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

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26

1 **Abstract**

2 Rodents that have multi-annual cycles of density are known to have flexible growth
3 strategies, and the “Chitty effect”, whereby adults in the high-density phase of the cycle
4 exhibit larger average body mass than during the low phase, is a well-documented feature of
5 cyclic populations. Despite this, there have been no studies that have repeatedly monitored
6 individual vole growth over time from all phases of a density cycle, in order to evaluate
7 whether such variation in body size is due to differences in juvenile growth rates, differences
8 in growth periods, or differential survival of particularly large or small voles. This study
9 compares growth trajectories from voles during the peak, increase and crash phases of the
10 cycle in order to evaluate whether voles are exhibiting fast or slow-growth strategies. We
11 found that although voles reach highest asymptotic weights in the peak phase and lowest
12 asymptotes during the crash, initial growth rates were not significantly different. This
13 suggests that voles attain larger body size during the peak phase as a result of growing for
14 longer.

15

16 **Keywords:** Chitty effect; juvenile growth; multi-annual density cycles; rodent; body size.

17

18

1 **Introduction**

2 Within populations of mammals, body size is often correlated with biologically
3 significant processes such as survival and reproduction, with larger individuals better able to
4 compete for resources and having higher reproductive output (Cuthill and Houston 1997;
5 Blanckenhorn 2000; Gaillard *et al.* 2000). However, there is evidence from a wide range of
6 taxa suggesting that animals exhibit submaximal growth rates, and that this strategy may be
7 selectively advantageous depending on the individual's internal state and the environmental
8 conditions encountered (Arendt 1997; Case 1978; Nylin and Gottard 1998; Blanckenhorn
9 2000). Life-history theory predicts that faster growth rates incur a cost, due to there being
10 trade-offs in the allocation of resources between growth and other requirements, such as
11 somatic development, immune responses, reproduction and survival against predation (Arendt
12 1997; Mangel and Stamps 2001; Blanckenhorn 2000; Lima 1998). Therefore, within a
13 population, mixed strategies of growth and reproduction may exist (see, for example, Fleming
14 1996; Koseki and Maekawa 2000).

15 Microtine rodents are multivoltine, live in a highly seasonal environment, and have
16 flexible growth strategies. Ecologists have been interested for decades in understanding the
17 causes of cyclic fluctuations in abundance observed in many vole and lemming populations at
18 northern latitudes. One controversial issue has been the relative contributions of trophic
19 interactions and changes in the quality of individuals to the demographic changes that
20 underpin such cycles (Krebs 1978). It has long been noted that changes in abundance are
21 accompanied by changes in characteristics of individuals, including their body weights.
22 Indeed, the so-called "Chitty effect" (Chitty 1952; *sensu* Boonstra and Krebs 1979), whereby
23 adults in the increasing and high-density phase of the cycle exhibit larger average body mass
24 (20-30% heavier) than during the low-phase, is an important feature of cyclic populations
25 (Mihok *et al.* 1985; Chitty 1987; Lidicker and Ostfeld 1991; Norrdahl and Korpimäki 2002),

1 and it has been argued that understanding the Chitty effect is fundamental to explaining
2 population cycles (Krebs *et al.* 1978). Such phase related changes in body size are widely
3 accepted to be a consequence of variation in environmental conditions, rather than due to
4 genetic differences between individuals (Stenseth 1999; Ergon *et al.* 2001a; Klemola *et al.*
5 2003; Turchin 2003). Oli (1999) suggests that the observed variation in body size is due to a
6 phase-related trade-off in the dynamic allocation of energy between growth and reproduction,
7 reproduction being suppressed during the late-increase and peak phases, such that resources
8 are allocated to somatic growth (longer continuous growth).

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

20 This paper aims to evaluate whether field voles (*Microtus agrestis* L.) in Kielder
21 Forest, UK are exhibiting submaximal growth rates, and whether submaximal growth rates
22 and asymptotic weights (upper asymptotic size) are linked to particular phases of the multi-
23 annual cycle. While the multi-annual cycles of density exhibited by voles at Kielder have
24 lower amplitude than cycles found in Fennoscandia owing to higher estimated densities in the
25 low phase (Lambin *et al.* 2000), clear crashes in population density are observed and are

1 known to be associated with the Chitty effect (Ergon *et al.* 2001a). Further, we test whether
2 the predictions of Oli (1999) regarding a trade-off between growth and reproduction apply not
3 only between years (phases) but also within years (though not specifically considered by Oli).
4 We evaluate whether voles born early in the year (typically reproducing in their year of birth)
5 exhibited a short-growing strategy when compared to individuals born late in the year (which
6 typically delay reproduction until the following year).

7

8 **Methods**

9 *Hypotheses tested*

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

23

24 *Study site and trapping methods*

1 The study took place in Kielder Forest (55°13" N, 2°33" W), a commercial plantation
2 forest where field voles exhibit multi-annual cycles (details of study area in Lambin *et al.*
3 2000) with a 3-4 year periodicity, during a longitudinal study undertaken between 2001 and
4 2007. Voles were trapped in four similar-sized clear-cuts (referred to as BHP, KCS, PLJ and
5 ROB), in two areas of the forest approximately 12 km apart, between May 2001 and March
6 2007. Population size fluctuated during the study period, reaching peak densities during 2003
7 and subsequently crashing to low levels in 2004 (range: 31 voles/ha (95% CI 23-40) to 746
8 voles/ha (95% CI 674-817)). Clear seasonal patterns in density fluctuation were overlaid on
9 the multi-annual fluctuations, with summer peaks and over-winter declines in density (Figure
10 1). Vole density estimates for each primary session were calculated using Huggins's closed
11 capture models within a robust design (Kendall and Nichols 1997; Huggins 1989) fitted using
12 program MARK (White and Burnham 1999) using mixture models (Pledger 2000) to allow
13 heterogeneity in capture probabilities.

14 Populations were trapped in primary sessions every 28 days from March to November,
15 and every 56 days from November to March. Each site had a permanent 0.3ha live-trapping
16 grid consisting of 100 Ugglan Special Mousetraps (Grahnb, Marieholm, Sweden), in optimal
17 habitat dominated by *Deschampsia caespitosa* Beauv., *Agrostis tenuis* Sibth., and *Juncus*
18 *effusus* L. Traps were set at 5m intervals and baited with wheat and carrots. Traps were pre-
19 baited with a slice of carrot and a few grams of oats 3 days before each trapping session, set at
20 approximately 18:00 on the first day and checked five times ("secondary sessions") at roughly
21 12 hour intervals at dawn and dusk.

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

1 *Data-set analysed*

2 The average mass of captive born field voles at 2 weeks (approximate age at weaning)
3 was 11.3g (S.E.=0.43, n=18 animals, weighed at age 12-16 days). Examining animals from
4 Kielder Forest first caught weighing ≤ 12 g, revealed that 99% of these animals weighed 15g or
5 more on second capture (approximately 6 weeks old) (Begon *et al. In Press*). Thus in our
6 analyses we only included voles first caught weighing < 15 g, with voles first caught weighing
7 ≤ 12 g assumed to be ≤ 2 weeks old and voles first caught weighing > 12 g but less than 15g
8 assumed to be between 2 and 6 weeks old. Hence, in the analysis, vole age was defined based
9 on trapping interval, with age 1 being a ≤ 2 week old vole, age 1.5 being a 2-6 week old vole,
10 age 2 being age 1 plus 4 weeks and so on. In order to confirm that inclusion of voles that may
11 have been slightly older than 14 days at first capture did not bias our conclusions, all analyses
12 were also repeated on data only including voles first caught ≤ 12 g in weight. Throughout, we
13 only investigate growth rates and asymptotic weights of voles during their first 6 months.
14 Many voles will undergo sexual maturation over this time span and gestation would add
15 unwelcome noise to our data. We thus removed all records of reproductively active females,
16 defined as those recorded as having a perforate vagina or having been recorded as gestating in
17 the field, as well as any record from the month preceding such a record. In order to confirm
18 that any differences in growth rates observed between phases were not due to differential
19 proportions of reproductive females between phases or seasons, the analysis was repeated
20 using data on male voles only.

21 Voles were recorded as having been caught in the “peak” phase of the cycle if they were
22 born during the year of highest recorded density (2003 for all sites, 2002 and 2003 for ROB).
23 The “crash” year occurred in 2004 and was defined as the year with the lowest recorded vole
24 densities and no significant summer increase in density. The “increase” phase was defined as
25 being any year where vole densities increased over the summer following the crash phase

1 (2001, 2005 and 2006 for all sites; 2002 for all sites except ROB) (see Figure 1). We also
 2 investigated whether present density was a better predictor of vole growth rates than cycle
 3 phase which largely reflects past density. Voles were subdivided into an “early” cohort if they
 4 were born before the 21st June, and “late” cohort if they were born on or after the 21st June.
 5 The June solstice was selected a-priori as a time-point dividing the breeding season.

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

8

9 *Selection of growth curves*

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

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

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

22 *Von Bertalanffy:*
$$wt = asym\{1 - \exp(-r(age - I))\}$$

23 *Logistic:*
$$wt = asym\{1 + \exp(-r(age - I))\}^{-1}$$

24 Model fits were assessed by Akaike’s Information Criterion (Akaike 1973). Models with a
 25 difference of AIC (ΔAIC) of less than 2 may be considered similar in their ability to

1 account for the data (Sakamoto, Ishiguro & Kitagawa 1986). According to the principal
2 of parsimony, if two alternative models had indistinguishable AIC values ($\Delta AIC < 2$), the
3 model with fewer parameters was selected.

4

5

6 ***Data Analysis***

7 In order to test the hypotheses, growth curves, using the best growth model, were
8 compared between different phases of the cycle (peak, increase and crash), between the sexes,
9 and between the early and late cohorts, using the likelihood ratio test following Kimura
10 (1980). Growth curves were also compared between cycle phases for “early” voles and “late”
11 voles separately, in order to confirm that any observed differences between phases were not
12 due to variation in seasonal categories. Due to the longitudinal nature of the data, individuals
13 were repeatedly sampled over time, potentially leading to pseudo-replication. Hence, model
14 fitting was repeated on a randomly generated subset of data, utilising one data point per vole.
15 Model fitting was also repeated on a data set excluding the top 2.5% of outlying residual
16 values in order to confirm that the observed patterns were not driven by a small number of
17 particularly fast growing voles.

18

19 **Results**

20 Fifty-five juvenile voles (138 weights) met our criteria during the “crash” phase, 234
21 (721 weights) during the “increase” and 239 voles (697 weights) during the “peak” phase of
22 the multi-annual cycle. Of the “crash” voles: 31 were female and 24 were male, and 9 and 46
23 were from the early and late cohorts respectively. Similarly for “increase” voles: 103 were
24 female and 131 male, and 40 and 194 were from the early and late cohorts, while 105 of the

1 “peak” voles were female and 134 male; and 97 were from the early cohort and 142 from the
2 late cohort.

3 Field voles first caught when 2 weeks old or younger exhibited wide variation in
4 growth trajectories (Figure 2). The logistic growth model was the best descriptor of growth
5 (ΔAIC 30.63 for Gompertz; and ΔAIC 67.11 for Bertalanffy when compared to the Logistic
6 model) and was thus used in all subsequent analyses. Male and female voles had significantly
7 different logistic growth curves (Table 1, ΔAIC : 55.51). Males reached a significantly greater
8 estimated asymptotic weight (21.50g \pm 0.15g for males; 20.11g \pm 0.14g for females) and
9 decelerated more slowly (estimated deceleration point for males is at age 1.16 \pm 0.02
10 compared to 1.02 \pm 0.02 for females), but there was no significant difference in initial growth
11 rates (0.50g/28 days \pm 0.02 for males and 0.48 g/28 days \pm 0.02 for females).

12 Voles from „early” annual cohorts exhibited different growth strategies from voles
13 from late cohorts (after 21st June) (ΔAIC : 43.10; Table 2; Figure 3). There were significant
14 differences in the asymptotic weight reached, with early cohort voles reaching higher weights
15 than late voles (21.75g \pm 0.22g for early; 20.59g \pm 0.12g for late), and growth rate decelerating
16 at a younger age in late cohort voles (age 1.16 \pm 0.02 vs 1.07 \pm 0.01 for late), but there was no
17 significant difference in initial growth rates (0.46g/28 days \pm 0.03 for early and 0.52/28 days
18 \pm 0.02 for late) (Table 2).

19 There was no evidence that estimated vole mass at first capture (weaning) varied
20 between the different phases of the cycle (mean weight at age 1: 9.67 (n=33) for “crash”; 9.94
21 (n=125) for “increase”; 9.92 (n=144) for “peak”; $F_{2,299}$ =0.48, p =0.62). However, growth
22 curves were significantly different between the cycle phases (Table 3; ΔAIC = 95.34; Figure
23 4). There were significant differences in the asymptotic weight reached, with peak phase voles
24 reaching a weight of 21.79 \pm 0.16g, compared to 20.14 \pm 0.17g for increase phase voles, and
25 19.82 \pm 0.50g for crash phase voles. Growth rates of voles during the peak phase decelerated

1 at a later age category (1.14 ± 0.02) than increase or crash voles (1.05 ± 0.02), but there was no
2 significant difference in initial growth rates between the phases (crash growth rate 0.46
3 ± 0.06 g/28 days; increase 0.51 ± 0.03 g/28 days; peak 0.49 ± 0.02 g/28 days).

4 Analyses of the hypothesis that growth curves were significantly different between
5 phases (Δ AIC between the coincident model and the best model where the asymptotic weights
6 and age at inflection differed but growth rate was constant) was robust to the exclusion of
7 individuals who contributed one or more outlier observations (remaining data $n=499$
8 individuals; $n=1472$ weights; Δ AIC: 93.84); when undertaken on a dataset only comprising
9 individuals first caught ≤ 12 g in weight ($n=302$ individuals; $n=910$ weights; Δ AIC: 24.49); and
10 when model fitting was repeated on a randomly generated subset of data, utilising one data
11 point per vole ($n=528$ weights; Δ AIC: 21.58). Moreover, the pattern and significance of the
12 differences between the growth curves for the crash, increase and peak phases remained when
13 late and early cohort voles were analysed separately (Early voles: $n= 146$ individuals, $n= 392$
14 weights, Δ AIC 10.49; Late voles: $n= 382$ individuals, $n= 1164$ weights, Δ AIC 63.60) and
15 when males and females were analysed separately (Males: $n= 289$ individuals, $n= 822$
16 weights, Δ AIC 47.50; Females: $n= 239$ individuals, $n= 734$ weights, Δ AIC 48.65). Parameter
17 estimates were very similar to those when the sexes and the cohorts were analysed together.

18 Vole density was not a better predictor of vole growth rates than cycle phase. Voles
19 from low, medium and high densities (based on the range of densities divided into three
20 categories) differed significantly (Δ AIC= 5.84 when compared to the coincident model), with
21 voles born during months of high density reaching significantly higher asymptotic weights
22 than those from low or medium density. There was, though, no support for a model with
23 different growth trajectories for voles born in years with low, medium or high densities in the
24 spring (March/April) of the year of birth (Δ AIC= 1.63). Overall, phase was a better predictor

1 of growth rates than density ($\Delta AIC= 35.04$ for current density; and $\Delta AIC= 14.04$ for spring
2 density when compared to the best phase model).

3

4 **Discussion**

5 The most striking finding of this analysis of growth trajectories in field voles during a
6 population cycle is that initial growth rates were remarkably consistent between phases of the
7 cycle, and between sexes and the season of birth (early or late). However, there is strong
8 evidence that the age at which growth rates decelerate, and also the asymptotic weights
9 reached, vary between cycle phases. The main aim of this paper was to evaluate whether the
10 „Chitty Effect“, whereby adults in the high-density phase of the cycle exhibited larger average
11 body mass than during the low-phase of the cycle, could be explained by variation in juvenile
12 growth rates in the different cycle phases. The Chitty effect is clearly present in Kielder voles,
13 albeit at a lower magnitude than the 20-30% reported in previous studies (Mihok *et al.* 1985;
14 Chitty 1987; Lidicker and Ostfeld 1991; Norrdahl and Korpimäki 2002), with the difference
15 between the asymptotic weights of voles observed during the crash/increase phase and
16 between those during the peak being 1.84g (representing 8.8% of the total body weight of an
17 average vole). However, this difference was not due to voles exhibiting faster growth rates,
18 but rather to voles growing for longer.

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

24 It should be noted that due to lower numbers of voles being observed during the crash
25 period, there was only limited power to detect significant differences in initial growth rates

1 during this phase, and such differences cannot therefore be ruled out altogether. Also, further
2 laboratory work would be necessary to evaluate whether this (apparently consistent) growth
3 rate represents a physiological maximum. Nonetheless, the present results do not support the
4 hypothesis that individuals exhibit sub-maximal juvenile growth rates during certain phases of
5 the cycle due to variable environmental conditions.

6 Although the Chitty effect has received much attention, there is relatively little
7 evidence evaluating its relevance to broader life-history theory and predicting trade-offs
8 between growth strategies and other biologically significant processes in multivoltine
9 organisms (Stenseth and Ims 1993; however see Lambin and Yoccoz 2001). Reproduction,
10 particularly sexual maturation of juveniles, is known to be inhibited during times of high
11 population density in cyclic *Microtus* rodents (Boonstra 1989; Boyce and Boyce 1988;
12 Myllymäki 1977; Ostfeld *et al.* 1993). Suppression of reproduction may arise due to limited
13 availability or poor quality of food resources; due to suppression by dominant individuals or
14 by puberty-delaying hormones secreted by littermates; and by pre- or post-natal stress (see Oli
15 1999 for a more detailed review). It has been suggested that the Chitty effect is a
16 consequence, not a cause, of cyclic population fluctuations, and of phase-related changes in
17 demographic processes, especially the age at first reproduction (Oli 1999; Lidicker and
18 Ostfeld 1991).

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

1 hypothesis. Further empirical work is now necessary to evaluate the further consequences of
2 this, and in particular whether there is also differential survival of the different size classes.

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

11

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18

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

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11 **Figure 2:** Plot of individual trajectories of the 528 voles considered in this study, showing the
12 variation in individual growth with increasing age.

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

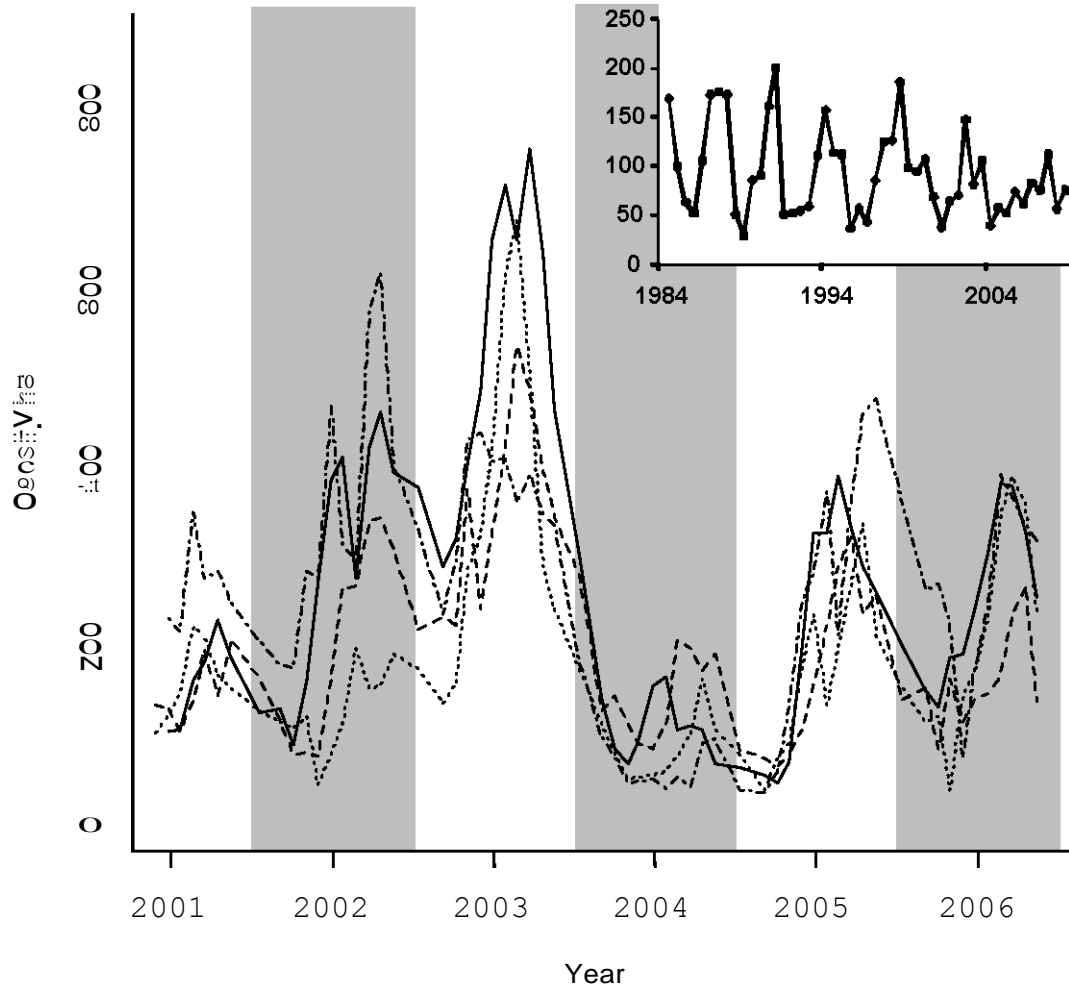
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18 **Figure 4:** Logistic growth curve fitted to the weight at age data for the field voles from the
19 peak (filled black circles), increase (grey filled circles) and crash (black filled triangles)
20 phases of the cycle.

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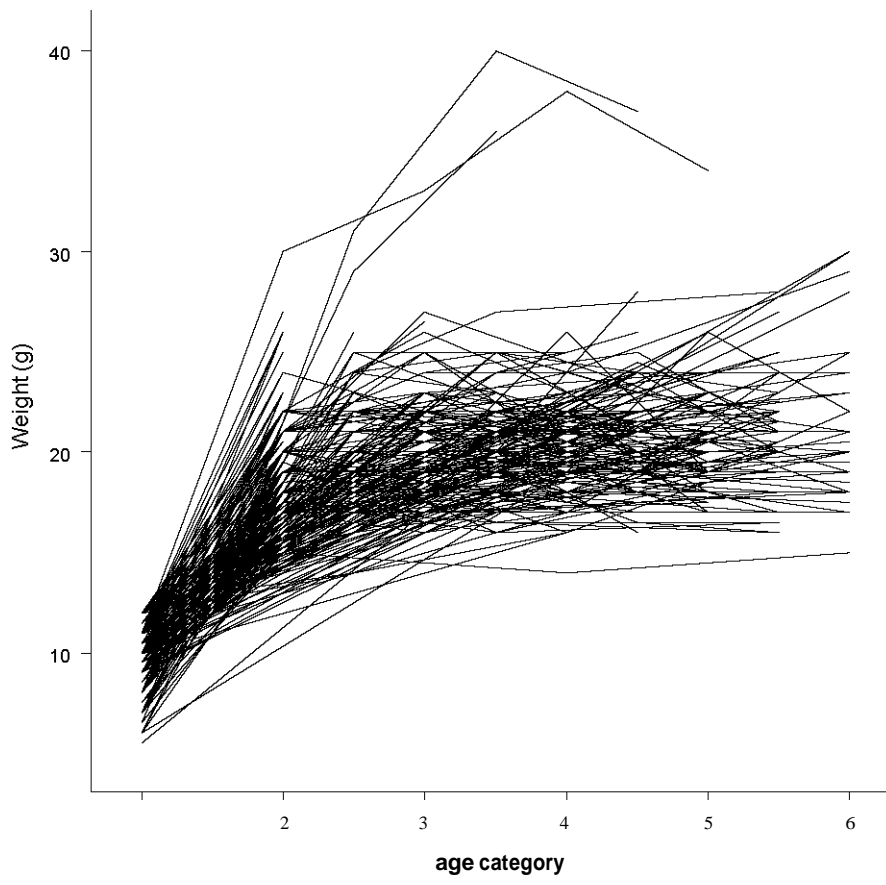
Figure 1



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1 Figure 2

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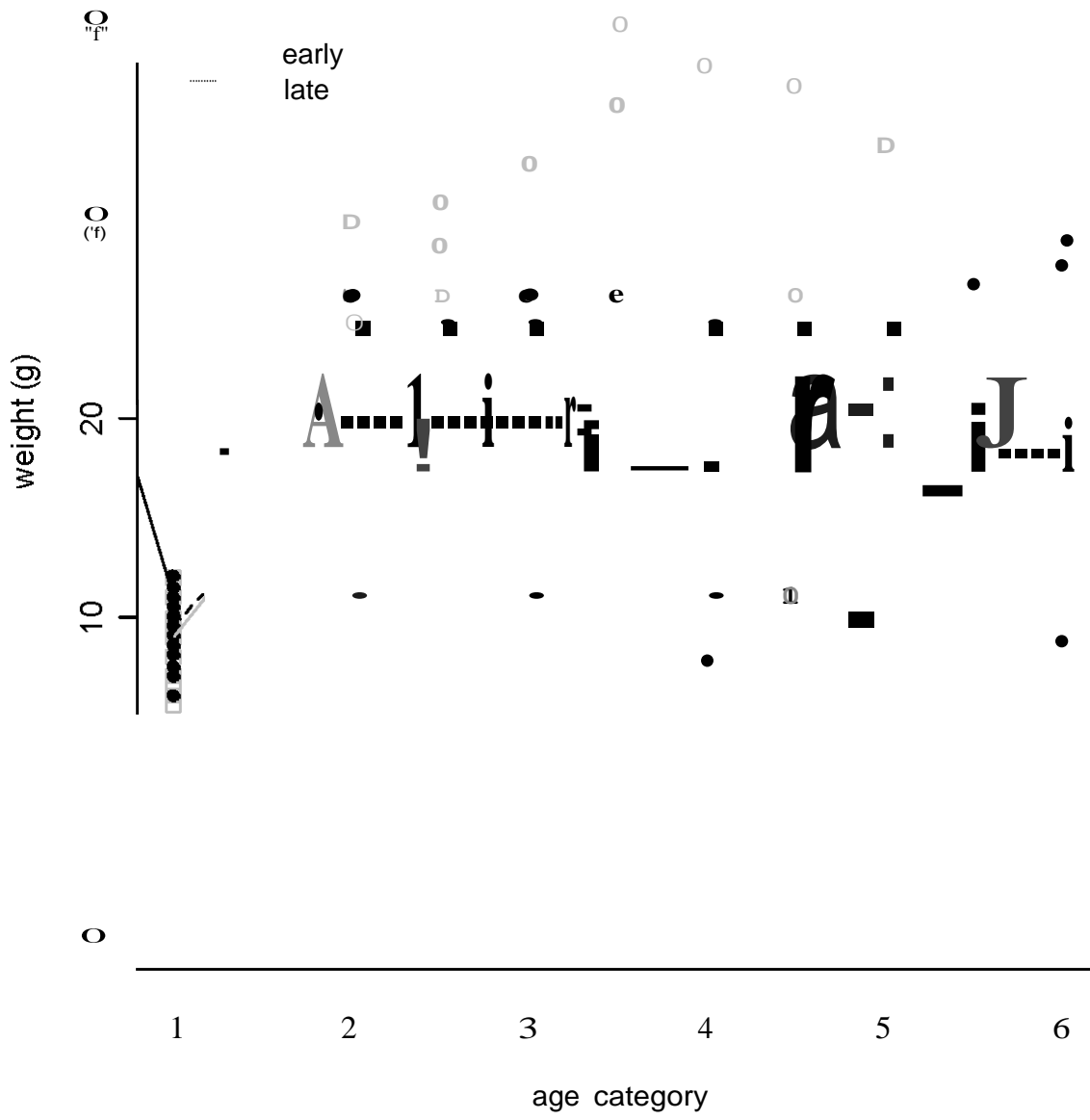
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1 Figure 3

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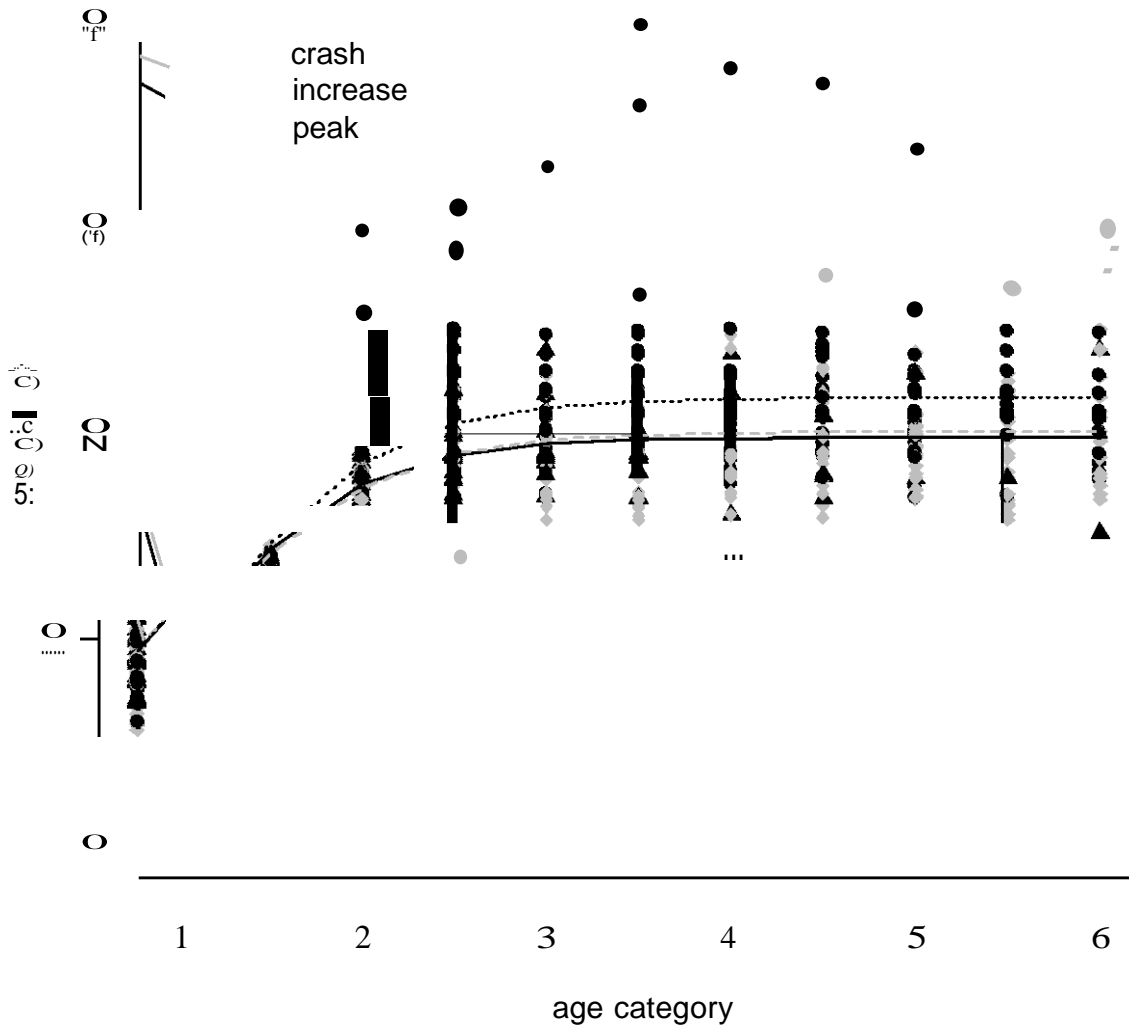
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1 Figure 4

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Table 1: Likelihood ratio test for the parameters of the logistic growth curves in females and males. The base case is where two separate curves are fitted for the female and male voles; the coincident results are for a single curve fitted through the data; *Asym* assumes that the asymptotic weight is equal for the two separate curves; *I* assumes that the age at inflection point is the same for the two curves; *r* assumes that the growth rate is the same for the two curves. The best models (lowest AIC) are indicated in bold with the delta AIC reported between the other models.

		Base Case	Coincident	Asym	I	r
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
	Δ AIC	1.35	55.51	44.99	29.11	0
	Number of parameters	6	3	5	5	5

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1 **Table 2: Likelihood ratio test for the parameters of the logistic growth curves in early**
 2 **voles (born before the 21st June) and late voles (born after 21st June).** The base case is
 3 where two separate curves are fitted for the early and late voles; the coincident results are for
 4 a single curve fitted through the data; Asym assumes that the asymptotic weight is equal for
 5 the two separate curves; I assumes that the age at inflection point is the same for the two
 6 curves; r assumes that the growth rate is the same for the two curves. The best models (lowest
 7 AIC) are indicated in bold with the delta AIC reported between the other models.

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		Base Case	Coincident	Asym	I	r
Early	Asymptotic weight (g)	21.75	20.82	20.89	21.48	21.92
voles	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	Asymptotic weight (g)	20.59	20.82	20.89	20.67	20.52
voles	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
	Δ AIC	0	43.10	21.68	10.90	1.51
	Number of parameters	6	3	5	5	5

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1 **Table 3: Likelihood ratio test for the parameters of the logistic growth curves in voles**
2 **during the crash, increase and peak phases of the population cycle.** The base case is
3 where three separate curves are fitted for the crash, increase and peak phases; the coincident
4 results are for a single curve fitted through the data; *Asym* assumes that the asymptotic weight
5 is equal for the three separate curves; *I* assumes that the age at inflection point (age at which
6 growth rate decelerates) is the same for the three curves; *r* assumes that the growth rate is the
7 same for the three curves. The best model (lowest AIC) is indicated in bold.

		Base Case	Coincident	Asym	I	r
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

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