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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.

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 arvicolines 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 arvicolines 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°26′N, 116°04′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 kruylovii*, *Leymus chinensis*, and *Artemisia frigida* (Jiang, 1985).

We established our trapping plot inside a 0.7-ha enclosure (70 m × 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 × 13 cm × 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 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 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