

Individual growth rates in natural field vole, *Microtus agrestis*, populations exhibiting cyclic population dynamics

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Abstract Rodents that have multi-annual cycles of density are known to have flexible growth strategies, and the “Chitty effect”, whereby adults in the high-density phase of the cycle exhibit larger average body mass than during the low phase, is a well-documented feature of cyclic populations. Despite this, there have been no studies that have repeatedly monitored individual vole growth over time from all phases of a density cycle, in order to evaluate whether such variation in body size is due to differences in juvenile growth rates, differences in growth periods, or

differential survival of particularly large or small voles. This study compares growth trajectories from voles during the peak, increase and crash phases of the cycle in order to evaluate whether voles are exhibiting fast or slow growth strategies. We found that although voles reach highest asymptotic weights in the peak phase and lowest asymptotes during the crash, initial growth rates were not significantly different. This suggests that voles attain larger body size during the peak phase as a result of growing for longer.

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Introduction

Within populations of mammals, body size is often correlated with biologically significant processes such as survival and reproduction, with larger individuals better able to compete for resources and having higher reproductive output (Cuthill and Houston 1997; Blanckenhorn 2000; Gaillard et al. 2000). However, there is evidence from a wide range of taxa suggesting that animals exhibit sub-maximal growth rates, and that this strategy may be selectively advantageous depending on the individual's internal state and the environmental conditions encountered (Arendt 1997; Case 1978; Nylin and Gotthard 1998; Blanckenhorn 2000). Life history theory predicts that faster growth rates incur a cost, due to there being trade-offs in the allocation of resources between growth and other requirements, such as somatic development, immune responses, reproduction and survival against predation (Arendt 1997; Mangel and Stamps 2001; Blanckenhorn 2000; Lima 1998). Therefore, within a population, mixed

strategies of growth and reproduction may exist (see, for example, Fleming 1996; Koseki and Maekawa 2000).

Microtine rodents are multivoltine, live in a highly seasonal environment, and have flexible growth strategies. Ecologists have been interested for decades in understanding the causes of cyclic fluctuations in abundance observed in many vole and lemming populations at northern latitudes. One controversial issue has been the relative contributions of trophic interactions and changes in the quality of individuals to the demographic changes that underpin such cycles (Krebs 1978). It has long been noted that changes in abundance are accompanied by changes in characteristics of individuals, including their body weights. Indeed, the so-called Chitty effect (Chitty 1952; sensu Boonstra and Krebs 1979), whereby adults in the increasing and high-density phase of the cycle exhibit larger average body mass (20–30% heavier) than during the low phase, is an important feature of cyclic populations (Mihok et al. 1985; Chitty 1987; Lidicker and Ostfeld 1991; Norrdahl and Korpimäki 2002), and it has been argued that understanding the Chitty effect is fundamental to explaining population cycles (Krebs 1978). Such phase-related changes in body size are widely accepted to be a consequence of variation in environmental conditions, rather than due to genetic differences between individuals (Stenseth 1999; Ergon et al. 2001a; Klemola et al. 2003; Turchin 2003). Oli (1999) suggests that the observed variation in body size is due to a phase-related trade-off in the dynamic allocation of energy between growth and reproduction, reproduction being suppressed during the late-increase and peak phases, such that resources are allocated to somatic growth (longer continuous growth).

Although phase-related changes in body sizes are well documented, most studies investigating variation in body sizes within and between populations in the wild have tended to utilise cross-sectional population data (but see Iverson and Turner 1974; Hansson 1995; Ergon et al. 2001b; Aars and Ims 2002) rather than repeated measurements of individual mass through time (longitudinal data), and have not investigated all phases of the density cycle. Hence, such studies cannot address directly the question of whether such changes in body size arise from variation in juvenile growth rates (as addressed in this study), in growth periods, or due to the differential survival of particularly large or small voles. Understanding how body size variation arises is crucial if we are to understand whether such variation is adaptive to the changing environmental conditions observed through the cycle, or whether voles are constrained to exhibit smaller body sizes.

This paper aims to evaluate whether field voles (*Microtus agrestis* L.) in Kielder Forest, UK are exhibiting submaximal growth rates, and whether submaximal growth rates and asymptotic weights (upper asymptotic size) are

linked to particular phases of the multi-annual cycle. While the multi-annual cycles of density exhibited by voles at Kielder have lower amplitude than cycles found in Fennoscandia owing to higher estimated densities in the low phase (Lambin et al. 2000), clear crashes in population density are observed and are known to be associated with the Chitty effect (Ergon et al. 2001a). Further, we test whether the predictions of Oli (1999) regarding a trade-off between growth and reproduction apply not only between years (phases) but also within years (though not specifically considered by Oli). We evaluate whether voles born early in the year (typically reproducing in their year of birth) exhibited a short growing strategy when compared to individuals born late in the year (which typically delay reproduction until the following year).

Materials and methods

Hypotheses tested

This analysis aimed to evaluate whether variation in the distribution of asymptotic weights in cyclic populations, the Chitty effect, arises from variation in juvenile growth strategies. We first consider between-year variation, and test the main hypothesis that voles born during the peak density years of the cycle exhibit faster growth and reach higher asymptotic weights than voles born during the increase phase, as a result of higher initial growth rates and/or delayed deceleration in growth, whereas voles born during the crash phase reach the lowest asymptotic weights for equivalent reasons. We also test subsidiary hypotheses on within-year variation in growth strategies in order to ascertain whether differences in growth between years of the cycle were not due to variation in population structure. Specifically, we evaluate whether voles from early cohorts exhibit faster (or slower) growth strategies than late-born voles, whether growth patterns differ between males and females, and whether differences in the proportions of these sub-groups might account for any phase-related differences.

Study site and trapping methods

The study took place in Kielder Forest (55°13'N, 2°33'W), a commercial plantation forest where field voles exhibit multi-annual cycles (details of study area in Lambin et al. 2000) with a 3- to 4-year periodicity, during a longitudinal study undertaken between 2001 and 2007. Voles were trapped in four similar-sized clear-cuts (referred to as BHP, KCS, PLJ and ROB), in two areas of the forest approximately 12 km apart, between May 2001 and March 2007. Population size fluctuated during the study period, reaching

peak densities during 2003 and subsequently crashing to low levels in 2004 [range: 31 voles/ha (95% CI 23–40) to 746 voles/ha (95% CI 674–817)]. Clear seasonal patterns in density fluctuation were overlaid on the multi-annual fluctuations, with summer peaks and over-winter declines in density (Fig. 1). Vole density estimates for each primary session were calculated using Huggins's closed capture models within a robust design (Kendall and Nichols 1997; Huggins 1989) fitted using program MARK (White and Burnham 1999) using mixture models (Pledger 2000) to allow heterogeneity in capture probabilities.

Populations were trapped in primary sessions every 28 days from March to November, and every 56 days from November to March. Each site had a permanent 0.3-ha live-trapping grid consisting of 100 Ugglan special mousetraps (Grahnb, Marieholm, Sweden), in optimal habitat dominated by *Deschampsia caespitosa* Beauv., *Agrostis tenuis* Sibth., and *Juncus effusus* L. Traps were set at 5-m intervals and baited with wheat and carrots. Traps were pre-baited with a slice of carrot and a few grams of oats 3 days before each trapping session, set at approximately 1800 hours on the first day and checked 5 times ("secondary sessions") at roughly 12-h intervals at dawn and dusk.

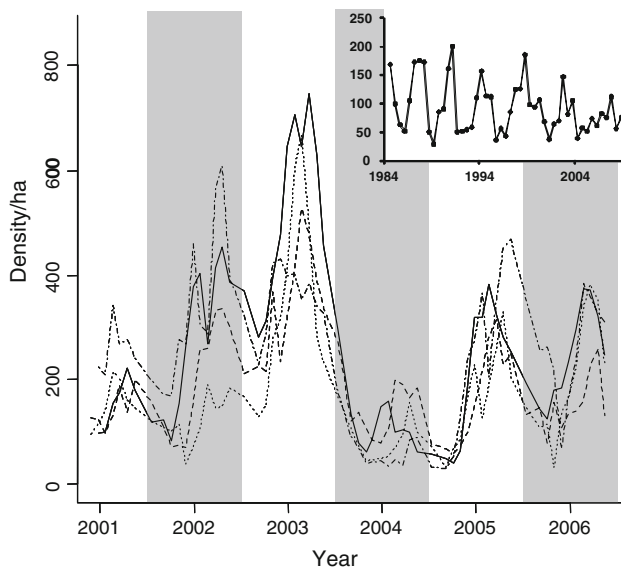


Fig. 1 Density of field voles per hectare throughout the period of study, for each of the four populations studied (indicated by different line types). Alternate years are highlighted in grey. The peak phase of the vole abundance occurs in 2003 (apart from one site where the peak occurred in 2002 and 2003), with the crash phase occurring in 2004. Densities were estimated using Huggins's closed capture models within a robust design, and for ease of interpretation, confidence limits are not included. Inset graph shows field population estimates based on indirect signs [the vole sign index; see Lambin et al. (2000) for details], indicating the cyclical nature of the field vole population beyond the time period of the current study

Individual animals were identified using subcutaneous microchip transponders (AVID, East Sussex, UK) injected into the skin at the back of the neck. Mass (measured to the nearest 0.5 g using a Pesola spring balance), sex and reproductive status were recorded at the time of first capture in each primary session.

Data-set analysed

The average mass of captive born field voles at 2 weeks (approximate age at weaning) was 11.3 g (SE = 0.43, $n = 18$ animals, weighed at age 12–16 days). Examining animals from Kielder Forest first caught weighing ≤ 12 g, revealed that 99% of these animals weighed 15 g or more on second capture (approximately 6 weeks old; Begon et al. 2009). Thus in our analyses we only included voles first caught weighing < 15 g, with voles first caught weighing ≤ 12 g assumed to be ≤ 2 weeks old and voles first caught weighing > 12 g but < 15 g assumed to be between 2 and 6 weeks old. Hence, in the analysis, vole age was defined based on trapping interval, with age 1 being a ≤ 2 -week-old vole, age 1.5 being a 2- to 6-week-old vole, age 2 being age 1 plus 4 weeks and so on. In order to confirm that inclusion of voles that may have been slightly older than 14 days at first capture did not bias our conclusions, all analyses were also repeated on data only including voles first caught ≤ 12 g in weight. Throughout, we only investigate growth rates and asymptotic weights of voles during their first 6 months. Many voles will undergo sexual maturation over this time span and gestation would add unwelcome noise to our data. We thus removed all records of reproductively active females, defined as those recorded as having a perforate vagina or having been recorded as gestating in the field, as well as any record from the month preceding such a record. In order to confirm that any differences in growth rates observed between phases were not due to differential proportions of reproductive females between phases or seasons, the analysis was repeated using data on male voles only.

Voles were recorded as having been caught in the "peak" phase of the cycle if they were born during the year of highest recorded density (2003 for all sites, 2002 and 2003 for ROB). The "crash" year occurred in 2004 and was defined as the year with the lowest recorded vole densities and no significant summer increase in density. The "increase" phase was defined as being any year where vole densities increased over the summer following the crash phase (2001, 2005 and 2006 for all sites; 2002 for all sites except ROB; see Fig. 1). We also investigated whether present density was a better predictor of vole growth rates than cycle phase which largely reflects past density. Voles were subdivided into an "early" cohort if they were born before 21 June, and "late" cohort if they were born on

or after 21 June. The June solstice was selected a priori as a time-point dividing the breeding season.

All analyses were undertaken using the statistical software R (R Development Core Team 2007) using the package nlme (Pinheiro et al. 2007).

Selection of growth curves

We analysed growth curves to estimate growth rate, asymptotic weight and the age at which maximum growth occurs (point of inflection), the latter indicating therefore at what age the juvenile rapid growth phase slows down. Clearly these three parameters of the growth curve are related: for example, an individual exhibiting a fast growth rate for a prolonged time will reach a high asymptotic weight.

In order to determine which growth curve best fitted the overall data, three models were fitted to the observed vole weight at age data: Gompertz, von Bertalanffy, and logistic (Pruitt et al. 1979; Ricker 1979; Ricklefs 1983). Parameters in the growth curve equations are defined as follows: wt is the dependent variable (vole mass in g), vole age is the explanatory variable, asym is the upper asymptotic size, r is the growth rate constant, and I is the age at the inflection point (Zullinger et al. 1984). Growth equations are:

$$\text{Gompertz: } wt = \text{asym} \times \exp\{-\exp -r(\text{age} - I)\}$$

$$\text{Von Bertalanffy: } wt = \text{asym}\{1 - \exp(-r[\text{age} - I])\}$$

$$\text{Logistic: } wt = \text{asym}\{1 + \exp(-r[\text{age} - I])\}^{-1}$$

Model fits were assessed by Akaike's information criterion (AIC; Akaike 1973). Models with a difference of AIC (ΔAIC) of less than 2 may be considered similar in their ability to account for the data (Sakamoto et al. 1986). According to the principal of parsimony, if two alternative models had indistinguishable AIC values ($\Delta\text{AIC} < 2$), the model with fewer parameters was selected.

Data analysis

In order to test the hypotheses, growth curves, using the best growth model, were compared between different phases of the cycle (peak, increase and crash), between the sexes, and between the early and late cohorts, using the likelihood ratio test following Kimura (1980). Growth curves were also compared between cycle phases for early voles and late voles separately, in order to confirm that any observed differences between phases were not due to variation in seasonal categories. Due to the longitudinal nature of the data, individuals were repeatedly sampled over time, potentially leading to pseudo-replication. Hence, model fitting was repeated on

a randomly generated subset of data, utilising one data point per vole. Model fitting was also repeated on a data set excluding the top 2.5% of outlying residual values in order to confirm that the observed patterns were not driven by a small number of particularly fast growing voles.

Results

Fifty-five juvenile voles (138 weights) met our criteria during the crash phase, 234 (721 weights) during the increase and 239 voles (697 weights) during the peak phase of the multi-annual cycle. Of the crash voles: 31 were female and 24 were male, and nine and 46 were from the early and late cohorts, respectively. Similarly for increase voles: 103 were female and 131 male, and 40 and 194 were from the early and late cohorts, while 105 of the peak voles were female and 134 male; and 97 were from the early cohort and 142 from the late cohort.

Field voles first caught when 2 weeks old or younger exhibited wide variation in growth trajectories (Fig. 2). The logistic growth model was the best descriptor of growth (ΔAIC 30.63 for Gompertz, and ΔAIC 67.11 for Bertalanffy when compared to the logistic model) and was thus used in all subsequent analyses. Male and female voles had significantly different logistic growth curves (Table 1; ΔAIC 55.51). Males reached a significantly greater estimated asymptotic weight (21.50 ± 0.15 g for males;

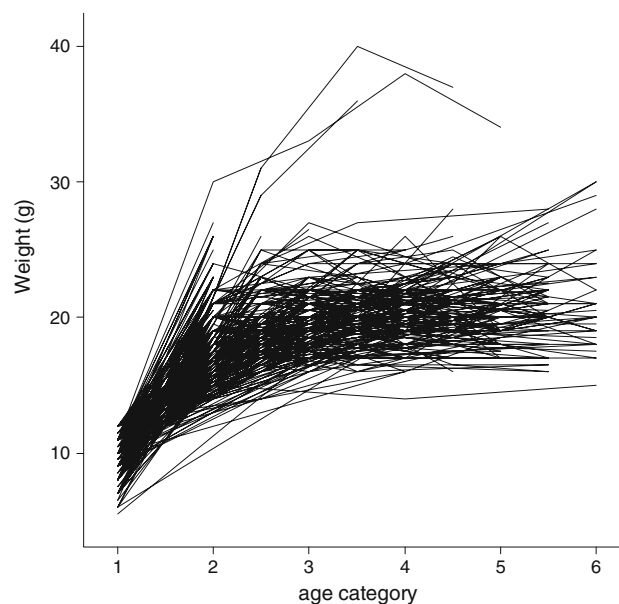


Fig. 2 Plot of individual trajectories of the 528 voles considered in this study, showing the variation in individual growth with increasing age

Table 1 Likelihood ratio test for the parameters of the logistic growth curves in females and males

	Base case ^a	Coincident ^b	Asym	<i>I</i>	<i>r</i>
Female					
Asymptotic weight (g)	20.11	20.84	20.87	20.33	20.15
Age category of inflection	1.02	1.09	1.06	1.09	1.02
Growth rate (g/age category)	0.48	0.50	0.55	0.47	0.49
Male					
Asymptotic weight (g)	21.50	20.84	20.87	21.31	21.47
Age category of inflection	1.16	1.09	1.13	1.09	1.16
Growth rate (g/age category)	0.50	0.50	0.46	0.52	0.49
ΔAIC	1.35	55.51	44.99	29.11	0
Number of parameters	6	3	5	5	5

The best models [lowest Akaike information criterion (*AIC*)] are indicated in *bold* with the Δ*AIC* reported between the other models. *Asym* Assumes that the asymptotic weight is equal for the two separate curves, *I* assumes that the age at inflection point (age at which growth rate decelerates) is the same for the two curves, *r* assumes that the growth rate is the same for the two curves

^a Base case is where two separate curves are fitted for the female and male voles

^b Coincident results are for a single curve fitted through the data

Table 2 Likelihood ratio test for the parameters of the logistic growth curves in early voles (born before 21 June) and late voles (born after 21 June)

	Base case ^a	Coincident ^b	Asym	<i>I</i>	<i>r</i>
Early voles					
Asymptotic weight (g)	21.75	20.82	20.89	21.48	21.92
Age category of inflection	1.16	1.09	1.12	1.10	1.16
Growth rate (g/age)	0.46	0.49	0.42	0.47	0.50
Late voles					
Asymptotic weight (g)	20.59	20.82	20.89	20.67	20.52
Age category of inflection	1.07	1.09	1.08	1.10	1.07
Growth rate (g/age)	0.52	0.49	0.54	0.51	0.50
ΔAIC	0	43.10	21.68	10.90	1.51
Number of parameters	6	3	5	5	5

The best models (lowest *AIC*) are indicated in *bold* with the Δ*AIC* reported between the other models. For abbreviations, see Table 1

^a Base case is where two separate curves are fitted for the early and late voles

^b Coincident results are for a single curve fitted through the data

20.11 ± 0.14 g for females) and decelerated more slowly (estimated deceleration point for males is at age 1.16 ± 0.02 compared to 1.02 ± 0.02 for females), but there was no significant difference in initial growth rates (0.50 ± 0.02 g/28 days for males and 0.48 ± 0.02 g/28 days for females).

Voies from early annual cohorts exhibited different growth strategies from voies from late cohorts (after 21 June; Δ*AIC* 43.10; Table 2; Fig. 3). There were significant differences in the asymptotic weight reached, with early cohort voies reaching higher weights than late voies (21.75 ± 0.22 g for early; 20.59 ± 0.12 g for late), and growth rate decelerating at a younger age in late cohort voies (age 1.16 ± 0.02 vs. 1.07 ± 0.01 for late), but there was no significant difference in initial growth rates

(0.46 ± 0.03 g/28 days for early and 0.52 ± 0.02 g/28 days for late; Table 2).

There was no evidence that estimated vole mass at first capture (weaning) varied between the different phases of the cycle (mean weight at age 1: 9.67 (*n* = 33) for crash; 9.94 (*n* = 125) for increase; 9.92 (*n* = 144) for peak; *F*_{2,299} = 0.48, *P* = 0.62). However, growth curves were significantly different between the cycle phases (Table 3; Δ*AIC* = 95.34; Fig. 4). There were significant differences in the asymptotic weight reached, with peak phase voies reaching a weight of 21.79 ± 0.16 g, compared to 20.14 ± 0.17 g for increase phase voies, and 19.82 ± 0.50 g for crash phase voies. Growth rates of voies during the peak phase decelerated at a later age category (1.14 ± 0.02) than increase or crash voies

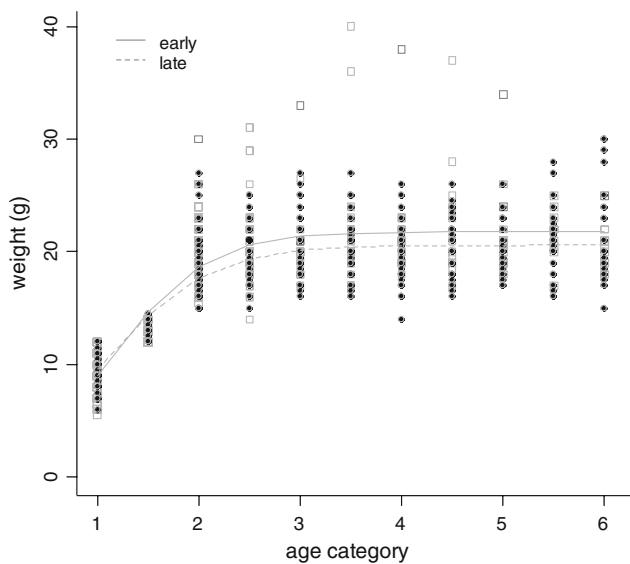


Fig. 3 Logistic growth curve fitted to the weight at age data for field voles born early in the season (before 21 June shown as *grey squares*), and those born late (after 21 June shown as *black filled circles*)

(1.05 ± 0.02), but there was no significant difference in initial growth rates between the phases (crash growth rate 0.46 ± 0.06 g/28 days; increase 0.51 ± 0.03 g/28 days; peak 0.49 ± 0.02 g/28 days).

Analyses of the hypothesis that growth curves were significantly different between phases (Δ AIC between the coincident model and the best model where the asymptotic weights and age at inflection differed but growth rate was

constant) were robust to the exclusion of individuals who contributed one or more outlier observations (remaining data $n = 499$ individuals; $n = 1,472$ weights; Δ AIC 93.84); when undertaken on a dataset only comprising individuals first caught ≤ 12 g in weight ($n = 302$ individuals; $n = 910$ weights; Δ AIC 24.49); and when model fitting was repeated on a randomly generated subset of data, utilising one data point per vole ($n = 528$ weights; Δ AIC 21.58). Moreover, the pattern and significance of the differences between the growth curves for the crash, increase and peak phases remained when late and early cohort voles were analysed separately (early voles, $n = 146$ individuals, $n = 392$ weights, Δ AIC 10.49; late voles, $n = 382$ individuals, $n = 1,164$ weights, Δ AIC 63.60) and when males and females were analysed separately (males, $n = 289$ individuals, $n = 822$ weights, Δ AIC 47.50; females $n = 239$ individuals, $n = 734$ weights, Δ AIC 48.65). Parameter estimates were very similar to those when the sexes and the cohorts were analysed together.

Vole density was not a better predictor of vole growth rates than cycle phase. Voles from low, medium and high densities (based on the range of densities divided into three categories) differed significantly (Δ AIC = 5.84 when compared to the coincident model), with voles born during months of high density reaching significantly higher asymptotic weights than those from low or medium density. There was, though, no support for a model with different growth trajectories for voles born in years

Table 3 Likelihood ratio test for the parameters of the logistic growth curves in voles during the crash, increase and peak phases of the population cycle

	Base case ^a	Coincident ^b	Asym	<i>I</i>	<i>r</i>
Crash phase					
Asymptotic weight (g)	19.82	20.84	20.95	20.04	19.97
Age category of inflection	1.05	1.09	1.09	1.09	1.04
Growth rate (g/age category)	0.46	0.50	0.56	0.46	0.50
Increase phase					
Asymptotic weight (g)	20.14	20.84	20.95	20.26	20.09
Age category of inflection	1.05	1.09	1.08	1.09	1.05
Growth rate (g/age category)	0.51	0.50	0.59	0.50	0.50
Peak phase					
Asymptotic weight (g)	21.79	20.84	20.95	21.62	21.81
Age category of inflection	1.14	1.09	1.10	1.09	1.14
Growth rate (g/age category)	0.49	0.50	0.44	0.50	0.50
Δ AIC	3.07	95.34	66.17	13.74	0
Number of parameters	6	3	5	5	5

The best model (lowest AIC) is indicated in *bold*. *Asym* Assumes that the asymptotic weight is equal for the two separate curves, *I* assumes that the age at inflection point (age at which growth rate decelerates) is the same for the two curves, *r* assumes that the growth rate is the same for the two curves

^a Base case is where two separate curves are fitted for the early and late voles

^b Coincident results are for a single curve fitted through the data

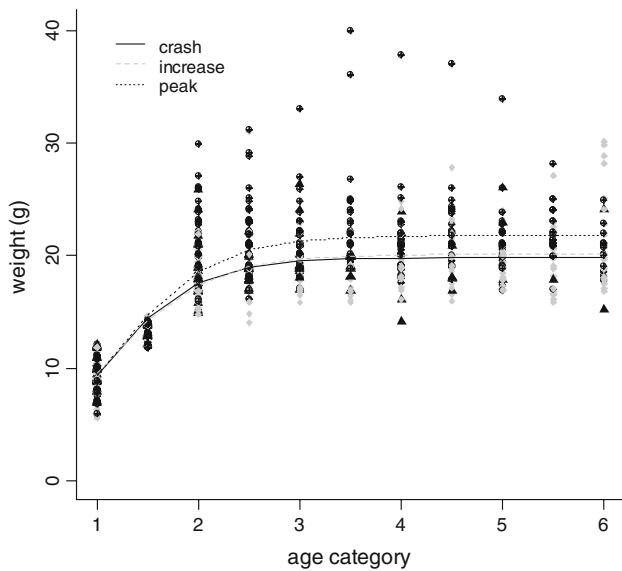


Fig. 4 Logistic growth curve fitted to the weight at age data for the field voles from the peak (filled black circles), increase (grey filled circles) and crash (black filled triangles) phases of the cycle

with low, medium or high densities in the spring (March/April) of the year of birth ($\Delta\text{AIC} = 1.63$). Overall, phase was a better predictor of growth rates than density ($\Delta\text{AIC} = 35.04$ for current density, and $\Delta\text{AIC} = 14.04$ for spring density when compared to the best phase model).

Discussion

The most striking finding of this analysis of growth trajectories in field voles during a population cycle is that initial growth rates were remarkably consistent between phases of the cycle, and between sexes and the season of birth (early or late). However, there is strong evidence that the age at which growth rates decelerate, and also the asymptotic weights reached, vary between cycle phases. The main aim of this paper was to evaluate whether the Chitty effect, whereby adults in the high-density phase of the cycle exhibited larger average body mass than during the low phase of the cycle, could be explained by variation in juvenile growth rates in the different cycle phases. The Chitty effect is clearly present in Kielder voles, albeit at a lower magnitude than the 20–30% reported in previous studies (Mihok et al. 1985; Chitty 1987; Lidicker and Ostfeld 1991; Norrdahl and Korpimäki 2002), with the difference between the asymptotic weights of voles observed during the crash/increase phase and between those during the peak being 1.84 g (representing 8.8% of the total body weight of an average vole). However, this difference was

not due to voles exhibiting faster growth rates, but rather to voles growing for longer.

These differences in the length of the juvenile growth period between voles during the peak phase and those during the increase and crash phase were not due to differences in population structure between phases. Separate analysis of males and females, and of early cohort and late cohort voles, found that the pattern and significance of the differences between the growth curves for the phases remained robust.

It should be noted that due to lower numbers of voles being observed during the crash period, there was only limited power to detect significant differences in initial growth rates during this phase, and such differences cannot therefore be ruled out altogether. Also, further laboratory work would be necessary to evaluate whether this (apparently consistent) growth rate represents a physiological maximum. Nonetheless, the present results do not support the hypothesis that individuals exhibit sub-maximal juvenile growth rates during certain phases of the cycle due to variable environmental conditions.

Although the Chitty effect has received much attention, there is relatively little evidence evaluating its relevance to broader life history theory and predicting trade-offs between growth strategies and other biologically significant processes in multivoltine organisms (Stenseth and Ims 1993; however, see Lambin and Yoccoz 2001). Reproduction, particularly sexual maturation of juveniles, is known to be inhibited during times of high population density in cyclic *Microtus* rodents (Boonstra 1989; Boyce and Boyce 1988; Myllymäki 1977; Ostfeld et al. 1993). Suppression of reproduction may arise due to limited availability or poor quality of food resources; due to suppression by dominant individuals or by puberty-delaying hormones secreted by littermates; and by pre- or post-natal stress (see Oli 1999 for a more detailed review). It has been suggested that the Chitty effect is a consequence, not a cause, of cyclic population fluctuations, and of phase-related changes in demographic processes, especially the age at first reproduction (Oli 1999; Lidicker and Ostfeld 1991).

Oli (1999), in particular, hypothesised that the Chitty effect was due to a trade-off between reproductive effort and somatic growth, in which individuals born during peak densities, especially those in the earlier cohorts, would suppress reproduction and thus have energy and resources available to allow them to grow for a longer period of time and reach a higher body mass, compared to those born in the low or early increase phase. Our finding that the Chitty effect is not due to differences in growth rates, but rather to differences in the length of growth periods, and that this applies to the earlier cohorts, directly supports this hypothesis. Further empirical work is now necessary to

evaluate the further consequences of this, and in particular whether there is also differential survival of the different size classes.

Finally, it is interesting to note that the contrast between those born early in the year (active reproduction, prolonged growth) and those born later (delayed reproduction, fore-shortened growth) does not support the idea of a trade-off. Neither, though, do the results support the idea that early cohort voles grow rapidly (as opposed to growing for longer) in order to arrive sooner at a weight that permits reproduction. This in turn suggests that those born later in the year either have fewer total metabolic resources available to allocate to different vital processes, or that they divert resources freed up by delayed reproduction to something other than prolonged growth.

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