Physiology & Behavior 189 (2018) 1–9

Contents lists available at ScienceDirect

Physiology & Behavior

journal homepage: www.elsevier.com/locate/physbeh

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

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ARTICLE INFO

Keywords:
Dominance hierarchy
Elo-rating
Fecal corticosterone metabolites
Female competition
Female-female interactions

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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https://doi.org/10.1016/j.physbeh.2018.02.039
Received 20 October 2017; Received in revised form 19 February 2018; Accepted 19 February 2018
Available online 21 February 2018
0031-9384/

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 und 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 × 39 × 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 × 24 × 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],

Rusu and Krackow [15], and Rusu et al. [22]. Furthermore, as an additional agonistic element, we included 'expel from nest box', i.e. one female displaced another one from a nest box. To investigate the impact of male presence on the frequency of socio-negative behavior among females, we compared for each group the mean number of agonistic interactions, as well as the frequency of socio-negative behavior among females on the first day of the study and the first day after males were introduced, using the Wilcoxon Signed Rank test.

2.3.3. Determination of social ranks

We used Elo-rating according to Albers and De Vries [52] to describe social hierarchies among females within each group. The method of Elo-rating provides a sequential estimation of individual dominance strength based on the actual sequence of agonistic interactions (for detailed information see [52]). To calculate Elo-rating values, we included all agonistic interactions within each of the 1-h observation units, either resulting in a winner and loser, or undecided. Based on the Elo-rating values, an estimated rank order can be derived at any moment in time. However, estimated ranks are only meaningful, if an assigned rank order is not altered by single interactions but is rather stable over time. We therefore carried out simulations (using the number of observed agonistic interactions per group) to obtain 95% confidence intervals of Elo-rating values reached by chance (when females would interact randomly). We only assigned females as 'dominant' or 'subordinate', when Elo-rating values were above or below this confidence interval, respectively. All females with values within the confidence interval were assigned as 'medium'.

The number of observed agonistic interactions over the course of the experiment varied between groups (range: 9–455). We therefore calculated the confidence intervals for each group separately. All simulations were run with 100 repeats (the values did not differ substantially if running 100 or 1000 repeats), with six females per group and with a starting value of 1000 for each female, applying the rules of the Elo-rating method according to Albers and De Vries [52]. For each interaction, two individuals were drawn at random, and winner/loser was assigned based on these individuals' current Elo-rating and a uniformly distributed random number. Minimum and maximum values for the confidence intervals leveled off after approximately ten interactions, suggesting that meaningful results can be obtained when ten or more interactions have taken place.

We assessed the hierarchical structure of each group by using the final Elo-rating values at day 33 of the experiment as an individual's characteristic for its social rank. On the basis of the simulation results, we assigned each female as 'dominant', 'medium' or 'subordinate'. In nine groups at least ten agonistic interactions were observed, and in one group, nine agonistic interactions were recorded over the course of the experiment. All ten groups were included in the analysis.

To investigate whether male introduction had an impact on the hierarchical structure of female group members, we carried out a linear mixed-effects model [53] fitted by residual maximum likelihood with individual Elo-rating values at day 33 as the response variable, and individual Elo-rating values at day 18 before male introduction as the explanatory variable. Group identity was incorporated as a random term to account for effects due to same group origin. We conducted this analysis with eight groups, as two groups only showed one, respectively five agonistic interactions in the first part of the experiment and the resulting Elo-rating values were not considered meaningful. The same model was carried out using the difference of the Elo-rating values at day 33 minus the Elo-rating values at day 18 as the outcome variable. We thus tested whether the observed slope of the relationship between Elo-ratings at day 33 and day 18 differed from a 1:1 relationship.

2.4. Nest box use

For all 22 groups we collected daily data on the females' nest box use on 30 consecutive days, between days 4–33. The location of each female was registered with a portable transponder reader (LID 500 Hand-Held Reader, TROVAN electronic identification systems) once a day at midday, when the mice were predominantly resting or sleeping in the nest boxes. Identifying transponder number was possible from outside the nest boxes without disturbing the mice.

Shared nest box use, specifically spatial association, was used as a measure for social preference (see also [23,24], a relation suggested in previous studies on house mice [15,37,54–56] and other mammals (e.g. [57,58]). We determined spatial associations according to the symmetrical index of Fager (I_{ij}-index) as modified by Kerth and König [57]. We calculated the expected probability that two females of a dyad meet in any of the nest boxes by chance, and compared this expected value with the observed data using a binomial test. Two females were regarded as 'preferred partners', when they showed a significant positive association, meaning that they shared nest boxes significantly more often than expected by chance. Females were regarded as 'non-preferred partners' when they shared nest boxes in the range of random expectation. Comparisons between the periods prior to and after male introduction were based on data of nest box use on days 4–18 and days 19–33, respectively.

2.4.1. Frequency of significant positive associations

To determine whether the presence of males altered the frequency of significant positive associations, we compared the proportion of 'preferred partner' dyads per group between the periods prior to and after male introduction with a Wilcoxon Signed Rank test. The proportion values can range from zero to one, with a value of zero indicating that no significant associations occurred, and a value of one that all dyadic associations of a group were higher than expected by chance.

In addition, we investigated the impact of male presence on female preference for specific social partners. We therefore tested whether the category of association between two specific female group members (preference category: either 'preferred' or 'non-preferred') in the absence of males was the same as in the presence of males. For this analysis we chose the two extremes in each group: the two females with the highest (significant) association and the two females with the lowest (non-significant) association. If more than one dyad in a group had the same highest or lowest association values, we randomly selected one. In two groups, all female dyads showed higher than random associations, resulting in only the 'preferred' pair to be used for analysis. In one group, one female in the lowest associated pair proved to have crippled genitalia and inner sexual organs at the end of the experiment, and the pair was excluded from analysis. This analysis was therefore carried out with 41 dyads altogether. We conducted a generalized linear mixed-effects model using a binomial error structure and the logit link function. The model was fitted with penalized quasi likelihood estimations (for details see [59]). We used the preference-category after male introduction as the binary response variable, the preference-category prior to male introduction as the fixed factor and group identity as a random term.

2.5. Monitoring stress hormones

For ten groups, we analyzed corticosterone metabolites (CM) in fecal samples using a 5α-pregnane-3β,11β,21-triol-20-one enzyme immunoassay (EIA). Details regarding the development, biochemical characteristics, and biological validation of this assay have been described by Touma and colleagues [60,61]. In fecal samples, circulating hormone levels are integrated over a certain period of time and are less affected by single stressful events and episodic fluctuations of hormone secretion [61,62], thus allowing us to assess longer-term endocrine profiles.

Fecal samples were taken at six defined time points during the experiment (days 1, 4, 11, 18, 25 and 33) from each individual female. Samples on day 1 were taken prior to the release of the females into the

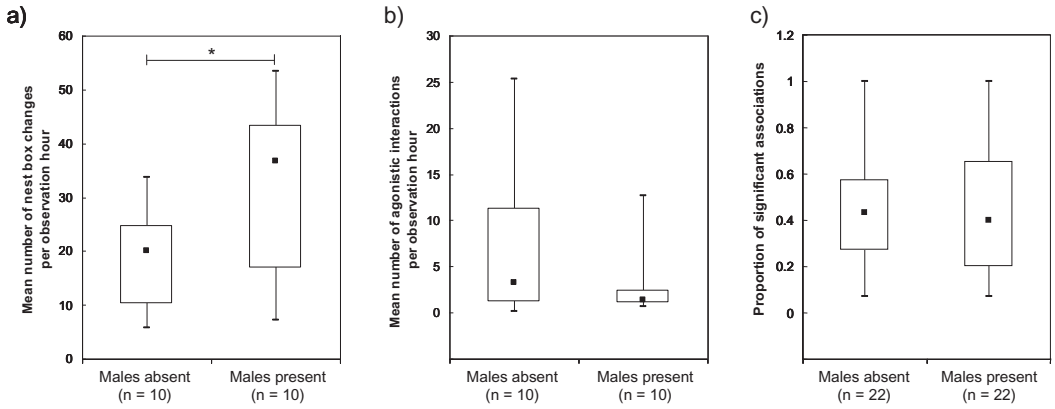

Fig. 1. Influence of male presence on a) mean number of nest box changes, b) mean number of agonistic interactions and c) proportion of significant associations (female dyads which shared nest boxes significantly more often than expected by chance). Data are shown as medians, box: interquartile range 25%–75%, whiskers: Min. – Max.. A significant difference between data collected when males were absent and when males were present is indicated by *.

enclosures, which we therefore defined as baseline levels of CM concentrations. As most social interactions and possible stress-responses were expected to occur during the first days after introduction to the group enclosure, we collected the second sample on day 4, followed by weekly intervals. We always sampled the females between 07:30 and 09:00 h in the morning, thus avoiding possible fluctuations in the steroid excretion due to the circadian activity pattern [61–67].

To obtain fecal samples from individual females, all females of one group were removed from the enclosure between 07:30 and 08:00 h and singly placed in Macrolon-II cages (18 × 24 × 14 cm), equipped with fresh bedding. After a period of 60 min females were released back into their enclosure. Fecal pellets were immediately collected from the cages and were frozen at −20 °C. Possible endocrine stress responses due to the sampling event could not have influenced the current or following sample, as elevated CM concentrations in reaction to stressful events are only traceable in the feces with a delay of 4–10 h, depending on the time of day and the activity rhythm of the animals (for detailed information see [60,62]).

Fecal steroid metabolites were extracted according to the method described by Palme et al. [68]. Briefly, the fecal samples were dried for two hours at 80 °C. Each sample was homogenized and shaken with 20 µl of 80% methanol per mg feces for 30 min on a multi-vortex. The ideal amount of dry feces for further processing was 50 mg, the minimal amount used was 20 mg. After centrifugation (10 min at 2500*g*), an aliquot of 500 µl of the supernatant containing steroid metabolites was frozen at −20 °C until analysis. To determine the amount of fecal CM, we used an EIA (5α-pregnane-3β,11β,21-triol-20-one enzyme immunoassay), a method specifically established and validated for mice by Touma et al. [60,61].

To investigate the effect of grouping females with unrelated, unfamiliar same-sex conspecifics on CM concentrations, we again carried out a linear mixed-effects model fitted with residual maximum likelihood. CM concentration was the response variable, the sampling bout (baseline level/day 1 or day 4) was used as a fixed factor and the individual was nested in group identity as a random term to account for potential similarities of individual females originating from the same enclosure.

We additionally carried out a linear mixed-effects model fitted with residual maximum likelihood to investigate potential factors altering CM concentrations. The difference in CM concentrations between the sampling bouts was the response variable, and we used male presence as a fixed factor. We additionally included mean number of agonistic interactions per group, individual activity and the final individual Elo-rating values as fixed factors as they may also affect CM concentrations. Furthermore, we included the change in CM over time, analyzed as the difference in individual CM concentration to the previous fecal sampling event (for days 4, 11 and 18 after grouping of females and thus before male introduction, and for days 25 and 33 after male introduction), as an ordered fixed factor and the interaction between male presence and the individual Elo-Rating values. In a stepwise backwards approach we removed the interaction from the model as it did not reach significance to investigate the main effects. Male presence nested in individual, which was again nested in trial identity, was used as a random term to account for potential similarities of females originating from the same enclosure in the absence and presence of males. We based this analysis on type three sum of squares to investigate each term independently.

To correlate behavior with hormone responses, we matched the time frames of fecal sampling and respective observations. We used behavioral data taken during the two preceding days (this means approximately between 10 and 38 h) prior to each fecal sampling event. Depending on the observation schedule, this time period might have included one or two observation units. For the analyses, we used the mean number of agonistic interactions occurring in each group per hour observation and the mean number of nest box changes per individual as a measure of individual activity per hour observation relating to the fecal sampling events on days 4, 11, 18, 25 and 33.

2.6. Statistics

Statistical models were carried out using R for Windows, Version 3.1.2 [69] and the packages 'nlme' [53] and 'MASS' [59]. The model assumptions of normality and homogeneity of variances were verified graphically and were always met. Nonparametric statistics were conducted using SPSS 13.0 (SPSS Inc. Chicago, IL, USA). All tests were two-tailed and effects were regarded as significant at $P \leq 0.05$.

3. Results

3.1. Group activity and agonistic interactions

Group activity, measured as the mean frequency of nest box changes per observation hour, increased significantly in the presence of males (Wilcoxon Signed Rank test: Exact Sig.: $P = 0.021$; $N = 10$, Fig. 1a). We further regularly observed females inspecting the cages with the males. In contrast, we found no significant difference in the mean frequency of agonistic interactions among females per observation hour between the time periods without and with male presence (Wilcoxon Signed Rank test: Exact Sig.: $P = 0.75$; $N = 10$, Fig. 1b). In most groups, highest frequencies were reached at the beginning of the experiment and leveled out over time.

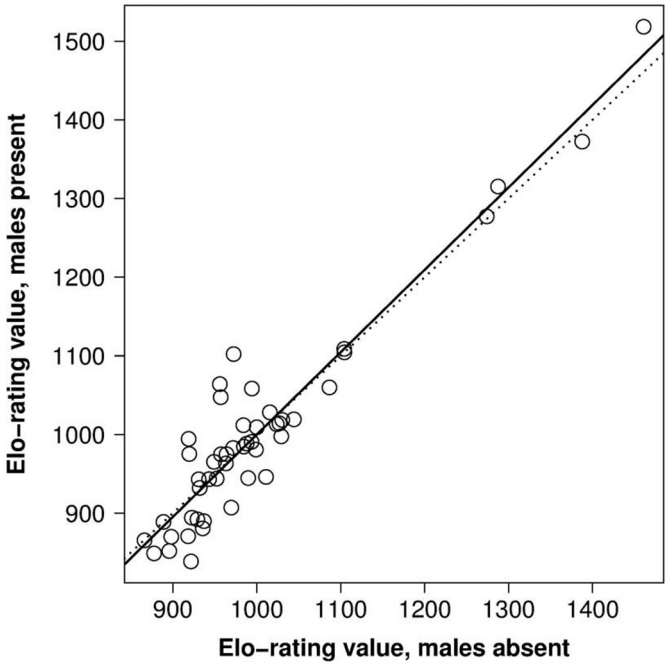

Fig. 2. Relation between individual Elo-rating values at day 18, in the absence of males, and at day 33, in the presence of males. The dashed line indicates a 1:1 relationship and the solid line reflects the line estimated by the statistical model.

3.2. Social hierarchies

In only four of the ten groups, one "dominant" female occurred, and none of the groups contained a female that was assigned "subordinate". Most females were classified as "medium" and showed rather similar Elo-rating values. Furthermore, social hierarchies were stable, independent of male presence. The final Elo-rating values at day 33 could be predicted by the Elo-rating values at day 18, prior to male introduction ($F_{1,39} = 399.46$, $P < 0.001$), and no significant difference from a 1:1 relationship was observed ($F_{1,39} = 0.81$, $P = 0.37$; Fig. 2). Comparing the scales on the axes, it is also visible from Fig. 2 that the Elo-ratings were in the same absolute range on both day 33 and day 18. Similarly, our random simulations of the Elo-ratings showed that they did not continuously diverge with increasing number of interactions but stabilized in their values over time. All four females, which were assigned as "dominant" at the end of the experiment already held this classification at day 18, i.e. before males were introduced.

3.3. Significant associations and partner preferences

The proportion of "preferred partner" pairs did not differ significantly between the time periods prior to and after male introduction (Wilcoxon Signed Rank test: Exact Sig.: $P = 1.0$; $N = 22$, Fig. 1c). Within groups, 7–100% of the pairwise associations among females were significantly higher than expected by chance in both periods.

However, even though the overall ratio of significant associations did not change significantly, 16 of the 41 extreme pairs (the highest and lowest associated dyad in each group) showed a change in their preference category ('preferred' versus 'non-preferred') in the presence of males. The preference category of the highest and lowest associated pairs after male introduction could thus not be predicted by the preference category of those dyads in the absence of males ($F_{1,18} = 2.2$, $P = 0.15$). Changes of the preference category occurred in both directions. Five out of 19 dyads which were classified as 'non-preferred' pairs in the presence of males were classified as 'preferred' prior to male introduction, and 11 out of 22 dyads classified as 'preferred' pairs after male introduction were classified as 'non-preferred' in the absence of males.

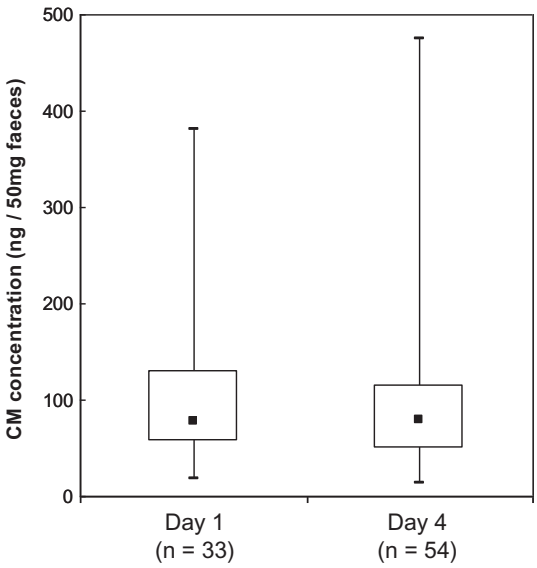

Fig. 3. Concentrations of corticosterone metabolites (CM) in the feces at day 1 (baseline) and day 4 of the experiment. Data are shown as medians, box: interquartile range 25%–75%, whiskers: Min. – Max.. Sample size differs between day 1 and day 4 as fewer individual fecal samples could be collected during the first than during the second sampling bout.

3.4. Stress hormone production

The grouping of unrelated, unfamiliar females in a rather large enclosure with several nest boxes, feeding and drinking sites did not induce elevated stress hormone levels lasting for the first three days. Such habituation period was expected to also overcome any anxiety related responses after transfer into the enclosure. The corticosterone metabolite (CM) concentration on day 4 of the experiment did not differ significantly from the baseline levels collected when females were still housed with same-sex littermates (day 1; $F_{1,26} = 0.17$, $P = 0.688$; Fig. 3) and may have been long enough to overcome any anxiety related responses after the transfer into the new environment.

We found no significant effect of the mean number of agonistic interactions per group ($F_{1,106} = 0.37$, $P = 0.55$) and of individual activity ($F_{1,106} = 0.03$, $P = 0.86$) on glucocorticoid production. In addition, time had no systematic effect on CM concentrations ($F_{2,106} = 0.13$, $P = 0.88$; Fig. 4) and the interaction between the presence of males and the individuals' final Elo-rating values was not significant ($F_{1,45} = 0.31$, $P = 0.58$). There was also no main effect of the final Elo-rating value ($F_{1,44} = 0.23$, $P = 0.64$) and of male presence ($F_{1,46} = 0.28$, $P = 0.60$; Fig. 4) on CM levels after removing the interaction from the model.

4. Discussion

Group living female house mice increased their activity in the presence of males. Nevertheless, we found no indication, neither on the physiological nor on the behavioral level, that male presence induced significant modifications in the females' behavior that suggest mate competition. The introduction of caged males to the enclosure, which allowed olfactory, acoustic and limited physical contact (but no mating), did not increase agonistic interactions or reinforce the dominance hierarchy among female group members. Furthermore, the presence of males did not alter the females' stress hormone production or the females' sociability.

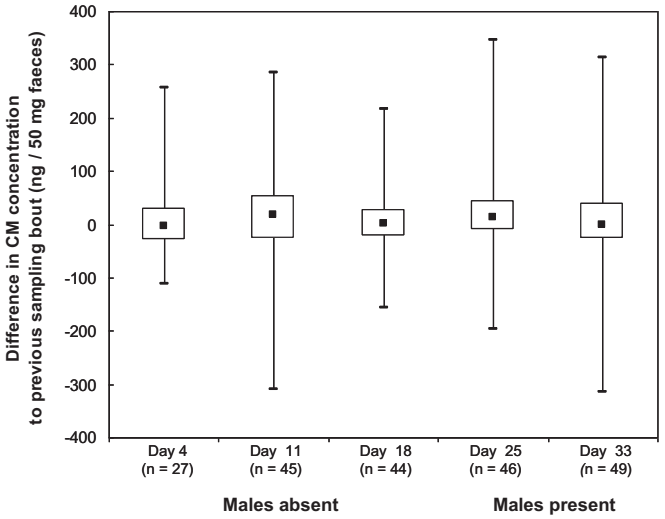

Fig. 4. Changes in concentrations of fecal corticosterone metabolites (CM) in relation to the previous sampling event, for the time periods before (days 4, 11, 18) and after male introduction (days 25, 33). Data are shown as medians, box: interquartile range 25%–75%, whiskers: Min. – Max. Sample sizes for each sampling bout refer to the data analyzed in the model.

4.1. Female relationships

Agonistic interactions among females were generally low, supporting previous research on wild-derived house mice [70,71,49]. Aggression did not increase after male introduction, even though overall group activity rose so that females were expected to meet and interact more frequently. Female-female mate competition in polygynous and monogamous mammals is indicated by intra-sexual aggression when breeding opportunities occur, as has been shown for example in red deer [17], Mongolian gerbils [72] and house mice [15,16] (for a review see [14]). Presence of or olfactory cues from unfamiliar males elicit estrous cycles in female house mice and signal the opportunity to reproduce [73,74]. In our study, male presence did not cause increased female-female aggression, suggesting that females did not compete over potential access to mating partners.

This finding is further supported by our results on the hierarchical structure among female group members. Dominance hierarchies are considered as a means to reduce direct and indirect costs of competition [75,76]. Females are therefore expected to develop social hierarchies whenever group members compete, as for example over mating partners. However, when within-group competition is low or absent, females are thought to have rather egalitarian relationships [3]. In our study, we found no pronounced hierarchical structure among female group members. Only in the minority of groups (40%), one female was assigned as dominant, and subordinates occurred in none of the groups. Most females were classified as ‘medium’. This situation remained unchanged when males were introduced.

That fact that male introduction did not influence the amount of positive associations towards other female group members either, additionally supports the conclusion of the previously discussed results. Males do not elicit mate competition and do not generally alter female sociality. Female preferences for social partners are reflected in preferential cohabitation (significant spatial associations) in house mice [40]. In this experiment, the proportion of such positive associations between female group members did not differ in the absence and presence of males, indicating that females do not generally get less social or choosier when males are present.

Interestingly, however, the introduction of males may affect female preferences for specific social partners. Overall, 16 of the 41 highest and lowest associated female dyads revealed modified preferences in the presence of males. Partners, that were preferred in the absence of males were no longer chosen when males were present, or vice versa. Given that social partner choice in the presence of males yields significant fitness benefits [40], partners for cooperative reproduction may only be chosen when reproductive opportunities are imminent, that is in the presence of males. This reasoning would be in line with Dugatkin and Sih's [77] statement, that individuals may display different partner preferences in different social contexts. However, further and more detailed studies are needed to prove that female preferences for specific social partners are indeed influenced by male presence.

Rodents mainly rely on chemical communication, and the females' estrous state affects odor cues important for inter-sexual interactions and mate choice [78,79,80]. The role of odor signals in competitive and aggressive interactions between females is rather little studied so far. In male house mice, major urinary proteins (MUPs) are crucial for intra-sexual competition and have recently been suggested to also mediate female-female interactions (for reviews see [81,11]). Production of these proteins was cyclic in females of a laboratory mouse strain [82], still variation across a wild-derived female's estrous cycle is considered to be much lower than variation between individuals (JM Hurst, cited in [11]). Virgin females synchronize in estrous when they experience olfactory cues from adult males [73,83,74]. As a consequence, all females in a group were expected to have experienced synchronous regulation in the proteins considered to be important in mediating intra-sexual communication. We therefore did not assume a substantial impact of the females' cycles on the question addressed here. Nevertheless, since we did not determine estrous stages to avoid a stress response due to regular handling, we cannot entirely exclude an impact of the sexual cycle on female-female competitive interactions.

4.2. Group life and corticosterone profiles

We did not find any indication for increased competition in the presence of males on the physiological level, either. Individuals that undergo disruption in social rank, involvement in agonistic encounters or that exhibit intra-sexual conflicts with group members (such as competition for mating partners), frequently show elevated corticosterone levels [84–90]. Glucocorticoid concentrations substantially increased during the mating season in wolves [91] or in Mongolian gerbils when founder females were replaced and competition for reproduction was elicited [72]. We therefore expected that mate competition among female group members, if existent, should be traceable on the physiological level by an increase in fecal corticosterone metabolites (CM). Introduction of males, however, did not affect female CM differences between consecutive sampling bouts.

The wild-derived females proved to be rather variable in their basal fecal CM levels taken at day 1 (see Fig. 3). The medians were in the range of those reported for males of several laboratory mouse strains [92] and for female laboratory mice [61,64,93]. Still, due to expressed sex differences in formed corticosterone metabolites [60,61], direct comparisons of CM levels between the sexes is problematic. In addition, an expressed diurnal rhythm in CM excretion and differences concerning the sampling regime (time of day and length of the collection interval) also impedes a direct comparison of CM levels between our and previous studies. Thus, future studies have to verify basal corticosterone levels in sexually mature females of a wild-derived genetic background.

Still, effects of male presence on female CM concentrations might have been “masked” by rank related differences among females. Apart from the fact that females may exhibit different baseline glucocorticoid levels depending on their social ranking (for details [89,94], females of different social status may also react differently on imposed stressors [72], which could prevent the detection of a general reaction pattern. In our study, we neither found a general rank effect, nor, more importantly, a differential effect of male presence on CM levels of females with different social rankings (there was no significant interaction between male presence and the individuals' Elo-rating values). Given the

formerly discussed finding of a relatively egalitarian social structure among females that lack a pronounced dominance hierarchy, this result is not very surprising.

In addition to the missing impact of male introduction on stress levels, group life among female house mice generally appeared to be free of lasting and severe stressors traceable in fecal CM concentrations, at least when resources such as nesting sites, food and water were not limiting, as in our study. CM differences did not vary considerably over time and CM concentrations did not even increase during the first four days after females were removed from their home cages, where they were housed with same-sex littermates, and grouped with unfamiliar, unrelated females. Our results are in line with previous studies by Brown & Grunberg [95] and Nicholson et al. [90], demonstrating that stress levels in female rats and mice, in contrast to those of males, are not strongly affected when housed in groups, even under relatively crowded conditions. Garratt and coworkers [93] also reported that co-housing of two previously unfamiliar females did not increase fecal corticosterone or decrease body weight after three days. Behavioral strategies in handling social and environmental challenges differ in male and female polygynous mammals, given their different social and reproductive roles. For social females, therefore, group life should generally not impose severe stress, which could have fatal consequences when chronic [96,97]. Nevertheless, it is surprising that this is even the case in groups of previously unfamiliar and unrelated female mice, especially as females in natural house mouse groups are generally kin [24,30,98,99]. However, the ability to behaviorally and physiologically deal with strangers might yet be an important characteristic of house mouse societies, as females occasionally emigrate from their natal territories and either integrate into another group or establish a new one [35,46,47].

4.3. Absence of female competition over males

Overall, we found no behavioral or physiological indication that male presence elicited competition among female group members, suggesting that females are not constrained in access to males, as has been observed in a free-living population [49]. This contrasts with Rusu & Krackow [15], who described elevated female aggression and the existence of dominance relationships in groups of three females living with one male in similar sized enclosures. The authors concluded that short estrous cycles and long copulation bouts constraint access to the mating partner when females are reproductively synchronized. Despite the fact that the proportion of adult males to adult females was the same, the discrepancy between Rusu & Krackow [15] and our data might be explained by two lines of argument. First, in groups of three, females may not compete over males but over a social partner (two of the females compete over access to the third female). In larger groups, such constellations may be rare. Second, competition over males is mainly expressed in the presence of a single male (see also [15]). Cues from several males, however, signal unlimited access to males, given that reproducing females are free to move between male territories, as suggested by the occurrence of polyandrous mating behavior in female house mice [48,100].

The absence of female competition, on the other hand, is in line with findings of Palanza and colleagues [16] stating that female intra-sexual competition is regulated by the timing of female-female settlement in relation to male settlement. This conclusion is supported by game theory models [101,102], which suggest that prior social experiences and possession of a resource influence the intensity and outcome of competitive interactions. Females that interacted at the same time or prior to cohabitation with a male (symmetric contest, females were equal in terms of prior residence and association with male), as in our study, showed little aggression and a high degree of reciprocal tolerance [16]. Females that first cohabitated with a male for some days before other females were introduced (asymmetric contest, females were not equal in terms of possession of a resource), however, were highly aggressive and intolerant [16,41]. Our study supports the findings of Palanza and colleagues and shows that the social organization of female house mice differs from the clear-cut territorial dominance observed among males.

4.4. Conclusions

Our results showed that female house mice are not significantly stressed when exposed to a group of several unfamiliar and unrelated same-sex conspecifics. The females' ability to behaviorally and physiologically arrange with same-sex group members under a variety of circumstances may be an important feature of female house mouse societies. This is especially the case when females migrate and enter into another group or found a new reproductive group where female group members are unfamiliar and unrelated. This ability may yet be a necessary prerequisite to establish cooperative relationships in the context of reproduction, such as the communal nursing of young.

Declarations of interest

None.

Acknowledgements

We thank Sarah Hofmann, Meret Latscha and Nicole Zweifel for help with the data collection, Edith Klobetz-Rassam for processing the fecal samples, Gabriele Stichel for animal caretaking and Anna Lindholm for kindly revising the English. The editor and anonymous referees provided very helpful comments. Animal experimentation was approved by the Veterinary Office Zurich, Switzerland (Kantonales Veterinäramt Zürich, no. 158/2004). This work was supported by the University of Zurich.

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