ARTICLE

Temporal change in body mass of two sympatric hamster species and implications for population dynamics

Chuan Yan, Tongqin Xu, Xiaoping Cao, Fusheng Wang, Shuqing Wang, Shoushen Hao, Hefang Yang, Hongjun Li, and Zhibin Zhang

Abstract: Shifting of body size distributions of animals has been a long-time focus in population ecology, but the underlying mechanism of density-dependent changes in body size and its implications for population dynamics of animals are largely unknown. In this 26-year study, we investigated intrinsic and extrinsic factors affecting body mass of the Chinese striped hamster (*Cricetulus barabensis* Pallas, 1773) and the greater long-tailed hamster (*Tscherskia triton* de Winton, 1899) in the Northern China Plain. We proposed three hypotheses to explain body mass shifts in the two hamster species: growth, survival, and reproduction hypotheses. Our results showed that mean and maximum body masses of both hamster species were positively correlated with population density, and that this density-dependent change in body mass is more likely to be caused by a change in mortality rates, not by a change in growth rates or reproduction rates. The sustained decline of body mass during the study period was probably caused by increased mortality owing to an increase in the area of agricultural irrigation. Our results suggest that, under the condition of lacking survival and growth data, the maximum body mass (which represents survival rate), minimum body mass (which represents growth rate), and mean body mass are very useful criteria in revealing intrinsic and extrinsic effects on population dynamics and the underlying mechanisms.

Key words: *Cricetulus barabensis*, *Tscherskia triton*, Chitty effect, density dependence, body mass, growth rate, survival rate, reproduction rate, global warming, human disturbance.

Résumé : Si les variations des distributions de la taille du corps des animaux constituent depuis longtemps un sujet d'intérêt en écologie des populations, le mécanisme qui sous-tend la variation de la taille du corps selon la densité et ses répercussions sur la dynamique des populations d'animaux demeurent largement méconnus. Dans la présente étude portant sur une période de 26 ans, nous avons examiné les facteurs intrinsèques et extrinsèques qui influent sur la masse du corps du hamster rayé (*Cricetulus barabensis* Pallas, 1773) et du hamster-rat nain (*Tscherskia triton* de Winton, 1899) dans la plaine de Chine septentrionale. Nous avons proposé trois hypothèses pour expliquer l'évolution de la distribution de la masse du corps chez les deux espèces de hamsters, soit les hypothèses de la croissance, de la survie et de la reproduction. Nos résultats indiquent que la masse moyenne du corps et la masse maximum du corps des deux espèces de hamsters sont positivement corrélées à la densité de la population et que cette variation de la masse du corps en fonction de la densité est plus probablement le fait de la variation des taux de mortalité que de celle des taux de croissance ou de reproduction. La diminution soutenue de la masse du corps durant la période d'étude découle probablement d'une mortalité accrue en raison de l'augmentation des superficies irriguées à des fins agricoles. Nos résultats donnent à penser que, dans des conditions où des données sur la survie et la croissance ne sont pas disponibles, la masse du corps maximum (qui représente le taux de survie), la masse du corps minimum (qui représente le taux de croissance) et la masse du corps moyenne sont des critères très utiles pour cerner les effets intrinsèques et extrinsèques sur la dynamique des populations et les mécanismes qui sous-tendent ces effets. [Traduit par la Rédaction]

Mots-clés : *Cricetulus barabensis*, *Tscherskia triton*, effet de Chitty, dépendance de la densité, masse du corps, taux de croissance, taux de survie, taux de reproduction, réchauffement planétaire, perturbation d'origine humaine.

Introduction

Body size or mass is a fundamental feature of animals, linking to many physiological and life-history traits of organisms such as metabolic rate, growth rate, and life span (Peters 1986). Previous studies have suggested that body mass of animal populations is closely associated with population density (Chitty 1952; Both 1998; Yom-Tov et al. 2007). In cyclic populations of voles and lemmings, body mass is found to be higher in high-density years than in low-density years, known as the "Chitty effect" (Chitty 1952; Boonstra and Krebs 1979). Boonstra and Krebs (1979) propose two alternative hypotheses for the origin of large individuals. Large

individuals could be a *r*-selected genotype adapted to increasing populations, or they could be an *α*-selected genotype adapted to high population density. Other hypotheses such as energy allocation and size-selective predation have also been proposed to explain this positively density-dependent body size change (Oli 1999; Sundell and Norrdahl 2002). However, a negative relationship is observed in some species (e.g., red deer, *Cervus elaphus* L., 1758: Mysterud et al. 2001; brown bear, *Ursus arctos* L., 1758: Zedrosser et al. 2006; lynx, *Lynx canadensis* Kerr, 1792: Yom-Tov et al. 2007) and food shortage in high-density years is suggested to be the explanation for these negative relationships (Yom-Tov et al. 2007). To disentangle these different views, it is necessary to

Fig. 1. Three hypotheses on the effects of growth, survival, and reproduction on the mean, maximum (Max.), and minimum (Min.) body masses (BM) of animals. Solid line indicates positive effect and broken line indicates negative effect. Growth hypothesis implies three positive associations between growth and three BM criteria. Survival hypothesis implies positive associations between survival and two (mean and maximum) BMs. Reproduction hypothesis implies a negative association between reproduction and mean BM.
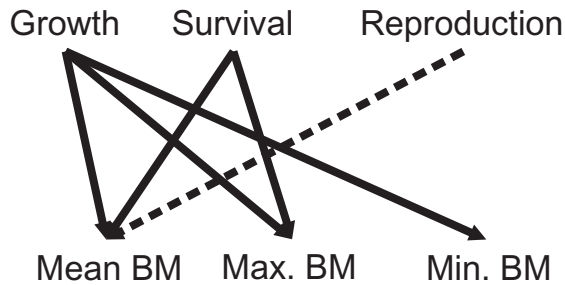
investigate this question in terms of long-term data sets from more species.

Several studies have demonstrated that animals tend to have smaller size as a result of on-going climate warming, such as some species of ectotherms, birds, and mammals (Sheridan and Bickford 2011). But increasing body size in response to global warming has also been observed (Gardner et al. 2011; Li et al. 2013). Interaction of temperature with precipitation would complicate the relationship between temperature and body size of animals (Boyce 1978; Yom-Tov and Geffen 2006). Climate may affect body size directly via Bergmann's rule, or indirectly through food availability (Gardner et al. 2011). It is necessary to clarify the direct and indirect effects of climate change on body-mass changes of animals.

It is likely that both intrinsic and extrinsic factors affect body-mass changes of animals at temporal scales. Previous studies suggest that a change in body mass may be affected by growth rate of body mass (McCay et al. 1935), mortality rates or life span (Deevey 1947), and reproduction rate (Sutherland et al. 2004). In this study, we propose three hypotheses to explain how the three basic factors affect body-mass change of a population (Fig. 1). First, high growth rate of body mass would increase body mass of animals at all ages; thus, we predict that high growth rate should be positively related with the mean, maximum, and minimum body masses of the population (growth hypothesis). Second, high survival rate should be positively related with the mean and maximum body masses, but not related to the minimum body mass (survival hypothesis). Third, high reproduction rate should be negatively related with the mean body mass of the population, but not related with the maximum or minimum body mass (reproduction hypothesis).

The effects of intrinsic and extrinsic factors on body-mass change can be inferred by looking at its association with growth rate, survival rate, and reproduction rate. For example, if the body-mass change of a population is adaptive because of genetic (Boonstra and Krebs 1979), energetic (Oli 1999), or metabolic (Sheridan and Bickford 2011) rates, the growth hypothesis should be applicable. If the body-mass change is caused by external factors affecting reproduction or mortality, the reproduction hypothesis or survival hypothesis may be applicable. Some factors may affect the three hypotheses of growth, reproduction, and survival rates. Understanding the effects of the three factors on body-mass changes of a population would be helpful in identify-

ing potential effects of intrinsic and extrinsic factors on population dynamics.

The Chinese striped hamster (*Cricetulus barabensis* Pallas, 1773) and the greater long-tailed hamster (*Tscherskia triton* de Winton, 1899) are dominant rodents in croplands of the Northern China Plain of China. Our previous studies indicate that both intrinsic and extrinsic factors affect the population dynamics of these hamsters (Yan et al. 2013), but it is still not clear how these factors affect body-mass changes over long temporal scales. The purpose of this study is to test the three hypotheses (i.e., growth, reproduction, and survival) in identifying potential intrinsic and extrinsic factors that affect body-mass change in the two sympatric hamster species and their population dynamics.

Materials and methods

Study site

The study area is located in Wugong village (38°5′N–38°9′N, 115°34′E–115°44′E), Raoyang County, Hebei Province in China. It lies in the warm temperate zone with four distinct seasons. Vegetation is mainly composed of crops such as wheat, corn, peanuts, and cotton. There are several sympatric rodent species, including Chinese striped hamster, greater long-tailed hamster, striped field mouse (*Apodemus agrarius* Pallas, 1771), house mouse (*Mus musculus* L., 1758), and brown rat (*Rattus norvegicus* Berkenhout, 1769) in the study site. Irrigation and ploughing are the most important agricultural disturbances faced by these rodents. During the past three decades, the area of flood irrigation has increased consistently in this region. Flood irrigation significantly increased crop yields, but it also destroyed the burrow systems of hamsters, which led to a sustained decline in hamster populations (Yan et al. 2013).

Studied species

The Chinese striped hamster and the greater long-tailed hamster are the predominant rodent species in croplands of Northern China Plain (Zhang et al. 1998). The Chinese striped hamsters reach sexual maturity around 3 months of age and breed all year, but the pregnancy rate in winter is very low. They have 3–5 births per year and the litter size ranges from 4 to 8. Their life span is about 10 months in the wild (Zhang et al. 1998). The greater long-tailed hamsters reach sexual maturity around 1.5 months of age and breed from March to September. They have 3–4 births per year and have a mean litter size of around 9. Their life span is about 1 year in the wild and 3–4 years in laboratory conditions (Zhang et al. 1998).

Body mass and population data

The abundance of rodents was surveyed monthly in croplands from 1984 to 2009 using wooden snare traps (Yan et al. 2013). The rodents captured were identified, weighed, and dissected to ascertain pregnancy. The sample sizes of the two hamsters every year are shown in Supplementary Table S1[1]. Monthly population abundance was estimated by trap success (%), defined as (total number of captured animals / total number of snare traps set) × 100. Annual abundances were calculated by averaging the monthly data. Annual mean body mass was calculated by averaging all the individuals captured in 1 year after excluding the pregnant females (sample size ≥ 30 per year; Fig. 2). The maximum and minimum body masses are also used for analysis (sample size ≥ 30 per year; Fig. 2). The pregnancy rate is defined as the number of pregnant females/adult females (sample size ≥ 30 per year; Fig. 2). Because the age of the two species is not easy to infer by visual examination, the body mass is used to identify age group. Adult is defined as body mass > 20 g for Chinese striped hamster and body

Fig. 2. Original data of mean, maximum, and minimum body masses (BM), pregnancy rate, and abundance of Chinese striped hamsters (*Cricetulus barabensis*) and greater long-tailed hamsters (*Tscherskia triton*) during 1984–2009. Open circles indicate small sample size (*N* < 30). Some pregnancy rate points are missing because of small sample size (*N* < 30).
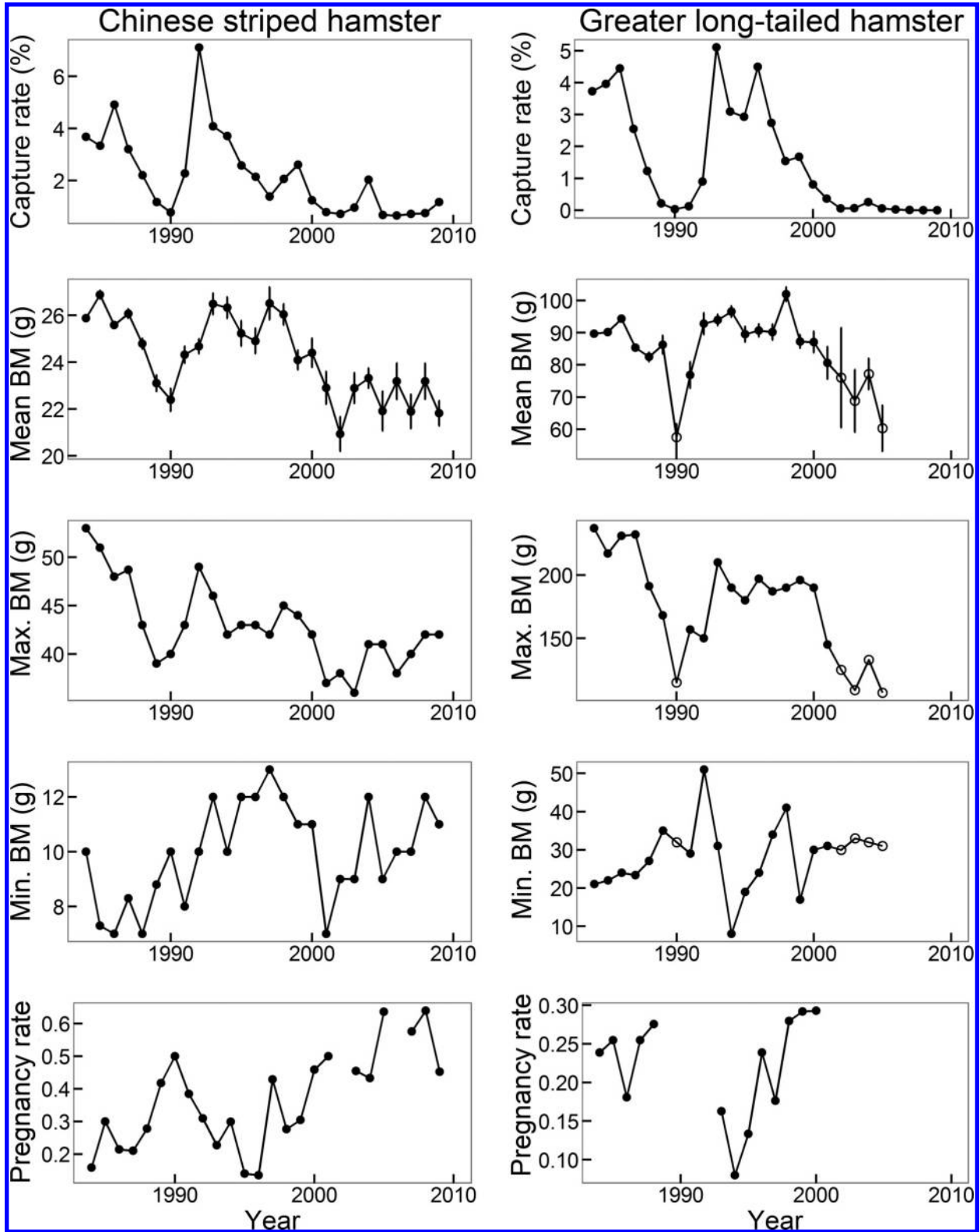

mass > 80 g for greater long-tailed hamster, from data collected on the reproductive status of these two hamsters in previous studies (Zhang 1985; Zhang et al. 1998). Juveniles (body mass ≤ 15 g for Chinese striped hamsters and body mass ≤ 40 g for greater long-tailed hamsters) are not mature; subadults (15 g < body mass ≤ 20 g for Chinese striped hamsters; 40 g < body mass ≤ 80 g for the greater long-tailed hamsters) have only a small percentage of being mature.

Fig. 3. Spearman's correlation analyses for Chinese striped hamsters (*Cricetulus barabensis*) and greater long-tailed hamsters (*Tscherskia triton*). The two plots are constructed by pairwise Spearman's correlations among body-mass criteria, population abundance, irrigation area, and pregnancy rate. Solid lines indicate positive correlations, while broken lines indicate negative correlations. T, annual temperature; P, population abundance; I, irrigation area; R, pregnancy rate; M, mean body mass; Max., maximum body mass; Min., minimum body mass. Line thickness denotes the value of the correlation coefficient and arrows denote possible causal directions.
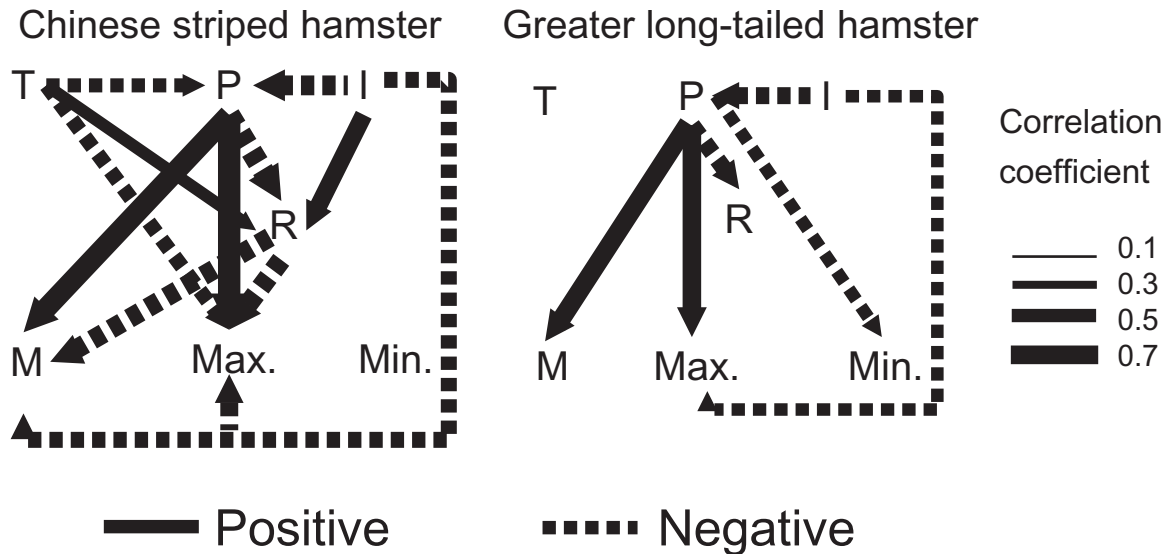
In this study, we define three body-mass criteria of a population to test the effects of growth rate, reproduction rate, and survival rate. First, the mean body mass is the mean value of body mass of all captured animals in a population within 1 year after excluding pregnant females. Second, the maximum body mass is the body mass of the individual with the highest body mass in a population after excluding pregnant females. The maximum body mass from a population can be used to indicate the maximum life span and then survival rate of the year. Third, the minimum body mass is the body mass of the individual with the lowest body mass in a population. The minimum body mass indicates the minimum body mass of a juvenile that becomes active outside its nest and can be captured by the use of traps. Animals with minimum body mass were mostly juveniles. Thus, the minimum body mass can be used to represent growth rate of the year. Because all three factors (i.e., growth, survival, and reproduction) may influence mean body mass (Fig. 1), we did not use mean body mass of juveniles or adults to represent growth or survival.

Hypothesis testing procedures

Because we lacked growth and survival data, the three hypotheses were tested based on correlations between mean, maximum, and minimum body masses and population abundance, pregnancy rate, and external factors (e.g., temperature, precipitation, irrigation). Growth hypothesis was confirmed by positive associations of population abundance with minimum body mass. Survival hypothesis was confirmed by positive associations of population abundance with the maximum body mass. Reproduction hypothesis was confirmed by negative associations of body mass with pregnancy rate, as well as evaluating the complex associations among pregnancy rate, body mass, and other factors.

Climate and agricultural data

Local data on annual temperature (°C) and annual precipitation (mm) were obtained from the China Meteorological Data Sharing Service System (http://cdc.cma.gov.cn). Annual data on irrigation area (ha) were obtained from the local Bureau of Agriculture of the Raoyang County. These data were presented in an earlier study (Yan et al. 2013).

Statistical analysis

Spearman's rank correlations (r_S) were used to identify associations among body mass, population abundance, reproduction, annual temperature, and irrigation area. Correlation analysis may report multiple associations, but it is difficult to disentangle various casual assumptions. Spurious noncausal effects may emerge when two variables share causal influences. Path analysis is a statistical tool that can break down noncausal relationships and also decompose direct and indirect effects (Lleras 2005). Therefore, it was used to identify the relative importance of the potential factors affecting the body mass of the two hamster species. Path analysis is based on a path diagram that included multiple casual assumptions with sufficient data points (i.e., degrees of freedom), as well as the requirement of normal distributions for all variables. The greater long-tailed hamsters did not have enough data for path analysis because the sample size in some years was too small to calculate pregnancy rate (only 13 years of data) and body-mass criteria. We also found no appropriate way to normalize their population abundance data. Therefore, path analysis was performed only on the normalized data from the Chinese striped hamsters. Path analysis was conducted in SPSS AMOS version 17.0 (SPSS Inc., Chicago, Illinois, USA).

Results

Chinese striped hamsters

As shown in Fig. 3, mean body mass of Chinese striped hamsters was positively correlated with population abundance ($r_S = 0.78$, $N = 26$, $P < 0.05$), but negatively correlated with pregnancy rate ($r_S = -0.73$, $N = 24$, $P < 0.05$) and irrigation area ($r_S = -0.6$, $N = 25$, $P < 0.05$). The maximum body mass was positively correlated with population abundance ($r_S = 0.84$, $N = 26$, $P < 0.05$), but negatively correlated with annual temperature ($r_S = -0.56$, $N = 26$, $P < 0.05$), pregnancy rate ($r_S = -0.74$, $N = 24$, $P < 0.05$), and irrigation area ($r_S = -0.67$, $N = 25$, $P < 0.05$). Pregnancy rate was also positively correlated with annual temperature ($r_S = 0.46$, $N = 24$, $P < 0.05$) and irrigation area ($r_S = 0.66$, $N = 23$, $P < 0.05$), but negatively correlated with population abundance ($r_S = -0.80$, $N = 24$, $P < 0.05$). Population abundance was also negatively correlated with annual

Fig. 4. Path analysis for Chinese striped hamster (*Cricetulus barabensis*). The path diagram is constructed by path analysis based on the casual assumptions after breaking down nonsignificant effects. T, annual temperature; P, population abundance; I, irrigation area; R, pregnancy rate; M, mean body mass; Max., maximum body mass; e1–e4, variances. Values beside single-headed arrows indicate estimates of standardized regression weight, while the value beside the double-headed arrow indicates an estimate of covariance.
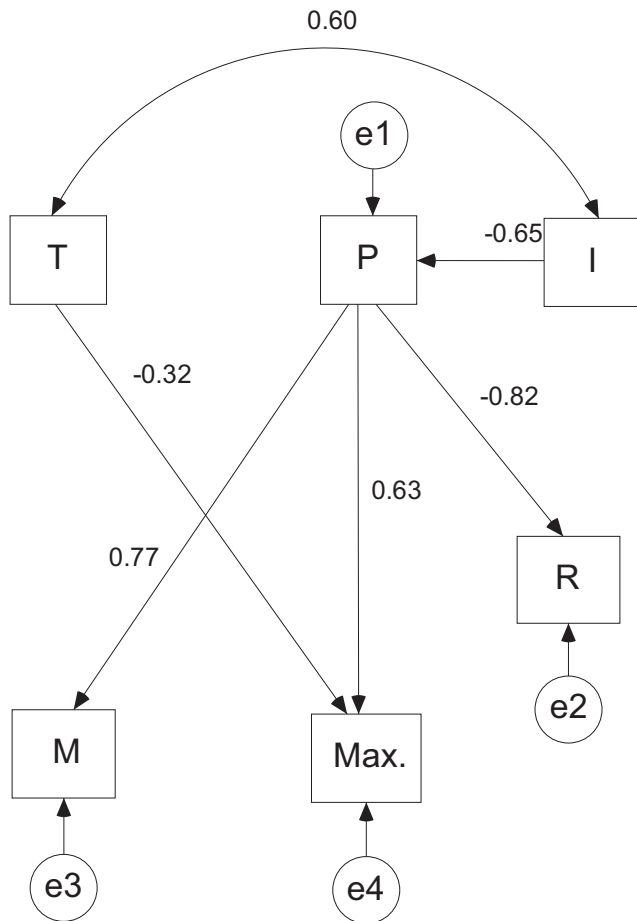
temperature ($r_S = -0.53$, $N = 26$, $P < 0.05$) and irrigation area ($r_S = -0.74$, $N = 25$, $P < 0.05$).

Path analysis was conducted based on the correlation structure of Chinese striped hamsters (Fig. 4; also see Supplementary Table S2[1]). After the model was selected by discarding nonsignificant coefficients ($P \geq 0.05$), the performance of the final pathway was adequate ($\chi^2_{(9)} = 13.7$, $P = 0.13$; comparative fit index (CFI) = 0.947) (Byrne 2009). The result showed mean and maximum body masses were directly positively associated with population abundance, suggesting that survival was high during high-density years. The maximum body mass was directly negatively associated with temperature, suggesting that survival was low during high-temperature years. Pregnancy rate and irrigation area were not directly associated with body mass, but irrigation area was indirectly negatively associated with population abundance, suggesting that reproduction was not a significant factor, but survival was low during high-irrigation years. The minimum body mass was not significantly associated with other variables, suggesting that growth rate was not significant in affecting body mass. Besides, population abundance had a negative effect on pregnancy rate. In summary, survival rate was a key factor in explaining

density-dependent and irrigation-linked body-mass changes in Chinese striped hamsters.

Greater long-tailed hamsters

Mean body mass of the greater long-tailed hamsters was positively correlated with population abundance ($r_S = 0.70$, $N = 18$, $P < 0.05$). The maximum body mass was positively correlated with population abundance ($r_S = 0.69$, $N = 18$, $P < 0.05$), but was negatively correlated with annual irrigation area ($r_S = -0.47$, $N = 18$, $P < 0.05$), suggesting that survival rate was high during high-density years or during low-irrigation years (Fig. 3). The minimum body mass was negatively correlated with population abundance ($r_S = -0.48$, $N = 18$, $P < 0.05$), suggesting that growth rate was low during high-density years, which would decrease the mean and maximum body masses. These results suggest that the high body mass during high-density years was mainly determined by high survival rate, not by the low pregnancy rate or the high growth rate. The positive effect of survival on body mass outweighed the negative effects of growth. The low body mass during high-irrigation years was related to low survival rates. Besides, pregnancy rate was negatively correlated with population abundance ($r_S = -0.63$, $N = 13$, $P < 0.05$). Population abundance was also negatively correlated with irrigation area ($r_S = -0.64$, $N = 25$, $P < 0.05$; Fig. 3), suggesting that irrigation may also have indirect effects on body mass through population abundance.

Discussion

The "Chitty effect" and underlying mechanisms

Consistent with previous studies on voles and lemmings (Chitty 1952; Boonstra and Krebs 1979), we found body mass of both hamster species during high-density years to be heavier (for both mean and maximum values) than during low-density years. These results support the previously observed "Chitty effect".

The Chitty–Krebs model emphasized the genetic adaption of high body mass during high-density years (Boonstra and Krebs 1979), but relatively recent literature have shown that larger individuals do not have higher fitness and that body size is not a highly heritable trait (Boonstra and Boag 1987; Lidicker and Ostfeld 1991). Oli (1999) proposed that the "Chitty effect" might result from limiting reproduction during high-density years that forced individuals to allocate more energy resources to body growth. Both hypotheses rely on fast body growth rate during high-density years to achieve a large body size. However, no significant correlation between population abundance and minimum body mass (which indicates growth rate) was found in the Chinese striped hamsters. Rather, we found a significant negative correlation between population abundance and minimum body mass in the greater long-tailed hamsters, suggesting that body growth rate is low during high-density years. These results do not support the earlier genetic or energy-allocation hypothesis, and thus do not support the growth hypothesis.

Although Spearman's correlation analysis showed, for the Chinese striped hamster, mean body mass to be negatively associated with pregnancy rate, path analysis showed pregnancy rate to be not significantly associated with mean and maximum body masses. No significant correlation between body mass and pregnancy rate was found in greater long-tailed hamsters. These results tend to reject the reproduction hypothesis.

Spearman' correlation analyses in both hamster species showed population abundances to be negatively associated with pregnancy rates (Fig. 3); path analysis confirmed such association for Chinese striped hamsters (Fig. 4). These results suggest that if reproduction rate was low during high-density years, survival rate would have to be high to achieve a high-density population. Indeed, this speculation was supported for both hamster species by

the observation that maximum body mass (which indicates survival) and mean body mass were significantly positively correlated with population abundance (Figs. 3, 4). Thus, the observed positive association of population abundance with mean and maximum body mass tends to support the survival hypothesis. Higher survival rate would increase the life expectancy of animals (Deevey 1947). If growth rate is constant, then longer life span implies larger body mass of animals.

In summary, our results tend to support only the survival hypothesis to explain the observed "Chitty effect" in both hamster species.

Impacts of extrinsic factors

For endothermic species, Bergmann (1847) described the pattern whereby larger animals are found in colder environments, while small animals are found in warmer environments (known as Bergmann's rule). This rule may also work on temporal scales (Yom-Tov 2001). Data on animal body size have accumulated over the past century and significant changes in body size in many species have been detected, but the changing pattern is not consistent (Gardner et al. 2011; Sheridan and Bickford 2011). Both decreases and increases in rodent body size in response to temperature change have been reported in the literature (Smith et al. 1998; Koontz et al. 2001; Yom-Tov and Yom-Tov 2004; Pergams and Lawler 2009). Body mass of woodrats (genus *Neotoma* Say and Ord, 1825) in an arid region of New Mexico, USA, was observed to decrease as temperature increased (Smith et al. 1998). The skull size in two species of Japanese rodents (large Japanese field mouse, *Apodemus speciosus* Temminck, 1844; Smith's red-backed vole, *Eothenomys smithii* (Thomas, 1905)) increased with elevated ambient minimal temperature (Yom-Tov and Yom-Tov 2004). Pergams and Lawler (2009) reported that 20 out of 28 museum rodent series collected on four continents showed a general increasing trend over the last 100 years. In this study, annual temperature has increased during the past 26 years (Yan et al. 2013). As for the Chinese striped hamsters, both Spearman's correlation analysis and path analysis showed that maximum body mass was significantly negatively correlated with increasing mean annual temperature, which is consistent with Bergmann's rule. However, Bergmann's rule works in situations of low growth rate during high-temperature years. In fact, we did not find the effect of growth rate on body-mass change. This may be a covaried effect of temperature with irrigation because they are highly positively correlated (Fig. 4).

In our previous study, we demonstrated that an increase in irrigation area decreased population abundance by destroying burrow systems of hamsters (Yan et al. 2013). During the study period, the irrigation area was consistently increased due to an increase in governmental investment on agricultural infrastructure. In this study, we found both mean and maximum body masses of the Chinese striped hamsters and maximum body mass of the greater long-tailed hamsters to be negatively correlated with irrigation area. The path analysis for Chinese striped hamster also indicated that irrigation might reduce maximum and mean body masses through population abundance. These results support our previous hypothesis that the increase in irrigation area during the past decades has resulted in continued population decline of hamsters by increasing mortality through flood irrigation.

To conclude, the present study suggests that changes in survival rates most likely contributed to the density-dependent and irrigation-related changes in body mass of the two hamster species populations. During high-density years, reproduction of hamsters was reduced, but survival increased, which resulted in large mean and maximum body masses during high-density years. High irrigation contributed to low mean and maximum body masses by increasing the mortality rate of hamsters.

References

Bergmann, C. 1847. Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. Göttinger Studien, **3**(1): 595–708.

Boonstra, R., and Boag, P.T. 1987. A test of the Chitty hypothesis: inheritance of life-history traits in meadow voles *Microtus pennsylvanicus*. Evolution, **41**(5): 929–947. doi:10.2307/2409183.

Boonstra, R., and Krebs, C.J. 1979. Viability of large- and small-sized adults in fluctuating vole populations. Ecology, **60**(3): 567–573. doi:10.2307/1936077.

Both, C. 1998. Experimental evidence for density dependence of reproduction in great tits. J. Anim. Ecol. **67**(4): 667–674. doi:10.1046/j.1365-2656.1998.00228.x.

Boyce, M.S. 1978. Climatic variability and body size variation in the muskrats (*Ondatra zibethicus*) of North America. Oecologia, **36**(1): 1–19. doi:10.1007/BF00344567.

Byrne, B. 2009. Structural equation modeling with AMOS: basic concepts, applications, and programming. 2nd ed. Psychology Press, London, UK. pp. 78–81.

Chitty, D. 1952. Mortality among voles (*Microtus agrestis*) at Lake Vyrnwy, Montgomeryshire in 1936-9. Philos. Trans. R. Soc. B Biol. Sci. **236**(638): 505–552. doi:10.1098/rstb.1952.0009.

Deevey, E.S., Jr. 1947. Life tables for natural populations of animals. Q. Rev. Biol. **22**(4): 283–314. doi:10.1086/395888. PMID:18921802.

Gardner, J.L., Peters, A., Kearney, M.R., Joseph, L., and Heinsohn, R. 2011. Declining body size: a third universal response to warming? Trends Ecol. Evol. **26**(6): 285–291. doi:10.1016/j.tree.2011.03.005. PMID:21470708.

Koontz, T.L., Shepherd, U.L., and Marshall, D. 2001. The effect of climate change on Merriam's kangaroo rat, *Dipodomys merriami*. J. Arid Environ. **49**(3): 581–591. doi:10.1006/jare.2001.0806.

Li, Y., Cohen, J.M., and Rohr, J.R. 2013. Review and synthesis of the effects of climate change on amphibians. Integr. Zool. **8**(2): 145–161. doi:10.1111/1749-4877.12001. PMID:23731811.

Lidicker, W.Z., Jr., and Ostfeld, R.S. 1991. Extra-large body size in California voles: causes and fitness consequences. Oikos, **61**(1): 108–121. doi:10.2307/3545412.

Lleras, C. 2005. Path analysis. *In* Encyclopedia of social measurement. Vol. 3. Elsevier B.V., Amsterdam, the Netherlands. pp. 25–30. doi:10.1016/B0-12-369398-5/00483-7.

McCay, C., Crowell, M.F., and Maynard, L. 1935. The effect of retarded growth upon the length of life span and upon the ultimate body size. J. Nutr. **10**(1): 63–79. PMID:2520283.

Mysterud, A., Yoccoz, N.G., Stenseth, N.C., and Langvatn, R. 2001. Effects of age, sex and density on body weight of Norwegian red deer: evidence of density-dependent senescence. Proc. R. Soc. B Biol. Sci. **268**(1470): 911–919. doi:10.1098/rspb.2001.1585.

Oli, M.K. 1999. The Chitty effect: a consequence of dynamic energy allocation in a fluctuating environment. Theor. Popul. Biol. **56**(3): 293–300. doi:10.1006/tpbi.1999.1427. PMID:10607522.

Pergams, O.R.W., and Lawler, J.J. 2009. Recent and widespread rapid morphological change in rodents. PLoS ONE, **4**(7): e6452. doi:10.1371/journal.pone.0006452. PMID:19649284.

Peters, R.H. 1986. The ecological implications of body size. Cambridge University Press, Cambridge, UK.

Sheridan, J.A., and Bickford, D. 2011. Shrinking body size as an ecological response to climate change. Nat. Clim. Change, **1**(8): 401–406. doi:10.1038/nclimate1259.

Smith, F.A., Browning, H., and Shepherd, U.L. 1998. The influence of climate change on the body mass of woodrats *Neotoma* in an arid region of New Mexico, USA. Ecography, **21**(2): 140–148. doi:10.1111/j.1600-0587.1998.tb00668.x.

Sundell, J., and Norrdahl, K. 2002. Body size-dependent refuges in voles: an alternative explanation of the Chitty effect. Ann. Zool. Fenn. **39**: 325–333.

Sutherland, D.R., Banks, P.B., Jacob, J., and Singleton, G.R. 2004. Shifting age structure of house mice during a population outbreak. Wildl. Res. **31**(6): 613–618. doi:10.1071/WR04010.

Yan, C., Xu, L., Xu, T., Cao, X., Wang, F., Wang, S., Hao, S., Yang, H., and Zhang, Z. 2013. Agricultural irrigation mediates climatic effects and density dependence in population dynamics of Chinese striped hamster in North China Plain. J. Anim. Ecol. **82**(2): 334–344. doi:10.1111/j.1365-2656.2012.02037.x. PMID:23030597.

Yom-Tov, Y. 2001. Global warming and body mass decline in Israeli passerine birds. Proc. R. Soc. B Biol. Sci. **268**(1470): 947–952. doi:10.1098/rspb.2001.1592.

Yom-Tov, Y., and Geffen, E. 2006. Geographic variation in body size: the effects of ambient temperature and precipitation. Oecologia, **148**(2): 213–218. doi:10.1007/s00442-006-0364-9. PMID:16525785.

Yom-Tov, Y., and Yom-Tov, S. 2004. Climatic change and body size in two species of Japanese rodents. Biol. J. Linn. Soc. **82**(2): 263–267. doi:10.1111/j.1095-8312.2004.00357.x.

Yom-Tov, Y., Yom-Tov, S., MacDonald, D., and Yom-Tov, E. 2007. Population cycles and changes in body size of the lynx in Alaska. Oecologia, **152**(2): 239–244. doi:10.1007/s00442-006-0653-3. PMID:17277929.

Zedrosser, A., Dahle, B., and Swenson, J.E. 2006. Population density and food conditions determine adult female body size in brown bears. J. Mammal. **87**(3): 510–518. doi:10.1644/05-MAMM-A-218R1.1.

Zhang, J. 1985. Study on the division of age group and the age composition of population of striped hamster in Beijing area. Acta Theriol. Sin. **5**(2): 141–150.

Zhang, Z.B., Yang, H.F., Wang, S.Q., Wang, F.S., Hao, S.S., Cao, X.P., Zhang, J.X., and Xu, Y.X. 1998. Ecology and management of rodent pests in agriculture. Ocean Press, Beijing.