Experiment 1 (Day 1 is the day of delivery). Prior to mating, the females were categorized as either infanticidal or noninfanticidal during a preliminary test to assess their behavior toward a newborn pup.

wounded the intruder (0.15 ± 0.05 visible wounds; $p < 0.01$). There was no effect of sex of the intruder on the location of wounds. Overall, most of the wounds were located on the vulnerable body regions, indicative of defensive attacks by lactating females. While no wounding indicative of offensive attacks was observed on the pelage of intruders of either sex into cages containing noninfanticidal females, this was not the case in cages containing infanticidal females. Infanticidal females inflicted more wounds characterized as resulting from both offensive ($p < 0.05$) and defensive ($p < 0.01$) attacks relative to noninfanticidal females. Infanticidal and noninfanticidal females were also compared for their rate and intensity of attack toward the intruder on the first test at 1000 h vs. second test at 1600 h on each day of testing, and, regardless of sex of intruder, no differences were found. Finally, no intruder was observed to enter the nest box within the 3 min test period, and none of the pups were thus attacked.

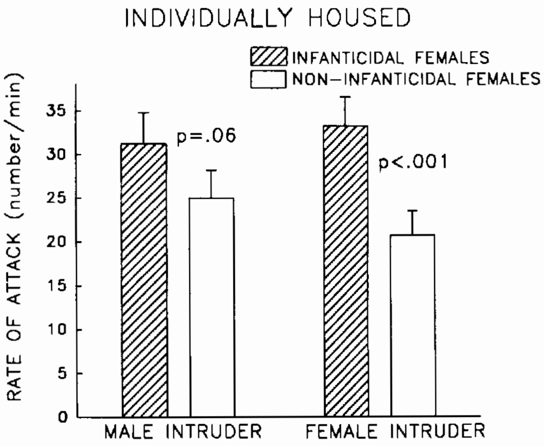

FIG. 2. Mean (+SEM) rate of attack during the first four days postpartum toward male vs. female intruders in Experiment 1. An intruder of each sex was tested one time on each day. Prior to mating, the females were categorized as either infanticidal or noninfanticidal during a preliminary test to assess their behavior toward a newborn pup.

NEST DEFENSE OF PREVIOUSLY INFANTICIDAL AND NONINFANTICIDAL FEMALES HOUSED WITH THEIR MATES

The objective of this experiment was to examine the behavior of lactating females (that had been infanticidal or noninfanticidal as virgins) toward male and female intruders during the first 4 days postpartum when the male that sired the litter was also present in the cage. In all other respects, the methods for this experiment were the same as those described for Experiment 1.

Methods

Adult virgin males and females were individually housed and screened for their behavior toward pups as described above. An infanticidal male was paired with either an infanticidal or noninfanticidal female ($n = 10$ pairs per group) in standard polyethylene mouse cages. Only infanticidal males were used as the studs in this experiment to control for the behavior of the male, which was not required in the prior experiment. When the female was visibly pregnant, the male-female pair was transferred into the larger testing cage containing the nest box as described above. Beginning on the day of birth of the litter, the same procedures described in Experiment I were used to examine behavior of the residents toward infanticidal intruder males and females during the first 4 days postpartum. The main difference between this study and Experiment I is that the male and female breeding pairs remained housed together throughout the period of testing for aggressive behavior toward intruders.

Results

In all of the cages pups survived to Day 4 after delivery (7.1 ± 0.6 live pups), which suggested that, similar to Experiment 1, no loss of pups occurred during the experiment. On 28/160 trials (18%), both the male and female attacked the intruder. On 68/160 trials (43%), only the female attacked the intruder. On 57/160 trials (36%), only the male attacked the intruder.

Ignoring the behavior of the male partner, for the infanticidal and noninfanticidal females that exhibited aggression, as in Experiment 1, infanticidal females showed an overall higher rate of attack ($p < 0.05$) than noninfanticidal females (Fig. 3), although on individual testing days, the mean differences between infanticidal and noninfanticidal females were not statistically different. Disregarding day of testing, the mean rate of aggression exhibited toward male vs. female intruders did not differ for infanticidal and noninfanticidal females. For the intensity of aggression measure (number of visible wounds on the intruder), too few infanticidal females and their mates and noninfanticidal females and their mates inflicted visible wounds on the intruder for meaningful quantitative comparisons.

For the 4 days of testing, only a few males (one or two per day) housed with noninfanticidal females attacked female intruders (5.5 ± 4.8 attacks/min for males showing aggression), and most aggression by these males was toward the male intruder (4–8 resident males attacked per day; 16.0 ± 3.7 attacks/min). The difference in rate of attack toward male vs. female intruders was not statistically significant due to the low number of males attacking females. For the males housed with infanticidal females, there was no significant difference in the number of males attacking male vs. female intruders (2–6 attacked per day). The rate of attack toward female intruders (6.0 ± 3.2 attacks/min) was lower than toward male intruders (19.5 ± 3.6 attacks/min), although again, the difference was not statistically significant.

When considered together without regard to whether the resident male or the female attacked the intruder, in cages containing noninfanticidal females, the rate of attack toward male intruders (20.4 ± 1.7 attacks/min) was significantly greater ($p < 0.01$) than toward female intruders (12.5 ± 1.7 attacks/min). In cages containing infanticidal females, there was no difference ($p > 0.1$) in the rate of attack toward male intruders (12.2 ± 1.7 attacks/min) or female intruders (13.3 ± 1.7 attacks/min). Both groups showed a significant increase in the rate of attack (exhibited by both the male and female resident) toward intruders between Day 1–3 postpartum. Finally, none of the intruders were observed to enter the nest box during the 3 min intruder tests.

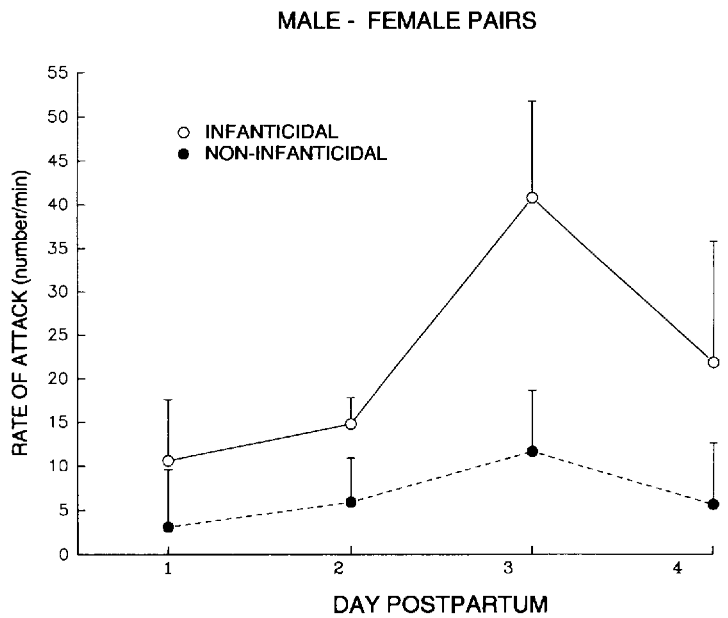

FIG. 3. Mean ($\pm$SEM) rate of attack toward intruders (both male and female combined) by females that remained housed with their mates throughout the first four days postpartum in Experiment 2 (Day 1 is the day of delivery). Prior to mating, the females were categorized as either infanticidal or noninfanticidal during a preliminary test to assess their behavior toward a newborn pup.

THE EFFECT OF PRESENCE OF A SECOND UNFAMILIAR, NONSIBLING FEMALE ON PUP SURVIVAL AND NEST DEFENSE IN PREVIOUSLY INFANTICIDAL FEMALES

In this experiment we examined survival of offspring and nest defense behavior in female mice housed with an unrelated and unfamiliar female. This housing condition was intended to mimic a situation in which two unrelated, unfamiliar, previously infanticidal (and thus highly aggressive) females might immigrate into the same territory. Only females which had exhibited infanticide on the screening test were examined, since in the prior two experiments these females had shown the highest levels of aggression toward intruders. Also, since most wild female mice are infanticidal, we wanted to conduct this experiment with females which might pose a threat to each other's young. The objective was to determine whether, relative to individually housed females in Experiment 1, survival of young as well as successful defense of the litter against infanticidal male and female intruders was enhanced or decreased.

Methods

All females used in this experiment ($n = 30$) had exhibited infanticide on the screening test. Fifteen females were paired with stud males, and then the remaining 15 females were paired with other stud males 4 days later. The objective was to have females produce litters which would be delivered about 4 days apart.

The females were placed together in the test chamber 2–3 days prior to delivery by the female that had been mated first (referred to as Female 1); the females were placed in the test chamber when Female 1 was visibly pregnant. The basis for this procedure is that female mice cannot be disturbed during the first week after mating without inducing abortion. Even mild disturbance, such as picking up the cage, will result in abortion prior to the secretion of placental lactogen from the placenta at the end of the first week of pregnancy (8,13,20). The females were individually identified by ear notches. The females in each pair had never come in contact prior to being paired. Each pair was observed for the first 10 min after being paired to determine dominance status, since preliminary studies had revealed that unfamiliar females of this stock would fight when paired, and a dominance hierarchy appeared to be rapidly established. In contrast, in another stock of wild mice (trapped in Northern Italy), intrafemale aggression was only observed after the females had been exposed to the odor of a male (25).

Day 1 postpartum was the day of delivery for Female 1. At this time Female 2 in the pair was still pregnant. We observed females in this experiment until the second litter delivered by Female 2 reached 4 days of age; in the majority of cases this entailed a total of 7 days of testing for nest defense against intruders. Beginning on Day 1 postpartum for Female 1, male and female intruders were introduced into the test chamber in the morning and afternoon as described for Experiment 1, and the behavior of each resident female was recorded. After the last test for aggression toward an intruder, the number of surviving pups produced by both females was recorded.

Results

The mean ($\pm$SEM) number of days between delivery for Female 1 and Female 2 was 3.4 ± 0.3 days (range: 2–6 days). The induction of estrus by males of this stock is more variable and not as rapid as in laboratory stocks of mice; after pairing males and females, the mean duration to mating (induction of ovulation in females) is 6 days based on hundreds of pairings (24).

In 11 of the 15 pairs (73%), the female that was the closest to delivery when the females were paired was the most likely to initiate attacks and defeat the female cage mate during the first 10 min of observation. In 3 cages Female 2 was the aggressor, and in one cage, no fighting was observed between the females. There was thus a significantly higher likelihood of the female that was closest to parturition being the aggressor (χ^2, $p < 0.01$).

In comparison to females housed individually in Experiment 1 in which 100% of litters survived to Day 4 after birth, in one-third (5/15) of the cages, no live pups remained after delivery by Female 2 (all of the pups belonging to both Female 1 and Female 2 disappeared after delivery by Female 2, although we did not observe any pups being killed). Females in these cages were thus not included in the following analyses. More specifically, for the 5/15 cages in which all pups disappeared, in 4 of these cages all pups disappeared on the day that Female 2 delivered, and in one cage, the pups disappeared on Day 2 after delivery by Female 2. In three of these 5 cages, Female 1 had been aggressive toward Female 2 when they were paired (and had also been aggressive toward male and female intruders during the intruder tests prior to delivery by Female 2), while in the remaining 2 cages, Female 2 had been aggressive toward Female 1 when first paired. In only one of the 10 cages in which pups survived throughout the entire period of testing had Female 2 been aggressive toward Female 1. The mean number of pups produced by both females in these 10 cages at the end of the intruder tests was 12.7, which suggests that no pups had been killed. It thus appears that there was not a progressive loss of pups in any cage during the 4 days of testing, and all pups in a litter disappeared at the same time.

On the days between delivery by Female 1 and Female 2, Female 1 showed a somewhat higher rate of attack toward male intruders (10.0 ± 2.7 attacks/min) than toward female intruders (5.1 ± 2.7 attacks/min), although the difference was not statistically significant ($p > 0.1$); for Female 1, 7/10 attacked both the male and female intruder. In contrast, for Female 2, few ($n = 3$) of these females exhibited attacks toward male (2.9 ± 2.4 attacks/min) or female (9.0 ± 2.5 attacks/min) intruders ($p > 0.1$). However, the rate of attacks toward male intruders by Female 2 was significantly ($p < 0.05$) less than by Female 1.

For the 4 days following delivery by Female 2, the rate of attack by Female 1 ($n = 3$–6/day) toward male intruders (12.4 ± 3.0 attacks/min) and female intruders (8.4 ± 3.1 attacks/min) was not significantly different ($p > 0.1$). On the 4 days after delivery by Female 2, the rate of attack by Female 2 ($n = 3$–4/day) toward the male intruders (7.0 ± 2.6 attacks/min) and female intruders (7.7 ± 2.3 attacks/min) was also not different.

In addition to the attacks exhibited toward the intruders, we also observed numerous incidents of aggression between the resident nonsibling pairs of females during the time that the intruder was in the cage; however, we did not record information about the number or intensity of these aggressive interactions between the resident females, and it was typically difficult to determine which female had initiated an attack.

EFFECT OF THE PRESENCE OF A FEMALE SIBLING ON PUP SURVIVAL AND NEST DEFENSE IN PREVIOUSLY INFANTICIDAL FEMALES

In this experiment we provided two female siblings (that had been together throughout life and had exhibited infanticide on the screening test) with the opportunity to mate with the same male and then remain together (without the male) while they reared their litters. We anticipated that this situation would lead to greater reproductive success than was observed in the prior experiment in which two unrelated and unfamiliar, previously infanticidal pregnant females were placed together shortly before delivery of their litters, and 33% of the litters disappeared. We then intended to conduct additional experiments to assess the relative contribution of genetic relatedness and familiarity to the expected increase in fitness.

Methods

Female siblings were reared together after weaning in groups of 3–5/cage. After being separated for one day to be screened for their behavior toward young, 18 female siblings that had been housed together since birth and that had exhibited infanticide on the screening test were housed together in groups of 2 per cage (9 sibling pairs). The females were individually identified by ear notches. An adult stud male was then placed into the cage with each pair of females. It was thus possible for the male to mate with both females. We did not want the female siblings to remain separated for a prolonged period of time, which mating with different males would have required. A previous study using wild mice trapped in Northern Italy has shown that placing female siblings separately with males leads to aggression and a decrease in reproductive success when they are placed back together (30).

About 3 days prior to the anticipated day of parturition for at least one visibly pregnant female in the pair, the females were placed together in the test chamber without the stud male. There were thus a number of differences between female pairs examined in this experiment and the previous study: these females were siblings and had been reared together, the females remained together while being given the opportunity to mate with one male, and they remained together throughout pregnancy.

Results

In all 9 cages only one female became visibly pregnant and delivered pups. In 3 cages all pups disappeared on the day of delivery prior to the first intruder test. These females were eliminated from further study. In only 3 cages did any pups survive to Day 4 after delivery, while in 3 cages some pups survived to Day 2 after delivery and then the entire litter disappeared; as in Experiment 3, we never directly observed any pups being killed. Of the 18 females that could have potentially become pregnant and produced offspring, only 3 females (17%) produced pups that survived to Day 4 postpartum.

There were too few cages with surviving pups to warrant conducting statistical analyses on rates of attack by the females toward male vs. female intruders throughout the 4 days after delivery. However, for the 6 cages with live pups on the day of delivery, in 4 of the cages no aggression toward the intruder of either sex was observed. For the 3 cages with pups surviving to Day 4, no aggression was observed on any day in one cage, while in the remaining 2 cages, aggression by the lactating female was observed toward the male and female intruders on 11/16 trials; the female that had not been pregnant did not attack the intruders of either sex. Thus, no aggression toward intruders was exhibited by the female sibling that had not produced a litter.

As was the case for the nonsibling pairs of females in Experiment 3, we observed aggression between the sibling females when an intruder was present. This type of aggression was not apparent at other times when investigators were in the animal room observing the females, although this was not systematically investigated. As in the previous study, we were typically not able to determine which female had initiated the attack against her sister.

GENERAL DISCUSSION

Relationship between Postpartum Aggression and Infanticide

In all of these experiments lactating females showed very high rates of aggression toward intruders of both sexes relative to aggression in most other laboratory or wild stocks which have been examined. Attacks typically had a very rapid onset, were relentless, and were potentially damaging in nature. A male or a female intruder may thus risk life-threatening wounds if they attempt to enter a lactating female's nest area (26,33). We confirmed in Experiments 1 and 2 that there is an increase in the rate of aggression toward intruders between Day 1 and Day 3 postpartum. However, our finding of a very high rate of aggression by virtually all females on the day of birth of their litters is in marked contrast to some studies conducted with laboratory stocks of mice in which little or no aggression is observed until 2–3 days postpartum (38).

When housed either by themselves (Experiment 1) or with their mates (Experiment 2), females that were infanticidal as virgins were more aggressive toward intruders than females that were noninfanticidal as virgins. This was reflected in the higher overall rate of attack by infanticidal females, particularly toward female intruders. In addition, the intensity of the attacks (the number of visible wounds on intruders) was significantly greater for infanticidal than noninfanticidal females. In mice there is a relationship between exposure to testosterone during fetal/neonatal life and, in adulthood, both aggression toward adults and infanticide when confronted with pups (44). However, recent findings suggest that while intrasexual aggression is related to levels of testosterone during fetal life in both male and female mice (40), infanticide is only related to fetal testosterone levels in male (34,41), but not female (24), mice.

In Experiment 1 infanticidal females showed both offensive and defensive types of attacks, while the noninfanticidal females only showed defensive attacks. Studies with both rats (4) and mice (5) have led to the hypothesis that defensive attack is motivated by fear while offensive attack is more commonly seen in encounters between adults of the same sex when competing for resources. It thus is likely that spontaneously infanticidal females are less fearful than spontaneously noninfanticidal females in this stock of mice.

In contrast to our findings here, postpartum aggression toward female intruders by Swiss mice is typically offensive in nature, while attacks toward male intruders are typically defensive (26). It has been proposed that maternal aggression may have evolved as a counter strategy to infanticide (21,27,28). A major difference between the male and female intruders in our experiments here and intruders (particularly females) in many laboratory stocks of mice is that all males and females which were used as intruders in these experiments were a potential threat to the young, since they all had exhibited infanticide when screened for their behavior toward young. In contrast, in most laboratory stocks of mice, the majority of virgin females are spontaneously parental toward pups and thus are not a threat to the survival of a lactating female's litter (17,39). We propose that the fact that most virgin females in this wild stock of mice are infanticidal has influenced the type of attack (more typically defensive rather than offensive) shown by lactating females toward female intruders.

Because all intruders had exhibited infanticide on a screening test, we were concerned about the possibility that at least some of the pups would be killed by the intruders, which would have led to incomplete data sets for animals tested in the experiments; the loss of litters in Experiments 3 and 4 due to housing females together made it very difficult to make quantitative comparisons.

We also were concerned that the extremely high aggressiveness of lactating females in this stock would lead to severe injury of at least some of the intruders. One consequence of this procedure was that we did not examine the possibility that, at least in some cases, after the intruder counter attacked, all of the pups would be killed (27); this decision was based on a preliminary study (with a small group of animals) in which we observed that after a male intruder counter attacked the resident lactating female, the entire litter was killed. In addition, it is also possible that at least some of the intruders would have been killed due to the very high aggressiveness of the lactating females (19).

Reproductive Success in the Presence of Another Female

When two sibling females were placed together with a stud male in Experiment 4, there was total suppression of reproduction in one female. Wild female mice are highly aggressive toward other females prior to pregnancy as well as during pregnancy and lactation (22,25). We predict that the female siblings had formed a dominance hierarchy and only the dominant female in each pair was able to ovulate, mate and produce offspring, similar to findings in a monogamous microtine, Microtus ochrogaster. Thus, females of this stock may be similar to males in that they form a dominance hierarchy which determines reproductive success. In an artificial territory with Swiss albino mice or the F_1 offspring of wild males and Swiss females, the dominant female in the colony had greater reproductive success than subordinate females (29). A similar inhibition of reproduction in subordinate females was also reported by Lloyd and Christian (16). In contrast, Parmigiani et al. (29) reported that in a strain of mice selected for a low level of aggression, there was no evidence of interfemale aggression, and when two females were housed with a male, both females successfully produced offspring.

In Experiment 4 there was also a dramatic loss of offspring for the one female in the sibling pair which did get pregnant and deliver pups: only 3 out of 9 litters produced by the one reproductively active female in a cage survived to Day 4 after birth. While we did not directly observe any of these females exhibiting infanticide, the finding that no pups were lost in Experiments 1 and 2 suggests that for the sibling females tested in Experiment 4, the nonpregnant sibling killed her sister's pups. In females from this stock, subordination may inhibit reproduction but not infanticide. The effect of social status on the behavior of these female mice toward pups may thus be markedly different than in male mice where subordination inhibits infanticide (45).

There was also a loss of litters in Experiment 3 in which two unrelated and unfamiliar pregnant females were placed together after having mated with different males (33% of the litters were lost). Thus, the loss of pups only occurred when another female was present in the cage (in Experiments 3 and 4), not when females were housed alone (Experiment 1) or with their mate (Experiment 2). The finding of a loss of litters due to the presence of another female contradicts previous work with both laboratory and wild mice demonstrating a reproductive advantage associated with communal nesting (14,36,37). This is what we had expected to observe in Experiment 4, yet only 3 out of 18 sibling females used in this study (17%) succeeded in becoming pregnant and producing pups that survived to Day 4 postpartum.

For the pairs of sibling females in Experiment 4, the loss of litters occurred even though the females were genetically related and had been together throughout life. In our study neither kinship nor familiarity appeared to result to the absence of infanticide among females, which does not support the hypothesis that closely related kin should always cooperate to rear young rather than exhibit infanticide. In fact, killing of kin by females has been observed in other species: dingo (9), prairie dog (11), yellow bellied marmot (1). These findings are consistent with the kin-competition hypothesis that aggression toward kin may be adaptive when there is intense competition for resources (2).

Laboratory stocks of mice show different levels of aggression, and, in particular, the less aggressive laboratory stocks are markedly different in their behavior than the wild population of mice studied here (38). It is possible that geographically separated wild mouse populations may also show different degrees of aggression, as well as differences in many other aspects of their physiology (7), and these differences may be responsible for the flexibility in social structure of this opportunistic species. In this regard, an interesting observation concerning this Canadian stock of wild mice is that even though they have been outbred in the laboratory for over a decade, there is a marked seasonal cycle in reproductive performance. Whereas virtually 100% of male-female pairs produce offspring when bred in the summer, only about 45% of pairs produce litters when bred between December and February (F. vom Saal, unpublished observation). This observation shows that for this stock of mice, seasonal changes in reproductive performance are not simply a facultative response to energetic constraints placed on small rodents during the winter in northern latitudes (7). These wild mice thus differ from wild mice trapped in a more temperate climate (Missouri) that were used in prior studies (17); 90-100% of pairs produced young throughout the year.

Relationship between Aggression and Social Structure in Mouse Demes

It is generally recognized that drawing inferences concerning the social structure of wild mice from laboratory experiments, even those using wild mice, in artificial settings is a tenuous process at best. However, the high frequency of infanticide and high level of intraspecific aggression of females in this Canadian stock of mice suggest that competition for resources, including mates, is intense. The observation that when sisters remained together in pairs in Experiment 4 only one female in each pair produced offspring is consistent with this hypothesis. What was not predicted was the additional observation that for two-thirds of the females that produced a litter, no pups survived and were likely killed by the nonpregnant sibling female. It is thus possible that in this stock, females do not breed together as a result of being adapted to a harsh environment in which there is much greater competition for resources than would be the case in more temperate climates. The social structure in this stock may thus not conform to the model that a mouse deme consists of a number of related females, a dominant male and a few subordinate males.

Our findings suggest that the best reproductive strategy for females in this stock may be to nest only with their mates rather than with other females, whether related or unrelated. Relative to nesting alone, a resident male mate provides an additional defender of the pups, particularly when the intruder is a male (as predicted, male residents were more likely to attack intruder males than intruder females in Experiment 2). The presence of the male is essential since male intruders that do counter attack and subdue a lactating female will always kill the entire litter (31). Females nesting with their mates can also mate during postpartum estrus, which occurs during the night after delivery, without leaving the nest site unprotected or attracting a strange male that is a threat to offspring into the nest area.

The implication for social structure in this stock of only having one successfully reproducing female when sibling females remained together is that aggression by females toward same-sex adult conspecifics and/or their infants may limit the reproductive output of reproductively active males (27,31,48). Thus, although house mice are polygynous in some situations, interfemale aggression as well as infanticide by females could prevent males from acquiring additional mates, thus leading to forced monogamy for males in this stock, as described by Wittenberger (47, p. 508) in other species. The present findings provide further evidence that house mice which live in markedly different climates show marked flexibility in their physiology and social structure (7).

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