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## Estimation of Seasonally Changing Growth Curves in Wild Japanese Field Voles, *Microtus montebelli*

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Seasonally changing growth curves were estimated from mark-recapture data on the Japanese field vole, *Microtus montebelli*, using a differentiated Gompertz equation. Trapping was carried out at the Kuju Agricultural Research Center of Kyushu University. The capture-release process was repeated more than 3300 times for 800 individual voles. Young born in the summer grew more rapidly and reached a larger asymptotic weight than those born in the remaining seasons. The asymptotic mass of young born in November (the last month of the breeding season) was quite small. These young seemed to over-winter in this subadult size. The maximum growth rates of the wild voles seemed to fluctuate seasonally, synchronizing with the length of daylight. Although the voles born in the field early in the breeding season became larger than laboratory-reared voles, they could not achieve the same growth rates as in the laboratory.

### INTRODUCTION

Growth and reproductive development of voles is variable and dependent on the season in which a vole is born (Barbehenn, 1955; Iverson and Turner, 1974; Negus et al., 1977). In many mammalian species, young born early in the year achieve adult body weights and sexual maturity at much younger ages than cohorts born later in the season (Lecyk, 1962; Lincoln and MacKinnon, 1976; Negus et al., 1977; Johnston and Zucker, 1980; Foster, 1981; Forger and Zucker, 1985; Lee and Zucker, 1990).

To show the seasonally changing growth, it is best to portray growth curves of individuals born in each season. Studies on growth in the field, however, are generally based on only the rates of weight increase between adjacent captures. This is because of the secretive nature of small rodents and the difficulty of obtaining samples of known age. Several methods have been introduced to generate growth curves of small rodents, such as, calculating average growth rates of captured animals in each mass-class (Delany and Monro, 1985), or calculating the regression of growth rate on body weight (Ford, 1981). However, since growth curves of many mammals are sigmoid, including those of murid rodents (Zullinger et al., 1984), the relationship between mass and mass gain should be theoretically considered to follow a differentiated sigmoidal equation.

Therefore, we hypothesize that the curve of mass gain on mass should reasonably fit a differentiated sigmoidal equation, if the growth curve of the targeted species is confirmed to follow the sigmoid model. The growth of Japanese field voles, *Microtus montebelli*, is known to be approximated by a sigmoidal curve, or Gompertz model (Yoshinaga et al., 1997). Our purpose in this paper is to introduce a method of predicting growth curves of wild animals using a differentiated Gompertz equation and to discuss the results of

seasonally changing growth curves for Japanese field voles.

## MATERIALS AND METHODS

The data used here were collected as part of a study on the space-use patterns of wild Japanese field voles at the Kuju Agricultural Research Center of Kyushu University, Oita Prefecture, Japan, from August 1994 to March 1996. A grid covering 6.75-ha area was trapped until April 1995, after which a 0.6-ha grid was trapped. Trapping was carried out at least three nights every month using Sherman live traps, excluding September and December of 1995 when radio-tracking was conducted. The condition of these voles and their weight to 0.01 g on an electronic balance were examined.

The mass growth for laboratory-reared Japanese field voles is approximated well by the Gompertz equation (Yoshinaga *et al.*, 1997). The Gompertz equation is

$$W(t) = A e^{-e^{-K(t-I)}} \quad (1)$$

where  $A$  = asymptotic weight,  $W(t)$  = weight (g) at age  $t$ ,  $K$  = growth rate constant ( $\text{day}^{-1}$ ), and  $I$  = age (days) at the inflection point (Ricklefs, 1967). The growth rate at  $t$  can be derived from differentiating  $W(t)$  with  $t$ :

$$\frac{1}{W(t)} \frac{dW(t)}{dt} = K e^{-K(t-I)} \quad (2)$$

Thus, the growth rate at  $W(t)$  can be calculated as follows:

$$\frac{dW(t)}{dt} = W(t) K \log_e \frac{A}{W(t)} \quad (3)$$

Growth rate-weight data in each month were fitted to the above equation (3) by an iterative least-squares technique (Zullinger *et al.*, 1984) in order to estimate the parameters,  $K$  and  $A$ .

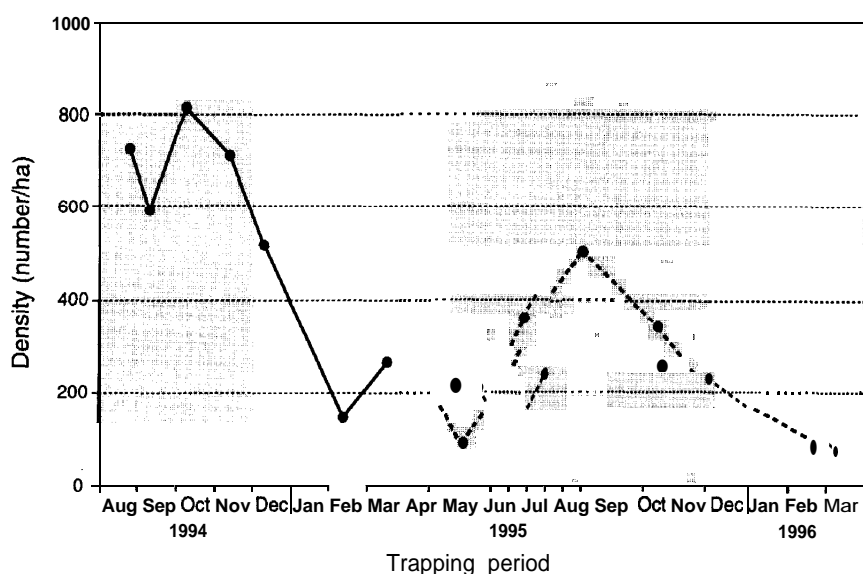
If, as was usually the case, an animal was not weighed precisely in the adjacent months, weights were estimated by linearly interpolating weights between adjacent captures. Weights were not interpolated over intervals greater than three months. Prior to analysis, data were partitioned into subgroups based on sex and capture month. Records of females showing signs of pregnancy (from abdominal palpation) were not used for the analysis.

Although the age at the inflection point could not be estimated from this procedure, the maximum growth rate at the inflection point was determined by multiplying  $K$  by  $A \cdot e^{-1}$ . Thus, the asymptotic weight, growth rate constant, and maximum growth rate were compared between growth curves. To show the results graphically, the constant value of 3 g was provided as the initial weight. This is the typical weight at birth in the laboratory (Yoshinaga *et al.*, 1997). Data of the laboratory-reared voles, taken from Yoshinaga *et al.* (1997) were also analyzed as a control.

## RESULTS

**Population density and breeding season**

Our study began in the middle of the high population density period in 1994, encompassed a low (winter) and high (summer) density period in 1995, and ceased before the onset of the breeding season in 1996 (Fig. 1). The number of voles captured at each trapping period, the proportion of recaptured voles, the number of juvenile recruits (for males < 25 g, for females < 20 g; Yoshinaga, submitted for publication) and the proportion of reproductively active adults are given in Table 1. The first pregnant or lactating females appeared in April. Males with descended testes and juveniles appeared at the same time. Reproduction apparently ended by November. The peak in population density coincided with the middle of the breeding season, and during winter the population density became low (Fig. 1). The proportion of recaptured voles declined in May and June 1995, following the extension in the trapping area.



**Fig. 1.** Estimated densities of the Japanese field voles on the study grids (solid line for a 6.75-ha grid and broken line for a 0.6-ha grid) at the Kuju Agricultural Research Center of Kyushu University during the trapping period. Shaded areas indicate breeding seasons.

**Table 1.** Numbers of Japanese field voles on the study grid at the Kuju Agricultural Research Center of Kyushu University. The numbers of juveniles (for males < 25 g, for females < 20 g) are given in parentheses.

Date	Total captured	Males	Females	% recaptured males	% recaptured females	% males with descended testes	% females with pregnancy or lactation
1994							
Aug 23-27	49	25(3)	24(1)	0.0	0.0	81.3	64.7
Sep 7-10	40	18(3)	22(1)	66.7	63.6	72.7	65.0
Oct 7-10	55	32(12)	23(3)	37.5	65.2	33.3	75.0
Nov 10-13	48	22(4)	26(4)	68.2	57.7	20.0	62.5
Dec 7-12	35	17(1)	18(1)	88.2	77.8	0.0	0.0
1995							
Feb 9-12	10	5(0)	5(1)	60.0	80.0	0.0	0.0
Mar 16-19	18	11(0)	7(0)	63.6	85.7	0.0	0.0
Apr 20-23	14	6(0)	8(1)	66.7	62.5	40.0	20.0
May 17-21	55	23(4)	32(3)	17.4	18.8	9.1	66.7
Jun 21-25	142	54(12)	88(16)	16.7	18.2	55.2	53.6
Jul 13-24	216	90(20)	126(17)	77.8	43.7	75.0	85.2
Aug 21-24	301	132(26)	169(12)	25.8	39.6	66.2	71.6
Oct 18-22	206	82(18)	124(20)	17.1	33.1	47.1	90.2
Nov 22-27	138	81(3)	57(1)	46.9	57.9	6.1	59.5
1996							
Mar 7-10	45	28(0)	17(0)	78.6	70.6	21.7	0.0

### Curve fitness

Predicted body mass values from differentiated Gompertz equations had correlation coefficients of 0.6-0.8 in almost all cases for the wild voles (Table 2). We could not determine the growth during April because of the small sample size ( $n = 3$  for males and  $n = 6$  for females). When comparing month to month parameters, it was found that voles born in the summer (the middle of the breeding season) grew more rapidly and became larger than those born in the remaining seasons. Voles born in November did not achieve the full adult weight. These relationships are shown graphically in Fig. 2. It appeared that the asymptotic weights were greater in the wild voles than in laboratory reared voles, except for the wild voles born in November, while the growth rate constants were much smaller in wild voles (Table 2).

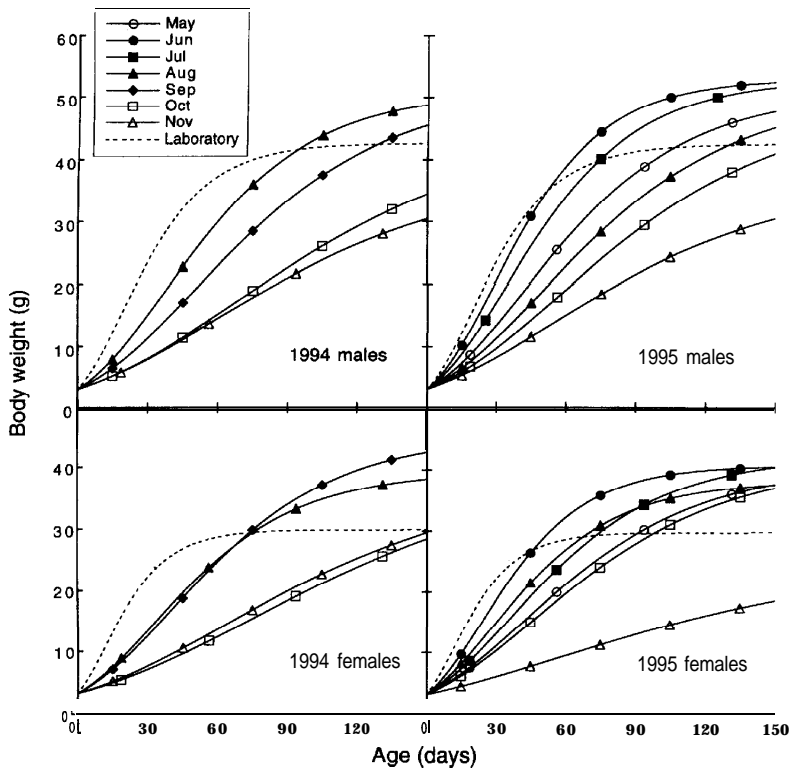
The maximum growth rates fluctuated seasonally in both years studied, and the highest rates were observed in June (Fig. 3). The peak of maximum growth rates occurred in the former half of the breeding season, during the increasing phase of population densities (Fig. 1). At the peak of population density, the growth rates had already begun to decline. The fluctuating pattern of growth rates seems to synchronize with the length of daylight (Fig. 3).

**Table 2.** Parameters of differentiated Gompertz curves fitted to the weight-growth rate data of the wild and laboratory-reared Japanese field voles.

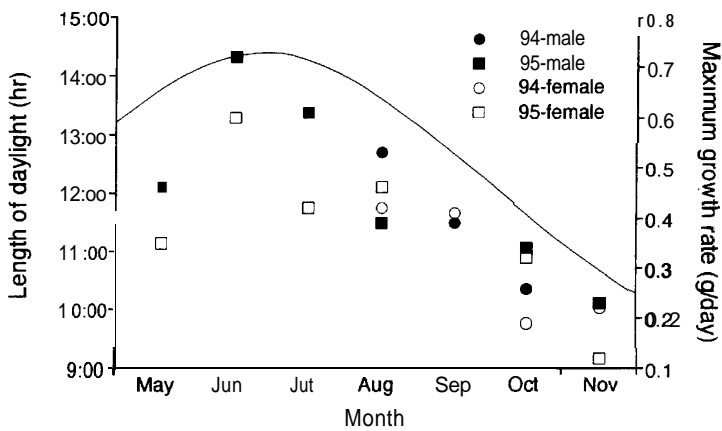
	n	Asymptotic weight (g) $\pm SE$	Growth rate constant (day <sup>-1</sup> ) $\pm SE$	Maximum growth rate (g/day)	Chisq	R
Males						
Aug-94	15	50.78 $\pm$ 1.71	0.028 $\pm$ 0.003	0.53	0.31	<b>0.89</b>
Sep-94	14	51.20f3.55	0.021 $\pm$ 0.006	0.39	0.62	0.68
Ott-94	16	45.76 $\pm$ 2.57	0.015 $\pm$ 0.003	0.26	0.27	0.78
Nov-94	16	38.27f2.25	0.016f0.004	0.23	0.26	0.76
May-95	8	51.10f3.10	0.025 $\pm$ 0.006	0.46	0.10	0.78
Jun-95	22	53.14f2.33	0.037 $\pm$ 0.004	0.72	0.86	0.71
Jul-95	31	53.16 $\pm$ 1.15	0.031 $\pm$ 0.003	0.61	0.67	0.84
Aug-95	26	51.01 $\pm$ 2.30	0.021 $\pm$ 0.004	0.39	1.36	0.67
Ott-95	35	49.56-t 1.68	0.018f0.002	0.34	0.65	0.82
Nov-95	32	37.151k1.77	0.017f0.003	0.23	0.79	0.71
Laboratory	26	42.52 $\pm$ 1.24	0.050 $\pm$ 0.004	0.78	0.85	0.84
Females						
Aug-94	16	39.27 $\pm$ 1.97	0.029 $\pm$ 0.009	0.42	0.71	0.65
Sep-94	19	45.11 $\pm$ 2.74	0.025 $\pm$ 0.007	0.41	0.56	0.54
Ott-94	18	41.07 $\pm$ 2.05	0.013 $\pm$ 0.003	0.19	0.16	0.68
Nov-94	15	38.32 $\pm$ 1.80	0.015 $\pm$ 0.003	0.22	0.13	0.78
May-95	13	41.00k1.24	0.023 $\pm$ 0.005	0.35	0.11	0.81
Jun-95	43	40.83 $\pm$ 1.22	0.040 $\pm$ 0.004	0.60	1.59	0.76
Jul-95	51	42.39t1.08	0.027 $\pm$ 0.003	0.42	1.16	0.73
Aug-95	43	38.29 $\pm$ 1.40	0.033 $\pm$ 0.006	0.46	3.51	0.65
Ott-95	25	41.53-t 1.62	0.021 $\pm$ 0.003	0.32	0.49	0.77
Nov-95	12	25.17k3.69	0.013f0.004	0.12	0.11	0.79
Laboratory	26	29.82 $\pm$ 0.71	0.068 $\pm$ 0.005	0.75	0.65	0.88

## DISCUSSION

Seasonally changing growth curves of the Japanese field voles were clearly demonstrated, using a differentiated Gompertz equation. Young born in the summer grew more rapidly and reached a larger asymptotic weight than those born in spring and autumn. The asymptotic mass of young born in November (the last month of the breeding season) was quite low and they seemed to over-winter at the subadult size. In *M. montanus*, these late season young are thought to become the breeding stock for the following spring (Negus *et al.*, 1977). Adult size and growth rate are influenced by the photoperiods and dietary factors (Pinter, 1968; Dark and Zucker, 1984; Horton, 1984; Forger and Zucker, 1985; Spears and Clarke, 1987). Pinter (1968) and Petterborg (1978) have shown that the rates of growth and sexual maturation of *M. montanus* raised during long photoperiods are significantly accelerated compared with those of voles raised in



**Fig. 2.** Estimated growth curves in body weight of wild Japanese field voles during breeding seasons in 1994 and 1995. Laboratory data included as a control are from Yoshinaga *et al.* (1997). Growth parameters for each curve are found in Table 2.



**Fig. 3.** Relationship of maximum growth rates (symbols) of wild Japanese field voles to the length of daylight (a solid line) at the study site. Growth data for two years are compiled.

short photoperiods. Growth and reproductive activity of *M. montanus* have also been shown to be stimulated by dietary factors under certain photoperiod conditions (Pinter, 1968). The growth rates of Japanese field voles fluctuated seasonally, which did not synchronize with population densities but with the length of daylight. Seasonally changing growth shown in this study seems to be based on the photoperiod.

It is also known that adults in peak populations appear to be larger than adults in early expanding or declining populations, called as "Chitty Effect" (Keller and Krebs, 1970). To understand more thoroughly underlying factors in seasonally changing growth, prediction of growth curves in the field population is necessary. The method introduced here is available for other wild animals which are continuously captured, if the fitness of the sigmoidal curve is first confirmed for known-age animals prior to conducting analysis.

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