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Clethrionomys gapperi: Is there a peak syndrome?

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Clethrionomys gapperi attained high fall numbers following high spring numbers (the result of winter breeding) in 1974; high fall numbers following average spring numbers in 1976; and average fall numbers following low spring numbers in 1978. Numerical increase was exponential in all three years, but the highest instantaneous rate of increase occurred in 1978. Survival of the overwintered (OW) cohort was also best in 1978. Spring growth in length and weight of the OW cohort was best in 1976, which was characterised by a very warm May and June. Late summer body weights for each sex and age class did not differ among years except for age class 2 males, which were larger in 1978 than in the other years. In 1978, the number of litters per OW females was higher, mean litter size (all ages of females combined) was larger, and the number of young of the year that attained sexual maturity was greater, than in the other years.

Overall, the results of 40 three-way comparisons do not support the concept of a "peak syndrome". Rather, they suggest the occurrence of a "low density" syndrome.

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1. Introduction

Krebs (1978) drew a useful distinction between the concepts of "density-dependence" and "self-regulation". In his words self-regulatory systems have "added an additional degree of freedom to the system, the individual with variable properties". He also distinguished between idealized "stable" populations and "cyclic" ones. He claimed, however, that Chitty's postulate that "... all species of animals have a form of behaviour that can prevent unlimited increase in population density" (Chitty 1967) would apply to both cyclic and stable populations. Under conditions of mutual interference, selection should favor "genotypes that have a worse effect on their neighbors than vice versa" (Chitty 1967). It follows that "high density" and "low density" or "increase" genotypes ought to be recognizable in any population in which the level of mutual interference varies. Cyclic populations, which alternate reasonably regularly between periods of high and low mutual interference offer the best opportunities for study of self-regulation. In ideal stable populations, on the other hand, regulation can only be studied by means of experimental perturbation (Krebs 1978). Fortunately, ideal populations are rare in the real world. Most "stable" populations exhibit at least occasional periods of exceptional abundance or scarcity. If self-regulation is a property of all populations, then qualitative differences between individuals from high-density and low-density episodes in "stable" populations should be detectable.

I suggested (Fuller 1985) that *Clethrionomys gapperi* in the southern Mackenzie District of the Northwest Territories of Canada are "stable" according to the fluctuation index, *s* (Stenseth & Framstad 1980). Nevertheless, the data contain several examples of "statistical peaks", defined as series of three successive years, having population sizes a, b, and c, such that a is less than b, which again is greater than c. Relative numbers (catch per 100 trap-nights) in May of 1973, 1974 and 1975 form one such peak. There are two statistical peaks in August numbers — 1973-1974-1975, and 1975-1976-1977. The mean annual catches confirm the peaks already mentioned and add a third in 1969-1970-1971.

In this report I compare a series of demographic variables and indices of individual "quality" in samples drawn from the (statistical) peak populations of 1974 and 1976, and the low-density population of 1978. According to the hypothesis of self-regulation, individuals from the two dense populations should resemble each other, and should differ in predictable ways from those that came from a low-density population.

2. Materials and methods

All materials used in this report were obtained by means of snap traps. Trapping methods have been described elsewhere (Fuller 1985). A problem that plagues all small mammal population studies is small samples in years of low numbers. In the present study about three times as much effort was expended in 1978 as in either of the other years (Table 1), and samples of comparable size were obtained. Trapping effort was spread rather evenly over the summer season (May to September) except for some concentration in May each year. Mean dates of capture were not singificantly different among years (Table 1), so that mean annual numbers can be compared meaningfully.

Table 1. Materials and summary statistics for 1974, 1976 and 1978.

	1974	1976	1978	10-yr average
Number of trap lines (N)	18	28	70	376
Number of trap nights (TN)	5733	7800	21 480	101 919
Mean number of TN/N (mean and *SE*)	318.5 27.49	278.6 10.10	306.9 4.28	271.1 6.01
Mean date of capture (mean and *SE*)	Jun. 27 10.2	Jul. 6 8.5	Jul. 7 4.9	Jul. 3 2.18
Total catch	531	466	502	3210
Mean catch per 100 TN (mean and *SE*)	8.68 1.211	6.02 0.803	2.32 0.253	3.18 0.167
May catch per 100 TN (mean and *SE*)	6.02 0.846	2.44 0.299	0.77 0.151	1.96 0.172
Aug. catch per 100 TN (mean and *SE*)	12.48 1.719	8.79 1.783	3.39 0.650	4.53 0.482
Sept. catch per 100 TN (mean and *SE*)	21.18 -	8.17 0.500	4.63 0.625	

Total length (TL) and length of tail vertebra (TV) were measured to the nearest millimeter and weight was recorded to the nearest 0.1 g. Body length was calculated as (TL − TV); weight of pregnant females was corrected by subtraction of the weight of the reproductive tract.

Skulls were preserved and cleaned in a dermestid beetle colony so that each individual could be placed in one of four age categories according to the morphology and development of the second upper molar (Martell & Fuller 1979, Mihok 1980).

Reproductive state was determined by dissection. Mature males had large testes and macroscopically visible tubules in the cauda epididymidis, or testes of moderate size and sperm in smears of testis and/or epididymis, or regressing testes and large accessory glands. Mature females had visible embryos, or placental scars, or in a few cases a copulation plug. This is a conservative criterion for judging females; nulliparous juveniles would not be recorded as mature until embryos were visible.

In this report age means chronological age as determined by the state of M^2; mature means sexually mature as revealed by the condition of the reproductive organs. I avoid use of the ambiguous term "adult", which could be interpreted as either an age class or a reproductive state.

Maximum and minimum temperatures in a Stevenson screen at the field station were recorded daily.

Statistical analyses were performed on an APPLE II plus computer (Trade mark of APPLE Computers, Cupertino CA) using the software package STATPRO (Copyright Wadsworth Electronic Publishing Company).

3. Results

3.1. Temperatures

May was warmer in 1976 than in the other two years (Fig. 1), but the relationship was reversed in the first half of June. For the balance of the summers there was little difference in mean maximum temperatures, but according to the mean minima 1978 was consistently colder than the other two years. The highest temperatures in the entire study (several days of 38°C) were recorded in the first half of August, 1976.

3.2. Numbers

Examination of scatter plots of relative numbers suggested that growth in numbers was exponential in all three years under consideration. Linear regressions were performed by the method of least squares on natural-log-transformed data, and non-linear regressions were performed by an iterative technique on untransformed data. Both methods were

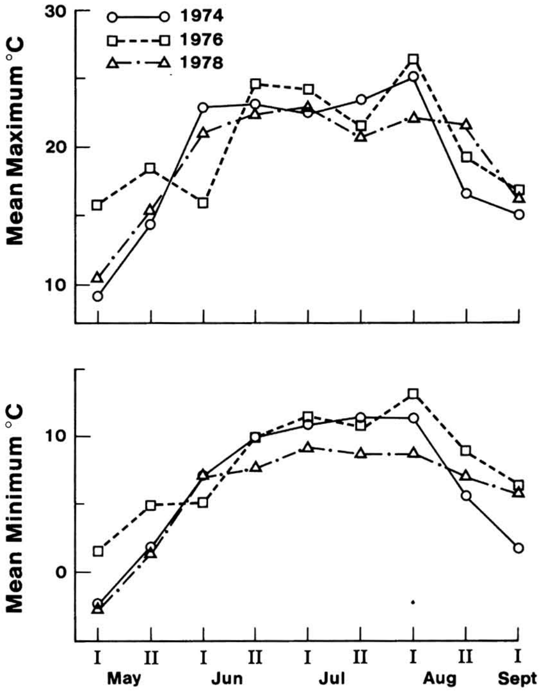

Fig. 1. Semi-monthly mean maximum and minimum temperatures measured at the field station.

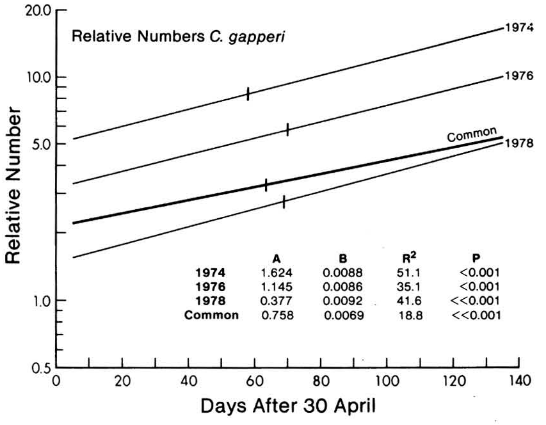

Fig. 2. Regression lines fitted by least squares to log-transformed data on relative numbers for the period 1 May to 30 September. The common regression line is based on the 10 years 1970-1979 inclusive. A = intercept. B = slope.

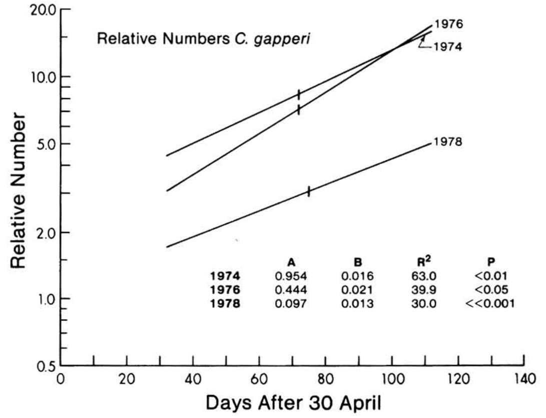

Fig. 3. Regression lines fitted by least squares to log-transformed data on relative numbers for the period 1 June to 20 August, the period of most rapid exponential growth. A = intercept. B = slope.

applied to a) data for the whole summer (i.e., 1 May to 30 September), and b) data for the main breeding season from about the time of first appearance of young to birth of all but the last few litters (i.e., 1 June to 20 August). Although trapping continued for three consecutive days, all captures were given the date of the middle day in the 3-day period. Calendar dates were converted to Day of Summer (DOS) for which day 1 equals 1 May.

Intercepts (antilog of intercept for linear model) were compared with mean May relative numbers; predictions from regression for DOS 105 were compared with mean August relative numbers, and predictions for DOS 140 with mean September relative numbers. Regressions based on the whole summer (Fig. 2) gave a better fit to observed values than those based on the breeding season only (Fig. 3), especially in 1976. In that year rapid increase during the breeding season was not sustained into September with the result that the number predicted by regression for September was too high by a factor of about 3.

According to the data in Table 2, linear and non-linear models gave similar estimates for both August and September numbers, but there were important differences in both slopes (Table 3) and intercepts (Table 2) between the two models. The near identity of slopes given by the linear model suggests that instantaneous growth rates were the same in both high density and low density years, whereas the non-linear model suggests that rates of increase were lower in one high density year (1976) than in the other two years. Table 2, however, shows that the intercept calculated by iteration for 1974 is much too low, although the August estimate is about right. It follows,

Table 2. Comparison of values from regression (May = intercept, August = DOS 105, September = DOS 140) and observed mean values.

	Predicted		
	Linear	Non-linear	Observed
May			
1974	5.08	3.89	6.02
1976	3.14	3.36	2.44
1978	1.46	0.92	0.77
August			
1974	12.83	13.09	12.48
1976	7.76	7.78	9.50
1978	3.82	3.25	3.25
September			
1974	17.40	19.62	21.18
1976	10.47	10.31	8.17
1978	5.29	4.96	4.63

Table 3. Slopes of regression lines calculated according to a linear model (least squares fit on ln-transformed data), and a non-linear model (iterative fit) of exponential increase.

	1974	1976	1978
Non-linear slope	0.0116	0.0080	0.0121
Linear slope	0.0088	0.0086	0.0092
R^2	0.51	0.35	0.42
F	16.72	15.16	50.59
p	<0.001	<0.001	<<0.001

therefore, that the calculated slope must be an overestimate. Even the slope derived from the linear model must be a slight overestimate. By analogous reasoning, both estimates of the 1976 slope were slight underestimates. For 1978 the non-linear model gave a nearly perfect match to observed values. True instantaneous daily rates of increase were probably 0.0085 or less in 1974, about 0.0090 in 1976, and about 0.0120 in 1978.

If the above interpretation is correct, then the instantaneous daily rate of increase was substantially greater in 1978 than in the two high density years. The "corrected" rates of increase are inversely related to May density, so it could be argued that the 1978 spring population consisted of *r*-selected, or "increase" types, whereas the 1974 and 1976 spring populations did not. Simple consideration of the ratio of September to May relative numbers would lead to the same conclusion. In both 1974 and 1976 the ratio was about 3.5:1, whereas in 1978 it was about 6:1 (Table 1).

Table 4. Monthly mean relative numbers of the OW cohort for each sex and for sexes combined. These data form the basis of the calculation of survival indices. M = males, F = females.

	May	June	July	Aug.	Sept.
1974					
TN	1950	1080	855	1338	510
M/100 TN	3.10	1.57	1.75	0.75	0.59
F/100 TN	2.92	2.22	1.05	0.97	0
Total	6.02	3.80	2.81	1.72	0.59
1976					
TN	2700	1500	1200	1800	600
M/100 TN	1.56	2.00	1.17	0.61	0
F/100 TN	0.81	1.07	1.58	0.50	0
Total	2.37	3.07	2.75	1.11	0
1978					
TN	5928	3855	6111	3570	2400
M/100 TN	0.54	0.57	0.44	0.34	0.13
F/100 TN	0.25	0.49	0.33	0.36	0.17
Total	0.79	1.06	0.77	0.70	0.29

Table 5. Survival indices (ratios of late summer relative numbers to spring relative numbers expressed as percentages). Horizontal lines indicate values that are not significantly different from each other at the $p = 0.05$ level. Zeros were given the value 1 for purposes of G-tests.

Ratio	Sex	1974	1976	1978	p*
August/May	M	24	39	63	<0.005
	F	33	62	144	<0.001
	Both	29	47	89	<0.001
August/June	M	48	31	60	<0.025
	F	44	47	73	NS
	Both	45	36	66	<0.01
September/May	M	19	0	24	<0.001
	F	0	0	68	<0.001
	Both	10	0	37	<0.001
September/June	M	38	0	23	<0.001
	F	0	0	35	<0.001
	Both	16	0	27	<0.001

* 3 × 2 *G*-test for independence.

3.3. Survival of the overwintered cohort

Overwintered (OW) individuals can be recognized with certainty on autopsy by the character of the roots on M^2. Since snap trapping was carried out extensively in many different habitats I assume that habitats from which animals were dispersing, as well as those habitats that were receiving dispersers, were included in the sampling. Given those two conditions, the relative number of OW individuals over time gives an estimate of survival.

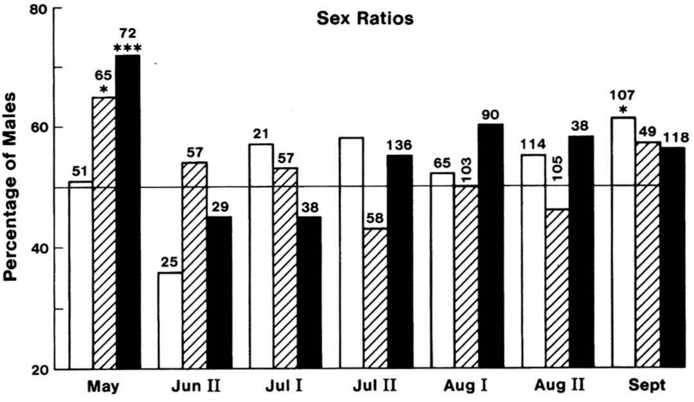

Fig. 4. Sex ratios expressed a percentage of males. Open bars are for 1974, hatched bars for 1976, and solid bars for 1978. * = $p<0.05$. *** = $p<0.001$. *G*-test for goodness of fit to 1:1 ratio.

Only in 1974 did the relative numbers decline smoothly over time (Table 4), and even in 1974 male survival did not change from June to July. In 1976 the highest number of males occurred in June, whereas female relative numbers increased until July. In 1978 both sexes reached their greatest relative numbers in June. Since the number of OW individuals in the population cannot increase over the course of a summer, and if immigration did not consistently exceed emigration, the results shown in Table 4 must mean that trappability is not constant.

Survival indices (*SI* = relative numbers in August and September expressed as percentages of relative numbers in May and June) were calculated for all four combinations of spring and fall months for each year. They were tested for independence by means of 3×2 *G*-tests, which were significant in 11 of 12 cases, and highly significant ($p < 0.005$) in 9 cases (Table 5). Pairwise contingency tests were then used to discover where the differences lie. For sexes combined, *SI*'s were different in each of the three years in three cases out of four (Table 5). Only in the fourth case (August/June) was the result partially in accordance with the expectation of the Chitty Hypothesis ($SI_{74} = SI_{76} \neq SI_{78}$) but *SI* in 1978 was higher than in the other two years, not lower. Females showed the same pattern ($SI_{78} > SI_{74} = SI_{76}$) in two cases out of four; in one case there was no difference between years, and in the fourth case each year differed from both of the others. For males, all four cases were contrary to expectation.

There is no pattern in the ratios of August numbers to spring numbers (Table 5); five different results are seen in the six cases. There is, however, a pattern in the ratios of September numbers to spring numbers. For males survival was the same in 1978 as in 1974 and significantly higher in both than in 1976. For females, survival in the two years of high numbers did not differ, and both years had significantly poorer survival than the year of low numbers.

Combining the sexes yielded a third outcome — *SI* for each of the three years differed significantly from that in both other years.

Overwhelmingly, however, the evidence points to the conclusion that survival of the OW cohort was best in the year of low numbers.

3.4. Sex ratios

In 16 of 21 samples the proportion of males was equal to, or greater than, the proportion of females (Fig. 4). However, only three of the deviations were significantly different from equality. Two of those occurred in May, perhaps because many females were pregnant then, which may have caused them to restrict their movements. In samples pooled over the whole summer the sex ratio differed from 1:1, in both 1974 and 1978, but not in 1976 (pooled *G*-test). There is no other discernible pattern in sex ratio that relates to differences in relative numbers.

3.5. Age composition

The proportions of three age classes, juvenile (age class 1), subadult (age class 2, and age

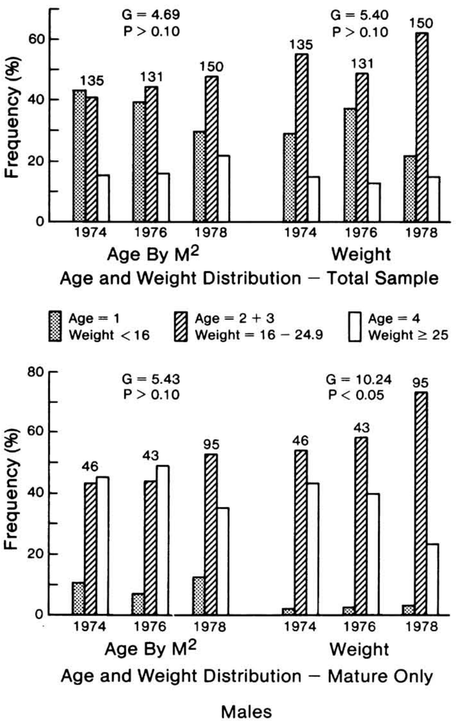

Fig. 5. Frequency distribution of males in the samples according to two criteria of age. Both mature and immature individuals are included on the upper portion of the figure, only mature individuals on the lower portion. Weight limits were chosen arbitrarily.

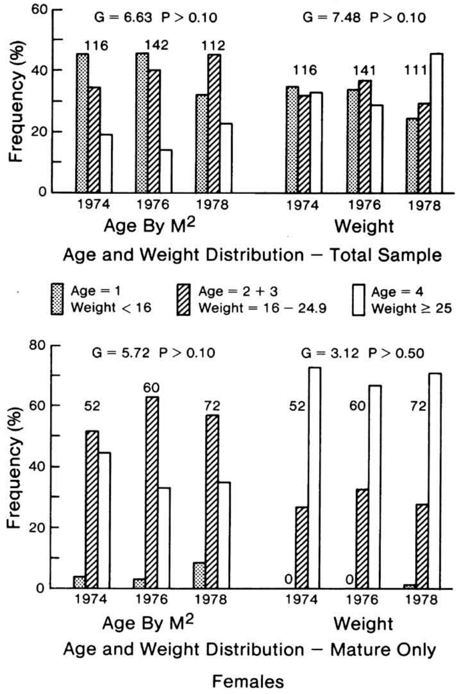

Fig. 6. Frequency distribution of females in the samples according to two criteria of age. Both mature and immature individuals are included on the upper portion of the figure, only mature individuals on the lower portion. Weight limits were chosen arbitrarily.

class 3 combined), and OW (age class 4), in samples taken from July 16 to the end of August were not significantly different among years for either sex and irrespective of whether one considered the whole sample or only the mature segment (Figs. 5 and 6). Only one male-female comparison was significant. The proportions of OW and subadults in the mature segment of the samples taken in 1976 were significantly different between the sexes.

Had weight been used as an index to age the same conclusion would have been reached for the total sample of males (Fig. 5; right). However, for the mature segment of the sample, the conclusion would have been that the 1978 sample differed from the other two in having more subadults and fewer OW. For females, the conclusion that frequencies of "age" classes did not change from year to year would still have held, but the weight criteria chosen greatly exaggerated the proportion of "adults" at the expense of the other two categories, particularly when only the sexually mature segment is considered (Fig. 6; right). Clearly, data obtained by capture-mark-release methods, in which weight is used as an index to age, must be interpreted with caution.

3.6. Body size

According to the conventional wisdom (see Krebs & Myers 1974 for a review), microtine peaks are usually characterised by OW adults that are heavier in the spring of a peak year than in the spring of any other phase. I have shown (Fuller 1977) that that is not the case for *C. gapperi*, although early spring growth was faster than predicted from spring temperature in the spring of the peak year. As a follow-up on that observation I have plotted mean length and weight for half months from early May to mid June for the two statistical peaks

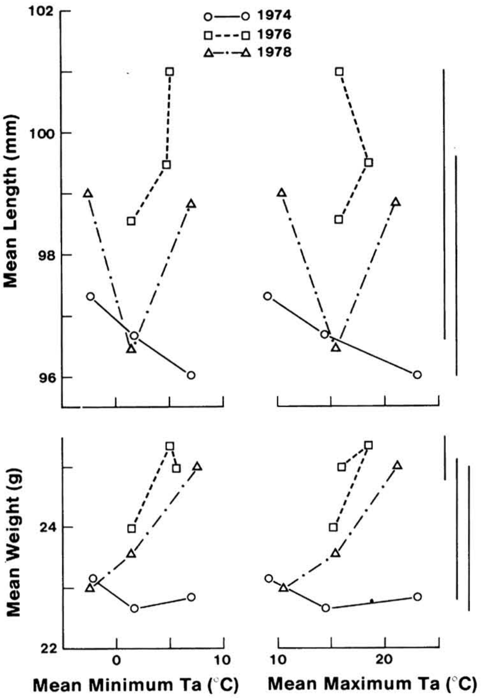

Fig. 7. Growth in mean length (upper) and mean weight (lower) of males by half months (early May, late May and early June) in relation to semi-monthly mean maximum and minimum temperatures.

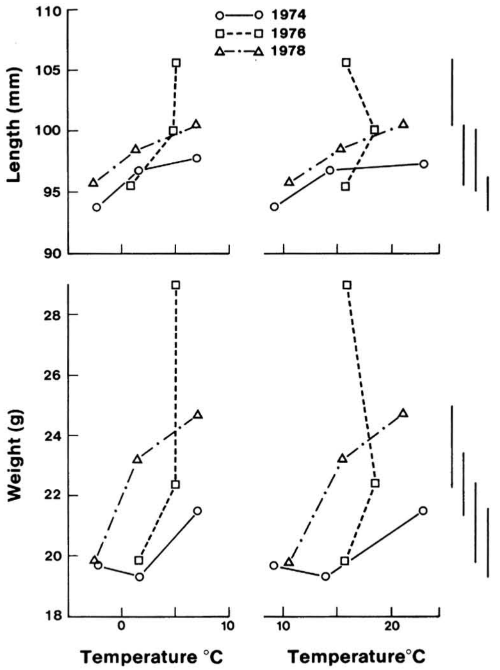

Fig. 8. Growth in mean length (upper) and mean weight (lower) of females by half months (early May, late May and early June) in relation to semi-monthly mean maximum and minimum temperatures.

and for 1978. Variances were so great for males that one can only say that by mid June the longest individuals were found in 1976, the shortest in 1974 (Fig. 7). There was no significant difference in weight among years in early May, but in late May 1976 individuals were significantly heavier than those in the other two springs. Females too were longer by mid June in both 1976 and 1978 than in 1974 (Fig. 8). Mean weights in mid June were significantly different for each of the three seasons.

Weights of all individuals caught in the last half of summer (16 July to 31 August) showed only one, marginal difference among years. OW females, females in age class 2, mature females of all ages combined, and immature females of all ages, had similar mean body weights in each of the three years. The same was true of males except for individuals of age class 2, which were significantly heavier (19.05±0.298 (n = 68)) in 1978 than in 1974 (18.20±0.256 (n = 50)). The 1976 sample mean (18.47±0.304 (n = 40)) was not significantly different from either of the others.

Distribution of body weights of all individuals (but not for the sexually mature segment only) in late summer does accord, at least in part, with expectation. Males had a different distribution in 1978 than in 1974 and 1976 (Fig. 9: $G = 25.517$, $df = 12$, $p < 0.025$). The major difference appears in the 22-25.9 g range. The same conclusions apply to females (Fig. 10: $G = 21.586$, $df = 12$, $p < 0.05$ for total sample; NS for mature only). Note that for neither sex was there a preponderance of heavy individuals in the years of high numbers.

3.7. Reproductive output

Reproductive output should provide direct evidence concerning the existence of an "increase type" if one exists. I chose the period 16 July to 31 August as the best time in which to analyse breeding. Total output is determined by three variables, namely, the proportion of young of the year that matures in the summer of birth, the number of litters per breeding female, and the number of young in a litter.

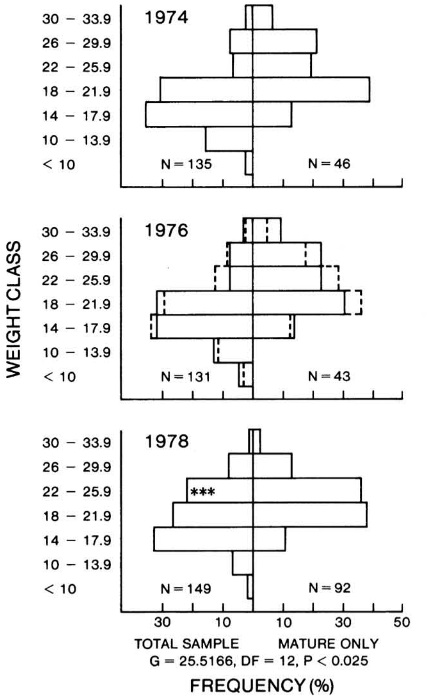

Fig. 9. Weight distribution of males captured in late summer (16 July to 30 August) by 4-gram weight classes. Both mature and immature individuals plotted to the left of the vertical line, mature only to the right. Broken lines on the middle figure show the composite distribution for all three seasons. *** = $p<0.001$.

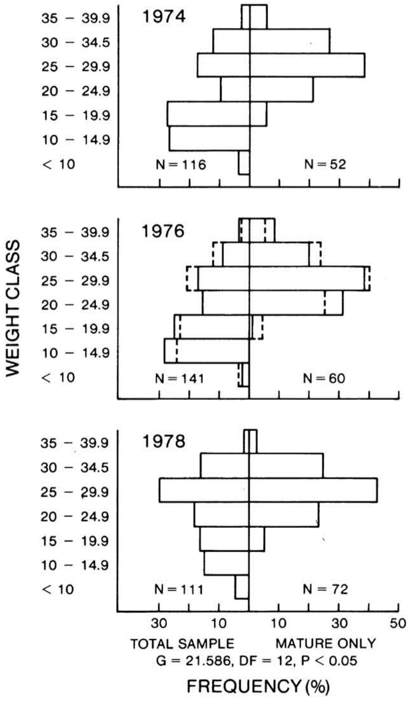

Fig. 10. Weight distribution of females captured in late summer (16 July to 30 August) by 5-gram classes. Both mature and immature individuals plotted to the left of the vertical line, mature only to the right. Broken lines on the middle figure show the composite distribution for all three seasons.

Proportion of young sexually mature

All females and most males of age class 3 became sexually mature in each year, but differences appeared in the proportions of age classes 1 and 2 that matured (Table 6). In both age class 1 and age class 2 significantly more young matured in 1978 than in either 1974 or 1976. The difference is particularly striking if the two classes are combined (i.e., all individuals without roots on M^2). Females in the group I have termed subadult (age classes 2 and 3 taken together) did not differ significantly among years but males did. Lumping all young of the current year, however, revealed a highly significant excess of mature individuals of both sexes in 1978.

Number of litters per breeding female

To get an estimate of the number of litters per breeding females I have counted the number of sets of placental scars plus the litter in utero (if any) for each female at the time of autopsy. Obviously, this underestimates the total contribution that individuals killed early might have made had they lived longer. Comparisons across years are sensitive to the distribution of captures over time, which was similar in 1974 and 1976 and shifted toward the early part of the sampling period in 1978. This bias may account in part for the small number of age class 3 individuals, and the large number of age class 2 individuals, in 1978. It should also result in a downward bias in the observed number of litters per female.

None of the females in age class 1 had placental scars (Table 7). The number of litters per female increased with the age class of the dam, but there were no differences among years in any age class of young of the year. OW females produced more litters per individual in 1978 than in 1974 in spite of the direction of the possible bias.

Table 6. Proportion of young of each age class sexually mature in samples caught from 16 July to 31 August.

Age class	Sex	1974			1976			1978			G	p
		n	Mat	%	n	Mat	%	n	Mat	%		
1	F	53	2	4	65	2	3	36	6	17	6.69	<0.01
	M	59	5	9	52	3	6	45	12	27	10.11	0.005
2	F	24	10	42	35	16	46	48	38	79	12.86	<0.001
	M	50	15	30	48	12	25	68	46	68	27.03	<<0.001
3	F	16	16	100	22	22	100	3	3	100	—	
	M	5	5	100	10	7	70	4	4	100	4.36	N.S.
1+2	F	77	13	17	100	18	18	84	44	52	32.62	<<0.001
	M	109	20	18	100	15	15	113	58	51	42.08	<<0.001
2+3	F	40	27	68	57	38	67	51	41	80	3.07	N.S.
	M	55	20	36	58	19	33	72	50	69	22.10	<<0.001
1+2+3	F	93	29	31	122	40	33	87	47	54	12.45	<0.001
	M	114	25	22	110	22	20	117	62	53	35.55	<0.001

Table 7. Number of litters (L) per breeding female (F) for females of different ages. Differences were detected by one-way ANOVA. * = significant difference between groups according to SNK test.

Age	1974				1976				1978			F	p
	L	F	L/F		L	F	L/F		L	F	L/F		
1	2	2	1.00		2	2	1.00		6	6	1.00	—	
2	12	10	1.20		24	16	1.50		44	35	1.26	1.616	N.S.
3	22	16	1.38		34	22	1.55		6	3	2.00	1.299	N.S.
2+3	34	26	1.31		58	38	1.53		50	38	1.32	1.730	N.S.
4	45	23	1.96	*	42	20	2.10	*	59	25	2.36	3.533	0.05

Table 8. Litter sizes, ages combined, according to number of embryos, number of new placental scars, and embryos plus new scars. * = significant difference between groups according to SNK test.

	1974			1976			1978		F	p
	n	Mean		n	Mean		n	Mean		
Embryos	29	5.59	*	21	5.86	*	46	6.39	3.144	<0.05
New scars	29	5.62	*	44	5.61		46	6.35	4.247	<0.025
Combined	58	5.61	*	65	5.69		92	6.37	7.480	<0.001

Number of young in a litter

Sample sizes were too small to allow meaningful comparisons between age classes of females, so all ages were lumped. Females had the largest litters in 1978, whether judged by embryos, or new scars, or a combination of the two (Table 8).

4. Discussion

The two years of high numbers began with markedly different spring temperatures, but from late June to mid August their temperature curves were similar. In contrast, mean temperatures were abnormally low throughout the summer of 1978. One might conclude from the above either that spring temperatures have no bearing on numbers in late summer, or that high summer temperatures promote high numbers. Consideration of instantaneous rates of increase suggests, however, that over the range of observed temperatures, temperature is irrelevant. The rate of increase in 1978, which had both a cold spring and a cold summer, was at least as great as, and probably greater than, the rate in either of the other two years (Table 3).

One explanation for the observed rate of increase in 1978 is that the population consisted mainly of "increase types" as predicted by Chitty (1967) and Krebs (1978). Alternatively, spacing behaviour without genetic involvement could provide an explanation. Presumably, female home ranges were fully occupied earlier in 1974 and 1976 than in 1978. If a female must obtain an exclusive home range before she can breed, as postulated by Koshkina & Korotkov (1975), then a high rate of reproductive output could be sustained for a longer time in a season of low initial density. The observed increase in proportion of mature subadult females (Fig. 10) is consistent with this explanation. The situation is less clear for males, which do not hold exclusive home ranges. The high maturation rate of subadult males may be an indication of an increase genotype, or a function of a low probability of encountering a mature male. My data shed no further light on this question.

Although temperature had no apparent effect on rate of increase, it has been shown (Fuller 1977) to be correlated with the growth of individuals in early spring (April to May). In the present account, growth from early May to mid June was fastest in both sexes in the warm spring of 1976 (Figs. 7 and 8) although there was little indication of a pause in growth when low temperatures returned in early June. Only the male weights may have shown such a pause. Furthermore, individuals grew at different rates in 1974 and 1978 even though mean temperatures, particularly the minima, were almost identical. This comparison may be unfair because many of the 1974 individuals were born during winter (Fuller 1985) and were not true members of an overwintered cohort. We must therefore look to 1976 and 1978 for possible evidence of the presence of a large genotype in the spring of a peak year. There was no significant difference in length of either males or females, or in male weights, between 1976 and 1978 June samples. However, 1976 females were indeed heavier in mid June, by about 20% on the average, than their 1978 counterparts (Fig. 8). It is still an open question whether this difference ought to be attributed to the predominance of a specific genotype, to the warm spring, or to an artifact of sampling.

Late summer weights have been shown to vary with density, hence it is not surprising that only one difference was found in this study. Analyses performed on an individual age class are subject to two biases, namely, the distribution of trapping effort, and the proportion sexually mature, in different years. Analyses of mixed age classes are subject also to varying proportions of each age class. The distribution of trapping effort was similar in 1974 and 1976 (mean dates August 19 and 12 for males; August 7 both years for females), but sampling ended earlier in 1978 (mean date August 1 for both sexes). This difference would be expected to bias the mean age, and probably also the mean weight, of young of the year downward in 1978, but males in age class 2 were larger in 1978 than in 1974. Since mature age 2 males averaged about 4 g heavier than immatures, the large proportion of mature individuals in the 1978 sample probably accounts for their greater average weight. The differences in distribution of body weights (Figs. 9 and 10) particularly the excesses of males in the 22.0 to 25.9 g class and females in the 25.0 to 29.9 g class in 1978, are also probably a reflection of the high proportion of young that matured that year.

Krebs & Myers (1974) claimed that "adult" survival is related to cyclic phase, being good in increase and peak phases and poor in decline and low phases. They also claimed that adult females survive better than adult males during the breeding season. My data (Table 5) generally bear out the last point. Female survival was better than male survival through August of all years, and through September in 1978. The number of OW's that survive until September is small, and their absence from the samples could just be a matter of chance. Of greater significance, my data suggest very strongly that survival of the OW cohort was better in the low phase than in either of the peak phase populations studied. Some age class(es) must survive well for a population to increase by a factor of about 6 (Table 1), and it is important for the OW cohort to do so because of the significant contribution it makes to total reproductive output. Unfortunately, I cannot get even an index to survival of young of the year from my data. The extreme paucity of age class 3 in 1978 suggests that the earliest summer litter did not survive well that year.

Krebs & Myers (1974) suggested that birth rates are determined by five components in addition to population size. One of the five, sex ratio, has not been correlated with cycle phase, but *Clethrionomys gapperi* seems to differ from *Microtus pennsylvanicus* and *M. ochrogaster* at least, in that there is an excess, rather than a deficit, of males. My criterion

Table 9. Pregnancy rates (P) for subadults and OW females. Significant differences are noted.

	n	P	%P	*G*	Result
Subadult					
1974	40	16	40		
1976	57	13	23	8.492	1976/78*
1978	51	25	49		
OW					
1974	23	11	48		
1976	20	6	30	3.166	N.S.
1978	25	14	56		
Combined					
1974	63	27	43		
1976	77	19	25	12.170	1974/76*
1978	76	39	51		1976/78*

"proportion of age class mature" (see Sect. 3.7) has elements of two of their criteria — age at maturity and pregnancy rate.

For comparison with my criteria I compiled pregnancy rates (Table 9). They did not differ among years in the OW cohort, but the rate was higher in 1978 than in 1976 in subadults and overall. Pregnancy rate in 1974 was intermediate and not significantly different from that in either 1978 or 1976. In terms of proportion sexually mature (Table 6) 1978 differed significantly from both 1974 and 1976 in age classes 1 and 2 and in all young of the year in both sexes. The difference in the number of females that actually produced at least one litter seems to me to be a better indication of the possible occurrence of an "increase type" than is pregnancy rate alone.

Obviously, too, if more individuals mature in age class 1 in one year than in another the mean ages at maturity will also be different in the two years.

Maturation rate of young of the year was inversely related to density, as already noted by Kalela (1957), Koshkina (1965), and Zejda (1967) for *C. rufocanus, C. rutilus* and *C. glareolus*, respectively. In the study population virtually all individuals of age class 3 matured every year, and individuals born after about 4 July all failed to mature in the season of their birth (Mihok 1979). Because these responses are both "all or none", the only chance for a graded response to density change occurs in a cohort born during a "window" that extends from about 20 June to 4 July. Each member of that cohort that has at least one litter contributes as much to the birth rate as 11 or 12 females would do assuming an increase of 0.5 embryos per litter.

Table 10. All possible outcomes of three-way comparisons, and number of cases in each class. There are 6 variants in class 2 for a total of 19 possible outcomes.

Class	Outcome	Cases
1	$1974 = 1976 = 1978$	10
2	$1974 \neq 1976 \neq 1978$	5
3	$(1974 = 1976) < 1978$	15
4	$(1974 = 1976) > 1978$	0
5	$(1974 = 1978) < 1976$	2
6	$(1974 = 1978) > 1976$	3
7	$(1976 = 1978) < 1974$	0
8	$(1976 = 1978) > 1974$	1
9	$(1974 < 1976) = 1978$	0
10	$(1974 > 1976) = 1978$	0
11	$(1974 < 1978) = 1976$	4
12	$(1974 > 1978) = 1976$	0
13	$(1976 < 1978) = 1974$	0
14	$(1976 > 1978) = 1974$	0
	Total	40

5. Conclusion

Finally, we come to the question asked in the subtitle — is there a peak syndrome in *Clethrionomys gapperi*? Three-way comparisons have 19 possible outcomes — one in which all three values are the same, six in which all three values differ, six in which one value differs from the other two, and six in which two values differ from each other but not from the third (Table 10). If there were a peak syndrome, and if the parameters chosen for comparison are part of that syndrome, the most commonly observed outcomes ought to be the two in which (1974 equals 1976), both of which differ from 1978. The value for 1978 may be either greater or less than that for the other two years depending on the nature of the parameter. For example, body weight in spring is expected to be less in 1978 than in the peak springs, whereas the rate of increase should be greater if the 1978 population contains a high proportion of "increase types". Any of the eight outcomes in which 1978 is indistinguishable from one of the peaks and different from the other are particularly damaging to the syndrome hypothesis, as are the two outcomes in which the peaks differ from each other but neither differs from 1978.

The outcomes of 40 comparisons were clearly not distributed according to chance (Table 10). Class 1 contains 10 cases when only about 2 would be expected by chance alone. Most of them have little bearing on the syndrome question, but three of them involve a reproductive parameter — mean number of litters per breeding female — which could be a feature selected for in an "increase type". Class 2, on the other hand, has only five cases, whereas about 12 would be expected by chance. Four of the 5 involved survival indices in females (Table 5), the fifth, June weight of OW females. In all five cases the observed outcome is contrary to the prediction from the syndrome hypothesis that the peak years should not differ from each other.

I will pass over the expected outcomes (classes 3 and 4) for the moment and deal with the 10 classes whose outcomes are at variance with the hypothesis. The first thing to note is that six of the ten classes are empty, and one contains only a single, trivial, case (length of OW females in June). It is also particularly striking that all four classes in which 1974 is the "odd" year (numbers 7, 8, 13, 14) contain only a single example. In contrast, only one of the four classes in which 1976 is the "odd" year (numbers 5, 6, 11, 12) is an empty class, and the other three classes contain 10 cases in total.

Both cases in class 5 involve size in June (length and weight of males). The outcome for class 5 matches the outcome of a comparison of spring temperatures (Fig. 1), which suggests that temperature plays a role in spring growth of males. All cases in class 6 are male *SI*'s (Table 5). Spring weights are supposed to be greater, and survival is supposed to be better in increase and peak years than in low and decline years, so classes 5 and 6 run counter to the syndrome hypothesis.

The four cases in class 11 are less seriously in conflict with the hypothesis because the trends are in the right direction. One of the cases is trivial (late summer weight), one involves male survival (Table 5), and two involve reproduction in females (Tables 7 and 8).

The 15 cases in class 3 deal mainly with reproduction ($n=12$). Nine comparisons of proportion of young sexually mature (Table 6) and two comparisons of litter size (Table 8) fall into this class, and are consistent with the presence of an "increase type" in the low population of 1978, or conversely, selection against high reproductive output in peak years. One comparison (slopes of regressions) suggests that the differences in reproductive parameters were actually translated into differences in rates of increase. The final two comparisons are of female *SI*'s (Table 5), and they run counter to the syndrome hypothesis.

What emerges from this analysis, then, is not the classical microtine peak syndrome of large body size and good survival of OW adults, coupled with a reduced birth rate. It is instead the appearance of an r-selected OW cohort, or "increase type", that survived better than its counterparts in peak years, even in an unfavourable spring and summer. Whether the differences in reproductive parameters are under genetic control, and hence self-regulatory (sensu Krebs 1978), or merely a density-dependent phenotypic response, cannot be determined from my data.

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