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Physiological Responses to Fasting and Refeeding in *Apodemus chevrieri* from Hengduan Mountain Region

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Authors' Contributions
WHZ conceived the study and participated in its design, coordination and drafted the manuscript. HJZ and DMH carried out the studies of body mass, food intake hormonal and biochemical markers. DZ carried out the studies of resting metabolic rate and organs morphology.

Key words
***Apodemus chevrieri*, Fasting, Thermogenesis, Serum leptin levels, Body mass.**

ABSTRACT

Physiological adaptations of mammals were the major strategies in response to the changing food resources. In order to investigate the physiological responses to fasting and refeeding in *Apodemus chevrieri*, body mass and body fat mass, resting metabolic rate (RMR), organs morphology, serum leptin levels and food intake were measured in the present study. The results showed that food deprivation decreased body mass and body fat mass. After refeeding, body mass can not be returned to the control value on refeeding 12 h, and it returned to control level on refeeding 7 days, but body fat mass can not be restored to the control level on refeeding 7 days. RMR and mass of liver decreased significantly in fasting groups, which can return to the control level after refeeding. Fasting for 12 h decreased serum leptin levels, and leptin levels can not recover to the control level after refeeding. Interestingly, there were no post-fasting compensatory increases in food intake. All of the results indicated that *A. chevrieri* can adjust their physiological functions to cope with food shortage, mainly by decreasing body mass, thermogenesis and serum leptin levels.

INTRODUCTION

Physiological adaptations of body mass and energy metabolism were the main strategies for small mammals to cope with the changing natural environment, which have great significance to improve their viability (Zhao and Wang, 2007). Availability of food resources play important roles in the survival, reproduction and evolution of mammals (Bacigalupe and Bozinovic, 2002). Small mammals declined body mass to reduce the total energy consumption under food restriction or deprivation, decreasing thermogenic properties or being food storage, ultimately to adapt to the extreme environment of food shortage (Zhan *et al*., 2009). Many previously studies showed that mammals can adapt food deprivation by the physiological regulation of body mass and energy expenditure. For example, food restriction decreased energy consumption (Liang and Zhang, 2003) and changed digestive tract morphology in small mammals (Bozinovic *et al*., 2007). Fasting reduced body mass, body fat mass, resting metabolic rate (RMR) and serum leptin levels in *Lasiopodomys brandtii* (Zhan *et al*., 2009). Food intake increased significantly in *Rattus norvegicus* and *Mus musculus* after re-feeding acclimation (Friedman and Halaas, 1998), which called post-fasting hyperphagia. However, *Mesocricetus auratus* (Schneider *et al*., 2000) and *Phodopus sungorus* (Day and Bartness, 2003) did not increase their food intake significantly in response to re-feeding. So the response for re-feeding in different mammals were not consistent completely. Leptin plays a major role in the regulation of body mass, energy inatke and energy expenditure (Schneider *et al*., 2000). Fasting can decrease serum leptin levels in animals, and serum leptin levels can be reversed after re-feeding (Hardie *et al*., 1996). In other species, food deprivation also decreased serum leptin levels, and increased food intake compared with that of control group (Friedman and Halaas, 1998).

Chevrier's field mouse, *Apodemus chevrieri* is endemic to Hengduan mountains region (Zheng, 1993). *A. chevrieri* were previous reported that seasonal changes in body mass and digestive tract morphology (Zhu *et al*., 2012), and temperature or photoperiod were the main factors to influence it's body mass regulation (Zhu *et al*., 2011). Moreover, food restriction alone may also reduce

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body mass in *A. chevrieri* (Zhu *et al*., 2013; Zhang *et al*., 2015), and it had significant plasticity in energy metabolism and behavior in *A. chevrieri* under random food deprivation and refeeding (Zhu and Wang, 2016). However, changes in thermogenic properties, serum leptin levels and body mass regulation in *A. chevrieri* under fasting and refeeding remain unknown. In the present study, body mass, RMR and serum leptin levels in *A. chevrieri* were examined in responses to fasting and refeeding. We hypothesized that *A. chevrieri* may decrease body mass, body fat mass, and thermogenesis in association with the decreases in serum leptin levels in response to fasting. We were also wanted to know whether *A. chevrieri* would show the post-fast hyperphagia phenomenon after re-feeding. We predicted that leptin levels, RMR and organ masses would involve in the regulation of body mass and energy metabolism in *A. chevrieri*.

MATERIALS AND METHODS

Samples

A. chevrieri were obtained from a laboratory colony, which were captured in farmland (26°15′-26°45′N; 99°40′-99°55′E; altitude 2,590m) from Jianchuan, Yunnan province. *A. chevrieri* were breed for two generations (120-150 days of age, weighing 36.1–47.6 g) at the School of Life Sciences, Yunnan Normal University, *A. chevrieri* were housed individually in plastic boxes (260 × 160 × 150 mm^3), which were maintained at room temperature (25 ± 1 °C) under a photoperiod of 12L:12D (lights on at 8:00 am), food (Kunming Medical University, Kunming, People's Republic of China) and water were provided *ad libitum*. All animal procedures were licensed under the Animal Care and Use Committee of School of Life Sciences, Yunnan Normal University (Permit No.: 13-0901-011).

After one month stabilization, 63 adult *A. chevrieri* were used in the present study and divided into seven groups (each group = 9) as follows: control group: food fed *ad libitum*; F12 h group: fasting for 12 h; F24 h group: fasting for 24 h; F36 h group: fasting for 36 h; R12 h group: fasting for 36 h and then refeeding for 12 h; R48 h group: fasting for 36 h and then refeeding for 48 h; R7 d group: fasting for 36 h and then refeeding for 7 d. Body mass showed no significant differences among the seven groups before the experiment ($F_{6,56}$=0.48, P>0.05).

Measurement of RMR

RMR were measured using AD ML870 open respirometer (AD Instruments, Australia) at 25°C within the thermal neutral zone (Zhu *et al*., 2008), and gas analysis was performed using a ML206 gas analysis instrument (AD Instruments). The temperature was controlled using a SPX-300 artificial climatic incubator (±0.5 °C) (Changsha, China), the metabolic chamber volume was 500ml and airflow rate was 200 ml/min, the method used for RMR is detailed in Zhu *et al*. (2012). Animals were stabilized in the metabolic chamber for at least 60 min prior to the RMR measurement, and oxygen consumption was recorded for at least 120 min at 1 min intervals. Ten stable consecutive lowest readings were taken to calculate RMR (Li and Wang, 2005). The method used for calculating the metabolic rate is detailed in Hill (1972, equation 4b).

Morphology

All animals were sacrificed after the collection of a blood sample, the visceral organs, including liver, brown adipose tissue (BAT), heart, lung, kidneys, spleen and gastrointestinal tract (stomach, small intestine, cecum, large intestine), were extracted and weighed (±1 mg). Before being dried and weighed, stomach and intestines were rinsed with saline to eliminate all the gut contents. The remaining carcass and all the organs were dried in an oven at 60 °C to constant mass (at least 72 h), and then weighed again to obtain the dry mass. The difference between wet carcass mass and dry carcass mass was the water mass of carcass. Total body fat was extracted from the dried carcass by ether extraction in a Soxhlet apparatus (Zhang and Wang, 2007).

Measurement of food intake

Food intake was measured following Rousseau *et al.* (2003). Briefly, animals were kept in metabolic cage (20 × 15 × 15 cm^3), and were fed at a set time (at 1100 h), and residual food was collected the following day. Residual food was dried in a vacuum dryer to a constant weight, which was recorded.

Measurement of serum leptin levels

Serum leptin levels were determined by radioimmunoassay (RIA) with the 125I Multi-species Kit (Cat. No. XL-85K, Linco Research Inc.). The lowest level of leptin that can be detected by this assay was 1.0 ng/ml when using a 100-µl sample size. And the inter- and intra-assay variability for leptin RIA were <3.6% and 8.7%, respectively.

Statistical analysis

Data were analyzed using the software package SPSS 15.0. Prior to all statistical analyses, data were examined for assumptions of normality and homogeneity of variance using Kolmogorov-Smirnov and Levene tests, respectively. Group differences in RMR and food intake were analyzed by one-way analysis of covariance (ANCOVA) with body mass as a covariate. One-way ANOVA for repeated

measures was applied to evaluate the effect of the fasting/re-feeding protocol on body mass, body composition, digestive tract morphology and serum leptin levels. To detect possible associations of serum leptin levels with body fat mass, we used Pearson-correlation analysis. Results are presented as means ± SEM, and $P < 0.05$ was considered to be statistically significant.

RESULTS

Body mass, body composition and digestive tract morphology

Body mass in *A. chevrieri* decreased significantly after fasting ($F=9.36$, $P<0.01$), which returned to control level in R7 d group (Table I). BAT mass in F24 h and 36h groups decreased significantly compared with that of control group, which also restored to the control level in R7 d group; mass of liver decreased significantly in F12 h group, which returned to control level after refeeding 48 h (Table II). Fasting increased stomach mass and stomach without contents mass significantly, and which returned to the control level after re-feeding. Maximum mass of the small intestine appeared in the F12h group, which returned to the control level after re-feeding 48 h (Table II). Dry mass of organs and digestive tracts showed no significant changes in response to fasting and re-feeding (Table III). Water content of organs also showed no significant differences in response to fasting and re-feeding, except for liver and stomach.

Table I.- Effects of fasting and refeeding on body mass and serum leptin levels in *Apodemus chevrieri.*

Parameters		Control	F12 h	F24 h	F36 h	R 12h	R48 h	R7 d
Body mass (g)	Initial	41.23±1.15	40.89±1.17	41.21±0.98	40.97±1.03	41.35±0.89	40.86±1.12	41.09±1.06
	Final	41.25±1.14^{a}	38.24±1.12^{b}	36.54±1.08^{bc}	32.15±1.01^{d}	35.98±0.98^{c}	39.29±1.11^{b}	41.54±1.12^{a}
Body fat mass (g)		5.42±0.45^{a}	4.56±0.31^{b}	3.78±0.33^{bc}	2.57±0.21^{d}	3.58±0.31^{c}	4.03±0.41^{b}	4.08±0.39^{b}
Wet carcass mass (g)		30.21±0.78^{a}	27.25±0.81^{b}	25.14±0.59^{bc}	20.22±0.46^{d}	23.18±0.35^{c}	27.14±0.52^{b}	30.48±0.61^{a}
Dry carcass mass (g)		11.54±0.23^{a}	10.18±0.24^{ab}	9.12±0.41^{b}	8.23±0.33^{c}	9.21±0.42^{b}	10.54±0.44^{ab}	11.78±0.51^{a}
Water of carcass (g)		18.68±0.54^{a}	17.07±0.48^{a}	16.02±0.52^{ab}	11.99±0.35^{c}	13.97±0.32^{c}	16.51±0.45^{ab}	18.70±0.53^{a}
Serum leptin levels (ng/ml)		1.78±0.23^{a}	1.45±0.19^{b}	1.43±0.20^{b}	1.41±0.16^{b}	1.46±0.19^{b}	1.44±0.21^{b}	1.51±0.18^{b}

Significant differences between groups are indicated by different superscript letters in the same row ($P<0.05$). Error bars represent SE.

Table II.- Effects of fasting and refeeding on wet organ masses and length of gastrointestinal tract in *Apodemus chevrieri.*

Parameters	Control	F12 h	F24 h	F36 h	R 12h	R48 h	R7 d
Heart(g)	0.22±0.02	0.21±0.01	0.21±0.01	0.19±0.02	0.20±0.01	0.20±0.01	0.22±0.03
Lungs(g)	0.29±0.05	0.27±0.03	0.28±0.03	0.27±0.04	0.26±0.03	0.28±0.03	0.28±0.03
Liver mass(g)	1.54±0.06^{a}	1.23±0.04^{b}	1.09±0.04^{c}	0.97±0.03^{c}	1.19±0.04^{bc}	1.37±0.05^{ab}	1.61±0.08^{a}
BAT mass(g)	0.22±0.02^{a}	0.19±0.01^{bc}	0.18±0.01^{b}	0.16±0.01^{c}	0.18±0.02^{b}	0.22±0.02^{a}	0.23±0.01^{a}
Kidney(g)	0.17±0.02	0.17±0.01	0.16±0.02	0.15±0.01	0.17±0.01	0.17±0.02	0.18±0.02
Spleen(g)	0.021±0.003	0.020±0.003	0.019±0.002	0.018±0.001	0.019±0.003	0.021±0.003	0.022±0.002
Stomach without contents mass(g)	0.16±0.02^{c}	0.26±0.02^{b}	0.36±0.04^{a}	0.33±0.03^{a}	0.34±0.02^{a}	0.29±0.03^{b}	0.19±0.03^{c}
Stomach mass(g)	0.43±0.05^{d}	0.58±0.05^{c}	0.73±0.06^{a}	0.55±0.03^{c}	0.69±0.02^{ab}	0.61±0.02^{bc}	0.46±0.03^{d}
Stomach mass length(mm)	22.32±0.13	23.24±0.22	21.54±0.31	23.01±0.29	21.39±0.25	23.16±0.19	22.18±0.22
Large intestine without contents mass(g)	0.09±0.01	0.10±0.02	0.09±0.01	0.08±0.01	0.09±0.03	0.11±0.02	0.09±0.01
Large intestine mass(g)	0.49±0.02	0.47±0.02	0.46±0.03	0.47±0.01	0.49±0.03	0.51±0.04	0.50±0.03
Large intestine length(mm)	158.23±3.69	156.32±3.32	155.62±3.95	157.29±2.89	154.23±3.56	155.12±3.28	157.36±2.88
Small intestine without contents mass(g)	0.47±0.05	0.49±0.06	0.47±0.06	0.45±0.06	0.47±0.04	0.46±0.06	0.47±0.05
Small intestine mass(g)	1.28±0.06^{c}	1.59±0.04^{a}	1.48±0.03^{b}	1.29±0.03^{c}	1.33±0.04^{c}	1.34±0.05^{c}	1.29±0.03^{c}
Small intestine length(mm)	446.34±6.32	451.12±5.63	453.63±7.69	446.32±6.63	450.69±6.03	449.59±5.56	450.98±5.31
Caecum without contents mass(g)	0.33±0.01	0.32±0.02	0.30±0.01	0.31±0.01	0.33±0.02	0.34±0.02	0.34±0.01
Caecum mass(g)	0.83±0.02	0.82±0.02	0.79±0.03	0.81±0.03	0.85±0.03	0.80±0.01	0.81±0.01
Caecum length(mm)	56.89±1.65	56.98±1.69	55.87±1.33	54.23±1.23	55.12±1.28	56.23±1.51	55.71±1.62

Significant differences between groups are indicated by different superscript letters in the same row ($P<0.05$). Error bars represent SE.

Table III.- Effects of fasting and refeeding on dry organ masses in *Apodemus chevrieri.*

Parameters	Control	F12 h	F24 h	F36 h	R 12h	R48 h	R7 d
Heart(g)	0.037±0.004	0.039±0.006	0.036±0.005	0.036±0.004	0.037±0.003	0.037±0.005	0.039±0.004
Lungs(g)	0.063±0.009	0.061±0.008	0.060±0.006	0.059±0.009	0.058±0.006	0.060±0.008	0.062±0.010
Liver(g)	0.502±0.023	0.489±0.019	0.482±0.013	0.486±0.015	0.492±0.022	0.521±0.023	0.526±0.029
Kidney(g)	0.035±0.003	0.034±0.004	0.032±0.002	0.032±0.003	0.033±0.002	0.035±0.001	0.033±0.002
Spleen(g)	0.003±0.001	0.003±0.001	0.002±0.001	0.002±0.001	0.003±0.001	0.003±0.001	0.003±0.001
Stomach(g)	0.086±0.012	0.076±0.008	0.077±0.009	0.075±0.006	0.082±0.009	0.083±0.011	0.084±0.015
Small intestine(g)	0.031±0.005	0.031±0.005	0.029±0.003	0.028±0.001	0.030±0.005	0.029±0.003	0.033±0.005
Cecum(g)	0.043±0.006	0.042±0.004	0.040±0.002	0.039±0.002	0.041±0.004	0.041±0.003	0.042±0.006
Large intestine(g)	0.041±0.003	0.038±0.002	0.038±0.004	0.036±0.003	0.039±0.006	0.038±0.005	0.042±0.006

Significant differences between groups are indicated by different superscript letters in the same row (P<0.05). Error bars represent SE.

RMR and food intake

There are significant effects of fasting and refeeding on RMR in *A. chevrieri* ($F_{6,56}$=4.89, P<0.01). During fasting, RMR decreased significantly in fasting 24 h group and returned to the control level after re-feeding 7 days (Fig. 1). There was no significant differences in the cumulative food intake of the re-feeding groups and the control group (Fig. 2).

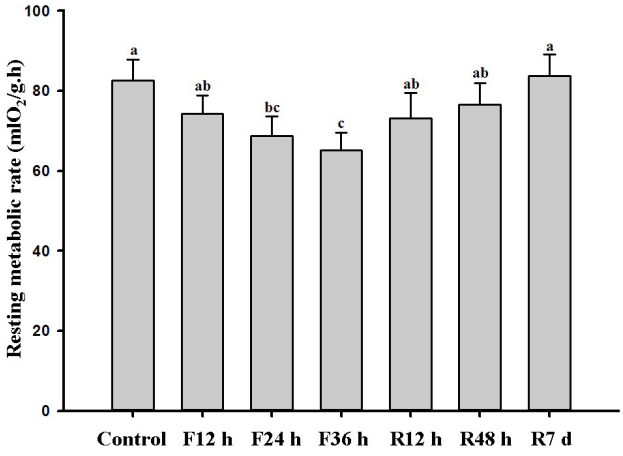

Fig. 1. Effects of fasting and re-feeding on RMR in *Apodemus chevrieri.* Error bars represent SE. Different letters indicate significant differences among the seven groups (P<0.05).

Body fat mass and serum leptin levels

Fasting and refeeding affects body fat mass significantly ($F_{6,56}$=4.23, P<0.01). Fasting for 24 h and 36 h, body fat mass decreased significantly, but it can not return to the control level after feeding 7 days (Table I). Food and refeeding also has remarkable effect on serum leptin levels ($F_{6,56}$=5.12, P<0.01). After fasting for 12 h, serum leptin levels decreased rapidly. After re-feeding 7 days, serum leptin levels did not return to the control group level (Table I). Serum leptin levels were positively correlated with body fat mass (r=0. 652, P<0.01).

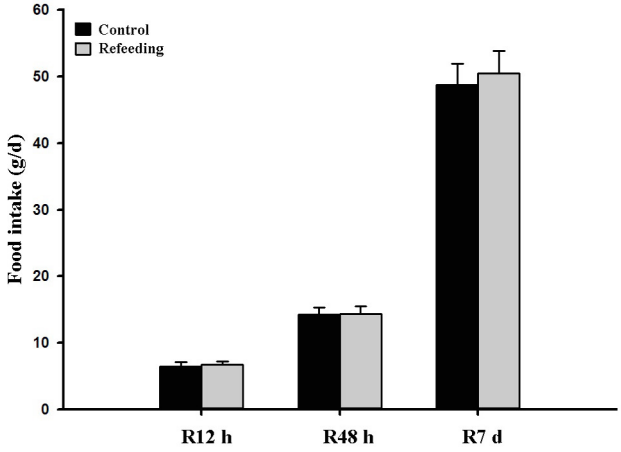

Fig. 2. Effects of fasting and re-feeding on food intake in *Apodemus chevrieri.* Error bars represent SE.

DISCUSSION

In the present study, fasting decreased body mass significantly in *A. chevrieri*, and it can return to the control level after refeeding, as shown by other rodent models (Kouda *et al*., 2004). The reduction in body mass was associated with reduced body fat mass, carcass mass and water of carcass (Mustonen *et al*., 2005). Fasting decreased body fat mass significantly, which suggested that *A. chevrieri* need to use body fat content to stay alive in response to food shortage. Moreover, body fat mass can not be restored to control level after refeeding 7 days, which indicated that the recovery of body mass may

related to the increase of carcass mass and water of carcass (Freminet, 1981). Previously study showed that the serum leptin levels decreased significantly during fasting (Tauson and Forsberg, 2002). In the present study, serum leptin levels decreased fasting for 12 h, which can not return to the control level after refeeding. We found a positive correlation between serum leptin levels and body fat mass, indicating that leptin may act as an "adiposity indicator". Body fat mass and serum leptin level did not recover to the control level after refeeding, indicating that *A. chevrieri* may still in malnourished condition after re-feeding 7 days (Flier, 1998).

When the internal or external environment has changed significantly, many small mammals can adjust their digestive tract morphology to adapt to the food quality or quantity changing, such as accelerating the turnover rates of food, or changing the volume of digestive tract (Sassi *et al*., 2007). In the present study, stomach mass and stomach without content mass increased in R 12 and 24 h groups, which may be related to that *A. chevrieri* can obtain a sustainable energy supply in a short time after fasting, *A. chevrieri* reduced the gastric mucosa secretion of digestive juice, leading to slow down the rate of digestion, so the food in the stomach retention time was relatively longer. In addition, the volume of the stomach may also increase in order to accommodate more food (Asfar *et al*., 2003). Stomach mass decreased significantly after fasting for 36h, which due to a longer period of fasting, there is no new food supplement, so its mass decreased. Under refeeding 12h, *A. chevrieri* had food to eat, and then the stomach mass increased, which returned to the control level after refeeding 7 days. Mass of small intestine was maximum at fasting 12h, which may be through the extension of food in the digestive tract of residence time, and increased the volume of gastrointestinal tract to improve food utilization during fasting (Chediack *et al*., 2012).

RMR was the main energy expenditure of small mammals, which plays an important role in the regulation of energy balance (Terblanche *et al*., 2007). Many animals regulate energy metabolism by altering RMR in order to adapt to changing environment (Nagy and Pistole, 1988). In the present study, fasting decreased RMR significantly, and it return to the control level after re-feeding. During periods of fasting, *A. chevrieri* cannot get enough energy intake to supply the body use, reducing RMR to decrease energy consumption to maintain the body's normal physiological activities. Moreover, the decreasing of RMR may relate to reducing of liver mass under fasting. After feeding, *A. chevrieri* can obtain enough energy from the food to maintain the body's normal physiological activity, so RMR returned to control levels, which suggested that change of RMR was one of the physiological mechanism for food shortage in *A. chevrieri* (Zhang and Wang, 2006). Animals usually increased food intake after re-feeding (Samec *et al*., 1998). In our study, *A. chevrieri* after refeeding did not increase food intake, indicating that *A. chevrieri* did not adopt feeding compensation strategy in response to food shortage (Wood and Bartness, 1996).

In summary, fasting reduced body mass, RMR and serum leptin levels. Serum leptin levels can not recover the control level after refeeding. All of the results indicated that *A. chevrieri* can adjust their physiological functions to cope with food deprivation by decreasing body mass, thermogenesis and serum leptin levels.

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Statement of conflict of interest

Authors have declared no conflict of interest.

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