



Impact of male presence on female sociality and stress endocrinology in wild house mice (*Mus musculus domesticus*)

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ABSTRACT

In group living animals, reproductive competition plays an important role in shaping social relationships and associations among female group members. In this study, we investigated the impact of male presence on the development of female-female competition and female sociality in groups of female wild house mice, using physiological and behavioral parameters. We predicted that, by eliciting intra-sexual competition, males influence social relationships among female group members and thus affect female associations to potential cooperation partners. To test this hypothesis we compared stress hormone production, the frequency of agonistic interactions, social hierarchies and social partner preferences in groups of unrelated, unfamiliar females in the absence and presence of males. Our results revealed no indication that the introduction of males into all-female groups of wild house mice elicited increased competition among female group members, neither on the physiological nor on the behavioral level. We found no effect of male presence on female glucocorticoid secretion, aggression, dominance hierarchies or on the females' sociability. Females thus seem not to intensely compete over access to males. This female ability to behaviorally and physiologically deal with even previously unfamiliar same-sex group members may be an important feature of female house mouse societies. In fact, it could be a necessary prerequisite to establish cooperative relationships between females in the context of reproduction, such as communal nursing of young.

1. Introduction

Conspecifics are a major environmental factor, in particular for group living animals. From a female's point of view, males may serve as potential mating partners and same-sex conspecifics as social and potential cooperation partners. On the other hand conspecifics are also competitors for limited resources when living in close proximity [1,2]. Conflicts are therefore inevitable when females form groups [3], despite any adaptive value of group living [4,5]. Among females, rivalry predominantly concerns reproduction, where individuals may not only compete over reproductive resources or the opportunity to reproduce, but also over access to mates [6–8]. Reproductive competition among females recently received substantial attention, since sexual selection in females has been documented in a wide range of taxa [9–14].

Female mate competition often emerges as increased intra-sexual aggression [15–17] and is assumed to play a role in shaping social

structure and spatial distribution among conspecifics [15,18,19]. The social structure, particularly spatial associations among female group members, is in turn linked to cooperative relationships, as for example shown in primates [20], bats [21], rodents [22–24], birds [25] or fish [26]. Thus, by affecting social structure, female-female competition may influence individual preferences for potential cooperation partners.

Wild house mice, *Mus musculus domesticus*, live in groups that are typically characterized by one territorial male, few, if any, subordinate males and several breeding and non-breeding females [27–33]. Females usually remain in their natal territory, but occasionally disperse and successfully immigrate into another breeding unit, where they encounter unrelated and unfamiliar same-sex conspecifics [27,34,35]. Female house mice belonging to the same breeding group may cooperate by communally nursing their young [35–39]. Thereby, females display preferences for specific cooperation partners, yielding

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significant fitness benefits [40]. At the same time, however, group living females may compete over access to males [15,41], especially due to the importance of genetic benefits of mate choice [42–44]. To understand the role of female intra-sexual competition for establishing social associations, we experimentally investigated the impact of male presence on female stress physiology and sociality in wild-derived house mice.

We predicted that male presence elicits competition among females and shapes female social structure. To test this hypothesis, we compared stress hormone production, behavioral parameters and social partner preferences in groups of unrelated, unfamiliar females in the absence and presence of males. We specifically hypothesized that male introduction into all-female groups 1) increases female stress hormone production, 2) leads to an increase of agonistic interactions between female group members, 3) reinforces the dominance hierarchy among females, and 4) decreases the females' sociability, i.e. reduces the number of association partners.

We focused on genetically unrelated females in this study as they compete most severely over reproduction [15,16,45]. Under natural conditions, unfamiliar non-sisters represent a social category that a maturing female mouse may encounter when emigrating from its natal territory. Such females may either enter another group or form a new one with previously unfamiliar and unrelated females [35,46,47].

2. Methods

2.1. Animal husbandry and enclosures

Animals were direct descendants of wild-caught and randomly bred house mice, *Mus musculus domesticus*, originating from three wild populations in the vicinity of Zurich, Switzerland (all populations shared the same karyotype, $2n = 24$). Mice in our breeding colony were housed in Macrolon-III-cages ($23.5 \times 39 \times 15$ cm) on standard animal bedding, with food (laboratory animal diet for mice and rats, no. 3804 & 3336, Provimi Kliba SA, Kaiseraugst, Switzerland), water and nest building material ad libitum. Pups were separated from their parents at the age of 23 days and housed with same-sex littermates.

The experiment was carried out in indoor enclosures, which were 7 m^2 in size and surrounded by 80 cm high aluminum walls. Each enclosure was filled with 1–2 cm of standard animal bedding, equipped with six nest boxes (15 cm diameter, 15 cm height), several PVC barriers for structuring, hay and paper towels as nest building material and three feeding and drinking sites.

Experimental animals were kept under standard laboratory conditions (14:10 h light:dark cycle, lights on at 07:30 h; 22 ± 1 °C, 50–60% relative humidity). Red light was automatically switched on from 17:30 to 22:00 h to allow for behavioral observations after the beginning of the dark phase.

2.2. Experimental procedure

We investigated 22 replicate groups, each with six adult virgin females (2–3 months of age) and two adult, sexually inexperienced males (2–7 months old). In each group, females were unfamiliar and genetically unrelated to each other (descending from different breeding pairs). The males were unrelated and unfamiliar to the females. Within a replicate, females did not differ more than one month in age and not > 2 g in weight at the onset of the experiment. All females were equipped with subcutaneously injected transponders (RFID tags; ID 100, TROVAN electronic identification systems) and obtained fur cuts and ear punches for visual individual identification during behavioral observations. Animals were not anaesthetized during these rapid procedures and resumed normal behavior immediately.

Females of one replicate were simultaneously introduced into the enclosure. The density used here can be considered below that reported for free-living house mice and for previous studies with wild mice,

where several up to 10 adults per m^2 have been documented [23,34,48,49]. During the first 18 days of the experiment, the animals remained in this all-female group. On day 18, two adult males were placed in separate cages (Macrolon-II-cages, $18 \times 24 \times 14$ cm) in the middle of each enclosure, for a period of another 15 days, days 19–33. The cages were positioned in a distance of 15–20 cm to each other and did not allow for direct interactions among the males. Females could inspect the cages and interact with the males through the cage lids (allowing olfactory, acoustic and limited physical contact, but no mating). Once per week we mixed the bedding of the two cages with the males and interchanged at the same time their position in the enclosure. Such treatment intended to expose all females to similar olfactory cues of the two sexually mature males independent of their individual spatial location. The males were expected to produce urine markings considered attractive for females [50] since they were exposed to olfactory cues from a potential male competitor. The introduction of caged males was intended to signal mating opportunities to the females without permitting them to mate. We did not determine the females' estrous stages since it would have required regular handling to use vaginal tissue inspection (vaginal smears). Such manipulation is considered invasive for wild-derived house mice (own observations) and is likely to have interfered with their stress response.

We collected data on the females' nest box use for all 22 groups. For ten groups, we carried out behavioral observations and sampled feces for endocrine analysis at regular intervals before and after the introduction of the males. Sample size was thereby comparable to other studies investigating female relationships [15]. To detect overt aggression, we checked the females for scars and wounds at least once a week. In two groups one female each had to be removed before male introduction due to wounds inflicted by her group mates. Both animals recovered and wounds healed within a few days without additional treatment. In another trial, a single female escaped from the enclosure after male introduction. We proceeded with the five remaining females in these groups.

2.3. Behavioral observations

For ten groups, behavioral observations were carried out 24 times, 12 times each before and after introduction of the males with at the most one observation unit per day, beginning at day 1. Observations took place during the females' activity period between 17:30 and 22:00 h (red light enabled the observations in the dark). Fur cuts and ear punches allowed visual identification of females in a group. During each observation unit we documented the behavior of all females belonging to the same group outside of nest boxes over one hour (all-occurrences recording; [51]). We continuously registered during direct observations the occurrence of individual females leaving and entering nest boxes and of agonistic interactions among individual females.

2.3.1. Group activity

We recorded for each replicates the number of nest box changes for each female as a measure for activity during a 1-h period. In two replicates, four and 17 of the 24 1-h observation units were excluded from analysis as none of the females appeared outside a nest box and no behavioral data were collected. For comparisons of the periods prior to and after male introduction, data were pooled for days 1–18 and 19–33 as follows. To determine the impact of male presence on female activity, we compared for each of the ten groups the mean frequency of nest box changes per observation hour between the time periods before and after male introduction. This was done using the Wilcoxon Signed Rank test.

2.3.2. Agonistic interactions

We recorded the frequency of agonistic interactions between females. The behavioral elements 'chase/flight', 'bite', 'attack', 'approach/retreat' and 'fight' were used according to Mackintosh [31],

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