



Original investigation

Density-related pattern of variation in body growth, body size and annual productivity in the common hamster

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ABSTRACT

Body size is one of the most influential life history traits, often covarying with population density. While decreasing in some organisms, such as large herbivores, body size may increase with population density in small ones, such as voles, the common hamster (*Cricetus cricetus* L.), the endangered Eurasian rodent, does not exhibit cyclic population dynamics but it does have large variation in population numbers and high reproductive capacity; yet, its density-related processes which affect morphological traits are still poorly understood. We analysed density-related changes in body growth rates and body size (length and weight) collected in a natural population over 9 years, separately for each sex and age category (subadult/adult). Annual population density, the maximum Jolly–Seber estimate of population size per hectare reached in that year, was found to increase linearly with productivity index and with the length of the breeding season. Body length growth rates increased with population density in adults, but not in subadults. In adults, body length was found to increase with population density; however, we found no relationship between body weight and population density. The evidence for changes in subadults' body size with population density was weak. These results suggest that, in years of peak numbers, adult hamsters grow faster, are longer and breed for longer time periods, thus having higher productivity index. Body size is therefore positively related to variation in population density, commonly referred to as the Chitty effect. Based on our findings, we conclude that variation in individual's body growth rate and size drives the variation in productivity which in turn causes the changes in hamster population density.

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Introduction

Body size is one of the most influential life history traits determining reproductive success (Peters, 1983). In mammals, larger individuals are usually more competitive, thereby producing more offspring of higher quality (Peters, 1983; Blanckenhorn, 2000). Body size can covary with population densities and these covariations differ among herbivores. In large herbivores, body size assessed through linear measurements or body weight may decrease with increasing population density and intraspecific competition as has been observed in red deer *Cervus elaphus* (Mysterud et al., 2001), caribou *Rangifer tarandus* (Couturier et al., 2010), roe

deer *Capreolus capreolus* (Richard et al., 2010; Kjellander et al., 2006) and chamois *Rupicapra rupicapra* (Garel et al., 2011). An opposite tendency has been documented in small herbivores, such as voles, which exhibit large fluctuations in numbers, referred to as population cycles (Chitty, 1952). During the high-density phase, individuals can be 20–30% larger than those in the low-density phase (Boonstra and Krebs, 1979), generally meaning that their average adult body weight is higher (Burthe et al., 2010). This phenomenon, known as the Chitty effect (Boonstra and Krebs, 1979), is often considered as an important biological characteristic of the vole population cycle (Krebs, 1996). It has been documented in voles (Boonstra and Krebs, 1979; Hansson, 1984; Lidicker and Ostfeld, 1991; Burthe et al., 2010), and has rarely been demonstrated in other rodents, such as the white-footed mouse (Wolff, 1993). In the North American red squirrel (*Tamiasciurus hudsonicus*), young individuals are known to grow faster in an environment with higher densities but no Chitty effect is present (Dantzer et al., 2013). At present, it remains unclear whether the lack of evidence

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in other rodents is caused by the absence of the change or the lack of long-term rodent population data from populations with high-enough temporal variability to detect a measurable change in body size.

Common hamsters (*Cricetus cricetus* L.) are small hibernating rodents with high reproductive capacity leading to occasional outbreaks in numbers (Grulich, 1986). Unlike annual voles, hamsters can be characterised as biannual rodents. Most individuals mature following the first hibernation when they are about one year of age. Adults can produce one to three litters of 4–6 offspring each (Franceschini-Zink and Millesi, 2008). They rarely survive to breed following the second hibernation. From an evolutionary perspective, the adults should therefore invest most resources into body growth and reproduction over survival until the next breeding season. Despite severe decline in their distribution range (Ulbrich and Kayser, 2004; Ziomek and Banaszek, 2007; Tkadlec et al., 2012; Rusin et al., 2013) and an increased conservation concern, most field studies on hamster demography are typically performed on a small-time scale (Ulbrich and Kayser, 2004; Franceschini-Zink and Millesi, 2008). Consequently, density-related processes acting in hamster populations are still poorly understood.

Using long-term data on body length and weight collected from a fluctuating population over 9 years, we focused on multiannual changes in the common hamsters' body growth rates and body size in relation to population density to see what pattern of body size changes the hamsters follow. Moreover, population productivity and length of breeding season are often implicated in mechanisms behind the rodent population cycles and may affect the size of individuals (Krebs, 2013). We therefore assessed their relationships to population density to obtain more insights into the causal links underlying the observed changes in morphology and population density.

Material and methods

Study site and trapping protocol

We studied a population of *Cricetus cricetus* L. in the suburbs of Olomouc, Czech Republic, from 2005 to 2013. The study plot of 20 ha in size is situated in the southern part of the town, with its midpoint at N49°34'34" E 17°17'00" at an altitude of 210 m. The site lies in the floodplains of the Morava River and consists of several smaller fields with a large variety of crops (cereals and alfalfa), thus providing both food and shelter for the hamster population.

Using a capture-mark-recapture method, we live trapped hamsters over the breeding season (April to late September) at monthly intervals for two consecutive days from 2005 to 2013. Live-traps, made of metal mesh and baited with wheat grains, were placed near the burrow entrances in the evening and checked on the following morning. Captured individuals were slightly narcotised by inhalation of isoflurane, and then measured and marked by passive transponders. The handling protocol lasted about 5 min. The body size was assessed using body length and body weight. Body length was determined by measuring the nasal-to-anal distance to the nearest 5 mm. Body weight was measured using Pesola spring scales to the nearest 5 g. We also recorded the sex and reproductive condition of the captured individuals and divided them into three age classes. Juveniles were small individuals with juvenile pelage, and body weight under 150 g. Subadults were individuals in adult pelage, and were caught before their first hibernation, hence usually 2–5 months old. Adults were all individuals after the first hibernation. Once processed, the animals were released close to the burrow where they were captured. Juveniles were excluded from the morphological traits' analysis due to the very low recapture rates. In total, we recorded 667 measurements of body length and

weight from 355 individuals. Of these, 158 individuals were captured and measured more than once. In total, we recorded 229 body size measurements from 119 adult males, 169 measurements from 79 adult females, 165 measurements from 119 subadult males, and 103 measurements from 72 subadult females.

Estimation of body growth rates

Body size growth rates can be measured in three ways as (1) increments per unit of time, (2) body size increments per unit of time and body size unit (proportional body growth rates) or (3) instantaneous rates of change. Here we measured growth as the instantaneous body growth rates defined as:

$$\frac{dw}{dt} \frac{1}{w} = \frac{\ln(w_{t+1}) - \ln(w_t)}{\Delta t}$$

where w is a body size measurement (body length or body weight), taken from the same individual in time t and $t+1$. In practice, it is obtained as the difference between two log body size measurements and then recalculated as a change in the parameter per week.

Estimation of annual population density, annual productivity index and length of the breeding season

We measured population density by applying the Jolly–Seber method to monthly capture-recapture data using the program Jolly (Pollock et al., 1990). Annual population density for each year of study was defined as the maximum population density expressed as the number of individuals per hectare, usually attained late in the growing season. We assessed the annual productivity as an index based on the number of captured subadults (not juveniles) divided by the number of adults captured during that year. Juveniles were excluded because they were few in numbers and their recapture rates were extremely low. Thus, the index not only reflects the number of offspring produced but also the ability of juveniles to survive until the subadult age. The productivity index does not include the increase in biomass due to somatic growth either. We then evaluated the variation in the length of the breeding season by counting the number of days between the capture of the first sexually mature individual in spring and the capture of the last juvenile produced in that season. We excluded two years in which no juveniles were caught. This method of estimation does not measure the absolute length of the breeding season. However, it can be used when the aim is to examine the differences among years. The estimates should be taken with caution because the last-born juveniles could be missed.

Statistical analysis

To assess the relationship between population density and the reproductive processes, we first examined whether population density is positively or negatively related to the productivity index and the length of the breeding season.

We then analysed covariation of body growth rates with population density by fitting linear mixed-effect models (LMMs) containing population density and sex as predictors using the function `lme` (package `nlme`, Pinheiro et al., 2017) implemented in R (R Development Core Team, 2017). Because somatic growth rates typically slow down with growing body size, we included body size (body length or weight) in the model structure. There was no need to account for seasonal variation in somatic growth rates as it was completely explained by body size. The year of study was set as a random effect to account for non-independent data from the same breeding season. In all models, we assumed normally distributed errors.

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