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Seasonal changes in and effects of familiarity on agonistic behaviors of rat-like hamsters (*Cricetulus triton*)

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The seasonal changes in agonistic behaviors and effects of familiarity on agonistic behaviors in wild-caught adult rat-like hamsters (*Cricetulus triton*) were observed in dyadic encounters in a neutral arena. The aggression of opposite- and same-sex encounters became higher or remained the same during the non-breeding season. This indicates that the hamsters were solitary during both seasons. Familiarity increased the aggression in male–male encounters and decreased the aggression in female–female encounters during both seasons. Familiarity also increased the aggression in female–male encounters during the non-breeding season and had no effect on the aggression in female–male encounters during the breeding season. These results may be related to the hamster's social structure. The more agonistic acts both male and female hamsters had, the more frequently they marked using flank glands during both seasons. This implies that flank gland marking can be used to advertise status and can be assessed by opponents to reduce the agonistic costs.

Key words: agonistic behaviors; *Cricetulus triton*; seasonal change.

INTRODUCTION

Agonistic interactions and effects of familiarity on social interactions in rodents are closely related to their lifestyle; for example, mating system, dispersal behaviors, reproductive conditions, spatial kin structure and social organization (Ferron 1982; Wolff 1985; Ferkin & Seamon 1987; Ferkin 1988a, b, 1990). Many species of small mammals are solitary when breeding with high aggression, and communal during the non-breeding season with low aggression (West & Dublin 1984). A large number of studies on vole species have shown that social interactions among conspecifics are less agonistic and more amicable during the non-breeding season (Wolff 1985; Ferkin & Seamon 1987). Agonistic interactions between dominant and subordinate individuals may cause dispersal (Brody & Armitages 1985). In Meadow voles (*M. pennsylvanicus*), females are philopatric and males are dispersal and solitary. Although familiarity can decrease the agonistic behavior in female–female encounters, it will increase the agonistic behavior in male–male encounters (Ferkin 1988b). In encounters of male or female golden hamsters, the dominant individual flank marks much more frequently than the subordinate to advertise its social status (Johnston 1985).

Rat-like hamsters (*Cricetulus triton*) mainly inhabit farmlands in the north of China and are one of the main rodent pests, seasonally breeding in spring and summer (Yang *et al.* 1996). Using multiple-capture live-traps and directly observing by digging their burrows in the field, the rat-like hamsters seem to live solitarily throughout the year and are polygamous or promiscuous. Males have larger home ranges than females; the females reside in a relatively fixed burrow with a smaller and more permanent territory than the males (Huang *et al.* 1995; Wang *et al.* 1996; Yang *et al.* 1996; Zhang, Zhang & Wang 1999; Zhang, Wang & Zhang 1999).

Based on this ecological information, we addressed the following questions about the

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agonistic behaviors of the rat-like hamster (*Cricetulus triton*): Do the agonistic behaviors between encounters remain high during the non-breeding season? Does familiarity affect the aggression between different encounters? Does flank marking signal the dominance relationship?

METHODS

Subjects

Rat-like hamsters were captured by live-traps made of wire meshes in farm land at the center of Hebei Province, north China. They were numbered, weighed, sexed, and their breeding condition was determined upon capture. Those weighing more than 100 g were assumed to have had a sexual experience, which has been clarified by Yang *et al.* (1996). During the breeding season, scrotal males and females with perforate vaginas and estrous cycles were classified as breeding and were used in the study; however, females with estrous cycles or pregnant or lactating females were not. Estrous females were judged by vaginal secretion detection and their behavioral responses to males. During the non-breeding season, adult-sized individuals were used.

Captured hamsters were sampled and sorted into two groups: unfamiliar or familiar. If two hamsters were caught from different sites that were separated by a river, a highway, or a railway dam, and with more than 1 km distance (the male's maximum activity range is 1 km) (Wang *et al.* 1996), we can unequivocally assume them to be unfamiliar with each other so as to ensure that they were socially naïve. If two hamsters were obtained from the same burrow entrance during two consecutive days or from neighboring burrow entrances of less than 5 m distance they were considered to be familiar.

About 140 hamsters in a non-breeding condition were trapped alive in early November (non-breeding season) 1995 and 1997, and 120 hamsters in a breeding condition were trapped between April and May 1996 and 1998. The hamsters captured in the field were housed individually in cages (40 cm × 25 cm × 15 cm) with wood shavings and cotton nesting as bedding. They were fed with rat chow and tap water ad libitum. A natural light/dark cycle and an approximate temperature of 20 ± 2°C was maintained throughout all experiments. Hamsters were acclimatized to the laboratory conditions 1 week prior to the experiment and all behavioral tests were conducted within the following 2 weeks.

Quantification of agonistic behavior

Staged dyadic encounters between either familiar or unfamiliar hamsters of the same or opposite sex were conducted in an observing room under red light conditions during the dark cycle. All hamsters were tested once. All behavioral tests were conducted during the dark phase of the corresponding light/dark cycle. After the experiments, the animals were continuously handled to breed for subsequent studies.

Paired encounters took place in a clear glass box (105 cm × 35 cm × 40 cm) that was partitioned into three equal parts by two removable opaque Plexiglas plates. Paired hamsters of approximately the same weight (within 10% difference) were randomly placed into two partitions at each end of the box. Following a 5-min acclimatization period, the two opaque partitions were removed and the hamsters were allowed to interact. The frequency of every behavior was continuously recorded for 5 min on a data sheet with a precalibrated time scale (10 s). Both hamsters' mutual aggression and one hamster's other defined behaviors having a duration of ≤ 10 s was taken as one unit. An act lasting > 10 s but ≤ 20 s was considered as two units, and so on. The glass box was thoroughly cleaned between trials with a hot 1 mol l^{-1} sodium hydroxide solution and rinsed with both water and ethanol.

The following definitions were used to describe the various social behaviors. Mutual attack referred to a physical struggle between two hamsters and included wrestling, rolling and biting; attack included biting, chasing and sideways postures; defense included fleeing and upright postures; marking was defined as hamsters arching their backs out and toward the wall and vigorously rubbing their flank glands against it. Subordinate hamsters deferred to a dominant attacker by fleeing, cowering, or exhibiting upright postures (Zhang 1997).

Behavioral differences were analyzed by two-tailed Wilcoxon matched-pairs signed-ranks test within pairs and two-tailed Mann–Whitney *U*-Wilcoxon Rank Sum W tests between pairs. Results were expressed as the group mean (±SE).

RESULTS

Seasonal changes in agonistic behavior

The following significant differences were detected in female–male encounters. There were more mutual aggressions between females and males (unfamiliar: $Z=3.67$, $P<0.01$; familiar: $Z=3.08$, $P<0.01$), more attacks by females (unfamiliar and familiar: $Z=2.53$, $P<0.01$), and more defense by males (unfamiliar: $Z=3.62$, $P<0.01$; familiar: $Z=3.29$, $P<0.01$) during the non-breeding season compared to during the breeding season (Figs 1a,2a).

In male–male encounters, there was no significant seasonal difference in mutual aggression (unfamiliar: $Z=1.33$, $P>0.05$; familiar: $Z=0.91$, $P>0.05$), nor in attack by winners (unfamiliar: $Z=0.53$, $P>0.05$; familiar: $Z=0.89$, $P>0.05$), nor in defense by losers (unfamiliar: $Z=0.44$, $P>0.05$; familiar: $Z=0.64$, $P>0.05$) were observed (Figs 1b,2b).

More mutual aggression between females (unfamiliar: $Z=2.32$, $P<0.05$; familiar: $Z=2.12$, $P<0.05$) occurred during the non-breeding season than during the breeding season. The act was manifested by more attacks by dominant females during the non-breeding season than by dominant females during the breeding season (unfamiliar: $Z=2.23$, $P<0.05$, familiar: $Z=2.57$, $P<0.05$), and more defense by submissive females during the non-breeding season than by submissive females during the non-breeding season (unfamiliar and familiar: $Z=2.19$, $P<0.05$) (Figs 1c,2c).

Effects of familiarity on agonistic behavior

Paired encounters between familiar females and males resulted in a strong mutual fight (attack) ($Z=2.01$, $P<0.05$), more attacks by females ($Z=2.16$, $P<0.05$) and more defensive behavior by males ($Z=2.08$, $P<0.05$) than did paired encounters between unfamiliar females and males during the non-breeding season (Fig. 1a). Familiarity did not influence agonistic acts between opposite sex individuals during the breeding season (mutual attack: $Z=1.66$, $P>0.05$; attack by females: $Z=1.03$, $P>0.05$; defensive behavior by males: $Z=1.28$, $P>0.05$) (Fig. 2a).

Paired encounters between familiar males resulted in significantly more mutual attacks (non-breeding season: $Z=2.40$; breeding season: $Z=2.16$, $P<0.05$), more attacks by the dominant male (non-breeding season: $Z=2.96$; breeding season: $Z=3.34$, $P<0.01$), and more defensive behavior by the subordinate male (non-breeding season: $Z=2.79$; breeding season: $Z=3.34$, $P<0.05$) than those found in paired encounters between unfamiliar males (Figs 1b,2b).

Paired encounters between familiar females resulted in fewer mutual attacks (non-breeding season: $Z=3.14$; breeding season: $Z=2.94$, $P<0.01$), fewer attacks by dominant females (non-breeding season: $Z=3.01$; breeding season: $Z=3.01$, $P<0.01$), and fewer defensive behavior by the subordinate female (non-breeding season: $Z=2.65$; breeding season: $Z=2.32$, $P<0.05$) than did paired encounters between unfamiliar females (Figs 1c,2c).

Flank marking and social status

In both unfamiliar female–male and familiar female–male encounters, females always defeated the male opponents. Females displayed more attacks (unfamiliar $Z=2.22$, familiar $Z=2.41$, $P<0.05$), more flank marking (unfamiliar $Z=2.09$, familiar $Z=2.28$, $P<0.05$), and less defensive behavior (unfamiliar $Z=2.22$, familiar $Z=2.41$, $P<0.05$) than did male opponents during the non-breeding season (Fig. 1a). There were no significant differences in attack (unfamiliar $Z=1.33$, familiar $Z=1.76$, $P>0.05$), defensive behavior (unfamiliar $Z=1.02$, familiar $Z=0.76$, $P>0.05$), and flank marking (unfamiliar $Z=0.98$, familiar $Z=1.11$, $P>0.05$) between unfamiliar female–male and familiar female–male encounters during the breeding season (Fig. 2a).

In both unfamiliar and familiar male–male encounters, one male always displayed more attacks (non-breeding season: unfamiliar $Z=2.80$,

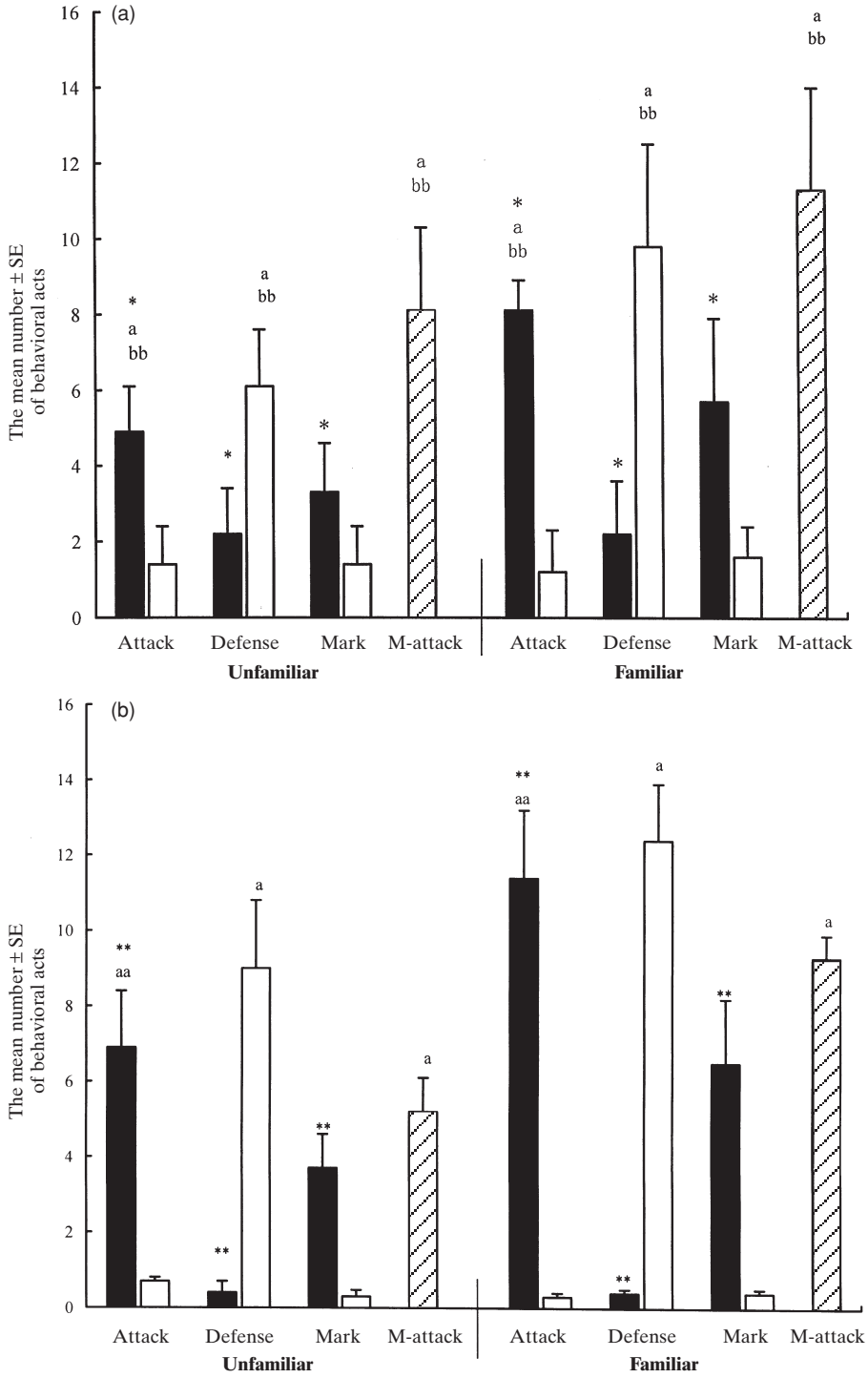

Fig. 1. Mean ± SE indicates the number of behavioral acts by pairs of rat-like hamsters (*Cricetulus triton*) within 5-min dyadic encounters between either unfamiliar or familiar hamsters during the non-breeding season in the different sexed encounters (a) and the same sexed encounters (b: males; c: females). (a) (■), female; (□), male; (b) (■), dominant males; (□) submissive males; (c) (■) dominant females; (□) submissive females. 'Mark' refers to flank gland marking; (▨) 'M-attack' refers to mutual attacks; $*P < 0.05$ and $**P < 0.01$ indicate significant differences between same category of social interactions of paired encounters, using two-tailed Wilcoxon matched-pairs signed-ranks test; a $P < 0.05$ and aa $P < 0.01$ indicate significant differences caused by familiarity using two-tailed Mann–Whitney *U*–Wilcoxon Rank Sum W tests between pairs; b $P < 0.05$ and bb $P < 0.01$ indicate significantly seasonal differences between corresponding paired encounters shown in Fig. 2 during both seasons, using two-tailed Mann–Whitney *U*–Wilcoxon Rank Sum W tests.

familiar 2.69, $P < 0.01$; breeding season: unfamiliar $Z = 2.80$, familiar $Z = 2.69$, $P < 0.01$), more flank marking (non-breeding season: unfamiliar $Z = 3.07$, familiar $Z = 2.99$, $P < 0.01$; breeding season: unfamiliar $Z = 2.70$, $P < 0.05$, familiar $Z = 3.19$, $P < 0.01$), and less defensive behavior (non-breeding season: unfamiliar $Z = 3.46$, familiar $Z = 3.28$, $P < 0.01$; breeding season: unfamiliar $Z = 2.56$, familiar $Z = 2.41$, $P < 0.05$) than did the other male (Figs 1b,2b).

In both unfamiliar female–female and familiar female–female encounters, one female also

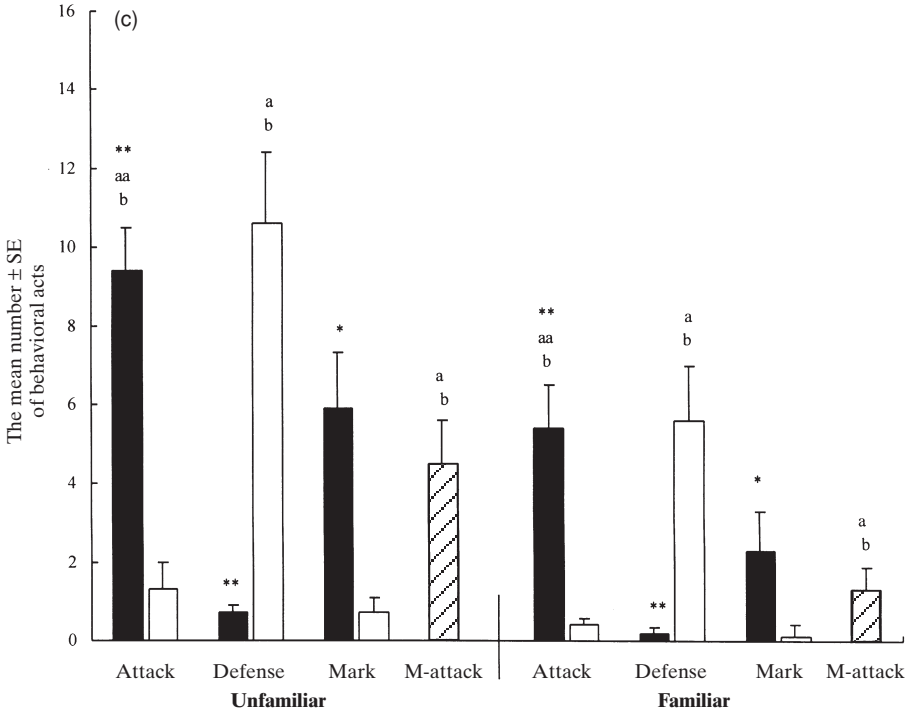

Fig. 1. *Continued*

displayed significantly more attacks (non-breeding season: unfamiliar $Z=2.80$, familiar $Z=2.73$, $P<0.01$; breeding season: unfamiliar: $Z=2.80$, $P<0.01$, familiar: $Z=2.33$, $P<0.05$), more flank marking (non-breeding season: unfamiliar $Z=2.29$, familiar $Z=2.34$, $P<0.05$; breeding season: unfamiliar $Z=2.33$, familiar $Z=2.09$, $P<0.05$), and less defensive behavior (non-breeding season: unfamiliar $Z=3.06$, familiar $Z=2.80$, $P<0.01$; breeding season: unfamiliar $Z=2.96$, familiar $Z=2.80$, $P<0.01$) compared to the other female (Figs 1c,2c).

DISCUSSION

The present study demonstrates that the aggression levels in opposite- and same-sex encounters become higher or remain the same during the non-breeding season; that familiarity increases the aggression in female–male encounters and decreases the aggression in female–female encounters during both seasons; and that the victorious individual in dyadic encounters displays more flank gland marking than the defeated opponent.

High aggression during the non-breeding season

Many species of small mammals are solitary when breeding with high aggression between familiar encounters, and communal during the non-breeding season with low aggression between familiar encounters (West & Dublin 1984; Wolff 1985). In winter-solitary species, aggression remains high during both the breeding and non-breeding seasons (West & Dublin 1984). About vole species, several studies indicate that social interactions among conspecifics become less agonistic and more amicable during the non-breeding season (Wolff 1985; Ferkin & Seamon 1987). The results of the present study on seasonal changes in agonistic behavior show that both familiar and unfamiliar rat-like hamsters became more aggressive during the non-breeding season than during the breeding season. Our data indicates that rat-like hamsters are solitary during both the breeding and non-breeding seasons. These results are in good agreement with previous field studies conducted by mark–recapture methods and laboratory observations (Wang *et al.* 1996; Zhang, Wang & Zhang 1999).

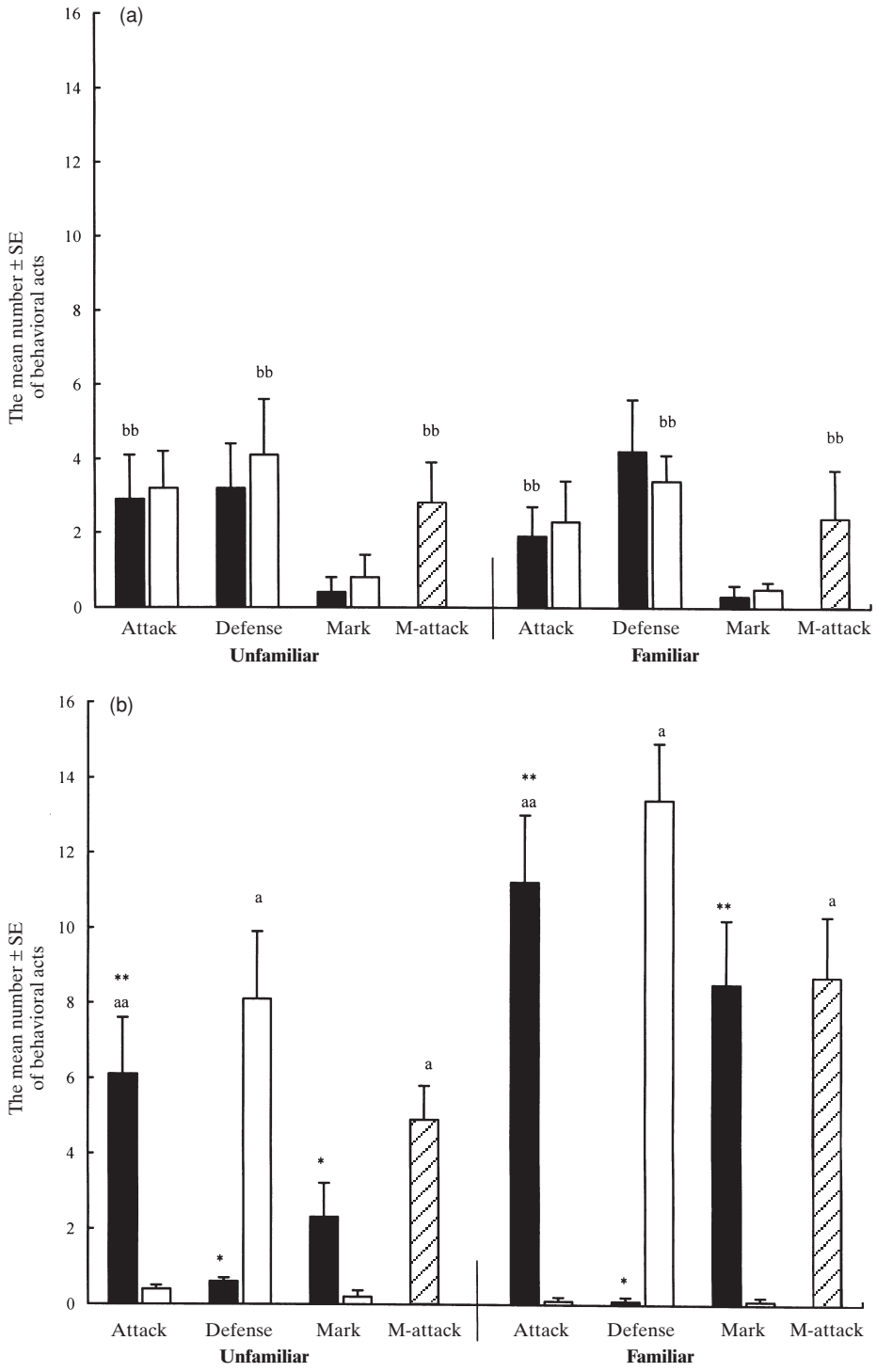

Fig. 2. Mean ± SE indicates the number of behavioral acts by pairs of rat-like hamsters (*Cricetulus triton*) within 5-min dyadic encounters between either unfamiliar or familiar hamsters during the breeding season in the different sexed encounters (a) and the same sexed encounters (b: males; c: females). (a) (■), female; (□), male; (b) (■), dominant males; (□) submissive males; (c) (■) dominant females; (□) submissive females. 'Mark' refers to flank gland marking; (▨) 'M-attack' refers to mutual attacks; $*P < 0.05$ and $**P < 0.01$ indicate significant differences between same category of social interactions of paired encounters, using two-tailed Wilcoxon matched-pairs signed-ranks test; a $P < 0.05$ and aa $P < 0.01$ indicate significant differences caused by familiarity using two-tailed Mann–Whitney *U*–Wilcoxon Rank Sum W tests between pairs; b $P < 0.05$ and bb $P < 0.01$ indicate significantly seasonal differences between corresponding paired encounters shown in Fig. 1 during both seasons, using two-tailed Mann–Whitney *U*–Wilcoxon Rank Sum W tests.

Different effects of familiarity on different encounters

Effects of familiarity on agonistic behavior in rodents are closely related to their lifestyle and dispersal pattern. Familiarity increases the aggression in solitary species, then stimulates their dispersion, and decreases the aggression in communal species (Ferkin 1988a, b, 1990). Agonistic interactions between dominant and subordinate

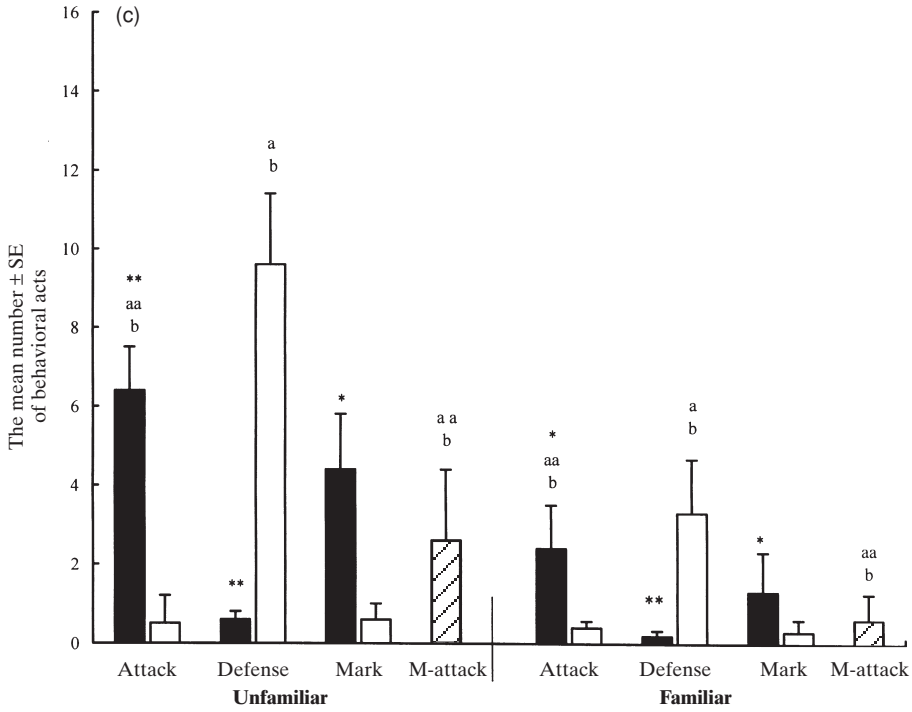

Fig. 2. *Continued*

individuals may cause dispersal (Brody & Armitages 1985).

In the present study, in encounters between males and females, familiarity increased their agonistic acts during the non-breeding season but had no effect on their agonistic acts during the breeding season. A possible explanation could be related to the mating system and competition for food resources during the non-breeding season. During the non-breeding season, competition for food would be more severe between neighbors than between non-neighboring hamsters. During the breeding season, solitary and promiscuous females did not form a fixed breeding pair bond with males. Only on sexually receptive (estrous) days, were females recipient to any (neighboring or non-neighboring) approaching males mating. On other days, females will launch an attack on approaching males (Zhang, Wang & Zhang 1999).

In the present study, in encounters between males, familiarity increased aggression. Male rat-like hamsters are prone to dispersal behavior (Wang *et al.* 1996; Zhang, Zhang & Wang 1999; Zhang, Wang & Zhang 1999) and would not have developed a long-term association with their neighbors. A neighboring male could become a rival for neighboring females and reduce their reproductive success by mating with a neighboring female. Although unfamiliar males may also decrease another male's reproductive success, it may be too costly for a male to fight with an unfamiliar male. Such encounters might be infrequent, because an unfamiliar male may simply be passing through.

We found that paired encounters between familiar female rat-like hamsters were less agonistic than encounters between unfamiliar females during both seasons. Female rat-like hamster philopatry coupling with solitary behavior (spatial exclusiveness) (Wang *et al.* 1996; Zhang, Zhang & Wang 1999, Zhang, Wang & Zhang 1999) would result in a high probability that neighboring females would become familiar with one another over time. This suggests that females may have a long association from pup-hood onwards. This social organization favors social tolerance between neighboring females once burrows are established.

Flank marking signals the dominance status

Scent rubbing in mammals is involved in advertising status and can be used by competitors to assess potential opponents (Gosling & McKay 1990). For example, in pairs of male or female golden hamsters, the dominant individual flank marks much more frequently than the subordinate (Johnston 1985). There is a pair of flank glands in both male and female rat-like hamsters, which are larger in males than in females during the breeding season and are not sexually different during the non-breeding season (Zhang 1997). In the present study of rat-like hamsters, the greater the number of agonistic acts by the hamster, the more frequently it marks using its flank glands. The results indicate that in encounters between same- or opposite-sex rat-like hamsters, the winners always displays more flank gland marking, which can be used to advertise status advertise and can be assessed by opponents to reduce the agonistic costs (Gosling 1982).

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