Relatedness and spatial distance modulate intergroup interactions: experimental evidence from a social rodent

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Abstract

Kin selection theory predicts that individuals should generally behave less aggressively or more amicably towards relatives than nonkin. However, how individuals treat conspecifics depends on genetic relatedness but also on the ecological context, which influences the benefits and costs of their interactions. In this study, we used microsatellite DNA markers and behavioral tests to examine the influence of kinship and proximity on the social behavior of Mongolian gerbils Meriones unguiculatus living in different social groups, and whether these effects varied with sex and season. We recorded the duration of 4 behavioral categories (investigative, neutral, amicable, and agonistic) during a 10-min pairwise test. We found that genetic relatedness had significant effects on the duration of investigative, neutral, and amicable behavior, but not on agonistic behavior. We also found significant interaction effects of relatedness and distance between burrow systems (i.e., spatial distance) on investigative, neutral, and amicable behavior, which suggests that the effects of kinship on social behavior were restricted by spatial proximity. The interaction effect between sex and relatedness on amicable behavior showed that male gerbils became more intimate with individuals of the same sex that had higher pairwise relatedness than females. Furthermore, both male and female gerbils enhanced their aggression during the food-hoarding season, but the intensity of these changes was significantly higher in females. Overall, our results suggest that the effects of kinship and spatial proximity on social behavior exhibit sexual or seasonal patterns, thereby implying ecological context-dependent responses to out-group individuals in Mongolian gerbils.

Key words: familiarity, kinship, Meriones unguiculatus, seasonality, social behavior
and Bro-Jørgensen 2011). In many cases, animals exhibit their peak aggression during the breeding season (BS) (e.g., eastern broad-toothed field mouse, *Apodemus mystacinus*: Vachova and Frynta 2004), and they behave less amicably toward kin during the BS compared with other times of the year (e.g., black-tailed prairie dog, *Cynomys ludovici*: Hoogland 1986). Thus, how individuals treat conspecifics depends on their genetic relatedness, but also on the ecological context, which influences the benefits and costs of cooperative and competitive interactions.

Evidence increasingly indicates that unrelated conspecifics that engage in frequent interactions due to their close spatial proximity may develop “kin-like” behavior (Arnberg et al. 2015; Meshriy et al. 2011; Sanchez and Hudgens 2015). Unrelated individuals may gain immediate shared benefits from mutualism or reciprocity (Clutton-Brock 2002, 2009; Madden et al. 2012). For instance, as the home range overlap increases, there is a higher probability of nest-sharing among unrelated female dusky-footed woodrats *Neotoma fuscipes* (Innes et al. 2012), thereby suggesting that proximity can lead to social tolerance in this species. In addition, many territorial species are less aggressive toward known neighbors than they are toward strangers (Macie et al. 2013; Monclús et al. 2014; Temeles 1994), and individuals may save time and energy by averting a costly and unnecessary fight with familiar neighbors (Fisher 1954; O’Connor et al. 2000).

Mongolian gerbils *Meriones unguiculatus* are geographically widespread in the typical steppe, desert steppe, or desert areas of northern China, Mongolia, and the Trans-Baikal region of Russia (Wilson and Reeder 2005). Mongolian gerbils live in social groups comprising 2–18 individuals throughout the year (Liu et al. 2009), where each group occupies an exclusive territory and all group members share the burrow system (*Ågren* et al. 1989a). The reproduction and recruitment of Mongolian gerbils occur mainly from March to August (Liu et al. 2007, 2009), and they start to store food from September to October (*Ågren* et al. 1989a, 1989b). Thus, there are 2 distinct annual life-history stages in Mongolian gerbils: the BS (March to August) and food-hoarding season (FHS) (September to October). Previous studies have shown that the home-range size of a social group increases with the number of male gerbils in the group during the BS, whereas it is positively correlated with the number of female group members during the FHS (Wang et al. 2011a). In addition, field observations and genetic data have demonstrated that social groups are basically family groups (*Ågren* et al. 1989a, 1989b; Wang et al. 2011b), and that inter-group genetic distances and geographic distances are positively related (Wang et al. 2017). Trespassing by neighbors and chases involving individuals from adjacent groups are frequently observed during the BS (*Ågren* et al. 1989a, 1989b), and females commonly copulate with neighboring males (*Ågren* 1984a, 1984b; *Ågren* et al. 1989a). Consequently, the gerbils that live in different social groups may be kin. These characteristics make the Mongolian gerbil a suitable model species for investigating the influence of kinship and spatial proximity on social behavior, which have not been thoroughly examined in this species.

In this study, we conducted an experiment to test our hypothesis that the social behavioral traits of individuals living in different groups are affected by genetic relatedness and spatial distance (distance between burrow systems) in a natural population of Mongolian gerbils *Meriones unguiculatus*. We predicted that gerbils may exhibit higher rates of amicable interactions and allocate less time toward exploring genetically and spatially close individuals. We also tested whether these effects on social behavior differed between sexes and seasons. The social associations and home-range overlap frequently occur among individuals from adjacent social groups during the BS (*Ågren* et al. 1989b; Wang et al. 2011a), and fewer intergroup social connections are established during the FHS than the BS (Deng et al. 2017). Thus, we predicted that the effects of kinship and spatial proximity on social behavior might be stronger during the BS than the FHS. In addition, multiple breeding females can be found at the same time in natural populations of wild gerbils and reproductively active male gerbils mainly defend the territories (*Ågren* et al. 1989b). Therefore, we predicted that these effects may be stronger in males but not in female gerbils given that females usually encounter relatively lower reproductive competition than males (Clutton-Brock and Huchard 2013b).

### Materials and Methods

#### Study site, trapping, and animal identification

Our studies were conducted at Houhatai (42°23′61.3″N, 116°06′52.4″E, altitude 1300 m), which is located about 25 km north of Shangdu, Zhenglan Qi, Inner Mongolia, China. The study site is a typical steppe area. The average monthly temperature ranged from −13.9°C to 21°C and the annual total precipitation was 324.6 mm during 2014.

Our trapping plot comprised a 2-ha (100 m × 200 m) grassland dominated by *Leymus chinensis*, *Artemisia sieversiana*, *Thalictrum petaloideum*, *Stellera chamaejasme*, *Klasea centauroides*, and *Aster alticicus*, which provided food or cover for gerbils. The sympatric small mammals comprised the Daurian ground squirrel *Spermophilus dauricus*, Daurian pika *Ochotona dauurica*, and striped dwarf hamster *Cricetus barabensis*. The potential predators of Mongolian gerbils were the steppe polecat *Mustela eversmanii*, corsac fox *Vulpes corsac*, and some raptors such as the common kestrel *Falco tinnunculus* and upland buzzard *Buteo hemilasius*. No livestock grazed on the study site during our study period.

Mark-recapture experiments were conducted from April 29 to October 24 at 2-week intervals in 2014, where each trapping session lasted for 3 consecutive days. We did not trap during the winter to avoid mortality. Mongolian gerbils were live-trapped using wire mesh live traps (28 cm × 13 cm × 10 cm) baited with fresh peanuts. To enhance the likelihood of successful trapping, we used a concentric circle trapping method (Liu et al. 2007). The trap station was arranged in 3 or 4 concentric circles within a burrow system to cover most of the range. In total, around 380 traps were set each time to cover all of the trap stations. The traps were set at 05:00–06:00 h from May to August, and checked every 1–2 h until about 1100 h. The traps were then closed between 11:00 and 15:00 h to avoid trap mortality due to the heat, and trapping was resumed at 16:00 h and continued until 19:00 h. Trapping started between 06:30 and 07:30 h, and continued until 17:30 h during September and October. We also checked the traps every 1–2 h during this period. Gerbils were active during the trapping periods employed in this study (Liu et al. 2007).

All of the captured gerbils were toe clipped when initially captured to allow permanent identification. The clipped toes were preserved in 95% ethanol for subsequent genetic analyses. All of the burrow systems were marked and their coordinates were recorded with a tape. In the field, a typical Mongolian gerbil burrow system comprises entrance holes, feeding chambers, nest chambers, and tunnels (Scheibler et al. 2006). The core area of the burrow system usually has about 10–20 entrances holes in the ground, which form
a burrow entrance cluster (Ågren et al. 1989a). There are areas with few or no entrances between the burrow systems, so it is easy to determine the distribution of the burrow systems based on the burrow entrance clusters (Ågren et al. 1989a, Wang et al. 2011a). Therefore, coordinates were used to calculate the distance between each 2 burrow systems according to the Pythagorean Theorem, where the distance from the center point of the core area of the burrow system was the average distance between all of the burrows in one social group and those of another social group. The distance between burrow systems was used as an index of the spatial distance between Mongolian gerbils living in different social groups.

The following data were recorded for each captured gerbil: location, sex, body mass, and reproductive condition (male: testes scrotal or abdominal, ventral scent glands invisible, clear contour or large visible pores surrounded by secreted substance; female: vulva closed or open, pregnant, lactating) (Liu et al. 2007). Age was estimated based on body mass and the developmental stage of the ventral sebaceous gland (juvenile: <30 g and with no sign of ventral gland; subadult: 30–50 g, unless they had a ventral active gland wider than 4.2 mm; adult: >50 g) (Ågren et al. 1989a; Liu et al. 2007). We tested gerbils captured in the same burrow system in 2 consecutive trapping sessions as members of the same social group (Ågren et al. 1989a). After recording the data, all of the gerbils were taken to a tent beside the plot and only adults from different groups were selected for behavioral tests. The trapping and handling procedures for the Mongolian gerbils were approved by the Institutional Animal Use and Care Committee of the Institute of Zoology, Chinese Academy of Sciences (Ethical Inspection License No: IOZ13047).

Procedures in behavioral tests
To test the social behavior in pairwise encounters, we used a neutral arena (Olivier and Dalen 1982), which has been employed widely in rodent behavioral studies (Klatt et al. 2015; Shen et al. 2015; Zhang et al. 2001). Adult gerbils (>50 g) of the same sex captured from different burrow systems were selected for pairwise encounters in behavioral tests and they were matched randomly. Social behavior was tested by staging paired encounters in a rectangular neutral arena (42.5 cm × 31 cm × 19 cm), where each dyad was tested only once during a specific season in our study. The arena was divided into 2 equal compartments using a removable opaque partition. Two individuals were placed on either side of the partition and allowed to acclimatize to the novel environment for 5 min. The barrier was then removed and interactions were observed for a 10-min period. A digital voice recorder was used to record any behavior, which was observed continuously by a specific observer. We terminated the tests immediately if one of the following occurred: 1) continuous fighting physically for almost 1 min at a time; or 2) an actual injury occurred.

We measured the durations of the following 4 categories of behavior observed during each 10-min test in the arena: 1) investigatory behavior, including sniffing the nose, body, and anal zone of the other gerbil; 2) neutral behavior where the gerbils remained more than 5 cm apart without exhibiting any agonistic behavior and they ignored each other; 3) amicable behavior defined as the pair of gerbils located less than 5 cm apart and they exhibited affiliative behaviors such as remaining side by side, one over the other, or grooming; and 4) agonistic behavior such as upright boxing, defense, and wrestling. All of these behaviors have been observed in natural and captive populations of Mongolian gerbils (Hurtado-Parrado et al. 2015). The arena was cleaned thoroughly with 75% ethanol between tests to remove any odors from the previously tested individuals. At the end of each trial, all of the gerbils were released back into the burrow systems from which they were captured. Gerbils were housed individually in plastic cages (30 cm × 15 cm × 20 cm) during the behavioral tests and adequate food was provided. Animals were kept in the tent for less than 3 h.

Pairwise relatedness based on microsatellite markers
DNA was extracted from tissues using a TIANamp Genomic DNA Kit (TianGen Biotech Company Ltd, Beijing, China). Nine microsatellite loci (Mungi1, Mungi2, Mungi3, Mungi4, Mungi5, Mungi6, Mungi7, Mungi8, and Mungi9) developed for Mongolian gerbils were used to estimate relatedness (Neumann et al. 2001). Polymerase chain reaction (PCR) was conducted in a 10-μL reaction mixture containing 0.5 ng genomic DNA, 5 μL Premix Taq (TianGen Biotech Company Ltd), and 0.6 μM of the forward (fluorescently labeled with 5'-TAMARA, HEX, or FAM) and reverse primers. PCR was run under the following conditions: initial denaturation at 95°C for 5 min, followed by 30 cycles of denaturation at 94°C for 40 s, annealing at a specific temperature (Ta) for 45 s, and extension at 72°C for 1 min, with a final extension at 72°C for 5 min. The specific annealing temperature (Ta) for each locus was specified by Neumann et al. (2001).

Successful PCR amplification was verified by examining samples on agarose gels. Amplified fragments were electrophoresed on an ABI 3730 XL capillary sequencer (Applied Biosystems, Foster City, CA) and the allele size was determined with GENEMAPPER 4.1 software (Applied Biosystems).

Hardy–Weinberg equilibrium tests were conducted with GenePop 4.3 (Rousset 2008). Micro-checker 2.0 (Van Oosterhout et al. 2004) was used to test for the probability of null alleles. We calculated genetic diversity metrics comprising the observed heterozygosity (Ho), expected heterozygosity (He), number of effective alleles (Ne), and inbreeding coefficient (FIS) using GenAlEx 6.501 (Peakall and Smouse 2012). The pairwise genetic relatedness was estimated between test pairs using GenAlEx 6.501 (Peakall and Smouse 2012) with Lynch and Ritland’s estimator (Lynch and Ritland 1999). The polymorphic information content (PIC) and discriminatory power (DP) of loci were estimated using Cervus 3.0.7 (Kalinowski et al. 2007).

Statistical analysis
The behavioral data were examined using Shapiro–Wilk test to determine their normality and the results did not indicate normal distributions (P < 0.001). Thus, we transformed the data using the Box-Cox method (Gurka et al. 2006) in the MASS package (Ripley et al. 2018). We used linear mixed effects (LME) models to determine whether the durations of 4 social behaviors were affected by the pairwise relatedness, spatial distance, sex, and season. Relatedness, distance, sex, and season were treated as fixed effects, and pairwise encounter and month as random effects. The results were expressed as the mean ± standard error (SE). P < 0.05 was considered to indicate a statistically significant difference. LME models were analyzed using the lme4 package (Bates et al. 2013). All statistical analyses were performed with R software (R Core Team 2016).

Results
In total, 253 gerbils (137 females and 116 males) from 24 burrow systems were identified during the study period. We captured gerbils
1371 times during the BS and 609 times during the FHS. The distance between 2 burrow systems ranged from 11.6 m to 147.0 m with an average of 66.1 ± 1.6 m. We conducted 249 pairwise behavior tests and about 77.1% (192/249) pairwise encounters were observed aggression. Initially, the gerbils in the pairwise encounters generally sniffed each other (i.e., investigative behavior) or kept away and ignored each other (i.e., neutral behavior). After several investigative and neutral behaviors, the encounters became amicable or agonistic. Amicable and agonistic behaviors did not occur within 10 min in some tests (Table 1, Figure 1). The relatedness between pairs of individuals was relatively low (Table 1).

Genetic analysis
The *Mung* allele was not amplified by PCR and it exhibited relatively low polymorphism, so we excluded it from subsequent analyses. *Mung* allele deviated from Hardy-Weinberg equilibrium after sequential Bonferroni corrections for multiple comparisons (P < 0.01). Thus, we removed this locus from any further estimations of relatedness. The number of alleles per locus ranged from 8 to 11, whereas the mean *H* = 0.783 ± 0.020 and mean *H* = 0.789 ± 0.030. The mean PIC was 0.756 ± 0.022, the mean DP for 7 loci was 0.927 ± 0.014, and the mean *F* = −0.211 ± 0.020 (Table 2). We detected no evidence of null alleles.

Effects of relatedness and spatial distance on behavioral traits
The pairwise relatedness had significant effects on investigative, neutral, and amicable behavior. In particular, the durations of investigative behavior (t = 2.869, P = 0.0046) and amicable behavior (t = 5.432, P < 0.0001) increased significantly, whereas the duration of neutral behavior (t = −2.734, P = 0.0071) decreased significantly with increasing relatedness (Figure 1, Table 3). We also found a significant negative relationship between the durations of amicable behavior and spatial distance (t = −2.562, P = 0.0111, Table 3), and amicable behavior only occurred between individuals with a spatial distance of less than 40 m (Figure 1f). In addition, the interaction between relatedness and distance had significant negative effects on investigative behavior (t = −2.022, P = 0.0475) and amicable behavior (t = −7.503, P < 0.0001), but positive effects on neutral behavior (t = 4.764, P = 0.0001, Table 3). However, pairwise relatedness (P = 0.1248) or spatial distance (P = 0.5687) had no significant effects on the intensity of agonistic behavior (Figure 1g-h, Table 3).

The effects of relatedness and spatial distance on social behavior exhibited no consistent patterns in different sexes or seasons. The interaction between relatedness and sex had significant negative effects on amicable behavior (t = −2.307, P = 0.0235, Table 3). The interaction between relatedness and seasonality had significant positive effects on investigative behavior (t = 3.395, P = 0.0007), but negative effects on neutral behavior (t = −2.037, P = 0.0425, Table 3). In addition, there were significant negative interaction effects of sex and seasonality on neutral (t = −2.408, P = 0.0188) and agonistic behavior (t = −2.085, P = 0.0410, Table 3, Figure 2).

### Discussion
As expected, the social behavior in staged encounters between Mongolian gerbils was influenced by relatedness, spatial distance, and their interactions. Gerbils spent significantly more time sniffing related individuals and behaved more amicably with increasing pairwise genetic relatedness. Thus, gerbils were more indifferent to each other as the pairwise relatedness decreased. However, the significant interaction effects between relatedness and spatial distance on investigative, neutral, and amicable behavior indicate that the effects of kinship on social behavior were constrained by space. In addition, we found that amicable behavior occurred only between individuals with a spatial distance of less than 40 m, which is approximately the active range of Mongolian gerbils (Agren et al. 1989a).

Furthermore, amicable behavior was exhibited by both close relatives and distantly related gerbils. These results imply that familiarity may play a key role in social associations of Mongolian gerbils. It should be noted that a higher level of familiarity does not necessarily indicate closer spatial distance, but it implies a closer social distance based on frequent interactions. For example, female banner-tailed kangaroo rats *Dipodomys spectabilis* avoid inbreeding via the development of familiarity based on prior associations rather than by using spatial cues, even if males live in familiar spatial locations (Waser et al. 2012). Thus, the relatively low inbreeding coefficient in gerbils may be related to a similar behavioral strategy for inbreeding avoidance, although females commonly copulate with neighboring males (Agren 1984a, 1984b).

However, there were no significant effects of relatedness or spatial distance on agonistic behavior. We observed that 192 out of 249 pairs of encounters resulted in aggression, thereby confirming previous direct observations that most intergroup interactions between gerbils are aggressive (Agren et al. 1989a). Many studies have demonstrated that high relatedness increases the incidence of amicable behavior among relatives such as supportive behavior (Smith et al. 2003) and cooperation (Langergraber et al. 2007), and it can reduce the intensity of aggression (Dobson et al. 2012). However, we found no evidence that agonistic intergroup interactions between gerbils changed with variations in the genetic or spatial distance. Scheibler et al. (2004) also reported that the intensities of inter- and intra-family aggression in Mongolian gerbils were generally similar. This suggests that the effects of relatedness and familiarity on aggression may be limited in this species, which indicates a high level of competition for food or mate resources between intergroup individuals.

### Table 1. Pairwise relatedness (Lynch and Ritland’s genetic relatedness coefficients) and the duration (seconds) of 4 behaviors in encounters during the breeding season (BS) and food-hoarding season (FHS)

| Sex     | Season | Relatedness | Investigative behavior | Neutral behavior | Amicable behavior | Agonistic behavior | Sample size (No. of paired encounters) |
|---------|--------|-------------|------------------------|------------------|-------------------|--------------------|---------------------------------------|
| Female  | BS     | 0.019 ± 0.011 | 33.75 ± 2.89          | 496.66 ± 11.46   | 23.76 ± 10.35     | 34.20 ± 4.97       | 92                                    |
| Female  | FHS    | 0.028 ± 0.018 | 62.51 ± 12.46         | 396.68 ± 26.09   | 17.12 ± 11.99     | 114.51 ± 21.81     | 41                                    |
| Male    | BS     | −0.005 ± 0.010 | 36.35 ± 4.27          | 462.17 ± 12.96   | 6.81 ± 6.10       | 81.42 ± 11.07      | 78                                    |
| Male    | FHS    | 0.017 ± 0.009 | 44.18 ± 6.88          | 432.95 ± 22.86   | 0.00 ± 0.00       | 110.29 ± 22.02     | 38                                    |

Data represent the mean ± SE.
Figure 1. Relationships between the duration (seconds) of social behavior and pairwise relatedness (Lynch and Ritland’s genetic relatedness coefficients) and spatial distance (distance between burrow systems) in Mongolian gerbils (N = 209): (A, B) investigative behavior, (C, D) neutral behavior, (E, F) amicable behavior, and (G, H) agonistic behavior.
The LME models for testing the effects of pairwise relatedness (Lynch and Ritland’s genetic relatedness coefficients) and spatial distance (distance between burrow systems), sex, seasonality, and their interaction on the duration of social behaviors in Mongolian gerbils

| Behavioral category | Estimate | SE | t | P |
|---------------------|----------|----|---|---|
| Investigative behavior | | | | |
| Sex: Male | –0.9020 | 5.7218 | –0.158 | 0.8750 |
| Sex: Seasonal | 18.7815 | 9.2196 | 2.037 | 0.0718 |
| Sex: Relatedness | –0.1565 | 0.1363 | –1.148 | 0.2523 |
| Sex: Distance | 83.0134 | 28.9383 | 2.869 | 0.0046† |
| Sex: Seasonality | –22.1472 | 11.9224 | –1.838 | 0.0654 |
| Sex: Relatedness × Distance | –0.0271 | 0.2682 | –0.101 | 0.9197 |
| Sex: Relatedness × Seasonality | –18.4826 | 60.3405 | –0.306 | 0.7395 |
| Sex: Relatedness × Distance × Seasonality | –0.5388 | 0.2845 | –1.894 | 0.0603 |
| Sex: Relatedness × Distance × Seasonality | 201.9876 | 59.4921 | 3.395 | 0.0007† |
| Distance × Relatedness | –2.8057 | 1.3875 | –2.022 | 0.0475† |
| Distance × Relatedness × Seasonality | –358.4613 | 175.9891 | –2.037 | 0.0425† |
| Distance × Relatedness × Seasonality × Distance | 18.5908 | 3.9025 | 4.764 | <0.0001† |
| Amicable behavior | | | | |
| Sex: Male | –8.8841 | 10.0254 | –0.886 | 0.3760 |
| Sex: Seasonal | –2.7259 | 6.9205 | –0.394 | 0.6945 |
| Sex: Relatedness | –0.5665 | 0.2211 | –2.562 | 0.0111† |
| Sex: Distance | 251.6024 | 46.3225 | 5.432 | <0.0001† |
| Sex: Seasonality × Distance | –5.7055 | 13.8146 | –0.413 | 0.6797 |
| Sex: Distance × Seasonality | 0.5058 | 0.4339 | 1.166 | 0.2444 |
| Sex: Relatedness × Distance | –209.8539 | 90.9576 | –2.307 | 0.0235† |
| Sex: Relatedness × Seasonality | 0.0863 | 0.3388 | 0.255 | 0.7992 |
| Sex: Relatedness × Distance × Seasonality | 7.5315 | 71.0561 | 0.106 | 0.9158 |
| Distance × Relatedness | –14.3321 | 1.9096 | –7.505 | <0.0001† |
| Agonistic behavior | | | | |
| Sex: Male | 26.8136 | 12.7975 | 2.097 | 0.0379† |
| Sex: Seasonal | 59.4638 | 18.1132 | 3.283 | 0.0123† |
| Sex: Distance | 0.1795 | 0.3046 | 0.589 | 0.5687 |
| Sex: Relatedness | –100.1879 | 64.8515 | –1.545 | 0.1248 |
| Sex: Seasonality × Distance | –56.0029 | 26.8553 | –2.085 | 0.0401† |
| Sex: Distance × Relatedness | –0.1014 | 0.6008 | –0.169 | 0.8664 |
| Sex: Relatedness × Distance | –129.0281 | 135.2281 | –0.954 | 0.3405 |
| Sex: Relatedness × Seasonality | 1.1538 | 0.6306 | 1.833 | 0.0734 |
| Sex: Relatedness × Seasonality × Distance | 142.8407 | 136.6413 | 1.045 | 0.2973 |
| Distance × Relatedness | 1.3495 | 3.1414 | 0.430 | 0.6706 |

†Significant P-values are indicated in bold. FHS, food-hoarding season.
adjacent territories (Ågren et al. 1989a). In our study, males were more aggressive against out-group individuals of the same sex than females during the BS, which probably reflects the patenty benefits of repelling intruding male gerbils. This finding supports the suggestion that intergroup encounters may have very different fitness impacts on males and females, and that responses to intruders may reflect differences in the benefit and cost trade-offs between the sexes (Mares et al. 2012; Nichols et al. 2015).

A second reason why agonistic interactions are less frequent and intense in females than males during the BS is that the risks associated with escalated conflict are usually higher for females than males (Cant and Young 2013; Clutton-Brock and Huchard 2013a). For example, a fatal injury to a female may also lead to increased mortality for any dependent offspring (e.g., ring-tailed lemurs, Lemur catta: Jolly et al. 2000). In addition, even when the risk of injury is relatively low, there may be an energy trade-off between chasing and pup feeding (Mares et al. 2012). Thus, lactating females may rarely engage in aggressive interactions (e.g., chacma baboons, Papio ursinus) (Huchard and Cowlishaw 2011).

In conclusion, our results demonstrate that the behavioral traits of Mongolian gerbils that live in different social groups are affected by kinship, spatial proximity, and their interaction. Furthermore, we showed that the effects of kinship and spatial proximity on social behavior exhibited sexual or seasonal patterns, thereby indicating the occurrence of context-dependent responses to out-group individuals in Mongolian gerbils. Further studies are required to investigate the social association patterns and to quantify their costs and benefits in order to advance our understanding of behavioral interactions in social rodents.

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Figure 2. Interaction effects between sex and seasonality on the duration (seconds) of (A) neutral behavior and (B) agonistic behavior.
