

## Seasonal changes in chronic social interactions and physiological states in female rat-like hamsters (*Tscheskia triton*)

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### Abstract

We examined the behavioral characteristics and physiological states related to solitary lifestyle and dominant–subordinate relationships in female rat-like hamsters (*Tscheskia triton*), formerly known as *Cricetulus triton*. Wild adult hamsters were captured and caged singly in the laboratory during the non-breeding and breeding seasons. The experimental hamsters were subjected to 5 min staged dyadic encounters every day for 28 consecutive days by pairing two unfamiliar and weight matched females in a neutral arena. Aggressive behavior, defense and flank marking were quantified everyday within the first week and once each week during the last 3 weeks. Animals were then autopsied and their physiological and reproductive state assessed. Our results suggested that dominant–subordinate relationships could be established especially in non-breeding conditions, where the dominant displayed higher aggression and flank marking, and lower defense than its opponent. The breeding females followed this pattern except there was no difference in aggressive behavior, between the partners. The repeated encounters did not appear to reduce aggression or lead to amiable behavior or bonding. At the end of the experiment breeding females exhibited higher levels of serum estradiol, progesterone and corticosterone than non-breeding females. Both dominant and subordinate females in non-breeding condition had atrophied ovaries and uteri, whereas both dominant and subordinate females in breeding condition had hypertrophied ovaries and uteri. Non-breeding females possessed heavier and thicker flank glands than breeding females did. Dominant females displayed longer or thicker flank glands than subordinate did. Thus, our data suggest that the behavioral traits observed in our experiment support the solitary lifestyle of adult female rat-like hamsters and physiological state show some differences between social ranks or in both seasons.

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### 1. Introduction

Some seasonally breeding rodents exhibit conspicuous seasonal shifts in behavior [16,19,23,24,48,57]. For example, many vole species are solitary when breeding and show high aggression, but are communal during the non-breeding season and show low aggression [48]. In contrast, in some solitary rodents such as the Syrian hamster (*Mesocricetus auratus*), males show elevated aggression when in non-breeding condition, while long photoperiod induces their gonad enlargement

and gonad hormone production, and synchronously inhibits aggression [5,23,28]. In wild-captured, solitary adult rat-like hamsters (*Tscheskia triton*), both males and females remain highly aggressive during the non-breeding season [57]. These findings suggest that for some species there may be some correlations between traits of behavioral interactions and lifestyles. On the other hand, various studies have demonstrated that dominant–subordinate relationships are established quickly and maintained stably in many solitary male rodents [6,15,25], whereas the relationships in females are poorly known, especially in their non-breeding condition. Some limited studies have suggested that during the breeding season solitary females could not establish a stable social rank largely due to their reproductive status [18].

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Photoperiod is viewed as the most important proximate factor used by seasonally breeding rodents to mediate physiological regulation, such as the hypothalamic–pituitary–adrenal (HPA) axis and hypothalamic–pituitary–gonad (HPG) axis and endocrine status [4,8,43]. Those physiological changes can affect animals' behaviors, which then change seasonally with photoperiod [4,8,16,23,24,39,40,43].

Some studies have also demonstrated that there is a correlation between social rank or behaviors and the concentrations of some hormones [22,38]. For example, several authors have found that the level of testosterone was positively correlated with male dominance [20,42,47,58]. Further estradiol alone increase aggression and progesterone alone did not effect female aggression [1,17,36,47], while estradiol and progesterone together initially inhibited and later activated aggression [10,35]. With respect to the correlation between social dominance and blood glucocorticoid level, the traditional hypothesis is that the losers suffer more stress in social interaction, thus the level of glucocorticoid of subordinate individuals is higher than dominants. However, recent studies have shown that blood glucocorticoid level is not correlated with social dominance or is mainly altered in dominants [3,11,34].

Rat-like hamster (*T. triton*) is a solitary, non-monogamous species mainly inhabiting the farmland of North China, formerly known as *C. triton*. It breeds seasonally from late March to early September [50,56]. We have previously demonstrated that males are born with a pair of flank glands and a midventral gland, display high recruitment and are dispersal-prone; females are philopatric and have no stable mating association [51,55,56,59]. Males have high aggression during both the breeding and non-breeding seasons, and females are more aggressive during the non-breeding season [57]. There was also a correlation between social status, reproductive condition and flank gland marking in males [58]. Chronic exposure to predator odor could suppress aggression [52,53]. Our field capture observations suggest that individual adult male and females often live in two adjacent burrows and maintain a close social association (author's unpublished observations). Thus far, the social relationships and related physiological conditions of same sex adults, especially females remain unclear.

This study aimed (1) to examine whether female rat-like hamsters can establish stable dominant–subordinate relationships during the non-breeding and breeding seasons; (2) to determine the display of behaviors in the chronic social interaction encounter; (3) to investigate whether there are differences in physiological states of reproductive organs, and serum hormone levels between social ranks or the two seasons. We hypothesized that persistent undiminished aggression reflects the wild rat-like hamsters' solitary lifestyle, and physiological status should show some differences between social ranks or in both seasons.

## 2. Materials and methods

### 2.1. Animals and housing conditions

We captured rat-like hamsters using live-traps made of wire mesh in the farmland around Beijing during the non-breeding

season (October, 2003) and breeding season (April, 2004). The hamsters were maintained in a reversed light:dark regime of 14 h:10 h (breeding condition, lights on at 1700 h) or 10 h:14 h (non-breeding condition, lights on at 2100 h) at approximately 20 °C for 4 weeks prior to the behavior tests. The subjects were housed individually in plastic cages (40 × 25 × 15 cm). Food and water were provided *ad libitum*. Wood shaving bedding material (softwood fibers) was changed weekly. Female rat-like hamsters weighing more than 80 g were assumed to be adults [50]. Females with perforate vaginas and showing regular estrous cycles were classified as potential breeders.

### 2.2. Social encounter

Twenty non-breeding (mean body weight ± S.D. = 121.83 ± 5.95 g) and 28 breeding adult females (mean body weight ± S.D. = 127.24 ± 3.40 g) were utilized in the behavioral tests. Two body weight matched (within 10% difference) breeding or non-breeding females were assigned to a pair. All behavior tests were conducted in an observation room under dim, red illumination during the first 2 h of the hamsters' dark cycle. The staged dyadic encounters took place in a clear Plexiglass box (length × width × height = 60 cm × 40 cm × 100 cm), in which two screens were placed parallel with the lateral wall to reduce the intensity of aggression and give losers a place to avoid being attacked. The arena was partitioned as two equal compartments using a removable opaque partition, and an individual from each pair was placed in one half of the arena. Following a 3-min acclimatization period, the opaque partition was removed and the hamsters were allowed to interact for 5 min. Behaviors were recorded by digital video. The interactions between the same pairs were repeated once per day for 4 consecutive weeks. Behavior was recorded everyday during the first week and on the seventh day of the last 3 weeks. The arena was thoroughly cleaned between trials with both water and 75% ethanol.

All behaviors within 5 min were cataloged using the following definitions and quantified by their duration using the software OBSERVER V 5.0 (Noldus, NL). Behavior was defined as follows [15,17,29,45,57,58]: *aggressive behavior*: biting, chasing, and sideways postures; *defense*: fleeing, cowering, threatening, lying on their back on the ground and upright postures; *flank marking*: arching back and rubbing toward the wall; *locomotion*: moving and exploring the environment; *amiable behavior*: mutual grooming, sitting or lying together. Females from each pair were recorded as either a winner or a loser by quantitatively comparing their attack-score in every daily encounter bout. The individual with the higher attack-score was considered the winner. After 28 days, the female in each pair displaying more wins than losses was defined as dominant and its opponent as the subordinate.

### 2.3. Physiological assay and hormone determination

Body weights were recorded once each week. On the 29th day, all animals were sacrificed. Blood samples were collected, centrifuged at 4000 rpm for 30 min, and serum aliquots were stored in polypropylene micro-centrifuge tubes at –80 °C until

radioimmunoassay of estradiol, progesterone and corticosterone. Spleens, adrenal glands, uteri, ovaries and flank glands were dissected and weighed to the nearest 0.1 mg. Relative organ mass was given as milligrams of organ mass per 100 g body weight [54].

All samples for each hormone was quantified in a single radioimmunoassay (RIA) [33,52] by  $^{125}\text{I}$  RIA kits. Progesterone and estradiol kits were provided by the Beimian Institute of Biotechnology (Beijing, China), and corticosterone was provided by Diagnostic Systems Laboratories, Inc. (Texas, USA). The

human antiserum used was highly specific for the hormones; cross-reactivity with other steroid hormones was  $<0.01\%$ ; intra-assay variability was  $<10\%$  for all samples. The detectable ranges were 0.1–100.0 ng/ml, 10–2000 pg/ml, and 20–2000 ng/ml for progesterone, estradiol and corticosterone, respectively.

#### 2.4. Statistical analyses

Seasonal stability of dominant–subordinate relationships between both seasons was tested statistically by cross-tabs

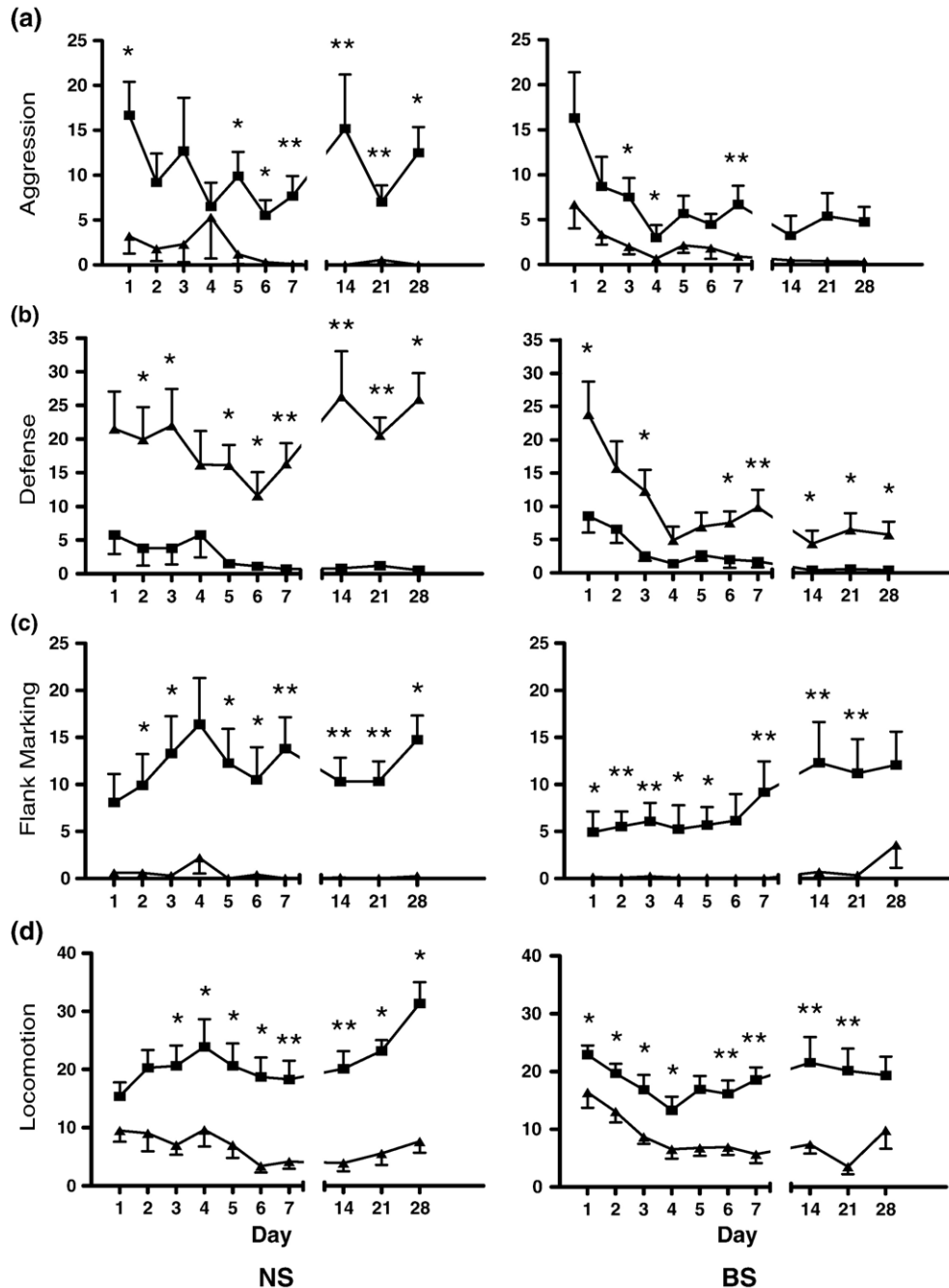


Fig. 1. Number of behavioral interactions (mean  $\pm$  SE) in 5 min tests over 4 weeks of dominant and subordinate females during the non-breeding season ( $n=10$ ) and during the breeding season ( $n=14$ ). (a) Aggressive behavior, (b) Defense, (c) Flank marking, (d) Locomotion. (■) Dominant females; (▲) subordinate females; BS: breeding season; NS: non-breeding season; \* $P < 0.05$  and \*\* $P < 0.01$  indicate significant differences.

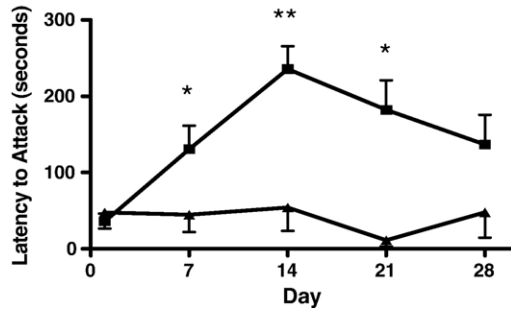


Fig. 2. Latency to attack (mean±SE) of pairs during non-breeding season ( $n=10$ ) and during breeding season ( $n=14$ ). (■) Breeding season (BS); (▲) non-breeding season (NS); \* $P<0.05$  and \*\* $P<0.01$  indicate significant differences.

Chi-square test. Behavioral data were statistically analyzed using a Wilcoxon matched pairs test between dominant and subordinate females within seasons and using a Mann–Whitney  $U$  test between seasons. Organ mass and hormone concentration were analyzed using a paired  $t$ -test between paired hamsters within seasons and using an independent two-tailed  $t$ -test between seasons if the data were normally distributed, or using Wilcoxon matched pairs test between paired hamsters within season, and otherwise using a Mann–Whitney  $U$  test between seasons. The level of significance was set at  $P=0.05$ .

### 3. Results

#### 3.1. Behavioral interactions in both seasons

During the non-breeding and breeding season, paired females rapidly exhibited apparent winner–loser relationships for every encounter and these relationships were maintained more stably during the non-breeding season than the breeding season. The differences between seasons were significant: in 10 non-breeding pairs, only two reversed their dominant–subordinate relationships, whereas nine out of 14 breeding pairs exchanged their social status more than one time ( $\chi^2=4.608$ ,  $P=0.032$ ).

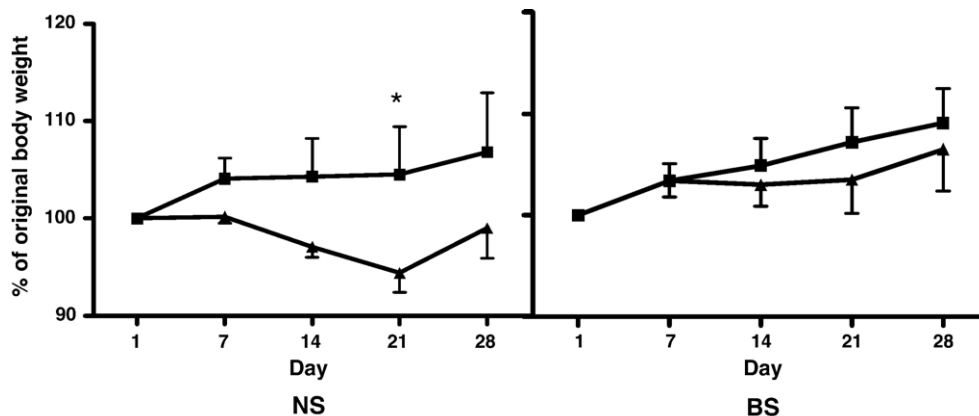


Fig. 3. Body weight percent of original (mean±SE) of dominant (■) and subordinate (▲) females during non-breeding season ( $n=8$ ) and during breeding season ( $n=12$ ) \* $P<0.05$  and \*\* $P<0.01$  indicate significant differences, using Chi-square test.

With few exceptions during the non-breeding season the dominant females displayed significantly higher aggressive behaviors, flank marking, locomotion and fewer defenses. In the breeding season, again, dominant females showed significantly higher rates of behaviors with aggressive behavior being less marked than in the breeding season (Fig. 1).

In addition, breeding females exhibited significantly longer latency to initial attack than non-breeding counterparts did (day 1:  $Z=-0.235$ ,  $P=0.841$ ; day 7:  $Z=-2.169$ ,  $P=0.031$ ; day 14:  $Z=-3.130$ ,  $P=0.001$ ; day 21:  $Z=-2.572$ ,  $P=0.011$ ; day 28:  $Z=-1.087$ ,  $P=0.305$ ; Fig. 2).

#### 3.2. Change in body weight

Change in body weight between dominant and subordinate females also exhibited a seasonal shift. The pattern of body weight change was the same in non-breeding season (6.9% increases) and breeding season (9.1% increases) for dominant females, however the difference is the decrease in body weight in subordinates: the body weights of non-breeding subordinate females were decreasing and most significant at day 21 (6.6% decreases), whereas in the breeding season the body weights of subordinate females were increasing by 6.5% (Fig. 3).

#### 3.3. Organ masses

There were no significant differences in relative masses of spleen, ovary or adrenal gland between dominant and subordinate females in both seasons. In contrast relative masses of uterus [ $t(38)=-5.140$ ,  $P<0.001$ ] and ovary [ $t(38)=-3.413$ ,  $P=0.002$ ] but not spleen or adrenal masses were significantly higher during the breeding season than the non-breeding season (see Table 1).

Flank glands were significantly heavier ( $Z=-2.236$ ,  $P=0.025$ ) and thicker ( $Z=-2.998$ ,  $P=0.003$ ) during non-breeding season than during the breeding season, while the length [ $t(77)=0.925$ ,  $P=0.358$ ] and width ( $Z=-0.035$ ,  $P=0.972$ ) did not show a seasonal difference. During the breeding season, the dominant females possessed significantly thicker flank glands than the subordinate females ( $Z=-2.223$ ,

Table 1  
Organ relative masses (g/100 g body weight) of dominant and subordinate female rat-like hamsters (*Tscheskia triton*) in both seasons (mean±SE)

	Spleen	Uterus	Ovary	Adrenal gland	n
<i>Non-breeding season</i>					
Dominant	0.106±0.019	0.093±0.009	0.012±0.001	0.015±0.001	8
Subordinate	0.105±0.015	0.101±0.016	0.014±0.001	0.015±0.002	8
<i>Breeding season</i>					
Dominant	0.098±0.008	0.219±0.029	0.020±0.002	0.015±0.002	12
Subordinate	0.159±0.040	0.204±0.020	0.020±0.002	0.016±0.001	12
<i>Between seasons</i>					
Non-breeding	0.106±0.015	0.097±0.009**	0.013±0.001**	0.015±0.001	16
Breeding	0.128±0.021	0.212±0.017	0.020±0.001	0.016±0.001	24

\* $P<0.05$ , \*\* $P<0.01$ . Using statistical test methods as described in the text.

$P=0.026$ ). During the non-breeding season, the dominant females possessed significantly longer ( $Z=-2.313$ ,  $P=0.019$ ), but not wider [ $t(29)=2.010$ ,  $P=0.054$ ] flank glands than the subordinate females (see Table 2).

### 3.4. Serum hormones levels

Serum estradiol [NS:  $Z=0.000$ ,  $P=1.000$ ; BS:  $t(10)=0.048$ ,  $P=0.963$ ], progesterone (NS:  $Z=-0.507$ ,  $P=0.612$ ; BS:  $Z=-1.067$ ,  $P=0.286$ ), and corticosterone [NS:  $Z=-0.845$ ,  $P=0.398$ ; BS:  $t(10)=0.495$ ,  $P=0.632$ ] concentrations were not different between dominant and subordinate females within either the breeding or non-breeding season. However in all females all hormones were at significantly lower concentrations during the non-breeding season compared to the breeding season (estradiol:  $Z=-2.888$ ,  $P=0.003$ ; progesterone:  $Z=-2.207$ ,  $P=0.027$ ; corticosterone:  $Z=-4.997$ ,  $P<0.001$ ; Fig. 4).

## 4. Discussion

In both seasons, paired females exhibited conspicuous winner–loser relationships at every test encounter. The dominant–subordinate relationship appeared to be more stably established in the non-breeding season than in the breeding season. Aggressive behaviors were indicative of dominance and were persistently significantly higher in non-breeding dominant females. In the breeding season the pairs exhibited a higher

frequency of reversal of the dominant–subordinate relationship during the duration of the experiment in comparison with their non-breeding counterparts. These results suggest that non-breeding female rat-like hamsters can establish stable dominant–subordinate relationships. Social rank is closely related to reproduction success, space use and defense of resources [2]. For the rat-like hamsters, because food is always scarce in the non-breeding season (winter), a stable relationship in which the dominant animal is highly aggressive favors its survival (e.g. occupancy of burrows, access to food) [50,59].

In addition, in the non-breeding season, dominant females displayed a shorter latency to initial attack and maintained a stably increase in body weight. These results confirm our earlier findings [56,57]. We previously found that males castrated while held on a long light cycle (14:10) became less aggressive, while intact males retained their agonistic behavior throughout both seasons [57,58]. Females also show some similar behavioral interaction patterns such as flank marking indicative of dominance, and defense indicative of submission across the seasons [15,26], and the exception is the higher aggression in dominant females in the non-breeding season. The lower aggression in breeding female rat-like hamsters may be due to the fluctuation of gonadal hormones in the estrous cycle [18].

Many small mammals are solitary with high aggression during breeding season, while communal with low aggression during non-breeding season [48,49]. In contrast, aggression remains high during both the breeding and non-breeding season

Table 2  
Relative masses (g/100 g body weight) and sizes of flank glands of dominant and subordinate female rat-like hamsters (*Tscheskia triton*) in both seasons (mean±SE)

	Mass (g)	Length (cm)	Width (cm)	Thickness (cm)	n
<i>Non-breeding season</i>					
Dominant	0.088±0.011	0.906±0.051*	0.588±0.034	0.108±0.005	8
Subordinate	0.074±0.016	0.732±0.048	0.487±0.037	0.103±0.005	8
<i>Breeding season</i>					
Dominant	0.066±0.012	0.912±0.053	0.590±0.033	0.097±0.003*	12
Subordinate	0.054±0.014	0.819±0.044	0.543±0.040	0.086±0.003	12
<i>Between seasons</i>					
Non-breeding	0.081±0.009*	0.811±0.038	0.536±0.026	0.106±0.004**	16
Breeding	0.060±0.009	0.865±0.035	0.567±0.026	0.092±0.003	24

\* $P<0.05$ , \*\* $P<0.01$ . Using statistical test methods as described in the text.



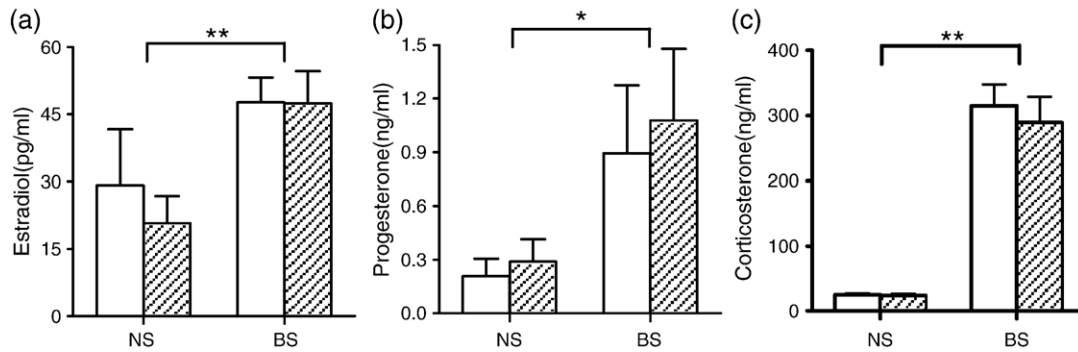


Fig. 4. Serum estradiol, progesterone, and corticosterone concentrations (mean  $\pm$  SE) of dominant (shaded bar) and subordinate (open bar) females in both seasons. BS: breeding season; NS: non-breeding season; \* $P$ <0.05 and \*\* $P$ <0.01 indicate significant differences.

in those rodents living a solitary life in winter [5,28,48]. In the present study, the chronic behavioral encounters revealed that female rat-like hamsters displayed persistently high aggression during non-breeding season, and diminishing aggression during breeding season. Additionally, amiable behavior was never exhibited. These behavioral traits indicated the low social tolerance and encouraged a solitary lifestyle.

Scent marking is one of the most common communication modalities in mammals [27]. Flank glands are important scent sources in golden hamsters (*M. auratus*) and rat-like hamsters and are closely correlated with an individuals' aggression and their social status [15,26,58]. For example, golden hamsters can discriminate between flank gland secretions from dominant and subordinate males [37], and the dominants exhibited hypertrophic glands [14]. Our present data showed that the flank glands of female rat-like hamsters were larger in dominants than those in subordinates, and also were heavier during the non-breeding season than those during the breeding season as described previously [51]. These results indicate that the changes in the flank glands and marking behavior were associated with the social status and aggressive intensity in female rat-like hamsters.

Seasonal shifts in behavior of many non-tropical animals is mainly regulated via the HPG axis under the influence of changes in photoperiod [8,21,43]. Our data showed that the breeding female rat-like hamsters had heavier ovaries and uterus, higher levels of estradiol and progesterone, but lower level of aggression than the non-breeding females. Therefore, our results indicated that the seasonal fluctuation of the level of estradiol and progesterone might be related to the seasonal changes of aggression and dominant–subordinate relationships in female rat-like hamsters [5,10,28,35].

Animals exposed to stressors exhibited an array of endocrine responses, of which the most important is to activate the HPA axis and consequently elevate the level of blood glucocorticoids [11]. Numerous studies in some avian and primates species found that blood corticosterone levels were different between seasons and within a social hierarchy [7,12,41,44]. Our results showed that corticosterone level displayed a similar seasonal shift but there was no differentiation between the dominants and subordinates. No consistent relationship has been found between social status and blood glucocorticoid level. In some

species the subordinates' glucocorticoid level is higher than the dominants' [11,58], whereas in others the dominants display an equivalent or even higher level of glucocorticoid [3,20,34]. The variation might be due to differences in social organization across animal species and physiological habituation after suffering long-term social stress. Dawkins pointed out that the function of glucocorticoids is to prepare the individual for action by making it ready for fight or flight, so there should be no expectation only that subordinates would have high glucocorticoids concentrations [13].

In addition, serum corticosterone level exhibited such a seasonal divergence, but the adrenal gland weights did not show corresponding weight changes. Levels of glucocorticoids are often positively correlated to adrenal gland size [31]. Although, it has also been reported that levels of glucocorticoids are higher in food-restricted rodents with smaller adrenal glands [30,32,46]. The postulated explanation is that the increases in the rate of steroidogenesis in undernourished rats lead to a decrease in adrenal gland weight [46]; similarly exogenous corticosterone administration reduces adrenal weights in adolescent rats [9]. These data support the solitary lifestyle of adult female rat-like hamsters, flank glands show differences between social ranks or in both seasons and reproductive organs only have seasonal changes.

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