



Optimal body weight of Brandt's voles for winter survival



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ABSTRACT

Winter survival is an important fitness component of non-hibernating small mammals in northern latitudes. Body sizes are related to many life history traits influencing the fitness of animals. Counterbalancing selective forces of survival selection may optimize autumn body weight to maximize winter survival of non-hibernating small mammals. Brandt's voles (*Lasiopodomys brandtii*) are non-hibernating and live in groups year round. We live trapped Brandt's voles in an enclosure and estimated weekly survival probabilities and daily proportional body weight growth rates of the voles from September 2003 to March 2004. Autumn body weight as an individual covariate explained about 43% of variation in autumn–spring survival of the voles. Survival of females and males peaked at body weight of about 33 g and 51 g, respectively, supporting stabilizing survival selection on body sizes of Brandt's voles. However, breeding selection may reduce the optimal body size of female voles. Brandt's voles did not lose body weight during the autumn and winter probably to enhance winter survival. Therefore, Brandt's voles adapt to the energetically demanding winter environments with optimal body size and maximized winter survival.

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1. Introduction

Seasonality may be a selective force for variation in many life history traits, such as body size, somatic growth, and fat or resource storage, of northern homeotherms (Boyce, 1979). The balance between the energy acquisition and expenditure of small mammals is subject to natural selection for survival through winter (Boratynski et al., 2010; Merritt and Zegers, 2002; Wunder, 1984). For instance, low temperatures increase resource and energy needs by non-hibernating small mammals to maintain body temperatures during winter in northern latitudes; as a result, small mammals may increase foraging time to augment energy acquisition. Meanwhile, winter food is low in quantity and quality in northern latitudes, increasing the energetic costs of winter food acquisition and assimilation and further resulting in body weight losses of small mammals (Ergon et al., 2004; Merritt and Zegers, 1991; Wunder, 1984). Therefore, northern non-hibernating small mammals may adjust their body sizes or physiology to adapt to unfavorable winter conditions (Boyce, 1979; Ergon, 2007; Ergon et al., 2004; Hansson, 1992; Wunder, 1984).

Winter survival is a fundamental fitness component of non-hibernating arviculines in northern latitudes. Small mammals may reduce or cease reproduction to enhance survival in low-resource environments during winters or in poor years, even with increases in body size (Ergon et al., 2004; Hansson, 1990; Merritt and Zegers, 2002; Ruf et al., 2006). Large body sizes can confer the benefits of reduced heat loss due to small surface-volume ratios, enhanced winter survival, and possibly increased future reproductive potential (Boyce, 1979; Sauer and Slade, 1988). However, winter energy conservation may select for small body sizes of small mammals challenged by low food availability and harsh (i.e., low ambient temperature and snow) environments (Hansson, 1992; Wunder, 1984). Voles may lose their body weight during late autumn and winter to reduce total winter metabolism or energy requirements when food resources are scarce (Hansson, 1990). Therefore, counterbalancing selective agents of large and small body sizes may result in optimal body sizes for winter survival, at which winter survival peaks, in arviculines in northern latitudes (Ergon et al., 2004). However, theoretical models for within-population optimal body sizes have been empirically tested primarily with the distribution patterns of body sizes and related energetic profiles (Chown and Gaston, 1997; Ergon et al., 2004; Sandell, 1989; Symonds, 1999). To our knowledge, few empirical studies have investigated the effects of body weight on autumn–spring survival of small mammals, directly assessing optimal body

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sizes with the fitness consequences of the variation in individual body sizes.

Brandt's voles (*Lasiopodomys brandtii*) are widely distributed on the Mongolian Plateau where winter is severe, with winter minimum temperatures reaching -40°C and snow cover lasting for 6–7 months. Brandt's voles are social, living in burrow systems as social groups year round (Zhong et al., 2007). A social group of voles excavates a complex underground burrow system with a nest chamber (about 20–50 cm deep below ground) and 2–4 about 1-m long food storage chambers per burrow system (G.M. Wang, unpublished; Schauer, 1987; Zhong et al., 2007). Brandt's voles cache winter food from September to October before the first snow falls. The voles close all burrow entrances but one near the center of a burrow system after snow falls and soil is frozen in November, becoming rarely active on ground during winter (G.M. Wang, unpublished; Zhong et al., 2007). Compared to other arvicolines living in shallow nest chambers, group nesting and huddling may provide thermal insulation, reducing the heat loss of Brandt's voles (Merritt and Zegers, 1991; Wang et al., 2006). However, it is unknown whether Brandt's voles would have net losses of body weight to conserve energy for winter survival, particularly with thermal insulation and huddling effects.

In this study, we test the hypotheses: 1) that there would exist an optimal body size in Brandt's voles for autumn–spring survival owing to natural selection for large body sizes to enhance survival (i.e., survival selection) and its counterbalancing selection against large body sizes to reduce total metabolism and energy requirements; and 2) that Brandt's voles would not lose body weight to reduce energy requirements during late autumn due to cached food and improved thermal insulation provided by burrowing and group nesting. Alternatively, Brandt's vole would lose body weight for energy conservation in the autumn and winter, like solitary arvicolines. We also test for sex-specific quadratic relationships between autumn–spring survival and autumn body weight using individual body weight as individual covariates for probabilities of survival. We predict that female voles would have smaller optimal body sizes than do males because of sexual selection or because of natural selection for small females to improve reproductive opportunities in resource-poor environments (i.e., breeding selection). This approach allows us to assess how individual life history traits influence the variation in individual's winter and spring survival.

2. Methods and materials

2.1. Study site

We conducted our field studies at the Inner Mongolia Grassland Ecosystem Research Station, Chinese Academy of Sciences in Inner Mongolia, China ($43^{\circ}26'\text{N}$, $116^{\circ}04'\text{E}$). The climate was semi-arid with average annual precipitation of about 350 mm and average annual temperatures of about -0.1°C (Jiang, 1985). Monthly average temperatures ranged from -40°C to 30°C , and most rainfall fell in June, July, and August. Snow cover lasted from November to March or April of the following year (Jiang, 1985; Zhong et al., 2007). Vegetation was dominated by *Stipa krylovii*, *Leymus chinensis*, and *Artemisia frigida* (Jiang, 1985).

We established our trapping plot inside a 0.7-ha enclosure (70 m \times 100 m), located at the center of a 4-ha grassland. The enclosure was constructed with cement brick walls about 50 cm deep below ground and steel wire mesh 1 m above ground to prevent movements of burrowing animals and mammalian predators into or out of the enclosure. The top of the enclosure was covered with nylon netting at about 2-m height to prevent predation by avian predators (e.g., *Bubo bubo*).

2.2. Establishment of Brandt's vole population

During the summer 2003, we live captured and marked about 40 Brandt's voles inside the enclosures until no unmarked voles were captured for 3 consecutive days. We then marked and released about 310 originally wild-caught Brandt's voles to our enclosure to establish the study population of Brandt's voles during July and August 2003. We observed that released Brandt's voles used existing burrow systems immediately after releases. The initial density of our established vole population was about 500 voles/ha (=350 voles/0.7 ha), at the low end of the observed density range (590–2300 voles/ha) of wild Brandt's vole populations in the same area (Zhong et al., 2007).

2.3. Live trapping of Brandt's voles

We live trapped Brandt's voles from September 20, 2003 to October 27, 2003 in 2- or 3- week intervals and then from March 6, 2004 to May 13, 2004 in 1- or 2-week intervals. We did not trap the voles from October 28, 2003 to March 5, 2004 when our enclosure was covered by snow because Brandt's voles did not move on the surface of snow. We placed 8–15 wire-mesh live traps (28 cm \times 13 cm \times 10 cm) in each burrow system. Traps were baited with peanuts and placed in 3–4 circles per burrow system with trap door opening facing a burrow entrance (Liu et al., 2009). We trapped the voles from 0900 to 1700 h in April, May, September, and October and from 1100 to 1400 h in March, with traps checked every 20–30 min during our trapping hours to avoid trap mortalities. We weighed captured voles to the nearest 0.1 g, using a portable electronic balance (Scout SE601F, Ohaus Corp., Parsippany, New Jersey, USA) and clipped a combination of toes for permanent identification (ID). We recorded sex, body weight, reproductive condition, and burrow system ID number for each capture and released captured voles back to the same burrow systems where the voles were captured. Each trapping week lasted for one to three days. We classified the voles weighing less than 25 g as juveniles, from 26 to 44 g as sub-adults, and equal to or more than 45 g as adults. Males were considered in reproductive condition if they had scrotal testes. Female were considered in reproductive condition if they had a bulging abdomen, enlarged nipples surrounded by white mammary tissue, or opened pubic symphysis. Our trapping and handling procedures of Brandt's voles in the field followed the guidelines approved by the Animal Care and Use Committee of the American Society of Mammalogists (Gannon et al., 2007) and were approved by the Institutional Animal Use and Care Committee of the Institute of Zoology, Chinese Academy of Sciences.

2.4. Statistical analysis

We used the Cormack–Jolly–Seber (CJS) models within the program MARK to estimate weekly probabilities of survival of Brandt's voles from September 2003 to May 2004 (Cormack, 1964; Jolly, 1965; Seber, 1965; White and Burnham, 1999). We conducted survival analyses in two steps. First, we built 16 models of all possible combinations of time and sex effects on probabilities of survival and capture. We estimated variance inflation factor, i.e., median \hat{c} hat, for our trapping data using the most complex model with time–sex interactions on both survival and capture probabilities (White and Burnham, 1999). The median \hat{c} hat was 1.38 for our data; thus, we used corrected quasi Akaike information criteria (QAICc) for model selection (White and Burnham, 1999). We used theoretic-information approach to select the most parsimonious model and competing models (Burnham and Anderson, 2002). The model with the lowest QAICc value or highest Akaike weight was

the most parsimonious model, and models with ΔQAICc value less than 2 were competing models (Burnham and Anderson, 2002). The ΔQAICc value of a model was computed as the difference in QAICc values between the model and the most parsimonious model. If sex effect on survival or capture probabilities was included in the most parsimonious model or competing models, we concluded that sex effect on survival or capture probabilities was significant. In the second step of survival analysis, we built models including mean autumn body weight of a vole as individual covariates of the probability of survival of the vole, based on the most parsimonious model from our first step modeling. Mean autumn body weight was calculated as the average of body weights of a vole over four trapping weeks from September 20 to October 27 of 2003. We tested for global and sex-specific relationships between survival and body weight (including both linear and quadratic terms of individual body weight). The former had identical quadratic regression for male voles and female voles; the latter had different quadratic regressions for male voles and female voles, respectively. We selected the most parsimonious models and competing models using the information-theoretic approach. We used analysis of deviance (ANODEV) to estimate the percent variation in survival probability explained by individual body weight (Skalski, 1996; Skalski et al., 1993).

We calculated the daily proportional body weight growth rate (hereafter, daily body weight growth rate) of a vole as the difference in body weight between two successive trapping weeks divided by initial body weight at the first trapping week and number of days between the two trapping weeks (Agrell et al., 1992). We calculated average autumn daily body weight growth rate of a vole over three trapping intervals from September 20 to October 27, 2003 ($n = 1-3$). We then calculated means and 95% confidence intervals (CIs) of mean daily body weight growth rates by age groups (as initially captured) and sexes. If the 95% CI of the mean daily body weight growth rate of a group included zero, we concluded that the average daily body weight growth rate of the group was not significantly different from zero (Zar, 1999). We used t tests to determine if mean autumn body weight differed between male voles and female voles as well as between male adults and female adults at the significance level of 0.05. Means were reported with ± 1 standard error (SE).

3. Results

We captured 431 voles during the entire study, including 50 juveniles, 95 sub-adults, and 27 adults of male voles; and 47 juveniles, 182 sub-adults, and 30 adults of female voles. We did not capture any pregnant female vole from September to October, but about 40% of male and female voles were in reproductive condition in March, 2004. In our first-step survival analysis, the best CJS model among the 16 models included time effects on probabilities of survival and capture but did not include the effects of sexes, with the Akaike weight of 0.93, whereas the second best model had the ΔQAICc value of 5.17. Survival of Brandt's voles was independent of sexes and changed through the study period, remaining relatively stable over the autumn and winter, but declining during the spring (Fig. 1).

In the second-step survival analysis, the CJS model with sex-specific quadratic effects of body weight on survival was the best model, with the Akaike weight of 0.99 (model 1, Table 1), whereas the second best model had the ΔQAICc of 8.94 (model 2, Table 1). Winter survival was a quadratic function of autumn body weight, with the coefficients of linear and quadratic terms being 0.151 (95% CI: 0.089–0.214) and -0.002 (95% CI: -0.003 to -0.001), respectively, for females; and 0.098 (95% CI: 0.045–0.150) and -0.001 (95% CI: -0.002 to -0.0004), respectively for males. The results of

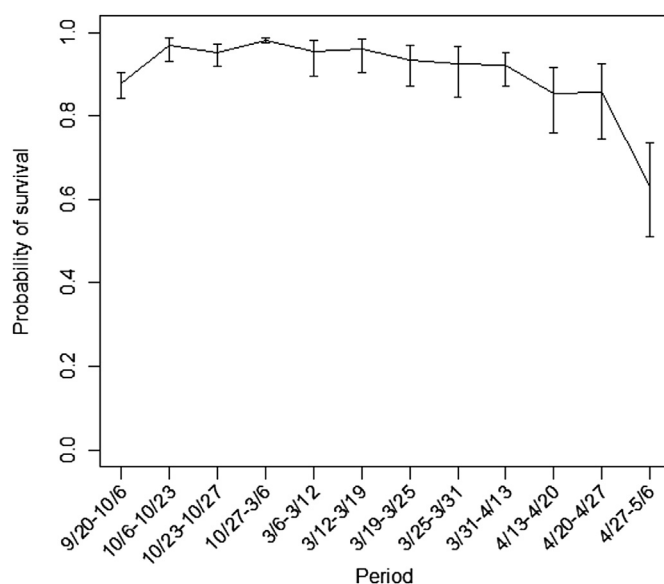


Fig. 1. Weekly survival probabilities of Brandt's voles (*Lasiopodomys brandtii*) in Inner Mongolia, China from September, 2003 to May, 2004.

ANODEV showed that the quadratic effects of body weight explained 42.3% of total variation in survival of Brandt's voles.

Optimal autumn body weights determined numerically by the most parsimonious model were about 33.4 g for females and 50.5 g for males (Fig. 2a). With data pooled over males and females (model 7), optimal body size was estimated about 39.7 g (the green line, Fig. 2a). Among captured voles, females weighed slightly less than did males (females: mean body weight [BW] = 34.37 ± 0.78 ; males: $BW = 37.68 \pm 0.57$; and $t = -3.41$, $df = 337$, $P = 0.0001$); however, mean body weight of female and male adults did not differ during the autumn (female adults: $BW = 49.85 \pm 0.84$, $n = 30$; male adults: $BW = 51.29 \pm 0.93$, $n = 27$; and $t = -1.15$, $df = 55$, $P = 0.25$). We tended to capture more males than females in the range of body weight between 35 g and 55 g (Fig. 2b). Male juveniles tended to have negative daily body weight growth rates during the autumn, with the 95% CI including zero (Fig. 3a); however, other age–sex groups had either positive or zero daily body weight growth rates during the autumn and winter (Fig. 3a, b).

4. Discussion

Brandt's voles did not suffer from greater mortality during winter than autumn and spring (Fig. 1). No females were captured in reproductive condition. We identified optimal autumn body weight, at which winter survival peaked (Fig. 2), supporting the prediction of the hypothesis that counterbalancing selections for large body sizes to enhance survival and against large body sizes to reduce total winter metabolism result in optimal body sizes of wintering Brandt's voles. Additionally, Brandt's voles did not lose body weight during the autumn and winter (Fig. 3), consistent with the hypothesis that Brandt's voles maintain or increase body weight during autumn and winter to enhance winter survival.

Food quality and quantity and reproductive condition are the main factors influencing winter survival of northern small mammals (Aars and Ims, 2002; Crespin et al., 2002; Ylonen and Eccard, 2004; Yoccoz and Mesnager, 1998). We did not capture any pregnant female vole during the late autumn. Therefore, the cessation of reproduction might enhance autumn and winter survival of Brandt's voles. Likewise, bank voles have pronounced seasonal variation in survival in Belgium, with survival lowest during spring

Table 1
The Cormack–Jolly–Seber models for probabilities of weekly survival of Brandt's voles (*Lasiopodomys brandtii*) in Inner Mongolia, China from September, 2003 to May, 2004. Symbol “ ϕ ” stand for probability of weekly survival; letter “ p ” for probability of capture; symbol “ bm ” for individual covariate of body weight; symbol “ bm^2 ” for squared body weight; and letter “ t ” for effects of time. Symbol “ g ” in the expression of survival models stands for sex-specific regression functions. Symbol “QAICc” is quasi Akaike information criterion corrected for small sample size. Symbol “ Δ QAICc” is the difference in QAICc between a model and the most parsimonious model.

Model	QAICc	Δ QAICc	QAIC weight	Model likelihood	Number of parameters	Deviance
1. $\{\phi(t + g[bm + bm^2]) p(t)\}$	3609.346	0	0.986	0.051	29	3550.580
2. $\{\phi(t + bm + bm^2) p(t)\}$	3618.282	8.936	0.011	0.001	26	3565.665
3. $\{\phi(t + g[bm]) p(t)\}$	3622.524	13.178	0.001	0.000	26	3569.907
4. $\{\phi(t) p(t)\}$	3623.372	14.026	0.001	0.000	24	3574.845
5. $\{\phi(t + bm) p(t)\}$	3624.656	15.31	0.001	0.000	25	3574.085
6. $\{\phi(g[bm + bm^2]) p(t)\}$	3803.664	194.318	0.000	0.000	18	3767.364
7. $\{\phi(bm + bm^2) p(t)\}$	3817.433	208.087	0.000	0.000	16	3785.195

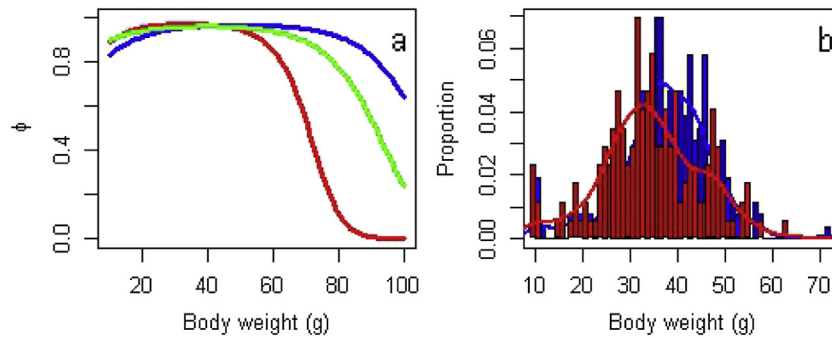


Fig. 2. Autumn (a) optimal body weight and (b) distributions of body weight of Brandt's voles (*Lasiopodomys brandtii*) in Inner Mongolia, China. The left panel (a) is the logistic regressions of weekly survival probabilities with the linear and quadratic terms of individual body weight as individual covariates; the red, blue, and green lines represent female voles, male voles, and the entire population, respectively. The ordinate is weekly survival probability (ϕ); and the abscissa is average autumn body weight. The right panel (b) is the histograms of mean body weight of male (in blue) and female (in red) voles. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and highest during winter inside the enclosure (Crespin et al., 2002). Survival through the winter or non-breeding season is an important fitness component of small mammals in northern-temperate regions (Ylonen and Eccard, 2004). High winter survival increases the reproductive potential of surviving individuals the following breeding season. Therefore, maximizing winter survival with the cessation of reproduction may be the optimal strategies of non-hibernating small mammals to adapt northern seasonal environments (Merritt and Zegers, 2002).

Ergon et al. (2004) predict an optimal wintering body size of arviculines based on the trade-off between the survival benefits and the energetic costs of foraging and food processing of large body sizes, mediated by the physiological constraints of energy assimilation. Optimal body sizes of Brandt's voles were between 30 and 50 g (Fig. 2). Optimal body sizes of Brandt's voles might evolve

to enhance winter survival under the trade-off between the survival benefits and the energetic costs of foraging of large body sizes. Li and Wang (2005) found that Brandt's voles housed in small cages in an outdoor enclosure increased energy intakes from August to November while losing body weight during autumn and early winter. Additionally, optimal autumn body weight differed between male and female Brandt's voles, with male adult Brandt's voles between 45 and 60 g surviving better than their female counterparts (Fig. 2a, b). Although Brandt's voles appear to be promiscuous (Huo et al., 2010), the voles were not sexually dimorphic during the non-breeding season, with mean body weights of adult males and adult females approximately equal ($P = 0.25$). Therefore, sexual selection is unlikely to be responsible for the difference in optimal body weight between the two sexes. Gestation, lactation, and parental care make reproduction more

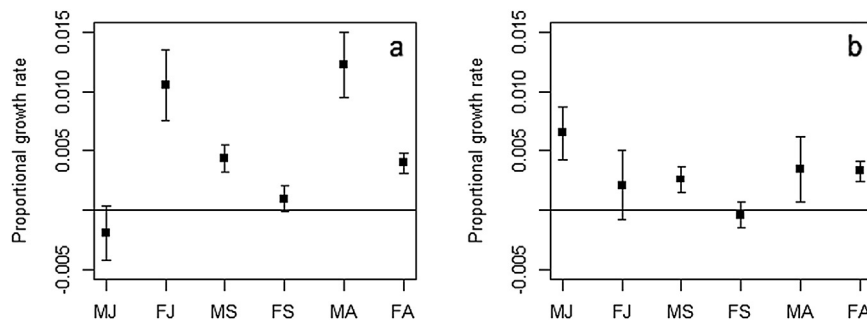


Fig. 3. Average autumn (a) and winter (b) daily proportional body weight growth rates of male and female Brandt's voles (*Lasiopodomys brandtii*) in Inner Mongolia, China. Vertical lines are the 95% confidence intervals. Letters “MJ” stand for male juveniles; “FJ” for female juveniles; “MS” male for sub-adults; “FS” for female sub-adults; “MA” for male adults; and “FA” for female adults.

energetically demanding for female voles than for male voles. High energetic demands for reproduction by female mammals may make females subjected to stronger breeding selection for small body sizes during the breeding season than to survival selection for large sizes during the non-breeding season (Sandell, 1989). Moreover, female voles can reproduce during winter with sufficient food and high temperatures, particularly under snow cover (Gliwicz and Taylor, 2002; Innes and Millar, 1994). Small optimal body sizes can lower the energy requirements for the reproduction of female voles, making winter reproduction possible (Sauer and Slade, 1988).

Our data support the prediction of the hypothesis that Brandt's voles would not lose body weight to reduce energy requirements during late autumn due to cached food and improved thermal insulation provided by burrowing and group nesting (Fig. 3). Although we did not collect data on temperatures in nest chambers and huddling effects on metabolic rates of Brandt's voles during winter, the metabolic rate of common voles (*Microtus arvalis*) declines by 30% when social group sizes increase from one to seven (Grodzinski et al., 1977). Additionally, temperatures in underground nest chambers of Taiga voles (*Microtus xanthognathus*) range from 4 to 7 °C, about 10–30 °C above ambient air temperatures during winter (Wolff and Lidicker, 1981). Future studies are warranted to investigate social effects on energy conservation and the energy expenditure of Brandt's voles in the wild.

In conclusion, counterbalancing selections for winter survival and for energy conservation may result in optimal body sizes during autumn. Breeding selection may result in smaller optimal wintering body size of female voles than that of male voles. Voles may cease reproduction and increase autumn body sizes to enhance winter survival.

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