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Fecal hormone variation during prolonged social interaction in male *Tscheskia triton*

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ABSTRACT

Agonistic behavior is crucial for conspecific members to maintain a social hierarchy, optimum population density, and high fitness. It is known that agonistic behavior and social ranking often interact with hormones such as testosterone (T) and glucocorticoids (GCs). The challenge hypothesis states that T levels in males are promoted by the agonistic behaviors of other males and has been widely testified in many taxa of vertebrates, even in humans, but seldom attempted in rodents. Here, we examined how fecal T and corticosterone (CORT) concentrations changed during prolonged social conflict in male greater long-tailed hamsters (*Tscheskia triton*). Dyads were subjected to 5 min staged encounters daily for 15 days during which agonistic and social behaviors were recorded and fecal hormone concentrations were determined by radioimmunoassay. Our results showed that pairwise male hamsters developed overt and stable dominant–subordinate relationships rapidly and that the agonistic behavior decreased over the course of the experiment. Dominant males exhibited more frequent flank marking and locomotion and shorter latency to initial attack than their subordinate counterparts. Testosterone levels were significantly increased in both dominant and subordinate males during early encounters, but T and CORT levels were higher in subordinate males. After five encounters, we found no difference between hormone levels and behavior for all males, implying some kind of behavioral and physiological habituation. This complex pattern of hormonal change during social conflict is discussed and correlations between behavioral and physiological habituation are hypothesized.

1. Introduction

Agonistic behavior is crucial for conspecific members to maintain a social hierarchy, optimum population density, and high fitness [1,2,14,41,47]. It is known that agonistic behavior and social ranking often interact with hormones such as testosterone (T) and glucocorticoids (GCs) [1,11,14,19,28,37,41,44,47,55,56]. For example, social dominance and agonistic behaviors can be enhanced by an increase in T levels or suppressed by castration in mammals [5,6,27,35,42,59]. Testosterone levels in males are also promoted by social competition between males with the degree of this change influenced by levels of social instability, access to females, paternal care and mating systems [22,32,38,55,56]. The challenge hypothesis has been proposed to explain interactions between agonist behavior and testosterone levels. This hypothesis states that T levels in males are promoted by the agonistic behaviors of other males [56] and this has been widely testified in many taxa of vertebrates, even in humans [33,54], but seldom attempted in rodents [see only 7,37,47].

Corticosterone (CORT), serving as a GC, is a reliable indicator of social stress, such as social defeat, in vertebrates [8,11,14,16,40,44,49]. It is commonly accepted (termed the subordination stress paradigm) that GC levels are often higher in subordinate animals than in winners of conflict or dominant individuals [31]. Few studies however, have not found support for a correlation between blood GC levels and social subjugation [3,49]. Such a discrepancy might be caused by studying species with different levels of social interaction whereby an individual may show physiological habituation following periods of intense agnostic behavior accordingly [41,49].

In rodents, behavioral and physiological habituation is common [40]. For example, in greater long-tailed hamsters (*Tscheskia triton*, formerly rat-like hamster, *Cricetulus triton*) it has been shown that agonistic behavior declines as a result of familiarity from continuous encounters with between individuals [51,60]. Furthermore, social challenges are often accompanied by social stress [14,44,47,56]. Here, we examined how these two processes interact to shape agonistic behavior in male–male encounters and the role of physiological habituation.

To determine whether physiological habituation can arise from behavioral habituation to continuous social competition, we utilized

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consecutive feces hormone sampling during chronic social interactions. Blood-sampling is an accurate and sensitive technique widely employed to measure hormone concentrations and to indicate endocrine conditions [21]; however, it requires animal handling which can artificially increase GC levels [34,50] and for rodents often only provides limited data at a single point in time [50]. Feces sampling overcomes these issues and is emerging as a popular tool to measure hormone levels [9,20,50,53].

The greater long-tailed hamster is a solitary, polygamous rodent dispersed throughout farmlands in northern China [57,59,60]. Males possess a pair of flank glands and a midventral gland for chemical communication; females are philopatric and have no stable mating association with males [46,59–61]. Our previous work has shown that intense agonistic behavior between individuals of the same sex [51,60] and resulting social ranks are correlated to hormone levels [51,59], and that flank gland size and marking behavior are associated with social rank and reproductive hormones [51,59,60]. More recently, we observed that long-term social interactions (male–male, female–female) and subsequent social rank were not related to levels of sex hormones or GC [60, authors' unpublished data], suggesting that T and CORT levels may differ during the early and late stages of chronic dyadic encounters.

Here, we aimed to ascertain a relationship between hormone levels and agonistic behavior at the early and late stages of chronic social interactions. We staged 5 min dyadic encounters between male greater long-tailed hamsters every day, continuously observed their behavior and measured fecal T and CORT concentrations. As the challenge hypothesis posits, we predicted an increase in T levels for both males and that levels would be higher in the subordinate or defeated male. According to the subordination stress paradigm we predicted that CORT levels would be higher during newer encounters and decline over time as males' physiology habituated, and again that subordinate males would have higher CORT levels than dominants.

2. Materials and methods

2.1. Animals and housing conditions

Healthy male adult (>120 g) greater long-tailed hamsters were captured in farmlands in April of 2005 outside Beijing using live-traps made of wire mesh. Hamsters were housed individually in stainless steel cages (40 cm × 20 cm × 20 cm) containing cotton nesting materials for 3 months prior to behavioral tests. The housing room was maintained at 20 ± 2 °C with a reverse light/dark cycle (16L:8D with light on at 17:00) and food and water were provided *ad libitum*. All procedures complied with guidelines for animal use and care as stipulated by the Institute of Zoology, Chinese Academy of Sciences.

2.2. Behavioral procedures

We used the body mass asymmetry method to establish dominant–subordinate relationship for higher social stabilities as described by Earley et al. [14] and Wang et al. [52]. We selected 20 males and assigned them into ten fixed pairs, each pair of which consisted of a heavy (167.8 ± 1.96 g; $n = 10$) and light male (2 ± 2.95 g; $n = 10$).

Establishing dominant–subordinate relationships was performed following the protocols of Wang et al. [51]; namely, the staged dyadic encounters took place in a neutral arena (Plexiglass box measuring 60 cm × 40 cm × 100 cm), in which two screens were placed parallel with the lateral wall that reduced intensity of aggression and provided a buffer for losing males to avoid further attack by winning males. The arena was divided into equal compartments using a removable opaque partition and males were placed into each compartment for an acclimatization period of 3 min. The opaque partition was then removed and males were allowed to freely interact for 5 min. This was repeated once each day for fifteen consecutive days for each dyad. Encounters were recorded using digital video and all behavioral tests were conducted under dim red illumination during the first 2 h (09:00–11:00) of the dark cycle. The arena was thoroughly cleaned between trials with water and 75% ethanol. After these tests, we placed each dyad close together to allow them to have continuous sensory contact with no physical interaction following Bartolomucci [4].

All behaviors during the 5 min encounters on days 1, 3, 5, 7, 9, 11, 13 and 15 only were quantified using OBSERVER V5.0 (Noldus, NL). Behaviors were defined as follows [23,45,51,59,60]: *aggression*, including attack, sideway posture, biting, and chasing; *defense*, fleeing, upright, cowering, threatening, and lying on their back on the ground; *flank marking*, arching back and rubbing toward the wall; *locomotion*, moving and exploring the environment; and *initial attack latency* was the time delay between the begin of dyadic encounters and the first attack by each male. Among them, aggression and defense were defined as agonistic behaviors. Males 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 15 days, the male in each pair displaying more wins than losses was defined as dominant and the other male as subordinate [51].

2.3. Hormone analysis

2.3.1. Feces sampling

Fresh feces was collected over 2 h and commenced 5 h [24,34,50] after a staged encounter. We collected feces on day 0, 1, 3, 5, 7, 9, 11, 13 and 15 and all samples were stored at − 20 °C until radioimmunoassay.

2.3.2. Hormone extraction and radioimmunoassay

Fecal samples were dried at − 80 °C for 24 h in a series vacuum freeze dryer (Christ, Delta 1 A, Osterode, Germany), and then thoroughly crushed with a mortar and pestle. A 100 mg fecal sample was extracted with 1 ml of water and 2 ml of dichloromethane for five min on a vortex (Haimen Kylin-Bell, Haimen City, China), fragmented for 1 min using ultrasonic wave and shaken vigorously on a motorized shaker for 1 h. After centrifugation at 4000 rpm for 30 min, 1 ml of the bottom (dichloromethane) layer was stored in a polypropylene micro-centrifuge tube and evaporated to dryness with pure N_2. The dried samples were stored at − 80 °C until radioimmunoassay of T and CORT.

Each dried sample was first dissolved in 600 μl phosphate buffer solution (0.1 M, pH 7.0) and then quantified in a single radioimmunoassay (RIA) [29,58] by ^{125}I RIA kit. Testosterone kits were provided by the Beimian Institute of Biotechnology (Beijing, China) and corticosterone kits 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 2–2000 ng/dl and 10–2000 ng/ml for T and CORT respectively. The formula to calculate feces hormone levels was as follows:

Feces hormone content (ng/g) = hormone concentration (ng/ml) × 0.6 (ml) × 2/0.1 (g).

2.3.3. Comparisons between fecal and serum hormone levels

To compare T and CORT levels present in feces with those in blood, twelve additional adult males (>120 g) were randomly selected and assigned into three groups of four: intact group (I), castrated group (C), and castrated + testosterone treatment group (C + T). We collected feces and serum samples of three groups four weeks after males were castrated. In the C + T group castrated males received 10 mg/kg testosterone propionate in gingili at 09:00 and we collected feces samples for 2 h. On the following day, all hamsters were euthanized between 09:00 to 10:00. A cage containing a hamster was encased in a plastic bag and a cotton ball soaked in ether was placed inside. Once animals became unconscious they were removed from the cage and decapitated so arterial blood from the neck could be collected. The

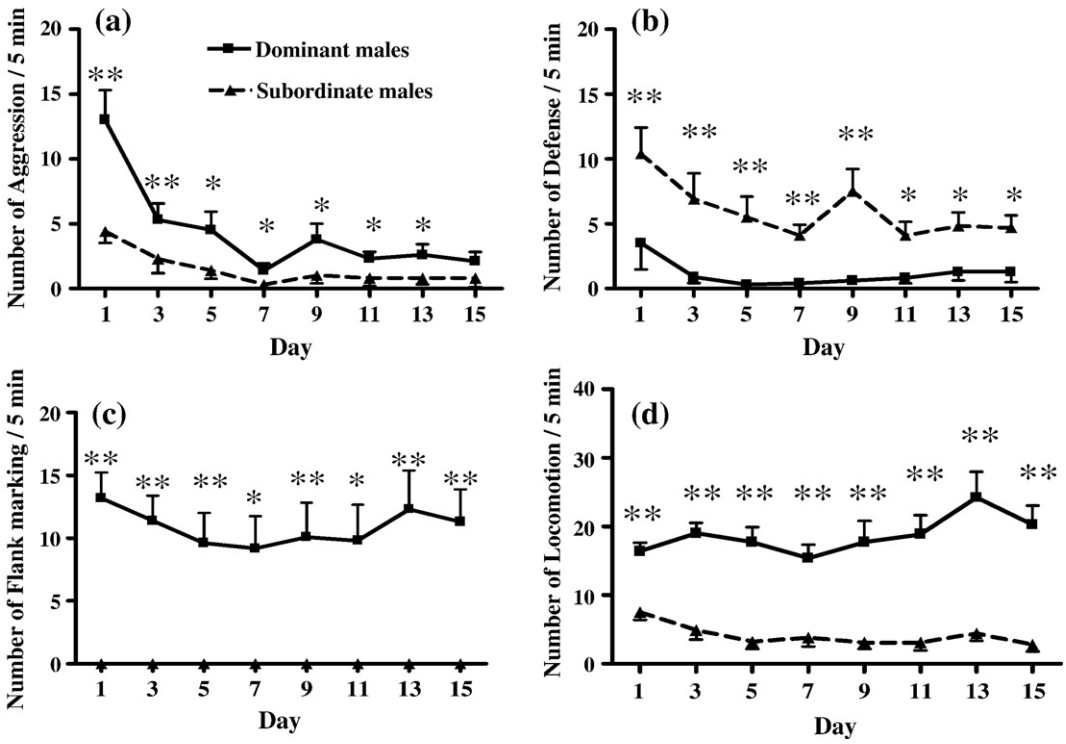

Fig. 1. Numbers (mean ± SE) in 5 min of aggression (a), defense (b), flank marking (c) and locomotion behaviors (d) of dominant ($n = 10$) and subordinate males ($n = 10$) during the 15-day chronic social interaction. *$P<0.05$ and **$P<0.01$ (indicating significant differences between dominant and subordinate males).

whole process from sealing the cage to decapitation took less than 3 min. Blood samples were then centrifuged at 4000 rpm for 30 min, and serum aliquots were stored in a polypropylene micro-centrifuge tube at −20 °C until radioimmunoassay of testosterone and corticosterone. Hormone radioimmunoassay kits were the same as above.

2.4. Statistical analysis

One-way ANOVAs with repeated measures were used to determine differences between behaviors and hormones levels within (sampling-time groups) and between groups (dominant and subordinate groups). Differences in behavior and hormone levels between dominant and subordinate groups were analyzed using two-tailed paired *t*-tests (if data were normally distributed) or non-parametric Wilcoxon matched pairs test (if data were not normally distributed). Correlations between behavior and hormone levels were analyzed using a Pearson Correlation (if data were normally distributed) or Spearmen Correlation (if data were not normally distributed). The level of significance (α) was set at 0.05 for all tests.

3. Results

3.1. Behavior

The winner–loser relationship quickly formed in every encounter (Fig. 1). Heavier males displayed higher levels of aggression than their lighter counterparts ($F_{1,18} = 10.445$, $P = 0.005$) on every test day except Day 15 (Fig. 1a), while lighter males showed higher defensive behavior ($F_{1,18} = 14.337$, $P = 0.001$; Fig. 1b). Consequently, all males in the heavy group were classified as dominant and their lighter opponents as subordinate. Flank marking behavior ($F_{1,18} = 25.297$, $P<0.001$; Fig. 1c) and locomotion behavior ($F_{1,18} = 52.074$, $P<0.001$; Fig. 1d) was also more common in dominant males from the first encounter (Fig. 1c). From a visual inspection of Fig. 1 it is apparent that agonistic behaviors declined temporally, but flank marking and locomotion did not.

Latency to attack in dominant and subordinate males increased over the duration of the experimental period (dominant: df = 7, $F = 2.506$, $P = 0.024$; subordinate: df = 7, $F = 6.070$, $P<0.001$; Fig. 2), but was significantly shorter in dominant males (Fig. 2).

3.2. Fecal hormone concentration

Fecal T and CORT concentrations were correlated with concentrations of these hormones in blood samples, thus indicating that hormone levels in the fecal samples reliably reflect hormone levels in the blood (Fig. 3). We found no significant difference in fecal T and CORT between heavy (dominant) and light (subordinate) males prior to the commencement of staged encounters (T: $t = 0.436$, $P = 0.672$; C: $t = 0.473$, $P = 0.644$); however, following the first encounter subordinate males showed higher T and CORT levels than dominant males (T: $F_{1,18} = 4.476$, $P = 0.049$; C: $F_{1,18} = 8.085$, $P = 0.011$). This pattern was maintained across the

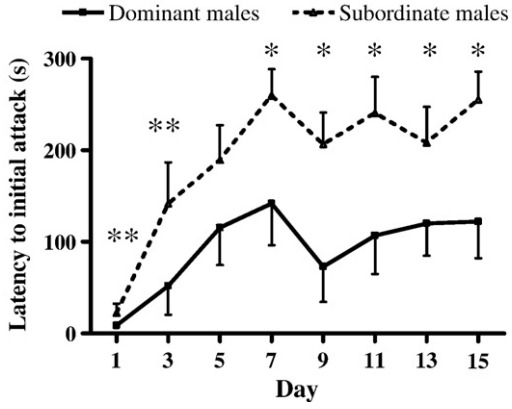

Fig. 2. Latency to attack for dominant ($n = 10$) and subordinate ($n = 10$) hamsters during 15-day chronic social interactions between paired males. *$P<0.05$ and **$P<0.01$ (indicating significant differences between dominant and subordinate males).

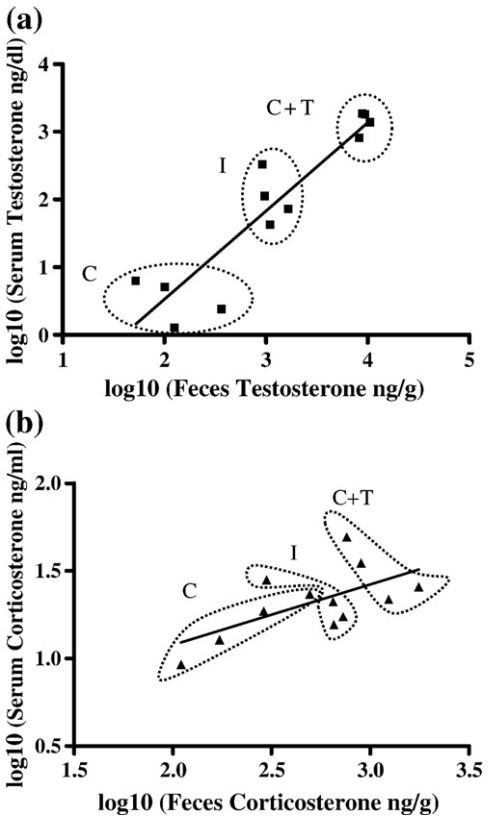

Fig. 3. Scatter plots showing log10 [feces hormones] and log10 [serum hormones] of intact males (I, $n=4$), castrated males (C, $n=4$) and castrated with testosterone treatment males (C+T: $n=4$). (a): Testosterone, (b): corticosterone.

experimental period (T: $F_{1,\ 18}=4.476$, $P=0.049$; C: $F_{1,\ 18}=8.085$, $P=0.011$; Fig. 4).

Compared with their baseline hormonal data collected on Day 0, subordinate males showed significantly higher T levels on Day 1 ($t=2.729$, $P=0.015$) and Day 3 ($t=2.754$, $P=0.014$) and higher C levels on Day 1 ($t=3.139$, $P=0.006$), Day 3 ($t=2.463$, $P=0.025$), Day 9 ($t=2.267$, $P=0.038$), Day 13 ($t=2.253$, $P=0.039$) and Day 15 ($t=2.453$, $P=0.026$). This pattern was not found for dominant males as T levels showed a significant increase on Day 3 only ($t=2.488$, $P=0.025$; see Fig. 4).

3.3. Correlations between hormones and agonistic behaviors

There was a positive correlation between hormone levels and defense behavior (T: $r=0.291$, $P=0.013$; cor: $r=0.399$, $P=0.001$) in subordinate males across the experimental period; however, this pattern was strongest between Day 1 and 5 only (T level: $r=0.444$, $P=0.018$; C level: $r=0.562$, $P=0.002$). No correlation was found between hormone levels and aggressive behavior for any group of males.

4. Discussion

4.1. Behavioral habituation: agonistic behavior was weakened

Under chronic social encounters, agonistic behaviors tend to be mild and low, and chemical communication gradually increases to a relatively higher level, characterizing the formed dominant–subordinate relationships [1,13,17,25,45,51]. Concurrent with this idea, our results showed that all heavier male greater long-tailed hamsters dominated their lighter opponents and exhibited more frequent aggressive behavior, flank marking and a shorter later to initial attack everyday social encounters across fifteen consecutive days. After dominance–subordination was developed in the initial 5 days, agonistic behavior became weaker and latency to attack greater.

4.2. Testosterone and social interaction

Social rank is closely related to reproductive success, use of space and the defense of resources. Dominant individuals often gain more benefits than subordinates in this regard [2]. In vertebrates, it is generally accepted that increased T concentrations increases male aggression and social dominance [27,42,60], whereas social challenge also influences T level [36,47,55]. However, such interactions can shift before and after social relationships are established. Increases in the level of T usually occurs when males suffer high social challenges, e.g. to establish dominance hierarchies, to defend territory and females, and competition with other males for access to females [44,47]. In periods of high social instability, T levels are often positively correlated with agonistic behavior [38]. For example, aggressive behavior displays in the Japanese quail (*Coturnix coturnix*) were positively correlated with plasma T levels only before the stable social relationship was established [38]. Our results showed some support for the challenge hypothesis whereby T levels of both dominant and subordinate males were elevated, and in subordinate males T levels were positive correlated with agonistic behavior during the early stages of social conflict [55,56].

Of note is that T levels exhibited a more rapid elevation and reached a higher concentration in subordinate males. Elevation in T therefore appears to adjust agonistic motivation, which may enhance the desire of losers to compete again for status [26,32,36]. For example, saliva T elevation in men more likely appeared in those losers who showed competition again, while T changes of winners were unrelated to decisions to compete again [32]. Likewise, in marmosets (*Callithrix kuhlii*), intruder males suffer a greater number of defeats by residents

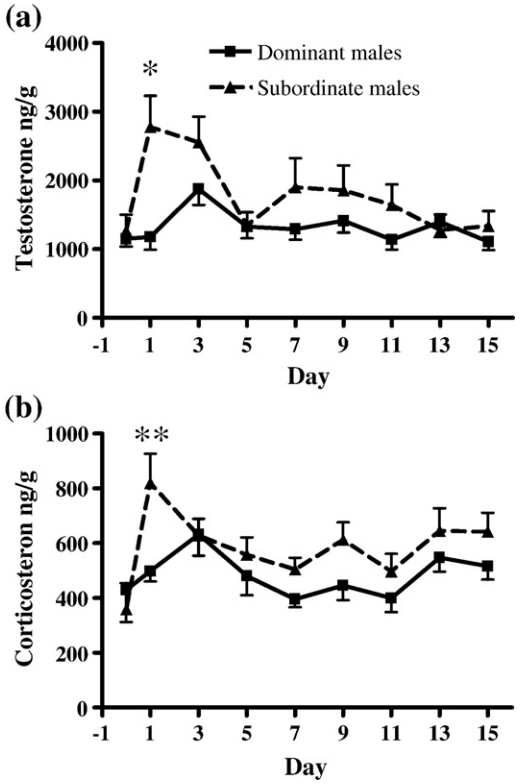

Fig. 4. Changes of fecal testosterone (a) and corticosterone (b) levels (mean ± SE) in dominant ($n=10$) and subordinate males ($n=10$) during the 15-day social interaction period. Hormone levels at day zero denote hormone levels before social interactions (heavy mass group: $n=7$, lighter mass group: $n=8$). *$P<0.05$ and **$P<0.01$ (indicating significant differences between dominant and subordinate males).

and show enhanced T levels at 2–6 h and 24 h [41]; however, we did not observe this increase in aggression of subordinate males. This type of discrepancy between T levels and aggression was probably the result of differences in body mass between dominant and subordinate males, which might counteract the increase in aggression owing to T levels of subordinate males.

In addition, our data shows that once dominant–subordinate relationships were established, differences in T levels between dominant and subordinate males disappeared. This pattern has been observed in mice (*Mus musculus*) undergoing a 10 day social interaction [28] and in golden hamsters undergoing a 12 day social interaction [10] and might partially reflect a physiological habituation to chronic social competition.

It is likely that increased fecal testosterone levels are related to changes in plasma binding proteins rather than testosterone itself. Changes in plasma binding proteins would enhance testosterone access to the liver and consequent catabolism [30]. Food intake would have changed between dominants and subordinates during the experimental period, and might affect fecal levels. An important caveat as previous work suggests that food restriction for four weeks significantly decreased testosterone levels of greater long-tailed hamsters [30]. In this study, after a 5 min encounter each day males were kept in separate cages. Food and water was provided *ad libitum* but in theory, subordinate males might reduce their food intake under higher social stress. It is possible then that changes in food intake might have affected testosterone levels detected using the fecal sampling method; this should be explored in further studies on this species.

4.3. Corticosterone and social interactions

There are considerable controversies over the relationship between GC levels and social status [11,31]. Recent research appears to contradict the traditional belief that animals in lower social status should have higher CORT levels [3,11]. However, our results clearly showed that fecal CORT Levels in subordinate males dramatically increased after the initial social interaction and stayed higher as compared to either their baseline CORT levels or the CORT levels of dominant males. In addition, fecal CORT levels were positively correlated with the frequency of defensive behavior in subordinate males, but not in dominants. The elevated CORT Levels of subordinate males suggested that they suffered a greater level of social stress than dominant males as predicated by the subordination stress paradigm [31].

In social conflicts, acute social stress elevates GC levels within 20–40 min to prepare animals for fight or flight [12,24,48] and is essential to their survival [40]. However, long-term high GC levels can result in harmful effects, such as reproductive and immune suppression [8]. Under chronic stimulation, physiological habituation usually occurs to eliminate the negative influences of elevated GC concentrations on the health of animals [8,24,40,41,43,44]. We found physiological adaptation as well as behavioral adaptation occurred in during the later periods of social conflict. In addition, CORT and CRF might have been influenced by differences in food intake and gut motility between dominant and subordinate males [15,18,39]. Teasing apart these effects should form the basis of future studies of this nature.

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References

[1] Albers HE, Huhman KL, Meisel RL. Hormonal basis of social conflict and communication. In: Pfaff DW, Arnold AP, Etgen AM, Fahrbach SE, Rubin RT, editors. Hormones, brain and behavior, vol. 1. San Diego: Academic Press; 2002. p. 393–433.
[2] Archer J. The biology of aggression. Cambridge, UK: Cambridge University Press; 1988.
[3] Arnold W, Dittami J. Reproductive suppression in male alpine marmots. Anim Behav 1997;53:53–66.
[4] Bartolomucci A, Palanza P, Sacerdote P, Panerai AE, Sgoifo A, Dantzer R, et al. Social factors and individual vulnerability to chronic stress exposure. Neurosci Biobehav Rev 2005;29:67–81.
[5] Bahrke MS, Yesalis CE, Wright JE. Psychological and behavioural effects of endogenous testosterone and anabolic–androgenic steroids. An update. Sports Med 1996;22:367–90.
[6] Brain PF, Haug M. Hormonal and neurochemical correlates of various forms of animal "aggression". Psychoneuroendocrinology 1992;17:537–51.
[7] Buck CL, Barmes BM. Androgen in free-living arctic ground squirrels: seasonal changes and influence of staged male–male aggressive encounter. Horm Behav 2003;43:318–26.
[8] Buckingham JC. Glucocorticoids: exemplars of multi-tasking. Br J Pharmacol 2006;147:258–68.
[9] Capezzuto A, Chelini MOM, Felippe ECG, Oliveira CA. Correlation between serum and fecal concentrations of reproductive steroids throughout gestation in goats. Anim Reprod Sci 2008;103:78–86.
[10] Coopera MA, Karomb M, Huhmana KL, Albers HE. Repeated agonistic encounters in hamsters modulate AVP V_{1a} receptor binding. Horm Behav 2005;48:545–51.
[11] Creel S. Social dominance and stress hormones. Trends Ecol Evol 2001;16:491–7.
[12] Dawkins MS. Evolution and animal welfare. Q Rev Biol 1998;73:305–28.
[13] Drickamer LC, Vandenbergh JC, Colby DR. Predictors of dominance in the male golden hamster (*Mesocricetus auratus*). Anim Behav 1973;21:557–63.
[14] Earley RL, Edwards JT, Aseem O, Felton K, Blumer LS, Karom M, et al. Social interactions tune aggression and stress responsiveness in a territorial cichlid fish (*Archocentrus nigrofasciatus*). Physiol Behav 2006;88:353–63.
[15] Enck P, Holtmann G. Stress and gastrointestinal motility in animals: a review of the literature. J Gastrointest Motil 1992;1:83–90.
[16] Fano E, Sánchez-Martin JR, Arregi A, Castro B, Alonso A, Brain P, et al. Social stress paradigms in male mice: variations in behavior, stress and immunology. Physiol Behav 2001;73:165–73.
[17] Ferris CF, Axelson JF, Shinto LH, Albers HE. Scent marking and the maintenance of dominant/subordinate status in male golden hamsters. Physiol Behav 1987;40:661–4.
[18] Glowa JR, Barrett JE, Russell J, Gold PW. Effects of corticotropin releasing hormone on appetite behaviors. Peptides 1992;13:609–21.
[19] Goymann W, Landys MM, Wingfield JC. Distinguishing seasonal androgen responses from male–male androgen responsiveness—revisiting the challenge hypothesis. Horm Behav 2007;51:463–76.
[20] Hambly CH. Faecal corticosterone concentrations indicate that separately housed male mice are not more stressed than group housed males. Physiol Behav 2006;87:519–26.
[21] Harper JM, Austad SN. Effect of capture and season on fecal glucocorticoid levels in deer mice (*Peromyscus maniculatus*) and redbacked voles (*Clethrionomys gapperi*). J Gen Comp Endocrinol 2001;123:337–44.
[22] Hirschenhauser K, Winkler H, Oliveira RF. Comparative analysis of male androgen responsiveness to social environment in birds: the effects of mating system and paternal incubation. Horm Behav 2003;43:508–19.
[23] Huhman KL, Bunnell BN, Mougey EH, Meyerhoff JL. Effects of social conflict on POMC-derived peptides and glucocorticoids in male golden hamsters. Physiol Behav 1990;47:949–56.
[24] Huhman KL, Moore TO, Ferris CF, Mougey EH, Meyerhoff JL. Acute and repeated exposure to social conflict in male golden hamsters: increases in plasma POMC peptides and cortisol and decreases in plasma testosterone. Horm Behav 1991;25:206–16.
[25] Johnston RE. Scent marking by male golden hamsters (*Mesocricetus auratus*). I. Effects of odors and social encounters. Z Tierpsychol 1975;37:75–98.
[26] Josephs RA, Sellers JG, Newman ML, Mehta PH. The mismatch effect: when testosterone and status are at odds. J Pers Soc Psychol 2006;90:999–1013.
[27] Kalin NH. Primate models to understand human aggression. J Clin Psychiatry 1999;60(Suppl 15):29–32.
[28] Kudryavtseva NN, Amstislavskaya TG, Kucheryavy S. Effects of repeated aggressive encounters on approach to a female and plasma testosterone in male mice. Horm Behav 2004;45:103–7.
[29] Li Z. Radioimmunoassays of hormones. Beijing: Sciences and Technology Press; 1985 [In Chinese].
[30] Liang H, Zhang Z. Food restriction affects reproduction and survival of F1 and F2 offspring of rat-like hamster (*Cricetulus triton*). Physiol Behav 2006;87:607–13.
[31] Mateos C. The subordination stress paradigm and the relation between testosterone and corticosterone in male ring-necked pheasants. Anim Behav 2002;69:245–55.
[32] Mehta PH, Josephs RA. Testosterone change after losing predicts the decision to compete again. Horm Behav 2006;50:684–92.
[33] Moore IT. Advancing the challenge hypothesis. Horm Behav 2007;51:461–2.
[34] Mostl E, Palme R. Hormones as indicators of stress. J Domest Anim Endocrinol 2002;23:67–74.
[35] Ogawa S, Robbins A, Kumar N, Pfaff DW, Sundaran K, Bardin CW. Effects of testosterone and 7alpha-methyl-19-nortestosterone (MENT) on sexual and

aggressive behaviors in two inbred strains of male mice. Horm Behav 1996;30:74–84.
[36] Oliveira RF, Hirschenhauser K, Carneiro LA, Canario AVM. Social modulation of androgen levels in male teleost fish. Comp Biochem Physiol B 2002;132:203–15.
[37] Oyegbile TO, Marler CA. Winning fights elevates testosterone levels in California mice and enhances future ability to win fights. Horm Behav 2005;48:259–67.
[38] Ramenofsky M. Agonistic behavior and endogenous plasma hormones in male Japanese quail. Anim Behav 1984;32:698–708.
[39] Rivier CL, Plotsky PM. Mediation by corticotrophin releasing factor (CRF) of adenohypophysial hormone secretion. Annu Rev Physiol 1986;48:475–94.
[40] Romero LM. Physiological stress in ecology: lessons from biomedical research. Trends Ecol Evol 2004;19:249–55.
[41] Ross CN, French JA, Patera KJ. Intensity of aggressive interactions modulates testosterone in male marmosets. Physiol Behav 2004;83:437–45.
[42] Rowe EA, Swanson HH. A comparison of central and peripheral effects of testosterone propionate on social interactions in the male golden hamster. J Endocrinol 1977;72:39–40.
[43] Sapolsky RM, Romero LM, Munck AU. How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory, and preparative actions. Endocr Rev 2000;21:55–89.
[44] Schuett GW, Harlow HJ, Rose JD, Kirk EAV, Murdoch WJ. Levels of plasma corticosterone and testosterone in male copperheads (*Agkistrodon contortrix*) following staged fights. Horm Behav 1996;30:60–8.
[45] Siegel HI. Aggressive behavior. In: Siegel HI, editor. The hamster reproduction and behavior. New York: Plenum; 1985. p. 261–88.
[46] Song MJ, Zhang ZB, Neumann K, Gattermann R. Sex-biased dispersal of greater long-tailed hamster (*Tscherskia triton*) revealed by microsatellites. Can J Zool 2005;83:773–9.
[47] Soto-Gamboa M, Villalón M, Bozinovic F. Social cues and hormone levels in male *Octodon degus* (Rodentia): a field test of the challenge hypothesis. Horm Behav 2005;47:311–8.
[48] Summers CH, Summers TR, Moore MC, Korzan WJ, Woodley SK, Ronan PJ, et al. Temporal patterns of limbic monoamine and plasma corticosterone response during social stress. Neuroscience 2003;116:553–63.
[49] Tamashiro KLK, Nguyen MMN, Sakai RR. Social stress: from rodents to primates. Front Neuroendocrinol 2005;26:27–40.
[50] Touma C, Sachser N, Mostl E, Palme R. Effects of sex and time of day on metabolism and excretion of corticosterone in urine and faeces of mice. J Gen Comp Endocrinol 2003;130:267–78.
[51] Wang DW, Zhang JX, Wang ZL, Zhang ZB. Seasonal changes in chronic social interactions and physiological states in female rat-like hamsters (*Tscheskia triton*). Physiol Behav 2006;89:420–7.
[52] Wang ZL, Wang DW, Zhang ZB. Effects of body weight on dominance hierarchy and agonistic behaviors in male greater long-tailed hamsters (*Tscheskia triton*). Acta Theriol Sin 2007;27:26–32 [In Chinese].
[53] Wasser SK, Monfort SL, Wildt DE. Rapid extraction of faecal steroids for measuring reproductive cyclicity and early pregnancy in free-ranging yellow baboons (*Papio cynocephalus cynocephalus*). J Reprod Fertil 1991;92:415–23.
[54] Wingfield JC. A continuing saga: the role of testosterone in aggression. Horm Behav 2005;48:253–5.
[55] Wingfield JC, Ball GF, Dufty AM, Hegner RE, Ramenofsky M. Testosterone and aggression in birds: tests of the challenge hypothesis. Am Sci 1987;75:602–8.
[56] Wingfield JC, Hegner RE, Dufty AM, Ball GF. The 'challenge hypothesis': theoretical implications for patterns of testosterone secretion, mating systems and breeding strategies. Am Nat 1990;136:829–46.
[57] Yang H, Wang S, Hao S. An investigation on populations of rat-like hamsters (*Cricetulus triton*) their predication and the integrated management in the non-irrigated area on North China Plain, China. In: Wang Z, Zhang Z, editors. Theory and practice of rodent pest management. Beijing: Science Press; 1996. p. 229–46. [In Chinese].
[58] Zhang JX, Cao C, Gao H, Yang ZS, Sun LX, Zhang ZB, et al. Effects of weasel odor on behavior and physiology of two hamster species. Physiol Behav 2003;79:549–52.
[59] Zhang JX, Zhang ZB, Wang ZW. Scent, social status, and reproductive condition in rat-like hamsters (*Cricetulus trition*). Physiol Behav 2001;74:415–20.
[60] Zhang JX, Zhang ZB, Wang ZW. Seasonal changes in and effects of familiarity on agonistic behaviors of rat-like hamsters (*Cricetulus trition*). Ecol Res 2001;16:309–17.
[61] Zhang ZB, Zhu J, Yang HF. The estimation on the time-specific mortality of rat-like hamsters. Acta Zool Sin 1992;38:151–5 [In Chinese].