Food limitation and low-density populations of sympatric hamster species in North China

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Abstract

Although food has been proposed as a possible factor on population regulation of small mammals, evidence of food restriction in field conditions is still lacking. Food restriction is generally thought to occur in high-density years of oscillating populations of small mammals. By using two body condition indices (muscle protein concentration and cleaned carcass index), we investigated variations of body condition of the greater long-tailed hamster (*Tscherskia triton*) and the striped hamster (*Cricetulus barabensis*) in the Raoyang County of the North China Plain during a population decline- and low-phase from 1998 to 2003. Our laboratory experiments showed that food restriction reduced muscle protein concentration and cleaned carcass index of greater long-tailed hamster. We found there were significant differences in body condition of hamsters over the six years. Both the muscle protein concentration and cleaned carcass index of *T. triton* were significantly and positively correlated with its yearly trap successes, which reflected yearly population densities. Muscle protein concentration of *C. barabensis* was positively correlated with the total yield of the wheat. This observation supported the hypothesis on the in-phase relation between food resources or availability and rodent abundances. During the four seasons, muscle protein concentration of two species was highest in autumn, and lowest in summer. These two body condition indices of wild *T. triton* in summer and in low phases were similar to 60% food restricted animals raised in the laboratory, but significantly lower than non-food-restricted animals. Our results indicated that malnutrition occurred in summer when food was not abundant, and in low density years with low grain production (an index reflecting food abundance of rodents) in our study region. Therefore, we concluded that food limitation may play an important role in seasonal and inter-annual population fluctuation of these two hamster species.

Contents

Introduction

Food availability has been emphasized as a major limiting factor that influences population variations of most vertebrates (Cameron and Eshelman, 1996; Huitu *et al*., 2007). Food per animal may determine body condition related to food restriction. Some previous laboratory studies have shown that food restriction has remarkable effects on the physiological condition, reproduction and immune level of immunity of rats (Sakamoto *et al*., 2000). For example, Liang and Zhang (2006) demonstrated that food restriction during the pregnancy period of the greater long-tailed hamster negatively affected the body growth of F_1 offspring, and delayed the physical development and neurodevelopment of both F_1 and F_2 offspring. However, evidence of food impact in fluctuating wild populations is still lacking, and thus the underlying mechanisms are not fully understood (Lindell, 1997; Norrdahl and Korpimäki, 2002; Ramsey *et al*., 2002).

Many population densities of small mammals experience fluctuations in demography (Boonstra, 1994;

Krebs *et al.*, 1995; Norrdahl and Korpimäki, 1995; Krebs, 1996; Tkadle and Zejda, 1998). There are three possible phase patterns between food and population density: in-phase, out-of-phase and phase with a time-lag (Krebs and Myers, 1974). The time-lag reflects the ability of animal population tracking changing food resource (Mihok and Boonstra, 1992; Boonstra *et al.*, 1998a; Norrdahl and Korpimäki, 2002). If the time lag is close to zero or very small, food availability should be higher in the increase phase or high-density phase of animal populations, and lower in the decline phase or low-density phase. The out-of-phase relation is generally accepted by ecologists because food availability would decrease with an increase of population density and it would become lowest when population reaches peak phase. Food shortage is usually thought to occur in high-density years of oscillating populations of small mammals (Boonstra, 1994). Andersson and Jonasson (1986) found a negative correlation between the density of rodents and frequency of food plants during two four-year cycles on alpine heath. The out-of-phase relation may be more likely for more oscillating animals and their food resources. For example, many tree species produce massive crops of large seeds in low-density years of small rodents (Willson and Traveset, 2000; Jansen *et al.*, 2004; Xiao *et al.*, 2005; Li and Zhang, 2007), which often results in "predator satiation" and benefits forest regeneration (Janzen, 1970). However, in theory, if animals could track fluctuations of food resources more quickly, an in-phase relation is also possible. The in-phase relation is likely possible when populations of animals and their food resources change slowly.

Body weight and body composition (such as muscle protein content and muscle fat content) are generally affected by food and nutrition, and they are feasible to evaluate (Johns *et al.*, 1984; Munoz *et al.*, 1994; Lynch and Barbano, 1999). For example, higher muscle protein concentration indicated that animals have a better body condition (Norrdahl and Korpimäki, 2002), and a high percentage of cleaned carcass weight also relate to good individual quality (Cardoso and Stock, 1996). As a result, muscle protein content and cleaned carcass index are taken as reliable indices of body condition for vertebrates and have been used to study individual quality of wild rodents during population cycles across years and seasons (Reeds *et al.*, 1988; Fuller *et al.*, 1990; Cardoso and Stock, 1996).

The greater long-tailed hamster (*Tscherskia triton* (De Winton, 1899)) and striped hamster (*Cricetulus barabensis* (Pallas, 1773)) are two sympatric rodent pests across the Northern China Plain where wheat, corn and peanut are the main crops. Most crops are harvested in autumn (from August to October), except wheat, which is harvested in spring (from March to May). Crop seeds comprise over 90% of the diets of these two rodent species in autumn, and a large number of crop seeds is stored in their burrows for over-wintering (Wang *et al.*, 1992, 1996). Population abundance of both rodent species oscillates greatly among seasons and years and populations of both species change slowly over the years. Population density of *T. triton* generally reaches a peak in autumn, while that of *C. barabensis* generally peaks in spring, and both species exhibit an approximate 10-year cycle in population size (Zhang *et al.*, 1998). Although the behaviour, reproduction, genetics and ecology of the two hamsters have been well-documented (Wang *et al.*, 1996; Zhang *et al.*, 1998; Xie and Zhang, 2006), the mechanism underlying their population dynamics remains unclear.

In this study, we investigated the seasonal and yearly variation of muscle protein content and cleaned carcass index of the two hamster species during a decline and low phase of their populations from 1998 to 2003 in the croplands in the Raoyang County of the North China Plain using field trapped animals. We wanted to test the season- or density-dependent food restriction hypothesis. We also compared muscle protein content and cleaned carcass index of wild animals with lab-raised animals. We predicted that 1) food restriction would occur in low-density years of hamsters if the in-phase relation hypothesis holds; 2) food restriction would occur in summer, as high temperature plus poor food resources may reduce body condition of hamsters.

Materials and methods

Study sites and trapping procedures

The study area was located in croplands around Wugong village (38.04 - 38.21N, 115.31 – 115.53E), Raoyang County, Hebei province, north China. This area lies in the warm temperate zone with four distinct seasons: spring (from March to May), summer (from June to August), autumn (from September to November) and winter (from December to February). The annual precipitation is about 552.6 mm, mostly in summer. The average temperature is 12.3° across the year; summer is very hot, averaging about 26.4°. Wheat, corn, and peanuts are major crops in the area.

Two or four locations were established in the two study sites with more than 1 km in between for long-term survey of the greater long-tailed hamster and striped hamster populations. In each location, we selected four plots for trapping animals using snare-wooden traps every month. The plots were kept at least 50 m apart. Each plot consisted of two trapping lines, and the distance between the trapping lines was 20-30 m. Twenty-five traps spaced about 10 m apart were set along each trapping line. Traps baited with fresh peanuts were set in the late evening and collected in the morning. Trapping at each plot was conducted for three consecutive days in the middle of each month from 1998 to 2003. Every plot was rotated for three months in order to minimize the potential effect of removal trapping. All captured animals were numbered, weighed, killed and dissected after capture, with the permission of the Institute of Zoology, Chinese Academy of Sciences. The wooden snare traps kill rodents promptly without causing obvious pains to the captured animals. Population density was calculated by using trap success. We defined monthly or yearly trap success as: total number of captured animals divided by total valid number of traps for the month or the year (12 months).

The head skulls of all captured hamsters were initially fixed in 90% ethanol in the field, and then preserved in 95% ethanol for long-term storage. To eliminate the influence of reproduction, pregnant hamsters were excluded. Muscles used for measurements of body condition were cut from the neck of the skull, where the muscle was adequate and representative to reflect the whole body protein content (see below).

We chose 230 greater long-tailed hamsters and 280 striped hamsters from the total number (all trapped animals from 1998-2003) and divided them into five age groups according to the degree of tooth wear following Lu *et al*. (1987). There were a total of 25 juvenile, 95 sub adult, 56 adult-I, 30 adult-II and 24 old greater long-tailed hamsters, and 44 juvenile, 71 sub adult, 85 adult-I, 68 adult-II and 12 old striped hamsters.

Measurement of body condition

The cleaned carcass index is defined as follows: cleaned carcass body mass without internal organs (g)/ total body mass (g). Cleaned carcass body means the body after viscera removal; it includes the body after removing all internal bodily organs (i.e. heart, lung, stomach, intestine, kidney, testis or ovary). The hair and skin are kept in the cleaned carcass.

The protein concentration of muscle was measured following the Kjeldahl method for determining nitrogen content (Munoz *et al*., 1994; Lynch and Barbano, 1999). We used 98% H_2SO_4, 40% NaOH, 2% Boric acid solution, 0.01N HCl, tablet of mixed K_2SO_4 and $CuSO_4$ in the extraction. Neck muscles (0.1-1.0 g) were cut out from the samples that were fixed in 95% ethanol, and then put into the oven at 60°Celsius scale for 48 h. Dry weight of each sample was determined using an electronic balance with precision of 0.0001g. The nitrogen concentration was determined using the Kjeldahl instrument (produced by Foss Company, USA). Nitrogen concentrations were converted to protein concentrations by multiplying by 6.25 (the protein /N mass ratio).

In this study, samples from 1998 to 2003 were preserved in ethanol. To test whether ethanol preservation affects muscle protein concentration, we placed muscle samples in 95% ethanol for 16 months and measured protein concentration every two months.

Laboratory food restriction on the greater long-tailed hamster

To establish reliable body condition indices of food restriction, a laboratory experiment was conducted for greater long-tailed hamsters based on our previous work (Liang *et al*., 2004; Liang and Zhang, 2006). Sixteen female and 16 male wild adult greater long-tailed hamsters of similar body mass were weighed and randomly assigned to one of two experimental groups. All animals were housed individually in plastic cages (40 cm x 25 cm x 15 cm) with wood shavings as bedding and maintained on a 16L: 8D light cycle (lights on at 21:00 h) and approximately 20 ℃. Tap water was available *ad libitum*. Two experimental groups were designed for testing the effects of food restriction on the body condition of the great long-tailed hamster. One was the control group, in which eight females and eight males were provided with *ad libitum* food and water. The other was for the food restriction group, in which eight females and eight males were provided with *ad libitum* water but with 40% less food than the daily intake of the control group. The trial was conducted for four weeks. Animals were weighed every week. After four weeks, the animals were killed and anatomized. Body mass (g), body mass without internal bodily organs (g) and body length (cm) were measured. A piece of muscle was cut from the back neck of the skull for protein concentration measurement as described above.

Statistical analyses

All data are normally distributed and presented as the mean ± standard error. Statistical analyses of muscle protein concentration and cleaned carcass index were performed using the SPSS statistical package by general linear model (GLM). Muscle protein concentration and cleaned carcass index were set as dependent variable, while year, season, age group and sex were set as factors. Effects of factors were considered statistically significant if $P < 0.05$. Correlation analyses were used to test the relationship between two body condition indices with trap success, average air temperature and yield of main crops. The climate data and crop yield data were obtained from the Bureau of Agriculture and Bureau of Meteorology, Raoyang County. We used repeated measures of GLM to test the difference of protein concentration between muscles preserved in ethanol and fresh muscle. In the food restriction experiment, muscle protein concentration and cleaned carcass index between control and food restriction groups were compared by using the Student's t-test. Results were considered significant if $P < 0.05$.

Results

Annual population abundances

As shown in Fig. 1, the annual trap success of all trapped animals of the two hamster species in the Raoyang County showed a decline since 1998. The similar decline pattern indicated that they might be driven by some external factors.
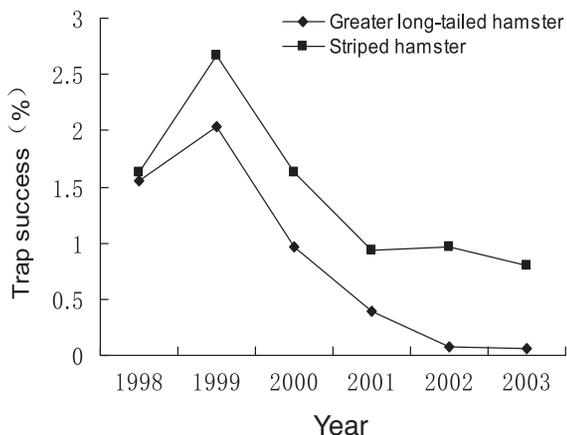
Table 1. Effect of food restriction on muscle protein concentration and cleaned carcass index of greater long-tailed hamster.

	Control group	FR group
Female		
Muscle protein concentration (g/100g)	81.416±0.206	76.468±0.277*
Cleaned carcass index (g/g)	0.805±0.058	0.717±0.029*
Male		
Muscle protein concentration (g/100g)	81.982±0.475	70.478±0.423*
Cleaned carcass index (g/g)	0.755±0.042	0.724±0.038*

* $P < 0.05$.

Laboratory food restriction experiment

The food restriction laboratory experiment revealed that muscle protein concentration in the food restriction (abbreviation: FR) group was significantly lower than that in the control group (female: $t_{14} = - 2.212$, $P = 0.044$; male: $t_{14} = - 2.805$, $P = 0.014$). Cleaned carcass index in FR hamsters was also significantly lower than the control group (female: $t_{14} = - 2.492$, $P = 0.028$; male: $t_{14} = -2.742$, $P = 0.027$; Table 1). Therefore, we used these two indices to represent the body condition related to the food restriction of the hamster species in the field during 1998 - 2003.

Muscle protein concentration

No difference was found for muscles preserved in ethanol (84.031 g/g, $N = 16$) and fresh muscle (86.969 g/g, $N = 16$) ($F = 0.665$, $P = 0.721$). Ethanol had no
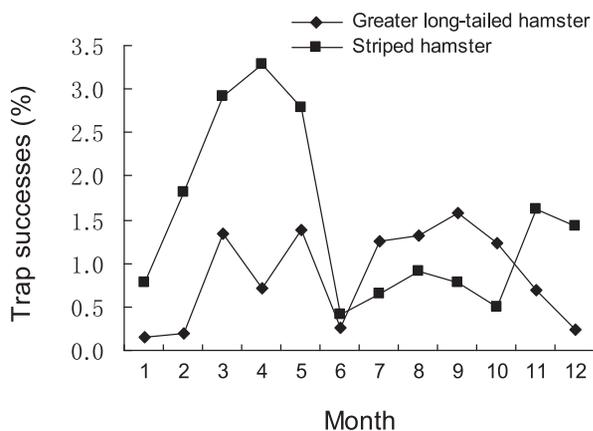
Fig. 1. Yearly (left) and seasonal (right) population dynamics of greater long-tailed hamster and striped hamster.

	Spring	Summer	Autumn	Winter	
Greater long-tailed hamster	82.722±1.127[a]	70.869±1.501[b]	84.008±1.047[a]	75.390±1.587[b]	*Table 2*. Seasonal differences of muscle protein concentration (g/100g) in greater long-tailed hamster and striped hamster.
Striped hamster	75.186±0.885[a]	72.766±1.026[b]	77.374±0.797[a]	72.664±1.205[b]	

The mean values with different letters on top of the data point are significantly different.

significant effect on muscle protein concentration.

There were significant seasonal differences in muscle protein concentration in the greater long-tailed hamster with individuals in spring and autumn displaying higher muscle protein concentration than in summer and winter ($F_{3, 226} = 12.19$, $P < 0.001$). This pattern was also found in striped hamsters ($F_{3, 276} = 2.68$, $P = 0.049$; Table 2).

Muscle protein concentration in greater long-tailed hamsters differed significantly among the six study years ($F_{5, 224} = 3.71$, $P = 0.004$). Muscle protein concentration in 1999 was significantly higher than in

1998, 2000, 2001, 2002 and 2003 (Fig. 2A). There was a significant positive correlation between muscle protein concentration and yearly trap success (%) ($R = 0.943$, $P = 0.005$, $N = 6$), indicating a strong relation between muscle protein concentration and population abundance (Fig. 2B).

In the striped hamster, muscle protein concentration showed no significant difference over the years ($F_{5, 274} = 1.30$, $P = 0.269$). However, when analysing it with the crop production (Table 3), muscle protein concentration was positively correlated with total yield of wheat ($R = 0.831$, $P = 0.041$, $N = 6$; Fig. 2C). The cor-
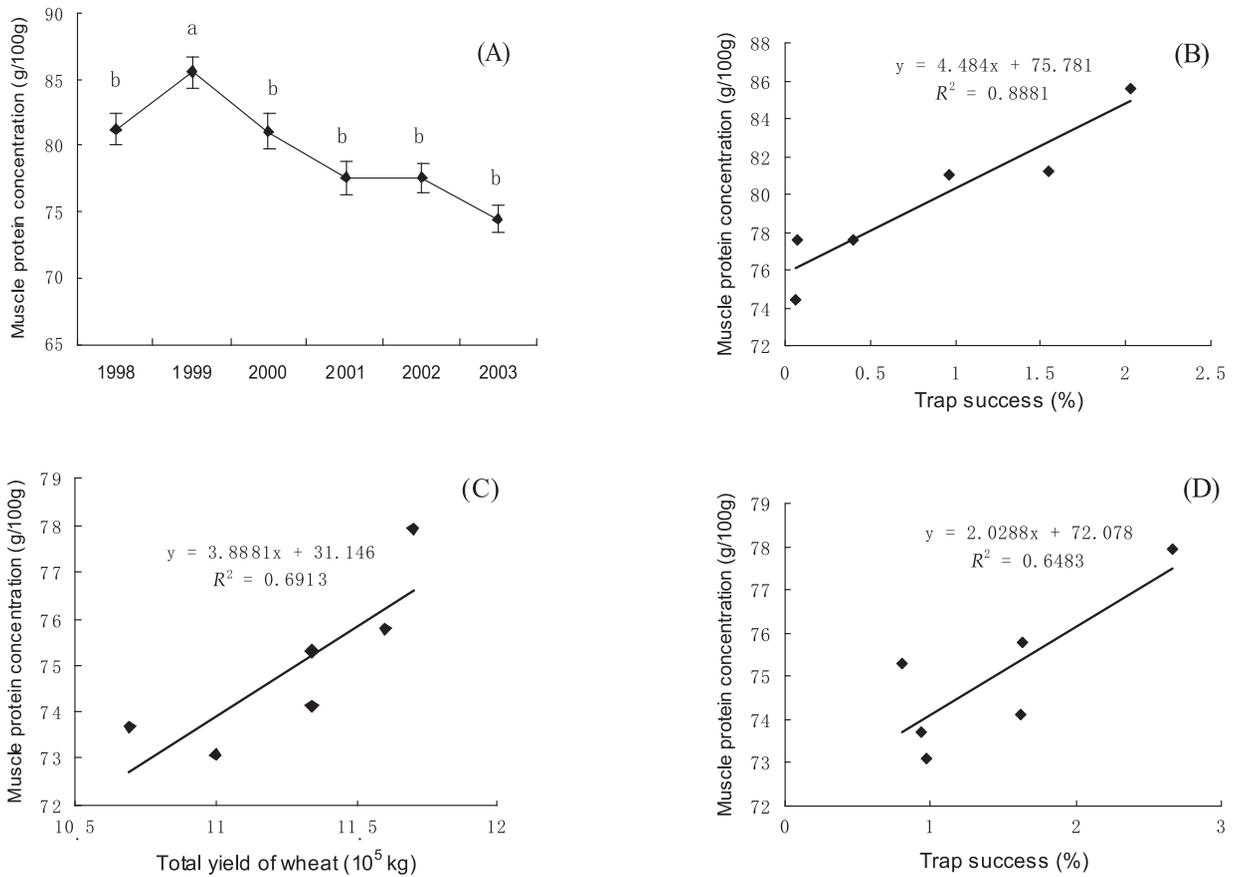
Fig. 2. Annual dynamics of muscle protein concentration in greater long-tailed hamster (A), Correlation of muscle protein concentration with trap success in greater long-tailed hamster (B), Correlation of muscle protein concentration with total yield of wheat in striped hamster (C), Correlation of muscle protein concentration with trap success in striped hamster (D). The mean values with different letters on top of the data point are significantly different.

Year	Wheat		Corn		Peanut	
	Yield per ha. (kg/ ha.)	Total yield (10^5kg)	Yield per ha. (kg/ ha.)	Total yield (10^5kg)	Yield per ha. (kg/ ha.)	Total yield (10^5kg)
1998	6000	11.60	7875	13.91	2700	0.36
1999	5850	11.70	7500	13.00	2625	0.53
2000	6075	11.34	7650	13.77	2775	0.74
2001	**5625**	10.69	7875	13.91	**2550**	0.43
2002	6000	11.00	**7350**	**12.74**	2700	**0.36**
2003	6075	11.34	**7125**	**12.83**	2850	0.38

Table 3. Annual dynamics of average yield of main crops in Wugong village, Raoyang country, China.

Note: Bold numbers indicate years with the low yield

relation between muscle protein concentration and trap success (%) was significant ($R = 0.806$, $P = 0.05$, $N = 6$; Fig. 2D).

Muscle protein concentration of female striped hamsters was significantly larger than in males ($F_{1, 278} = 5.64$, $P = 0.019$) [mean ± SE muscle protein concentration: female (76.3 ± 0.7 g/100g, $N = 131$) and male (73.9 ± 0.6 g/100g, $N = 149$)], but showed no difference among age groups ($F_{4, 275} = 0.78$, $P = 0.538$). This pattern was not found for greater long-tailed hamsters.

Cleaned carcass index

The cleaned carcass index for greater long-tailed hamsters ($F_{3, 226} = 4.47$, $P = 0.005$), but not striped hamsters ($F_{3, 276} = 0.41$, $P = 0.746$) showed significant seasonal differences, with higher values in autumn and winter than in spring and summer (Fig. 3).

There were significant inter-annual differences in the cleaned carcass index for greater long-tailed hamsters ($F_{5, 224} = 2.53$, $P = 0.032$). Analysis of least significant differences (LSD) showed that 2001 was the lowest year in cleaned carcass index of the six years (Fig. 4A). The cleaned carcass index of the greater long-tailed hamster was significantly and positively correlated with yearly trap success ($R = 0.819$, $P = 0.046$, $N = 6$) (Fig. 4B).
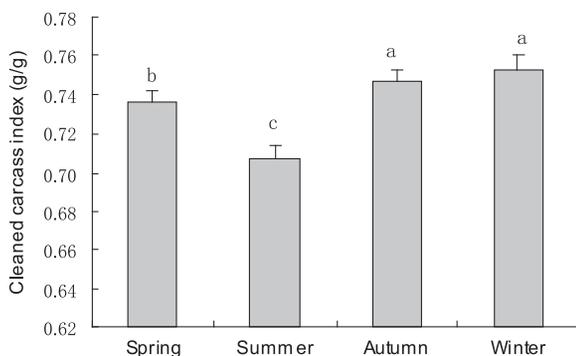
Significant inter-annual differences were also shown for the cleaned carcass index in striped hamster ($F_{5, 274} = 8.44$, $P < 0.001$). This analysis also indicated that the cleaned carcass index in 2001 was lowest (Fig. 4C). The cleaned carcass index was approximately correlated with the total yield of wheat ($R = 0.768$, $P = 0.074$, $N = 6$) (Fig. 4D).

A significant difference among age groups in the cleaned carcass index was observed for greater long-tailed hamster ($F_{4, 225} = 9.38$, $P < 0.001$). As age increased, the cleaned carcass index also increased. The differences between the following groups were significant: juvenile and sub adult, juvenile and adult-I, juvenile and adult-II, juvenile and the old, sub adult and adult-II, sub adult and the old, adult-I and the old (Table 4). No difference of this nature was found for striped hamsters ($F_{4, 275} = 1.62$, $P = 0.171$). Males and females did not differ in cleaned carcass index for greater long-tailed hamster ($F_{1, 228} = 0.45$, $P = 0.504$), or for striped hamster ($F_{1, 278} = 0.15$, $P = 0.697$).

Comparisons between laboratory and field studies

It is notable that the muscle protein concentration of the greater long-tailed hamster in summer was significantly lower than that of the laboratory- raised control group and very close to the value for the food restriction group, while the protein concentration of the control group was similar to that seen in spring and autumn [mean ± SE muscle protein concentration: spring (82.3 ± 0.9 g/100g, $N = 74$), summer (72.6 ± 1.5 g/100g, $n = 39$), autumn (84.1 ± 0.8 g/100g, $N = 104$), control group (81.7 ± 1.6 g/100g, $N = 16$), and food restriction (73.7 ± 1.7 g/100g, $N = 16$)] (Tables 1 and 2). The average protein concentrations of the greater long-tailed hamster in 2001, 2002 and 2003 were similar to the value for the food restriction group [mean±SE muscle protein concentration: 2001 (79.2 ± 2.5 g/100g, $N = 25$), 2002 (77.8 ± 2.2 g/100g, $N = 11$), 2003 (77.7 ± 2.0

Fig. 3. Seasonal differences of cleaned carcass index in greater long-tailed hamster. The mean values with different letters on top of the data point are significantly different.
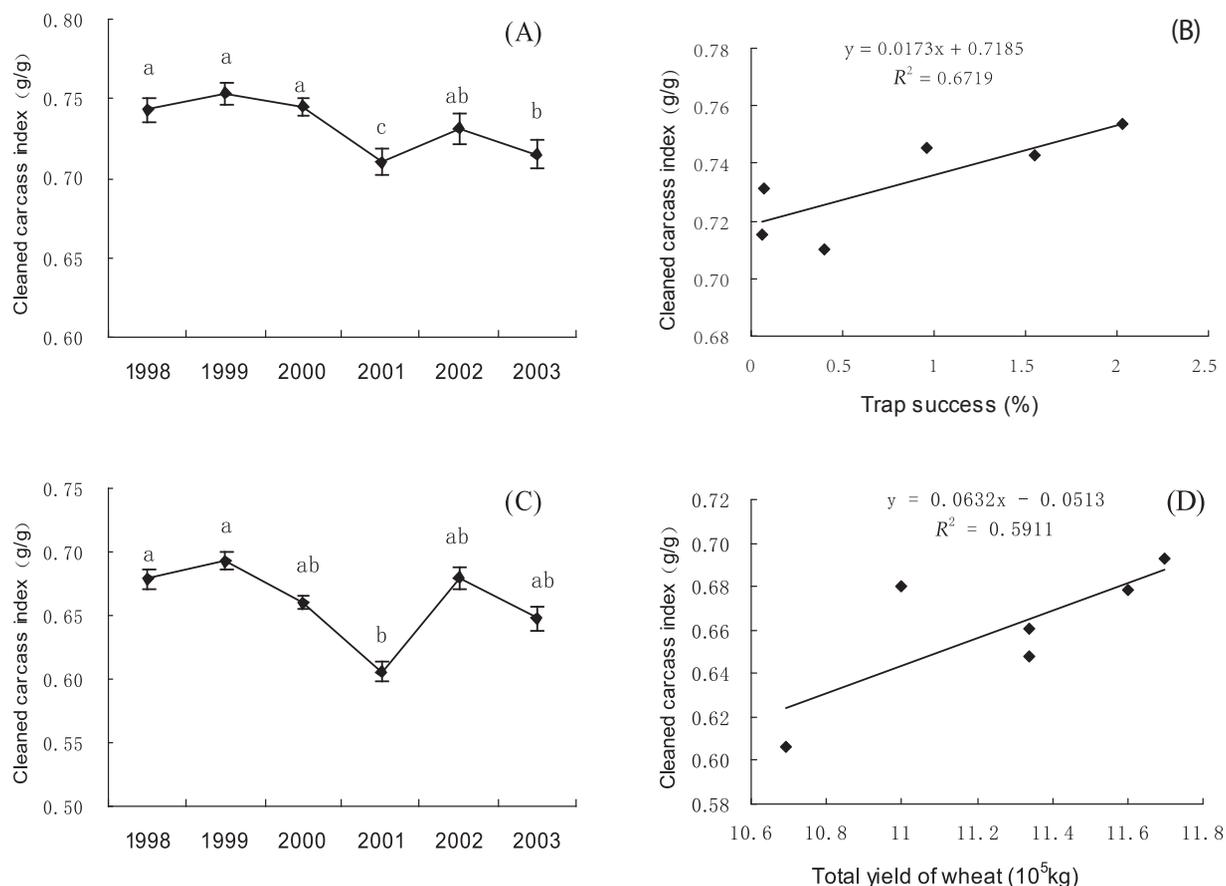
Fig. 4. Annual dynamics of cleaned carcass index in greater long-tailed hamster (A) and striped hamster (C), Correlation of cleaned carcass index with trap success in greater long-tailed hamster (B), Correlation of cleaned carcass index with total yield of wheat in striped hamster (D). The mean values with different letters on top of the data point are significantly different.

g/100g, $N = 35$), and food restriction (73.7±1.7 g/100g, $N = 16$)]. However, the average protein concentrations in 1998, 1999 and 2000 approached that of the control group [mean±SE muscle protein concentration: 1998 (81.0±0.9 g/100g, $N = 66$), 1999 (85.9±1.1 g/100g, $N = 42$), 2000 (81.2±1.1 g/100g, $N = 51$), and control group (81.7±1.6 g/100g, $N = 16$)] (Table 1, Fig. 4A).

The cleaned carcass indices of the greater long-

Table 4. Differences among ages of cleaned carcass index in greater long-tailed hamster.

Age group	Mean (g/g)
Juvenile	0.682±0.008[a]
Sub adult	0.721±0.005[b]
Adult-I	0.738±0.006[bc]
Adult-II	0.750±0.008[cd]
Old	0.756±0.009[d]

tailed hamster captured in autumn and winter were significantly higher than in the food restriction group raised in laboratory, while the cleaned carcass index of the food restriction group was very similar to values in spring and summer [mean±SE cleaned carcass index: spring (0.730±0.006 g/g, $N = 74$), summer (0.723± 0.008 g/g, $N = 39$), autumn (0.745±0.004 g/g, $N = 104$), winter (0.756±0.015 g/g, $N = 104$), and food restriction (0.721±0.008 g/g, $N = 16$)] (Table 1, Fig. 3). The cleaned carcass index of food restriction group was not different from that in 2001, 2002 and 2003, but was significantly lower than that in 1998, 1999 and 2000 [mean ± SE cleaned carcass index: 1998 (0.747±0.005 g/g, $N = 66$), 1999 (0.745±0.008 g/g, $N = 42$), 2000 (0.740±0.007 g/g, $N = 51$), 2001 (0.705±0.010 g/g, $N = 25$), 2002 (0.730±0.011 g/g, $N = 11$), 2003 (0.730 ±0.008 g/g, $N = 35$), and food restriction (0.721±0.008 g/g, $N = 16$)] (Table 1, Fig. 4A).

These results provide strong evidence that hamsters suffer seasonal and inter-annual food restriction under natural conditions.

Discussion

Yearly variation of body condition

Contrary to the conventional view, our results indicated that the body condition indices of both hamster species tended to be positively correlated with the population densities, which obviously supports the in-phase relation hypothesis. Furthermore, by comparing with the laboratory-feeding results, we found both morphological and physiological evidences of food restriction in greater long-tailed hamsters in the low-density years 2000-2003, revealing the fact that hamsters in our study were in poor body condition in low density years. This observation is not in agreement with several other observations (*e.g.,* Andersson and Jonasson, 1986; Boonstra, 1994). The possible explanation to this in-phase relation is that both crop production and hamster population fluctuated slowly, which made it possible that hamsters could track fluctuating food resources easily. The finding of food restriction in decline and low density years of hamsters suggests that food resources might be an important factor in causing population decline and low density of the hamster species.

Our discovery of a relationship between body condition and population abundance is notable because the population densities of the two hamster species were quite low during our research period compared with their peak density (trap success is over 10%). It is noticeable that, even during a low population phase, hamsters in summer, spring and winter still face malnutrition. Thus, malnutrition is not necessarily the result of over-consumption due to high population size. Instead, climate-driven grain production and subsequent grass seed production may be responsible for the annual variation of body condition. Indeed, grain production showed some variations in our study region during 1998-2003. Wheat production was lowest in 2001, while corn and peanut production were considerably lower in 2002 and 2003. The years with lower grain production corresponded well with the malnutrition found in 2001, 2002 and 2003, and a significant correlation between body conditions and grain yield was found in the striped hamster. This study indicates that high yield crop production does not necessarily mean food is not a limiting factor in population growth

of hamsters. In fact, mature crops were often harvested very quickly, within about one week. Furthermore, hamsters mainly eat or hoard fallen crop seeds on the ground, which is often proportional to the total yields. This is why the body condition index is closely related to crop production (an index of food availability).

Seasonal variation of body conditions

We found that both body condition indices of the two hamster species showed food restriction effect in summer, whereas in autumn there was no difference with the laboratory control group. This is seen by comparison of body conditions between laboratory and field studies. Previous studies have also shown seasonal changes in animal body mass and composition (Ryg *et al.*, 1990; Li and Wang, 2005). Parker (1993) found that body mass of black-tailed deer declined in winter, and the amount of body fat lost by deer over winter depended on the peak body mass attained during fall. Wang *et al.* (1993) investigated seasonal dynamics of lipid, protein and water contents, as well as the mitochondria protein contents of brown adipose tissue in plateau pika, and they found that total protein was highest in winter and lowest in summer. Thus in many cases, individuals in autumn have both higher body fat and protein content but suffer concurrent declines in protein mass in winter and summer (Virgl and Messier, 1992; Craig, 1997).

Major diet components of these two hamster species are crop seeds or grass seeds (Wang *et al.*, 1992, 1996). In this study region, most crops (especially ground seeds such as peanut and soybean, which are rich in protein) mature in autumn. Thus, hamsters have abundant food of high quality in autumn. This may explain why hamsters have their highest body condition in autumn. In temperate regions, hamsters need to deposit body fat in the body for over-wintering, which also contributes to the better body condition indices in autumn. In the other seasons, climate or food resources are not as favourable. In spring, over-wintering animals have consumed most of their autumn fat deposition, and are short of food. The cleaned carcass index of hamsters in spring showed this food restriction effect. During winter, mammals used 10-15% of their protein and 70-82% of their body fat reserves (Parker *et al.*, 1993) or voluntarily decrease food intake (Heldmaier and Steinlechner, 1981), and thereby lose body mass and fat by spring. By and large, deficiency of food might contribute to the lower body condition indices related to food availability.

Laboratory food restriction effect

Body condition is closely connected with food availability which determines growth, survivorship, and age of sexual maturity, reproductive status, and litter size (Fuller *et al*., 1990; Cameron and Eshelman, 1996; Norrdahl and Korpimäki, 2002). Although a large number of studies have attempted to assess body condition of field populations, controlled experiments with the target animal in a laboratory are necessary. In our laboratory experiment, the effect of food restriction on physiological and body-condition quality of the greater long-tailed hamster was assessed for the 40% food restriction group, because the amount of minimum crop yield was approximately 60% of maximum crop yield in the study site. Our laboratory experiment indicated that animals in the food restriction group had significant lower muscle protein concentrations and cleaned carcass indices. This showed that food restriction and malnutrition reduced body condition of these species. Our laboratory results are in accordance with some previous studies. For example, Voltura and Wunder (1998) found that food restriction had a great influence on body mass and body composition (reduced fat deposition) in prairie voles. Liang *et al*. (2004) found that food restriction reduced muscle protein concentration and relative fatness in a 50% food restricted group of the greater long-tailed hamster. Thus, body condition measures (including percentage of protein, water and fat in muscle, cleaned carcass, and organs) are widely used to evaluate body condition (Reeds *et al*., 1988; Fuller *et al*., 1990; Cardoso and Stock, 1996). Our results also indicate that cleaned carcass index and muscle protein concentration are two feasible criteria that reflect body condition related to food restriction in hamsters.

Implications of food restriction

Our findings provide both morphological and physiological evidence that hamsters may suffer food limitation under natural conditions. Food limitation in low-density years may also be linked to poor survivorship of the two hamster species in the same study site and in the same period (X.H. Yu and Z.B. Zhang, unpublished data). They also found that survival indices of the two hamster species were positively correlated with trap successes in the same study site during 1998-2003. Poor body condition may decrease and prolong population growth through maternal effects. Huck *et al*. (1986) found that food restriction of hamsters

(*Mesocricetus auratus* (Waterhouse, 1839)) affects sex ratio and growth of subsequent offspring. Food restriction in maternal individuals may have long-term consequences for the reproduction and survival of offspring (Ward and Read 1985), and thus play an important role in population regulation (Boonstra, 1994; Boonstra *et al*., 1998a; Tkadle and Zejda, 1998; Meikle and Westberg, 2001). Liang and Zhang (2006) reported that food restriction in pregnancy had negative effects on behaviour, growth, reproduction and survival of F_1 and F_2 offspring of greater long-tailed hamsters. Thus, changes in maternal quality occur in animals during the peak phase, carry over several generations and lead to population decline and a subsequent low phase of the population cycle. It is also important to note that genetic diversity is also very low during low phases of the greater long-tailed hamsters of the same site in the same period (Xie and Zhang, 2006), indicating that hamster population might suffer inbreeding effects and genetic drift during low phases. Thus, food restriction effects plus inbreeding effects may work together in producing the sustained low density phases of hamsters.

Acknowledgements

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