



The effect of aggression I: The increases of metabolic cost and mobilization of fat reserves in male striped hamsters

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ABSTRACT

Aggression can benefit individuals by enhancing their dominance and thereby their ability to acquire and retain resources that increase survival or fitness. Engaging in aggressive behavior costs energy and how animals manage their energy budget to accommodate aggression remains unclear. We conducted three experiments to examine changes in physiological, behavioral and hormonal markers indicative of energy budget in male striped hamsters subject to resident-intruder aggression tests. Body temperature, metabolic rate and serum corticosterone levels significantly increased in resident hamsters immediately after the introduction of intruders. Energy intake did not change, but the metabolic rate of residents increased by 16.1% after 42-days of repeated encounters with intruders. Residents had significantly decreased body fat content and serum thyroxine (T_4) levels, and a considerably elevated tri-iodothyronine (T_3)/ T_4 ratio compared to a control group that had no intruders. Attack latency considerably shortened, and the number of attack bouts and total duration of attacks, significantly increased in residents on day 42 compared to day 1 of experiments. These findings may suggest that the conversion of T_4 to T_3 is involved in defensive aggression behavior. The mobilization of fat reserves resulting in lean body mass is probably common response to the increased metabolic cost of aggression in small mammals. Aggressive behavior, which is important for the successful acquisition and defense of resources, may be of significance for adaptation and evolution of metabolic rate.

1. Introduction

Aggression is an important aspect of intra-specific competition that can allow individuals to gain access to and retain limited resources that enhance their survival and fitness (Briffa and Elwood, 2004; Haller et al., 2005; Careau et al., 2010; Seebacher et al., 2013). Aggression is frequently employed in the defense of territory or offspring, and in response to the threat of conspecific attack (Miczek et al., 2001, 2002). Aggression also occurs when individuals compete for food, water and other resources necessary for survival and reproduction (Miczek et al., 2002; Takahashi et al., 2012). The likelihood of success of aggressive competition has been found to be proportional to the metabolic investment (Briffa and Sneddon, 2007; Seebacher et al., 2013). For example, a significant positive correlation has been observed between overt aggressive behavior and metabolic rate in the Mozambique tilapia (*Oreochromis mossambicus*) (Ros et al., 2006). Therefore, aggression has been considered an ‘energetic wars of attrition’, where the winning contestant is the one that commits the greatest amount of energy to the contest (Payne and Pagel, 1997; Briffa and Elwood, 2004; Copeland

et al., 2011).

From the perspective of energy balance animals must either increase their energy intake, mobilize their energy reserves, or both, to meet increased energy costs. For example, the European hermit crab (*Pagurus bernhardus*) significantly elevates glucose concentration during fighting by mobilizing glycogen reserves (Briffa and Elwood, 2004). Having sufficient energy reserves appears to be a key factor determining the likelihood of an individuals' success in combat (Briffa and Elwood, 2004). In addition to fighting, non-hibernating small mammals need to meet the increased energy costs of metabolic thermogenesis under cold conditions, either by increasing their food intake or by mobilizing body fat reserves (Bartness et al., 2002; Wang et al., 2006; Zhao, 2011). Lactating animals typically increase their food intake and mobilize body fat reserves to meet the increased energy requirements of milk production (Hammond and Diamond, 1997; Speakman, 2008; Zhang et al., 2016).

Mobilization of fat reserves may result in a lean body mass if the increased energy consumption cannot be compensated for by energy intake. Conversely, mobilized fat reserves can recover rapidly when

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energy intake is increased. It is unclear how energy resources are mobilized during aggressive interactions, and what factors associated with energy intake and expenditure (hereafter “energy budget”) influence their mobilization during both short, and prolonged, bouts of aggression.

The striped hamster (*Cricetulus barabensis*) is a solitary and highly territorial rodent that is common in northern China and also found throughout Russia, Mongolia, and Korea (Zhao et al., 2014a). As described previously, these hamsters do not hibernate but rather feed on plant stems and leaves during summer and seeds in winter (Zhang and Wang, 1998; Song and Wang, 2003). Juveniles of both sexes leave their natal territory when close to sexual maturity to establish individual territories. Both females and males are highly aggressive to conspecifics both in the wild and under laboratory conditions. Indeed, the striped hamster is more aggressive than other rodent species, such as the Siberian hamster (*Phodopus sungorus*), Syrian hamster (*Mesocricetus auratus*), and laboratory mice and rats (Blanchard and Blanchard, 1977; Jasnow et al., 2000, 2002; Takahashi et al., 2012). In addition, the striped hamster displays considerable plasticity in metabolic rate and body fat in response to seasonal climatic changes (Zhao et al., 2014b). Basal metabolic rate has been observed to play important roles in physiological fat regulation (Tan et al., 2016, 2017). These characteristics suggest this species could be a suitable, new animal model for research on the physiological and behavioral aspects of aggressive behavior.

In this paper we present the results of three experiments on the effects of aggression on various physiological and metabolic indicators in the striped hamster. The first (Experiment 1) was designed to examine the effect of aggression, induced by introducing an intruder, on the body temperature, metabolic rate and corticosterone levels, of resident hamsters. The second (Experiment 2) examined the effect of brief periods of aggression on the energy budget, metabolic rate, serum thyroid hormones and body fat content, of resident hamsters. The third (Experiment 3) examined the effect of short, and extended, periods of aggression on the energy budget, body fat mobilization and aggressive behavior, of resident hamsters. We hypothesized that resident hamsters that were subject to incursions by intruders would develop a lean body mass due to mobilizing body fat to meet the increased metabolic cost of territory defense.

2. Materials and methods

2.1. Animals

Striped hamsters were obtained as previously described from colonies maintained at the College of Life and Environmental Science, Wenzhou University (Zhang et al., 2016). All animals were initially kept at $21 \pm 1^\circ\text{C}$ under a 12 L:12D (light:dark, lights on at 0800 h) photoperiod. Food (standard rodent chow, 17.6 kJ/g; Beijing KeAo Feed Company, Beijing, China) and water were provided ad libitum. All experimental procedures complied with the guidelines of the Wenzhou University Animal Care and Use Committee.

Experiment 1 was designed to test the effect of aggression on body temperature and metabolic rate. Sixty nine male hamsters of 3.5–4.5 months of age were randomly assigned into either a Resident ($n = 37$), or Control group ($n = 32$). Aggression was elicited using a resident-intruder model described previously (Jasnow et al., 2000). In brief, a male intruder was introduced into the home cage of each animal in the Resident group for 10 min. Intruders were identified by marking them with dye on their back. No intruders were introduced into the home cage in the Control group. Aggression was tested at 21:00, one hour after the light off. Experiment 1 lasted for only one day, and the aggression test was conducted only once. In detail, body temperature was measured (Resident, $n = 15$, Control, $n = 15$) for 55 min, including 10 min of aggression test. Rate of oxygen consumption was determined (Resident, $n = 7$, Control, $n = 7$) for 180 min, also

including a 10-min aggression test. Aggressive behavior was scored for 10 min when intruder hamster was placed in the home cage of resident hamster (Resident, $n = 15$), after which residents were sacrificed by decapitation. Ten non-intruder hamsters were sacrificed as controls (Control, $n = 10$). Serum was collected for the measures of corticosterone levels.

2.2. Body temperature (T_b)

An encapsulated thermo-sensitive passive transponder (diameter 2 mm and length 14 mm; Destron Fearing, South St Paul, USA) was implanted in the abdomen of 15 randomly selected hamsters in the Control and Resident groups on day 7 before intruders were introduced. A Pocket Reader was then used to receive and collect T_b data without disturbance. T_b was first measured for 15 min to obtain a baseline measurement (min 0–15). A male intruder was then introduced into the home cage of each resident hamster for 10 min (min 16–25). T_b was then measured for another 30 min (min 26–55) after intruders had been removed.

2.3. Intensity of attack behavior

Intensity of attack behavior was quantified as described by Jasnow et al. (2002): initial latency to attack, number of attacks (attack bouts), duration of attacks, and duration of intervals between two successive bouts of attacks. An “attack” was a combination of chasing and biting, and was operationally defined as the rapid approach of a resident toward an intruder in either a sideways or upright offensive posture in an attempt to bite the intruder (Huhman et al., 1990; Jasnow et al., 2002). Behavioral observations were conducted with a low-power (15 W) red light in the dark phase.

2.4. Rate of oxygen consumption

The oxygen consumption rate before, during, and after bouts of aggression was measured in seven randomly selected hamsters in both the Control and Resident groups. The rate of oxygen consumption was determined using an O_2 module high-speed sensor unit (994620-CS-HSP-01) for calorimetric measurements in an open-flow respirometry system (TSE, Germany). As described previously (Wen et al., 2017), air was pumped through a cylindrical sealed Perspex chamber at a rate of 1 L/min at a temperature of $21 \pm 0.5^\circ\text{C}$, which was the same temperature at which hamsters were kept. Gases leaving the chamber were dried and sampled using an oxygen analyzer at a flow rate of 0.38 L/min. Data were collected every 10 s by a computer connected via an analogue-to-digital converter (TSE, Germany). Measurements were first taken for 90 min to obtain a baseline measurement (min 0–90). A male intruder was then intruded to the chamber of resident hamster for 10 min (min 91–100) after which measurements resumed for 80 min (min 101–180). The consecutive rate of oxygen consumption over 2 min was averaged, corrected to standard temperature and air pressure conditions, and expressed as mlO_2/h . All measurements were made between 2100 and 2400 h.

2.5. Serum corticosterone levels

Twenty five subjects were selected randomly from the Control ($n = 10$) and Resident groups ($n = 15$) for the measurement of serum corticosterone levels. Male intruders were introduced into the home cages of Resi group as mentioned above, after which residents were sacrificed by decapitation immediately after the male intruder was removed. Trunk blood was collected from each animal and serum was separated from each blood sample by centrifugation ($3000\text{ g}/\text{min} \times 15\text{ min}$) and stored at -20°C . Serum corticosterone levels were determined using a commercial kit (Cayman Chemical Company, USA Item No. 501320), according to the kit instructions. The assay has a

range of 8.2–5000 pg/mL and a sensitivity of approximately 30 pg/mL, and the inter- and intra-assay variations are < 4.9% and 8.8%, respectively. In the experiment that had been previously performed in striped hamsters as the same method described in [Experiment 1](#), serum corticosterone and cortisol were determined using ELISA (corticosterone kit, No. 501320; cortisol kit, No. 500360, Cayman Chemical Company). Both kits were effective in striped hamsters according to the manufacturer's instructions, and the cross reactivity of serum corticosterone and cortisol was 0.14%. Serum corticosterone and cortisol concentrations of resident hamsters were higher by 23.3% and 12.0%, respectively, than that of control hamsters (corticosterone, $t_{26} = 3.92$, $P = 0.001$; cortisol, $t_{26} = 2.07$, $P = 0.049$), suggesting that corticosterone might be more suitable for evaluation of stress in this strain of hamsters. Therefore, corticosterone was used as a biomarker of stress in this study.

[Experiment 2](#) was designed to test the effect of aggression on residents' energy budget, body fat content, and serum T_3 and T_4 levels. Forty-eight adult male hamsters were randomly assigned to either a Resident (Resi, $n = 30$), or Control group (Con, $n = 18$). Aggression was elicited as described in [Experiment 1](#), except that male intruders were repeatedly introduced to the home cage of residents for 10 min periods at 3-h intervals; i.e. a total of 8 times of introduction per resident over 48-h, during which there was no aggression test in light phase. Intruders were housed individually after weaning, and before and throughout these experiments. The intruders in this experiment were not used previously, without a prior defeat. Although, intruders were randomly assigned into home cage of resident hamsters, they were not placed again into the same cage of residents, i.e. the intruder put in the residents cage was different one each time. [Experiment 2](#) lasted for 48 h, and there were four 10-min tests every 3 h during the dark phase in the first 24 h and also four 10-min tests in the second 24 h. As described in the [Experiment 1](#), aggressive behavior was observed during each aggression test throughout the experiment (supplementary material, Fig. S1).

2.6. Basal metabolic rate (BMR)

The BMR of fifteen Resident and nine Control hamsters was measured after the experiment described above in an open-flow respirometry system (TSE, Germany), as described in [Experiment 1](#). Animals were fasted for 3 h to correct for food special dynamic effects before being transferred into the chamber where they were allowed to acclimatize for 1 h before measurements began. BMR was measured for 2.5 h. The consecutive minimum rate of oxygen consumption over 10 min was used to calculate BMR, which was then corrected to standard temperature and air pressure conditions and expressed as mL O₂/h.

2.7. Serum tri-iodothyronine (T_3) and thyroxine (T_4)

The fifteen Resident and nine Control hamsters whose BMR had been measured were sacrificed and their blood serum was collected as described in [Experiment 1](#). Serum T_3 and T_4 levels were determined by radioimmunoassay using I¹²⁵ RIA kits (Beijing North Institute of Biological Technology, Beijing, China). Intra- and inter-assay coefficients of variation were 2.4% and 8.8% for T_3 , and 4.3% and 7.6% for T_4 .

2.8. Fat mass and fat content

After blood had been collected from hamsters, their liver, heart, lung, spleen, kidneys and gastrointestinal tract, were removed. The remaining carcass was weighed to determine its wet mass, dried to a constant mass in an oven at 60 °C for two weeks, then reweighed (to 1 mg) to determine its dry mass. Total body fat was extracted from the dried carcass by ether extraction in a Soxhlet apparatus, and the difference in weight before and after extraction was used to calculate the fat content of the carcass using the following equation: fat content of

dry mass (%) = fat mass of carcass (g)/dry carcass mass (g) × 100%; Fat free mass (g) = dry carcass mass (g) - fat mass of carcass (g).

[Experiment 3](#) was designed to determine the effect of aggression on the body fat content of resident hamsters who were subjected to incursions by intruder for 6 weeks. Twenty-six adult male hamsters were randomly assigned to either a Resident (Resi, $n = 16$), or Control (Con, $n = 10$) group. A male intruder was introduced into the home cage of each resident for 10 min per day over a 6 week period. Intruders were introduced during the first 2 h of the dark phase to control for circadian rhythmicity of behavior. Body mass and food intake were measured throughout the experiment on a daily basis. Food intake was calculated as the weight of food missing from the hopper every day, subtracting orts mixed in the bedding.

2.9. Gross energy intake (GEI) and digestibility

GEI, digestive energy intake (DEI), and digestibility were determined over the last two days of the experiment (days 41 and 42). A known quantity of food was provided, and 48 h later, any uneaten food and orts mixed with the bedding material were collected, along with feces from each animal. Food and feces were separated manually after drying at 60 °C to constant mass. Gross energy content of feces was determined using an IKA C2000 oxygen bomb calorimeter (IKA, Germany). GEI, DEI, digestibility and gross energy (GE) of feces were calculated as described previously ([Grodzinski and Wunder, 1975](#); [Zhao and Wang, 2006](#); [Wen et al., 2017](#)): GEI (kJ/d) = [food provided (g/d) × dry matter content of food (%) - dry spillage of food and uneaten food] × gross energy content of food (kJ/g); GE of feces = dry feces mass (g/d) × gross energy content of feces (kJ/g); DEI (kJ/d) = GEI (kJ/d) - GE of feces; and digestibility (%) = DEI/GEI × 100%.

2.10. Intensity of attack behavior

Resident/intruder aggression was elicited according to the methods described in [Experiment 1](#). The intensity of attack behavior was measured at the beginning (day 1), and the end (day 42) of this experiment, respectively.

2.11. BMR, serum T_3 and T_4 , and body fat

BMR was determined as described in [Experiment 2](#) after observing and recording attack behavior. Animals were sacrificed and serum was collected as described previously the day after BMR measurements were completed. Serum T_3 and T_4 levels, and body fat content were determined according to the methods used in [Experiment 1](#). In addition, the subcutaneous fat was collected from each subject and weighed (to 1 mg).

2.12. Statistical analysis

Data were analyzed using SPSS 21.0 statistic software. In [Experiment 1](#), the statistical significance of changes in T_b and O₂ consumption over time were tested with a Repeated-measures ANOVA, and the significance of differences between Resident and Control groups at any time points over the course of the experiment was analyzed with an Independent-sample *t*-test. In [Experiment 2](#), the significance between group differences in energy intake, digestibility, BMR, serum T_3 and T_4 levels, and fat content were tested with an Independent-sample *t*-test. Attack behavior was analyzed using one-way ANOVA, followed by a Repeated-measures. In [Experiment 3](#), the significance of changes in body mass and food intake over the course of the experiment were tested using a Repeated-measures ANOVA. Eta-squared (η^2) was used to measure effect size in ANOVA. The statistical significance of differences in aggressive behavior between day 1 and day 42 was analyzed with an Independent-sample *t*-test, as were the significance of differences of between-group differences in energy intake, digestibility, BMR, serum

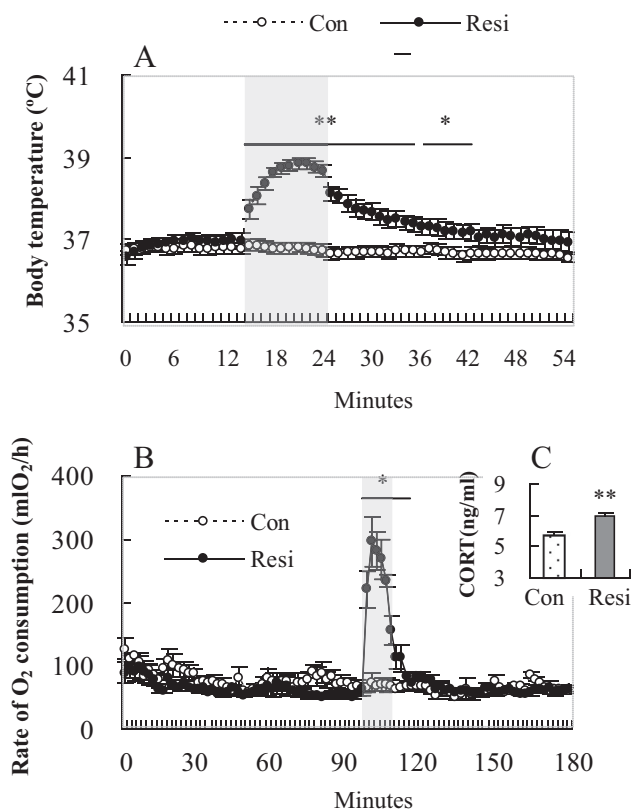


Fig. 1. Effect of aggression on the body temperature (A), rate of oxygen consumption (B) and serum corticosterone level (CORT, C), of striped hamsters. Data are means \pm s.e.m. Grey background indicates the period during which intruders were in the home cage of resident hamster. Grey circles indicate that data were collected from a combination of both resident and intruder hamsters. Resi, resident hamsters to which intruders were introduced for 10 min periods; Con, control group (no intruders). *, the effect of aggression was significant ($P < 0.05$); **, $P < 0.01$.

T_3 and T_4 levels, and fat content. All data are presented as means \pm s.e.m., P -values < 0.05 were considered significant.

3. Results

3.1. Experiment 1

3.1.1. T_b and attack behavior

T_b varied significantly throughout the experiment ($F_{54,1512} = 19.82$, $P = 0.001$, $\eta^2 = 0.414$, Fig. 1A). The T_b of the Control and Resident groups did not differ significantly before intruders were introduced (min 0, $t_{28} = 0.84$, $P = 0.41$) but did after this ($F_{1,28} = 15.31$, $P = 0.001$, $\eta^2 = 0.353$). The T_b of the Resident group increased significantly (min 16, $t_{28} = 3.26$, $P = 0.003$) when intruders were present, peaking 7 min after intruders were introduced (Control, 36.8 °C vs Resident, 38.9 °C), indicating that aggression had a significant effect on T_b (min 21, $t_{28} = 11.74$, $P = 0.001$). The T_b of the Resident group declined after intruders were removed, but remained significantly higher than that of the Control group after 42 min (min 42, $t_{28} = 2.13$, $P = 0.042$). The two groups did not differ significantly after 43 min (min 43, $t_{28} = 1.58$, $P = 0.125$, min 54, $t_{28} = 1.46$, $P = 0.156$). Resident hamsters showed intense aggressive behavior when intruders were present, during which the initial latency to attack averaged 209 ± 37 s, the number of attack bouts was 3.5 ± 0.7 , the total duration of attacks and intervals was 80 ± 19 s and 241 ± 25 s, respectively; and the average duration of attacks was 26 ± 4 s and the average duration of between-attack intervals was 110 ± 18 s.

3.1.2. Rate of O₂ consumption and serum corticosterone levels

There was no significant difference in O₂ consumption between the Control and Resident groups during the 90-min baseline measurement period before intruders were introduced (min 0, $t_{12} = 1.33$, $P = 0.217$, min 90, $t_{12} = 1.48$, $P = 0.171$, Fig. 1B). However, O₂ consumption increased almost fourfold after intruders were introduced (min 92, $t_{28} = 5.41$, $P = 0.051$, min 100, $t_{28} = 3.47$, $P = 0.035$). This was due to increased oxygen consumption by both residents and intruders during bouts of aggression, and the increased oxygen consumption of intruders by being placed into a novel environment with an aggressive conspecific male. O₂ consumption of the Resident group remained significantly higher than that of the Control 4 min after intruders had been removed (min 102, $t_{28} = 2.62$, $P = 0.022$, min 104, $t_{28} = 2.28$, $P = 0.042$), and then decreased to the baseline levels (min 106, $t_{28} = 1.19$, $P = 0.272$; min 180, $t_{28} = 1.19$, $P = 0.858$). There was a significant difference in serum corticosterone levels between the two groups ($t_{23} = 3.56$, $P = 0.002$); that of the Resident group was 21.9% higher than that of the Control group (Fig. 1C).

3.2. Experiment 2

3.2.1. Attack behavior over 48 h

The initial latency of residents in the fourth aggression test was shortened by 40.4% compared to the first test during the first 24 h, and it was shortened by 40.4% during the second 24 h; however the difference among the groups was not statistically significant ($F_{7,88} = 1.41$, $P = 0.211$, $\eta^2 = 0.101$, supplementary materials, Fig. S1A). The number of attack bouts ranged from 2 to 5 per aggression test over the 48 h ($F_{7,88} = 0.72$, $P = 0.655$, $\eta^2 = 0.054$, Fig. S1B). The cumulative time of attack did not change significantly ($F_{7,88} = 1.70$, $P = 0.119$, $\eta^2 = 0.119$, Fig. S1C). However, average time of attack of significantly increased in the final test compared to others ($F_{7,88} = 3.11$, $P = 0.006$, $\eta^2 = 0.198$, Fig. S1D). The cumulative and average time of intervals was not statistically different among the groups (cumulative, $F_{7,88} = 1.15$, $P = 0.339$, $\eta^2 = 0.083$, Fig. S1E; average, $F_{7,88} = 0.78$, $P = 0.604$, $\eta^2 = 0.059$, Fig. S1F).

3.2.2. BMR, serum T_3 and T_4 levels

The BMR of the Resident group was 15.3% higher than that of the Control group ($t_{22} = 2.50$, $P = 0.021$, Fig. 2A). Serum T_3 levels were not significantly different between the two groups ($t_{22} = 0.47$, $P = 0.642$, Fig. 2B), but the serum T_4 levels were 36.6% lower than that of the Control group ($t_{22} = 3.56$, $P = 0.002$, Fig. 2C). The serum T_3 to T_4 ratio (T_3/T_4), which indicates the rate of transformation from T_4 to T_3 , was significantly higher in the Resident group than in the Control group ($t_{22} = 2.08$, $P = 0.040$, Fig. 2D).

3.2.3. Fat mass and fat content

Although carcass mass was not significantly affected by aggression ($t_{22} = 0.74$, $P = 0.467$, Fig. 3A), there was a significant difference in fat-free mass between the two groups ($t_{22} = 4.02$, $P = 0.001$), that of the Resident group being 17.7% higher than that of the Control group (Fig. 3B). Both fat mass and fat content were significantly affected by aggression, which caused significant reductions in body fat (fat mass, $t_{22} = 2.21$, $P = 0.037$, Fig. 3C; fat content, $t_{22} = 3.49$, $P = 0.002$, Fig. 3D).

3.3. Experiment 3

3.3.1. Body mass and food intake

Body mass was not significantly affected by aggression ($F_{1,24} = 0.14$, $P = 0.713$, $\eta^2 = 0.007$) and did not change significantly during the experiment ($F_{20,460} = 1.42$, $P = 0.109$, $\eta^2 = 0.058$, Fig. 4A). Food intake was also unaffected by aggression ($F_{1,24} = 0.32$, $P = 0.577$, $\eta^2 = 0.013$, Fig. 4B), and did not vary during the experiment ($F_{20,460} = 1.66$, $P = 0.118$, $\eta^2 = 0.077$).

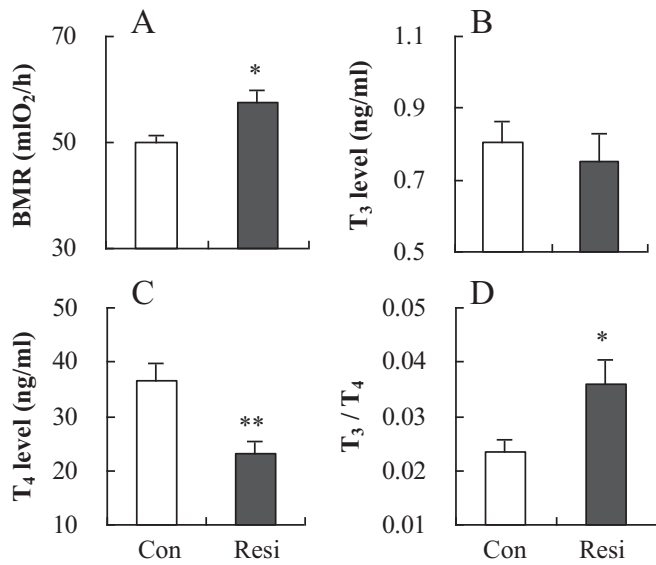


Fig. 2. Effect of aggression on the basal metabolic rate (BMR, A), serum T_3 (B) and T_4 levels (C) and T_3/T_4 (D) of striped hamsters. Data are means \pm s.e.m. Resi, resident hamsters to which intruders were introduced for 10 min periods at 3-h intervals over 48 h; Con, control group (no intruders). *, the effect of aggression was significant ($P < 0.05$); **, $P < 0.01$.

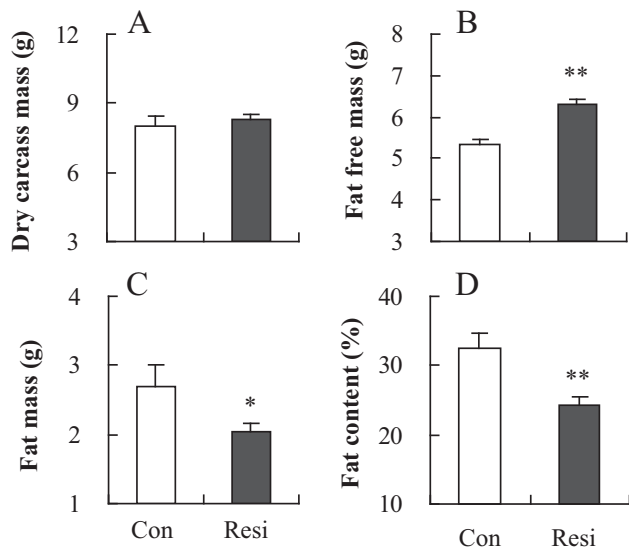


Fig. 3. Effect of aggression on the dry carcass mass (A), fat free mass (B), fat mass (C) and fat content (D) of striped hamsters. Data are means \pm s.e.m. Resi, resident hamsters to which intruders were introduced for 10 min periods at 3-h intervals over 48 h; Con, control group (no intruders). *, the effect of aggression was significant ($P < 0.05$); **, $P < 0.01$.

3.3.2. Attack behavior

Although residents did not always continue to attack the intruders, they displayed aggression toward them intermittently during the 10-min periods in which intruders were present. As described in the Method section, aggression behavior was characterized by a combination of chasing and biting, as well as upright offensive posture in which residents attempted to bite the intruder. We think that it's reasonable to conclude that all resident hamsters experienced social stress, and displayed elevated levels of aggression, when intruders were present. There was a significant difference in the initial latency to attack between day 1 and day 42, which was 61.6% less on day 42 compared to day 1 (day 1, 138 ± 22.9 s vs day 42, 53.4 ± 15.4 s, $t_{30} = 3.21$, $P = 0.004$, Fig. 5A). The number of attack bouts was significantly

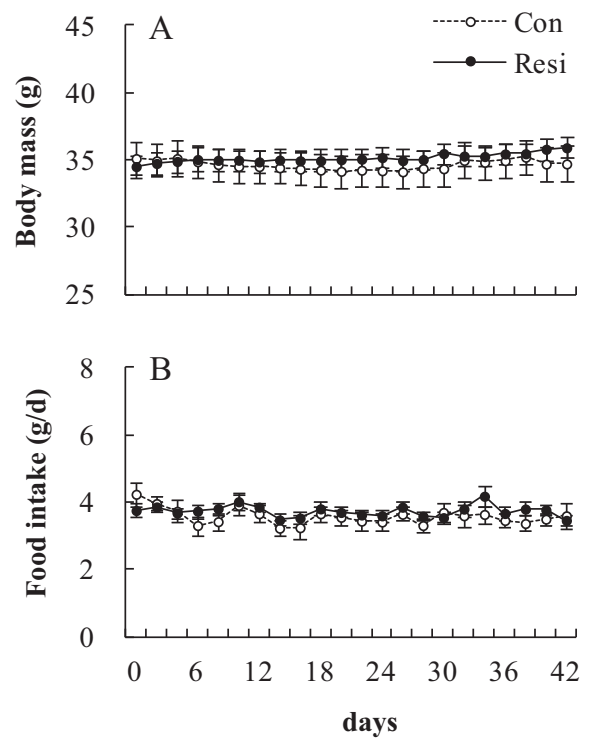


Fig. 4. Effect of aggression on the body mass (A) and food intake (B) of striped hamsters. Data are means \pm s.e.m. Resi, resident hamsters to which intruders were introduced for 10 min periods over 42 days; Con, control group (no intruders).

higher (by 2.4-fold) on day 42 relative to that on day 1 ($t_{30} = 4.96$, $P = 0.001$, Fig. 5B), and the total duration of attacks had also increased by 100.7% on day 42 compared to day 1 ($t_{30} = 2.67$, $P = 0.012$, Fig. 5C). However, the average duration of attacks did not change significantly between day 42 and day 1 ($t_{30} = 1.20$, $P = 0.242$, Fig. 5D), nor did the total duration of intervals between day 42 and day 1 ($t_{30} = 0.41$, $P = 0.685$, Fig. 5E). However, the average duration of between-attack intervals was significantly shorter on day 42 compared to day 1 ($t_{30} = 3.69$, $P = 0.001$, Fig. 5F).

3.3.3. Energy intake and digestibility

GEI and DEI did not differ between the Control and Resident groups, indicating that aggression had no significant effect on energy intake (GEI, $t_{24} = 0.84$, $P = 0.407$, Fig. 6A; DEI, $t_{24} = 0.66$, $P = 0.513$, Fig. 6B). There was no significant difference between feces of the Resident and Control groups ($t_{24} = 1.60$, $P = 0.123$, Fig. 6C), nor was there any difference in digestibility between the two groups ($t_{24} = 0.33$, $P = 0.743$, Fig. 6D).

3.3.4. BMR, serum T_3 and T_4 levels

The BMR of the Resident group was 16.1% higher than that of the Control group ($t_{24} = 2.50$, $P = 0.039$, Fig. 7A). Serum T_3 levels of the Resident group tended to be higher than those of the Control group, but this difference was not statistically significant ($t_{24} = 1.10$, $P = 0.282$, Fig. 7B). The serum T_4 levels of the Resident group were 18.7% lower than that of the Control group ($t_{24} = 2.13$, $P = 0.043$, Fig. 7C). The serum T_3 to T_4 ratio (T_3/T_4) was significantly higher in the Resident group than that in the Control group ($t_{24} = 3.71$, $P = 0.001$, Fig. 7D).

3.3.5. Fat content

The subcutaneous fat mass was significantly affected by aggression, and it was 47.9% lower in the Resident group than that in the Control group ($t_{24} = 2.71$, $P = 0.012$, Fig. 7E). The fat content of carcass was also significantly lower in the Resident group compared to that in the Control group ($t_{24} = 2.35$, $P = 0.027$, Fig. 7F).

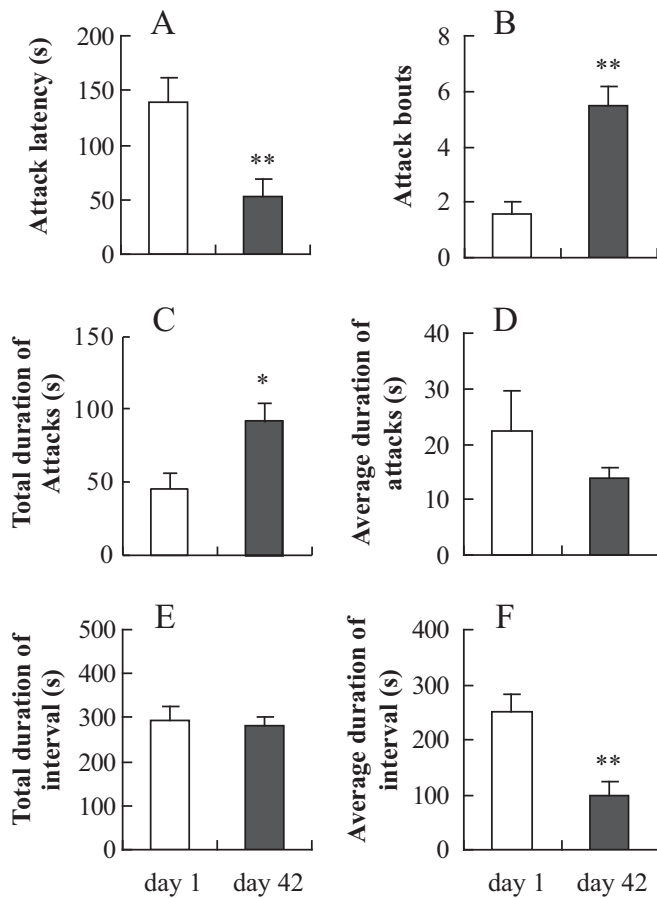


Fig. 5. Attack latency (A), number of attack bouts (B), cumulative and average time of attack (C and D), cumulative and average time of interval (E and F) in striped hamsters. Data are means \pm s.e.m. *, significant difference between day 1 and 42 ($P < 0.05$); **, $P < 0.01$.

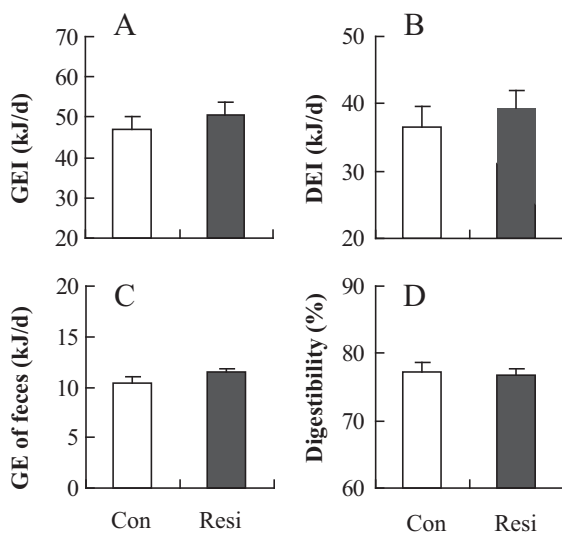


Fig. 6. Effect of aggression on gross energy intake (GEI, A), digestive energy intake (DEI, B), GE of feces (C) and digestibility (D) in striped hamsters. Data are means \pm s.e.m. Resi, resident hamsters to which intruders were introduced for 10 min periods over 42 days; Con, control group (no intruders).

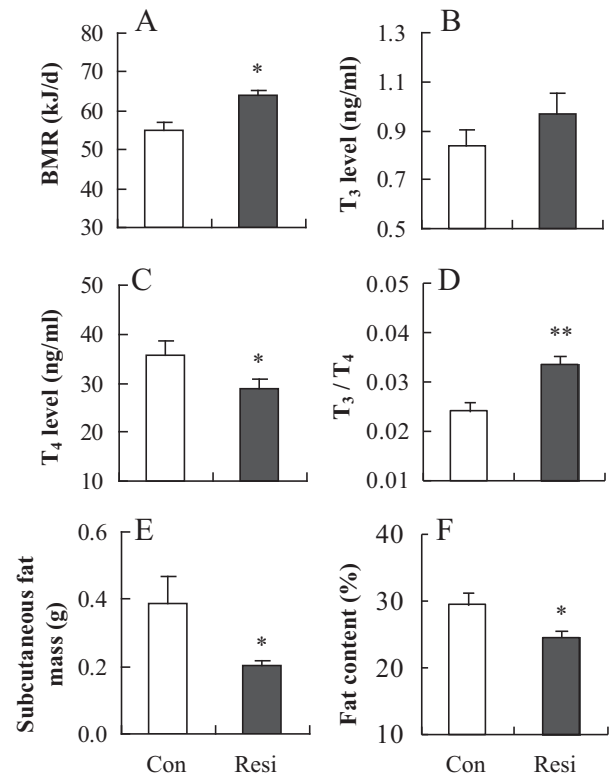


Fig. 7. Effect of aggression on the basal metabolic rate (BMR, A), serum T_3 (B) and T_4 levels (C), T_3 to T_4 ratio (T_3/T_4 , D), subcutaneous fat mass (E), and fat content (F), of striped hamsters. Data are means \pm s.e.m. Resi, resident hamsters to which intruders were introduced for 10 min periods over 42 days; Con, control group (no intruders).*, the effect of aggression was significant ($P < 0.05$); **, $P < 0.01$.

4. Discussion

The striped hamster is solitary, highly aggressive and territorial species (Zhang and Wang, 1998). We found that hamsters from a laboratory colony displayed intense aggression in the resident/intruder tests. Plasma corticosterone, an important indicator of physiological stress responses (Ylönen et al., 2006; Sheriff et al., 2011; Liesenjohann et al., 2013), was significantly elevated in resident hamsters after aggressive interactions with intruders. Aggression-induced increases in serum corticosterone levels, which may facilitate aggression required for territorial defense, have also been observed in variety of other animals, (Liesenjohann et al., 2013; Baird et al., 2014; Braasch et al., 2014). We found that the aggressive behavior was significantly affected by the duration of resident/intruder interactions; prolonged interaction considerably shortened the latency to initiate attack. The number of attack bouts and the total duration of attacks also increased significantly on day 42 relative to day 1, indicating that aggressive was intensified by repeated exposure to intruders.

Aggressive often has a cost in terms of energy investment (Payne and Pagel, 1997; Briffa and Elwood, 2004; Haller et al., 2005; Careau et al., 2010; Copeland et al., 2011; Seebacher et al., 2013). We found that the resident hamsters considerably increased their O_2 consumption following the introduction of intruders, which is indicative of a significant increase in metabolic rate. Similar evidence of elevated metabolic rate during aggressive confrontations has been observed in many other animal species (Payne and Pagel, 1997; Briffa and Elwood, 2004; Ros et al., 2006; Copeland et al., 2011; Seebacher et al., 2013). In addition, the T_b of resident hamsters increased markedly after intruders were introduced, which, given the close relationship between metabolic rate and thermogenesis, presumably is also indicative of increased metabolic rates (Refinetti, 2003; Hulbert and Else, 2004; Tokizawa

et al., 2015; Tan et al., 2017). Both the metabolic rate and T_b of resident hamsters rapidly declined after intruders were removed, indicating considerable plasticity of metabolic thermogenesis. Therefore, single, brief, aggressive confrontations could have only a transient effect on energy balance of resident animals.

However, when intruders were introduced more frequently within a 48 h period the BMR of resident hamsters increased by 15.3%, and after 6-weeks of repeated exposure to intruders was 16.1% higher than that of the control group. This suggests that increased metabolic rate may be a common response to the perceived risk of potential, or actual, attack in a variety of animals, particularly those that display intense territorial aggression (Haller et al., 2005; Careau et al., 2010; Copeland et al., 2011; Seebacher et al., 2013). There is evidence of a positive correlation between BMR and thermogenic capacity or exercise-induced aerobic capacity (Hayes and Garland Jr., 1995; Speakman et al., 2003, 2004; Sadowska et al., 2005; Boratyński and Koteja, 2008). Individuals with high thermogenic capacity are better able to survive extreme cold, and high aerobic capacity may be an indicator of physical condition and the ability to sustain a high level of locomotor activity (Henderson et al., 2002; Rezende et al., 2006; Boratyński and Koteja, 2008). This suggests that the ability to increase metabolic rate may be beneficial for resident hamsters because this increases their ability to acquire and retain resources that improve their prospects of survival and to withstand cold. It also suggests that aggression may be an important factor influencing the adaptation and evolution of metabolic rate.

Metabolic cost is one of the most important aspects of energy expenditure, and therefore plays a key role in the regulation of energy balance (Hulbert and Else, 2004; Speakman et al., 2004; Johnston et al., 2007; Shi et al., 2017; Wen et al., 2017). From the perspective of energy balance, animals usually increase energy intake to meet their metabolic costs when energy requirements increase (Hammond and Diamond, 1997; Speakman, 2008; Zhao, 2011). However, we found that neither food nor energy intake of resident hamsters was affected by long-term, repeated, aggressive interaction with intruders. This suggests that the metabolic cost of aggression in small mammals is not always compensated for by increased energy intake.

In addition to energy intake, stored energy in the form of glycogen and body fat is sometimes mobilized to meet increased energy costs (Speakman, 2008; Zhao, 2011; Zhao et al., 2014b). We found that the fat mass of resident hamsters decreased by 24.4% compared to the controls after intense, but short-term, aggressive encounters. Long-term aggressive encounters had no effect on body mass, but significantly reduced body fat content and fat mass. Aggression induced by the introduction of intruders significantly decreased the body fat mass of laboratory mice and rats (Meerlo et al., 1996; Kaliste-Korhonen and Eskola, 2000). However, in golden hamsters (*Mesocricetus auratus*) aggression caused significant increases in fat mass and fat content (Borer et al., 1988; Gattermann et al., 2002; Solomon et al., 2007). The discrepancy could be species specific, or reflect differences in the duration and intensity of aggression (Solomon et al., 2007). In the European hermit crab (*Pagurus bernhardus*), the trigger for the mobilization of energy reserves in defenders may be an important strategy for resisting attacker (Briffa and Elwood, 2004). Therefore, the mobilization of energy reserves appears to be a key factor in determining fighting success (Briffa and Elwood, 2004). In small mammals, exposure to cold has been found to induce notable increases in metabolic thermogenesis and significant reductions of body fat (Concannon et al., 2001; Wang et al., 2006; Zhao, 2011). C57Bl/6 J mice kept at 6–8 °C for 5 weeks displayed more intensive aggression than controls (Moshkin et al., 1993). This suggests that the efficient mobilization of body fat enhances fighting capacity and therefore the ability to repel intruders.

Thyroid function and thyroid hormones are associated with aggressive behavior (Kioukia-Fougia et al., 2002), and the hypothalamic-pituitary-adrenal (HPA) axis seems to play a key role in the development, elicitation, and enhancement of aggression in animals, including humans (Kruk et al., 2004; Böhnke et al., 2010; Sinai et al., 2015). This

has led some authors to hypothesize that higher individual serum thyroid hormones levels should be associated with aggressive behavior (Karlsson et al., 2015; Evrensel et al., 2016). We observed that serum T_4 levels decreased in the resident hamsters compared to controls, but T_3 levels were not significantly affected by aggression. Although these results do not provide clear support for the above hypothesis, neither do they refute it. Importantly, we also observed that the T_3/T_4 ratio was significantly higher in resident hamsters than in controls, suggesting that the rate of conversion of T_4 to T_3 may have been increased by aggressive behavior. Previous studies used absolute values of serum T_3 or T_4 levels to investigate the role of thyroid hormones in aggression in animals and humans (Kioukia-Fougia et al., 2002; Kruk et al., 2004; Böhnke et al., 2010; Sinai et al., 2015; Karlsson et al., 2015; Evrensel et al., 2016). Our results suggest that the conversion rate of T_4 to T_3 could be also involved in the defensive aggression behavior.

5. Conclusion

Aggression behavior of resident hamsters was significantly affected by the duration of resident/intruder encounters. Prolonged encounters considerably shortened the latency of initiating attacks, increased the number of attack bouts and the duration of attacks. The metabolic rate of resident hamsters increased significantly during both short and prolonged exposure to intruders. Resident hamsters did not change their energy intake, but did decrease their body fat content compared to controls. Interestingly, the serum T_3/T_4 ratio was considerably increased in resident hamsters, which suggests that the rate of conversion of T_3 to T_4 is affected by aggression. These findings suggest that increased metabolic rate is a common response to potential or actual aggressive interaction with intruders in small mammals, which is beneficial for the success of defense, and thus gains access to resources and enhances the capacity to survive. Our results also suggest that aggressive behavior could be an important influence on the adaptation and evolution of metabolic rate. The efficient mobilization of body fat, rather than increased energy intake, may enhance the fighting capacity, and thereby increase the likelihood of acquiring and defending resources from intruders.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.yhbeh.2017.12.015>.

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