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Original investigation

Growth patterns in free-ranging yellow-necked wood mice, *Apodemus flavicollis*

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ABSTRACT

Growth patterns are nearly unknown in free-ranging rodents. Here we analyse growth patterns (in body length) in relation to sex, year, and population density in a population of yellow-necked wood mice, *Apodemus flavicollis*. This population was studied by capture-mark-recapture at a mountainous site in central Italy during 1988–1995, and 2000–2005. In our study, (i) the growth of females was accelerated compared to males of comparable body length, (ii) growth rates strongly varied inter-annually, and (iii) there was a clear density-dependence mechanism between population density and intrinsic growth rate, with growth being decelerated at density increases in both males and females. The general implications of these patterns are discussed.

Introduction

Since several decades it has been increasingly clear that, studying growth trajectories of individuals is central for a deeper understanding of reproductive and population ecology, and even evolutionary trends of organisms and species (e.g., see Von Bertalanffy 1934, 1938, 1951, 1964; Beverton and Holt (1957); Shine and Charnov, 1992, Jackson and van Aarde, 2003; and later literature). Despite its potential relevance, and the fact that lots of studies have investigated growth patterns in free-living animals (e.g., Lack, 1954; Peterson et al., 1999; Stamps and Krishnan, 2004), very scarce data are available for free-ranging rodents. Most of the studies on rodent growth patterns came from laboratory investigations (e.g., Creighton and Strauss, 1986; Jackson and van Aarde, 2003; Aliaga-Rossel et al., 2009).

In this study we analyse the growth patterns of a population of free-ranging rodents, *Apodemus flavicollis* in central Italy. We used for this purpose a mice population studied by capture-mark-recapture for a long-term. We emphasize intersexual and inter-annual differences in growth patterns, as well the relationships between growth rates and density fluctuations in a species where population densities are known to differ substantially from year to year (Amori et al., 2010).

Material and methods

Study area and trapping design

The study area was located in central Italy (Majella National Park, 42°08′N, 14°05′E, 1000 m a.s.l.), and was characterized by a thermophilous beech forest (*Fagus sylvatica*). The vegetation belongs to the association *Geranio-Fagion*, which is very widespread in the study area.

Data were obtained through capture-mark-recapture (CMR; Gurnell and Flowerdew, 1982) from spring to fall (April to October) in 1988–1995 and 2000–2005. The field research was suspended in 1996–1999 because of lack of sufficient funds to support the project and logistic constraints. Mice were live-trapped in a 1.44 ha square grid, calculated including an outer boundary strip equal to half of the minimum distance between traps. In each month we performed a trapping session; each trapping session was 3-nights-long, for a total of 1200–1500 trap nights per year. We arranged a square grid of 100 live-traps, spaced 12 m apart (see Amori et al., 2000 for more details). Mice were captured by home-made live-traps $30 \times 8 \times 10$ cm; these traps allowed capture of all sized mice, from the small individuals to the very large and oldest ones. The animals captured were tranquillized with ether, ear-tagged (Le Boulengé-Nguyen and Le Boulengé, 1986), measured by a manual calliper (precision 0.02 mm) for body length, i.e. the distance in a straight line from the tip of the nose to the tail basis. Morphometric variables were taken from each captured individual every time that it was trapped, i.e. even on multiple captures. As the above-mentioned morphometric variables were highly correlated with each other, here we used only body length measurements in order to assess individual growth rates. Mice were released at the site of capture

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Table 1
Numbers of male and female *Apodemus flavicollis* captured at the study area, and divided by year. These numbers were used to calculate modelled population densities by POPAN method.

Year	Number captured	Number recaptured
1988	58	40
1989	50	61
1990	38	86
1991	53	96
1992	51	106
1993	37	108
1994	22	20
1995	73	215
2000	12	24
2001	25	41
2002	19	11
2003	32	19
2004	62	69
2005	41	18

after having taken these measurements, and recorded their sex and sexual status (i.e., active/inactive) (see Amori et al., 2000).

Statistical analyses

In order to assess growth rates and to build a growth curve, we used the difference of the body length between two consecutive captures of the same sample. We analysed independently datasets relative to males and females. Growth curves for males and females were generated by the linking of means method in the programme FiSAT II (Gayanilo et al., 2005). This method was used to estimate the von Bertalanffy (1938) growth function parameters L_∞ (the mean asymptotic body length) and k (growth coefficient), assuming that this function can describe the growth in the observed body length range.

In order to estimate the population size, we used the Jolly–Seber open population model using the POPAN procedure, calculated by the program Mark (version 4.3). The POPAN method allows the estimation of four parameters: apparent survival rate (ϕ), recapture rate (p), immigration/natality rate (*pent*), and population size (N), all being assessed either time-dependent or time-independent. For more details, see Gracceva et al. (2008).

All data were checked for normality and homoscedasticity prior to apply any parametric test. Alpha was assessed at 5%, and all tests were two-tailed. All analyses were performed by a Statistica 11.4 software. Monte Carlo permutations were generated by the EcoSim 7.0 software, and Monte Carlo ANOVA analyses were done under the module 'Standard tests' in this software (Gotelli and Entsminger, 2004). A total of 30,000 iterations was used for Monte Carlo ANOVA in order to avoid algorithm biases (Luiselli, 2008).

Results and discussion

The numbers of captured mice (including the recapture events) by year is given in Table 1. There was no difference in the body length (mm) of adult females and males, but the females grew faster ($F_{1,\ 97} = 8.7492$, $p = 0.00389$; Fig. 1) reaching adult size approximately after two months, while the male only reached adult size at 4–5 months ($k = 0.186$/month; $L_\infty = 112$ mm; Fig. 2). Growth tended to nearly stop after 6 months of life (Fig. 2). Obviously these values may not be totally realistic, and the von Bertalanffy growth function described by them should be considered as an approximation of growth in the observed size range.

There were significant inter-annual differences in individual growth rates ($F_{12,\ 85} = 7.3087$, $p = 0.00000$), with mice captured in the year 1994 showing a much higher growth rate than those captured in other years (Fig. 3A). Modelled population density varied significantly among years (Monte Carlo ANOVA, pseudo-$F = 21.43$, $p < 0.001$; see Fig. 3B). Overall, there was a significant inverse relationship between mean growth yearly rate and yearly modelled density (Fig. 4).

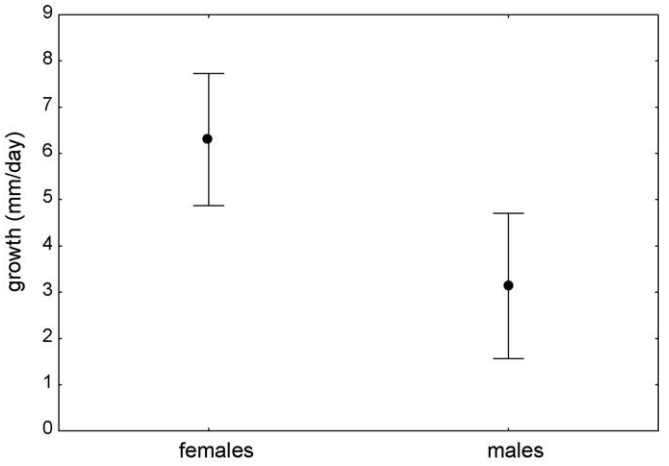

Fig. 1. Intersexual differences in individual growth rates (one-way ANOVA: ($F_{1,\ 97} = 8.7492$, $p = 0.00389$).

Our study revealed three main patterns: (i) in the field, female mice grew faster than males of comparable size (body length), (ii) growth rates strongly varied inter-annually, and (iii) there was a clear density-dependence mechanism between population density and intrinsic growth rate, with growth being decelerated at density increases in both males and females.

Concerning issue (i), the few data available on wild mice populations are contradictory: indeed, males grew faster in *A. sylvaticus* from a hot dry Mediterranean area in Portugal (Rosario and Mathias, 2004), whereas females grew faster in a laboratory group of *A. sylvaticus* (Quéré and Vincent, 1987). Although our data can be difficult to generalize given the scattered bibliographic information available, it remains that in our study area the intersexual difference in growth rates was clear and evident for a very long time-span. We suggest that the faster growth of females is linked to a reproductive advantage in the cold climate of our study area, as an earlier sexual maturity may increase the likelihood of producing an additional litter, especially because cold climate mice show a strong reproductive seasonality compared to conspecifics from warmer climates which are able to bear the whole year round (e.g., Amori et al., 2000).

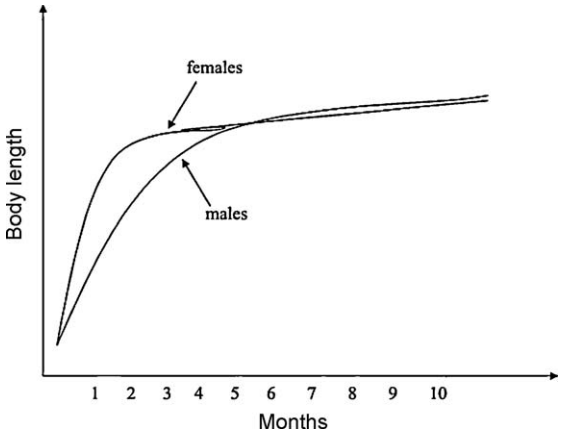

Fig. 2. Growth trajectories of male and female *Apodemus flavicollis* by von Bertalanffy (1938) growth function.