Extra-large body size in California voles: causes and fitness consequences

William Z. Lidicker, Jr. and Richard S. Ostfeld

Extra-large body size in microtine rodents is a ubiquitous feature of peak population densities, and it has been hypothesized that these giant individuals represent a genetically based morphotype that has high fitness under increasing and high densities, and may represent a key element of a genetic polymorphism driving multi-annual cycles (Chitty/Krebs model). We examine this large-size phenomenon (Chitty Effect) in the California vole utilizing three approaches: analyzing the weight distribution in a non-cyclic population over a 13 yr period with comparisons to cyclic populations, analyzing body composition, especially fat content, as a function of body size, and observing the microhabitat distribution of extra-large males in two populations, one of which cycles.

Extra-large body sizes occur in all populations, and can occur in any year except in the year following a cyclic peak. They are most likely to be found when favorable conditions prevail for an extended period. Analysis of covariance demonstrates that body composition (fat, water, fat-free dry weight) is influenced by season, sex, reproductive condition, as well as by body size. Fat accounts for only 45% of variation in body weight, and extra-large voles are sometimes fat and sometimes lean. Contrary to expectations of the Chitty/Krebs model, extra-large males tend to be in marginal microhabitats and to be negatively associated with reproductively active females.

We conclude that the Chitty Effect in California voles is the result of prolonged periods favorable to growth and survival, that these giant individuals do not have enhanced fitness under conditions of rapid population growth and high densities, and that large size may or may not be associated with obesity. Collectively, our data do not support the hypothesis that the Chitty Effect is caused by a genetic polymorphism, and instead we view it as an interesting epiphenomenon of vole density regulation.

W. Z. Lidicker, Jr., Museum of Vertebrate Zoology, Univ. of California, Berkeley, CA 94720, USA. – R. S. Ostfeld, Dept of Biology, Boston Univ., Boston, MA 02215, USA (present address: Inst. of Ecosystem Studies, New York Botanical Garden, Box AB, Millbrook, NY 12545, USA).

One of the most stimulating hypotheses proposed to explain the perplexing multi-annual fluctuations ("cycles") in numbers often exhibited by microtine rodents is that associated with Chitty and Krebs (Chitty 1958, 1960, 1967, 1987, Krebs 1964, 1978, Krebs and Myers 1974). Over the thirty-plus years that this hypothesis has been extant, it has evolved extensively and many versions are in the literature. However, its essential features have not changed. The hypothesis proposes that microtine cycles result from a self-regulative process involving a genetic polymorphism affecting aggressive behavior. Over the course of a cycle, varying selective regimes select differentially for two behavioral morphotypes producing the observed changes in density. The most generally accepted feature of these multi-annual fluctuations is the ubiquitous occurrence of especially large (that is, heavy) individuals during peak populations (Chitty 1952, Zimmermann 1955, Chitty and

Chitty 1962, Kalela 1962, Krebs 1964, Krebs and Myers 1974, Gaines et al. 1977, Boonstra and Krebs 1979, Tamarin et al. 1984, Taitt and Krebs 1985). Moreover, these big voles are generally considered to be assignable to one of the two genotypes involved in the presumptive polymorphism, namely the one favored at high densities (Chitty 1967, Stenseth 1978, Boonstra and Krebs 1979). In fact, this phenomenon, the "Chitty Effect" (Boonstra and Krebs 1979), is so characteristic of microtine cycles that its understanding is considered by some to be fundamental to unraveling the mechanism of multi-annual cycles (Krebs 1978, Chitty unpubl., cited in Taitt and Krebs 1985, Chitty 1987).

This paper reports our efforts to understand the large-size phenomenon in the California vole (*Microtus californicus* Peale), a species that often shows multi-annual density cycles of three to five years duration (Krebs 1966, Batzli and Pitelka 1971, Bowen 1982, Cockburn and Lidicker 1983, Ostfeld et al. 1985, Hestbeck 1986, Lidicker 1988). Because the Chitty Effect is presumed to be of such pivotal importance to these cycles, we feel that it is essential that we try to understand its causes and consequences. Specifically, we wish to examine some of the assumptions and corollaries of the Chitty/Krebs model as they may be applicable to this species.

The following are attributes of the large body size phenomenon according to the Chitty/Krebs model. It is these fundamental properties of the model that we investigated in the California vole: (1) Extra-large individuals are almost exclusively associated with peak populations; (2) Large individuals are favored by natural selection under high density conditions; and (3) Large individuals are heavy because they have grown to a larger than average size, that is, they are not merely obese.

The relevance of the Chitty Effect to the demographic mechanisms of multi-annual cycles depends on a close association between the occurrence of extra-large individuals and peak cyclic densities. To explore this relationship, we first examine the weight distribution in a population that does not exhibit multi-annual cycles and compare this with one that does, both populations being very closely related genetically.

Next, we examined body composition (fat, water, fat-free dry weight) as a function of body size to determine if large individuals tended to be especially fat, or alternatively did not differ in body composition from less heavy individuals. We reasoned that if extra-heavy individuals were merely obese, it would be less likely that the Chitty Effect was based on a genetic polymorphism.

Finally, to gain insights into whether or not extra-large individuals are favored by natural selection at high densities, we have observed the micro-spatial distribution and survival rates of extra-large males in two populations, one of which exhibits multi-annual cycles. We wished to determine if these males were associated with

the most favorable microhabitats and whether they cohabited with reproductively active females to a greater extent than other males. The distribution of extra-large females could not be examined in a similar fashion because these two data sets were based on live-trapping only, and hence female weights could not be corrected for pregnancy.

Large-size in a non-cyclic population
The data set

Samples of 1923 individuals collected over a 13 yr period on Brooks Island in San Francisco Bay (Lidicker 1973) allow us to examine the occurrence of large-sized individuals unencumbered by possible complications associated with multi-annual cycling of densities. Moreover, these samples are extensive enough that one can search for effects of season and density, as well as sex. It is especially noteworthy that the population exhibits only annual cycles in numbers, while originating from a population within a few kilometers of the Russell Reservation (see below) population which undergoes multi-annual cycles (Lidicker and Anderson 1962, Lidicker 1973). The Chitty/Krebs model is not explicit on non-cyclic populations, but since the Chitty Effect is closely associated with multi-annual cycling, there is the implication that extra-large individuals should be absent on Brooks Island.

The Brooks Island sample is enriched by the association of reproductive data, body length measurements, and age estimates for each individual. The reproductive data allow us to relate size with reproductive status, and to correct female weights for pregnancy. Based on known birth weight and gestation period and on some direct measurements, weights for embryos of various sizes were estimated by the following formula: 1 mm of embryo = 0.1 g. Body weights for pregnant females were corrected accordingly. Age estimates were based on the method of Lidicker and MacLean (1969). In an effort to assess body condition, we calculated the ratio of body mass (g) to body length (mm, not including the tail), reasoning that individuals that are heavy relative to their length would be in relatively good condition.

The first major decision was to choose which of the 1923 individuals in our sample constituted extra-large ones. The sample is composed of 1808 individuals that are at least 25 d estimated age. As such, all of these are potentially reproductively competent. During the breeding season, females can mate as young as 17 d of age and males at about 25 d old. Males in the 40 to 50 g range can be considered typical mature adults. Similarly, females in the 35 to 45 g range would be the most frequent cohort of actively breeding individuals (Lidicker 1973). Given this information, we considered that males of at least 55 g could reasonably be considered extra-large. This group consisted of 121 males or 12.6%

Table 1. Seasonal analysis of extra-large individuals from Brooks Island.

	Spring	Summer	Autumn-Winter	Totals
Males				
numbers	432	265	264	961
number extra-large	91	10	20	121
percent extra-large	21.1	3.8	7.6	2.6
percent of total sample	9.8	2.0	4.1	6.3
Females				
numbers	500	238	224	962
number extra-large	83	21	19	123
percent extra-large	16.6	8.8	8.5	12.8
percent of total sample	8.9	4.2	3.9	6.4
Both cases				
numbers	932	503	488	1923
number extra-large	174	31	39	244
percent extra-large	18.7	6.2	8.0	12.7

of the males in the sample (Table 1). Boonstra and Krebs (1979) used 56 g for their cut-off weights for large-size male California voles. To keep the female "extra-large" size category comparable, we designated the 123 individuals constituting the heaviest 12.8% of that sex as "extra-large." The group had a corrected body weight of at least 45.4 g (Boonstra and Krebs 1979, used 52 g as their threshold weight for females but included those in early to mid pregnancy). To be even more conservative, we also studied those males with weights of at least 60 g (n=60; 6.2%). The maximum weight recorded for a male from the Brooks Island population was 80.9 g. This is comparable to the 81 g maximum recorded for the Russell Reservation population, which shows multi-annual cycles. The heaviest female recorded was also 80.9 g, but when this weight is corrected for embryos, it becomes 62.5 g.

Seasonal distribution

The seasonal distribution of extra-large individuals is shown in Table 1, arranged by sex. These individuals occurred in all 13 years of the study. In this population, peak densities occur each year in about mid-June (Lidicker 1973), and it is this point that marks the beginning of the "Summer" (dry) season. "Autumn-Winter" be-

Table 2. Correlation matrix for large individuals from Brooks Island: males (n=121) above diagonal; females (n=120) below diagonal.

	Weight	Age	Body Length	Condition
Weight	–	0.373**	0.491**	0.872**
Age	0.287**	–	0.337**	0.233*
Body Length	0.424**	0.657**	–	0.005
Condition	0.898**	0.002	–0.017	–

* p < .01
** p < .005

gins with the start of the rainy season, usually mid-October; and "Spring" starts with mid-February. Whereas most big individuals occur in spring (71.3%), some are present in the population at all seasons (Table 1). Also, more large females than males occur in the summer. For all years, the number and percent of extra-large males decline *before* the end of the breeding season. Some large females generally persist into the summer season, however.

Considering only the subsample of 60 very large males (≥60 g), we find that these also occur in all years and all but seven in late winter or spring. Of the seven exceptions, two were found in summers following particularly high June densities, and five occurred in the autumn of 1959 when the island was still being colonized by this species.

Relationships between weight and other body metrics

Table 2 illustrates a correlation matrix for four variables: body weight, body length, estimated age, and body weight/body length ("condition index"; Lidicker 1973). The highest correlations are between body mass and the condition index. At first we thought that this implied that the heavier the individual, the more fat it contained. Later, we discovered (see below) that this index carries little information other than body weight, and so not much can probably be concluded from this. Highly significant (p < 0.005) correlations also occurred between body weight and both body length and age in both sexes. Not surprisingly, age and body length were also strongly correlated.

Because of possible character interactions, we did a step-wise multiple regression analysis using weight as the dependent variable. The condition index always entered first with body length second. Together they give R^2 values of 99.7 and 99.9 for males and females respectively. Eliminating the condition index gave quite

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different results. For both sexes, body length enters first but does not give statistically significant regression coefficients ($p > 0.05$). For males, age enters second giving an R^2 of 29.0 ($p < 0.05$). Age does not even enter for the female sample.

Conclusions

We conclude from this analysis that extra-large body sizes occur regularly in annually cycling populations as well as in multi-annual ones. In fact, they are present in every year that moderate to high densities are achieved. Large size is strongly influenced by season, being primarily a phenomenon of late winter and spring, although males and females show some minor but possibly important seasonal differences. Occurrences at other seasons are associated with particularly high numbers or especially favorable conditions. Heavy weights are significantly associated with big body lengths. Age correlations are positive, but add little information not already incorporated in body length. Although the highly significant positive correlations between body weight and our condition index might suggest that heavy individuals tend to be unusually fat, this conclusion must be tempered by our subsequent (see below) failure to show such a consistent relationship with our body composition studies.

Body composition versus size
Introduction

Because of the possibility that extra-large (heavy) individuals represent a genetically-based morphotype, we investigated fat content as a function of body size. The Chitty/Krebs model supposes that such a morphotype is genetically programmed to become structurally large. Therefore, if extra-heavy voles have merely accumulated fat, the argument that they represent a genetically based large-sized morph would be weakened. Questions that we posed were: (1) Is the condition index correlated with actual fat content? (2) As voles grow, does their body composition with respect to fat, water, and fat-free dry weight remain in the same proportions? In particular, do the extra-large individuals deviate in some consistent way from other individuals? and (3) Are there sex and seasonal variations in the answers to these questions?

To explore these issues, we did a complete fat extraction on a sample of 44 voles ranging in mass from 16.8 to 71.2 g. Female weights were corrected for pregnancies. These voles were collected mostly from the Russell Reservation (see below), but a few came from the Richmond Field Station, both in Contra Costa County, California. The sample was approximately equally divided by sexes and into two seasons. Half were collected in mid-winter (Winter Sample), and half were taken toward the end of the breeding season in late spring-early summer (Summer Sample). Whole carcasses, frozen immediately after being weighed and autopsied, were dried at 50°C to a constant weight, ground with mortar and pestle, and subjected to petroleum ether extraction for 48 h. Body content was divided into three fractions: fat, water, fat-free dry weight (FFDW). The condition index was also calculated for each individual.

A priori, we recognized multiple inadequacies in our sample. As always, a larger sample would be desirable. This was especially the case when we subdivided it by sex and/or season. Only 13 individuals qualified as "extra-large" (six males, seven females) by our Brooks Island criteria, and these were not from peak population densities. However, our primary purpose was to document ontogenetic changes in body composition, and for these a wide range of body weights was desirable. These limitations emphasize, however, that our findings must be considered preliminary.

Analysis of ratios

First, we regressed the condition index against body mass, and we did this for the total sample as well as for 11 different sub-samples based on sex, season, and reproductive status. All regressions were highly significant statistically ($p < 0.0001$) with R^2 varying from 0.92 to 0.98 (0.96 for the total sample). We conclude from this that the condition index gives almost no information that is not contained in body weight.

We next calculated body composition in terms of fat as a per cent of wet weight, fat as a percent of dry weight, percent water, and percent fat-free dry weight (FFDW). Then body proportions were regressed against body mass. With sample subdivisions for sex, season, and reproductive condition, 48 regressions were computed. For the total sample, none of the variables gave significant regressions or even suggested likely trends, and only three regressions had p-values less than 0.05.

Bivariate analyses

For the next phase of our analysis, we avoided use of ratios, as recommended by Packard and Boardman (1987). As they point out, ratios intended to eliminate size from the effects on the variable of interest often fail to do this, and the resulting ratios frequently remain highly correlated with body size (for example, our condition index). They recommend using analysis of covariance procedures as an alternative. Accordingly, we re-analyzed our unmodified data using the SAS regression and covariance procedures.

Table 3. Regression statistics for selected and statistically significant (p<0.05) relations between FFDW (g) and body size.

Regression		R^2	Slope (m)	p	Intercept (b)	p
Sample	Covariate					
Total	Body wt.	0.944	0.279	0.0001	0.037	0.9355
	Body len.	0.917	0.202	0.0001	−14.947	0.0001
Females	Body len.	0.906	0.180	0.0001	−12.353	0.0001
Males	Body len.	0.928	0.218	0.0001	−16.894	0.0001
Heavy	body wt.	0.814	0.218	0.0001	1.869	0.223
Light	Body wt.	0.934	0.306	0.0001	− 1.587	0.009
Long	Body wt.	0.822	0.196	0.0001	3.211	0.005
Short	Body wt.	0.963	0.280	0.0001	− 0.968	0.028
Winter	Body wt.	0.926	0.232	0.0001	1.396	0.053
	Body len.	0.896	0.231	0.0001	−18.961	0.0001
Summer	Body wt.	0.942	0.255	0.0001	− 0.296	0.588
	Body len.	0.887	0.196	0.0001	−13.971	0.0001
Females						
Summer	Body len.	0.924	0.185	0.0001	−12.523	0.0002
Winter	Body len.	0.937	0.210	0.0001	−16.652	0.0001
Males						
Summer	Body len.	0.887	0.257	0.0001	−21.333	0.0011
Winter	Body len.	0.719	0.212	0.0005	−15.959	0.0235
Males, winter						
Heavy	Body wt.	0.845	0.210	0.0001	2.466	0.099
Light	Body wt.	0.928	0.320	0.002	− 2.012	0.339
Females, light						
Summer	Body wt.	0.959	0.281	0.0001	− 1.062	0.073
Winter	Body wt.	0.990	0.389	0.005	− 3.115	0.064
Reproductivity						
Active	Body wt.	0.893	0.233	0.0001	1.165	0.167
Inactive	Body wt.	0.901	0.294	0.0001	− 1.218	0.135

Body length

Not surprisingly, body length (total length – tail length) is very strongly related to body weight ($R^2 = 0.871$, $p < 0.0001$). To test for non-linearity, we calculated regression residuals of body weight and plotted them against body length. They gave a classic random scatter ($R^2 = 0.000$, p=1.0) with no suggestion of a U-shaped distribution. Although it seems unlikely that throughout ontogeny this relationship remains linear, in our sample it clearly is. Regressing log body weight and body weight($^{3/4}$) against body length improved the regression only slightly. We conclude that over the weight range shown by our sample, body length and weight co-vary tightly (with a slope of 0.752). Because of this, no obvious sex or seasonal effects on the regression could be detected.

Water

In contrast to our results with percent water composition, when we regressed water content (g) against body size (weight, length), we found very tight correlations. No suggestion of non-linearity was indicated nor could sex or seasonal effects be discerned.

Weight and fat-free dry weight

Dry weight showed very tight correlations with total body weight ($R^2 = 0.943$, $p < 0.0001$) and body length ($R^2 = 0.893$, $p < 0.0001$). Subtracting fat from dry weight to give FFDW improves the correlations marginally ($R^2 = 0.944$ and 0.917, $p < 0.0001$, respectively). Each sex calculated separately gives a similar tight linear regression with males seeming to have a steeper slope.

Table 3 gives regression statistics for 22 selected regressions of FFDW against body size. Seasonal correlations are also high, with all four sex/seasonal groupings showing significant regressions. Even when the sample is divided by sex, season, and weight class (heavy and light), four subgroups continue to have a significant positive relationship between FFDW and body weight.
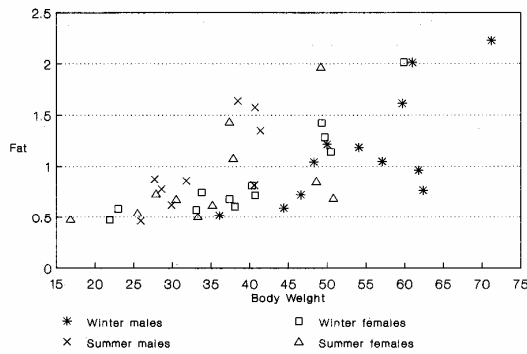
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Fig. 1. Fat content (g) as a function of body weight (g); n = 44. Sex and two seasonal categories are shown.

Male reproductive condition

Because of the possibility that fat deposition might be related to reproductive state, we investigated how seminal vesicle length and testes volume (calculated from testis length and width measurements) changed with body size. Both measures of male reproductive competence were highly significantly correlated with body weight and length ($p < 0.0001$ for both). In the case of

body length, a size of 124 mm clearly marked the threshold separating reproductively active from inactive individuals. R^2 for weights were consistently lower than for length, and in fact, there was a weight range of 36 to 42 g within which both active and inactive individuals occurred.

Fat

Most attention was given to this variable because of its theoretical significance. Fig. 1 shows how fat content relates to body weight in our sample, with sex and two seasons also indicated. Table 4 gives regression statistics for 21 statistically significant ($p < 0.05$) relationships between fat and body size.

In the undivided sample, body weight gives an R^2 of 0.448 and body length 0.303. A study of the regression residuals of fat content with these two variables shows no evidence of non-linearity. However variation among the residuals increases markedly with size. Among the six largest males (> 55 g), three are much fatter than predicted and three are much leaner. All six are from the winter sample. There are also three especially fat males weighing between 38.5 and 41.4 g taken in the summer sample and reproductively inactive (although two of them showed evidence of previous sexual competence).

Table 4. Regression statistics for statistically significant (p<0.05) relations between fat content (g) and body size.

|	Regression	R^2	Slope (m)	p	Intercept (b)	p
Sample	Covariate					
Total	Body wt.	0.448	0.025	0.0001	−0.05	0.775
	Body len.	0.303	0.017	0.0001	−1.12	0.030
	FFDW	0.407	0.092	0.0001	0.02	0.931
	Log fat: FFDW	0.431	0.844	0.0001	−2.06	0.0001
Females	Body wt.	0.535	0.030	0.0001	−0.236	0.336
Males	Body wt.	0.342	0.022	0.005	0.110	0.738
Heavy	Body wt.	0.286	0.033	0.027	−0.51	0.503
Light	Body wt.	0.239	0.022	0.010	0.073	0.787
Long	Body wt.	0.433	0.036	0.0007	−0.660	0.164
Short	Body wt.	0.468	0.038	0.0006	−0.380	0.221
Winter	Body wt.	0.595	0.031	0.0001	−0.401	0.141
	Body len.	0.465	0.027	0.0002	−2.67	0.005
Summer	Body wt.	0.336	0.029	0.007	−0.070	0.839
	Body len.	0.290	0.021	0.014	−1.50	0.113
Females, winter	Body wt.	0.796	0.036	0.0001	−0.514	0.057
Males, winter	Body wt.	0.539	0.041	0.007	−1.067	0.137
Males, summer	Body wt.	0.590	0.051	0.016	−0.729	0.229
Reproductivity – Females						
Active	Body wt.	0.572	0.044	0.003	−0.930	0.102
Inactive	Body wt.	0.463	0.028	0.031	−0.097	0.772
Reproductivity – Males						
Active	Body wt.	0.542	0.039	0.004	−0.924	0.139
Inactive	Body wt.	0.844	0.066	0.001	−1.147	0.025
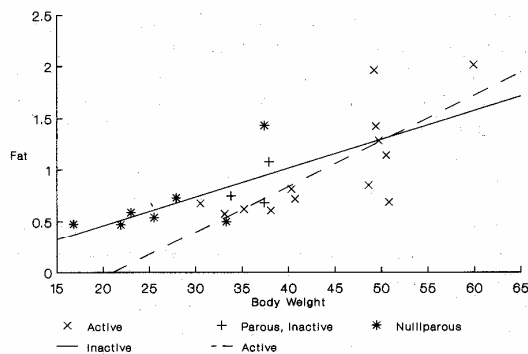
Fig. 2. Body fat content as a function of body mass in females, with three reproductive categories indicated; n = 23. The regression for the inactive individuals includes both "parous, inactive" and "nulliparous" categories.

Fig. 4. Residuals of fat content regressed on body weight plotted against seminal vesicle length, n = 21. Males with seminal vesicle lengths greater than 4.5 mm are reproductively competent. Males ≥55 g body weight (Chitty males) are indicated by *.

Dividing our sample by sex and reproductive status, we find that significant regressions of fat against body weight persist for males and females separately and for all four sex/reproductive categories (Table 4, Figs 2, 3). It is apparent, however, from Fig. 2 that most females (16:23 in the sample) add only a few 0.1 g of body fat as they grow from 17 to 51 g. Reproductive activity does not correspond well to fat content (Fig. 2), and the regressions of active and inactive females show no noticeable improvements over all females together (Table 4).

Overall, males show more variability than females and this pattern begins at a much smaller size (Figs 2, 3). Reproductively active and inactive males seem to have different regression trajectories with the latter being fatter. Active males show a shallower slope and intercept not different from zero. Inactives have a steeper slope and a y-intercept (− 1.15) significantly different from zero (Table 4, Fig. 3). As noted above,
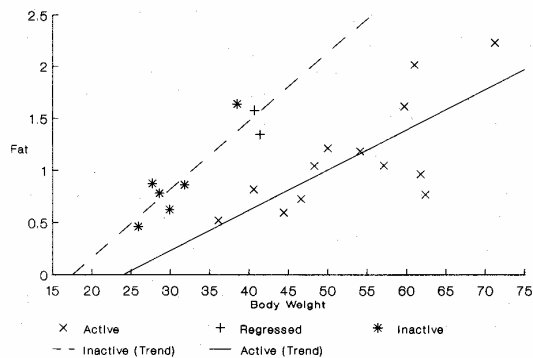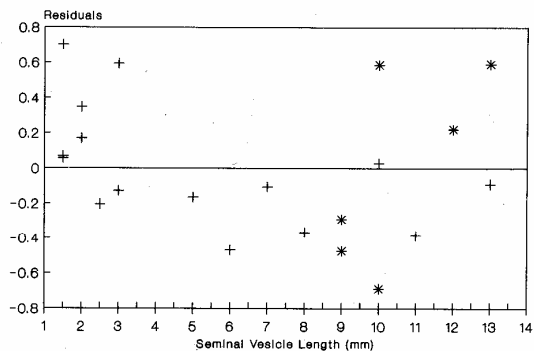
the extra-large males are strongly bimodal in fat content. When the residuals of fat versus body weight are plotted against testes volume and seminal vesicle length, we find a random scatter for the first and a definite U-shaped distribution for the second (Fig. 4). This last finding suggests that males are relatively fat when they are reproductively inactive and again when they have the largest possible seminal vesicle size.

Because of our special interest in the largest individuals, we divided our sample into heavy and light individuals. For males "heavy" meant ≥49.0 g and for females ≥39.0 g. Rather than improving the relationship between fat and size, this destroyed the significance of the correlation with body length and reduced it for body weight (Table 4). We also divided the sample on the basis of body length. Long males were defined as having a body length of > 130 mm, and long females were > 123 mm. This division improved the correlation between fat and body weight (Table 4).

Fig. 3. Body fat content as a function of body mass in males, with three reproductive categories indicated; n = 21. The regression for inactive individuals includes the "regressed" category.
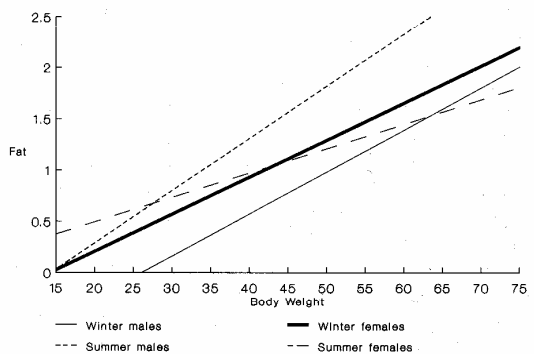

Fig. 5. Regressions of fat content on body mass for four sex and season categories; see Table 5 for regression statistics. Slopes are all statistically different from zero except for summer females.
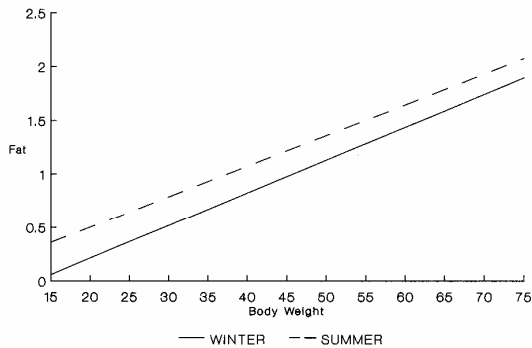
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Fig. 6. Fat content as a function of body weight, and according to two seasons. Y-intercepts are significantly differnt (p = 0.039), but slopes are not; see also Table 5.

Finally, we addressed the possible influence of season on fat content. Both winter and summer samples showed statistically significant positive regressions against both body length and weight (Table 4), and for winter the R^2 values were improved over the total sample. In spite of the vastly reduced sample sizes, three of four sex/season groups also continued to show positive and significant regressions on body weight (Table 4). Fig. 5 shows the regressions for these four subgroups, and Fig. 6 shows the two seasonal groupings only.

Analysis of covariance

While these bivariate analyses give useful insights, they are limited in their usefulness because of rampant factor interactions. We therefore subjected our data set to covariance analysis. Because fat and FFDW are the body components with least predictability from body size, we used each of these as dependent variables. The covariate body size was measured by body weight or body length. Independent variable were: sex, season, reproductive status, and, for weight as the covariate, we used two body length classes and two body weight classes when body length was the covariate.

The analyses for fat gave unequivocal results. There were no significant effects on regression slopes for either body length or body weight. For both size indices, there were significant effects on intercepts for season and reproductive condition. For body weight, the two length classes also showed significantly different intercepts. These results support our conclusions from the bivariate analysis, namely: 1) reproductively inactive females have a higher intercept than active ones, and hence have more fat for a given weight (see Fig. 2, Table 4); 2) reproductively inactive males start to accumulate fat at a smaller size and remain fatter than active males at equivalent body weights (Fig. 3); 3) winter individuals have a lower intercept than summer ones, and hence are less fat for a given weight (Figs 5, 6).

When FFDW was used as the dependent variable, slightly more complex results were obtained. With respect to body length, males and females have significantly different regression slopes (Table 3), with males increasing in FFDW faster. Seasonal influences on the y-intercept are not significant (p = 0.07). With respect to body weight, it is not surprising that shorter voles increase their FFDW content faster than do the longer individuals (p = 0.004; Table 3). As with fat, there are seasonal influences on y-intercepts, with winter voles having the higher intercept (p = 0.004; Table 3); and as one might expect, the effects of fat and FFDW are reciprocal. Thus the analysis of covariance affirms the sex and seasonal differences in FFDW relative to body size found with the bivariate analyses (Table 3).

Space use and survival in extra-large males

Introduction

Perhaps the most critical assumption of the Chitty/Krebs model is that the large morph is strongly favored by selection as densities increase and approach peak numbers. Without this, the postulated shift toward high frequencies of this high density type would not occur. Boonstra and Krebs (1979) analyzed survival rates in four species of *Microtus*, and concluded that for two species (*pennsylvanicus* Ord and *townsendii* Bachman) large adults are favored during periods of rapid population growth, and for two other species (*californicus* and *ochrogaster* Wagner) large size is advantageous at high densities. Thus, they raise the possibility that the particular selective advantage of being extra-large may not be the same in all species of cyclic microtines.

For *M. californicus*, Boonstra and Krebs (1979) analyzed data from six populations based on data in Krebs (1966). In addition to a positive correlation between survival advantage of large voles and mean density (statistically significant only for males), they concluded that during the breeding season, large males had a survival advantage of 11% and large females 4%. There was no advantage during the non-breeding season, as large individuals rapidly disappeared during the non-breeding period. Because the two-week survival rates that they calculated are subject to unknown errors due to dispersal and chance recapture failures, and because these limitations could be size-biased, we felt that their conclusions required further examination.

We examined the micro-spatial distribution of extra-large males to see if fitness criteria other than survival rates could be used to address this critical issue. We utilized data from two intensive live-trapping studies in which habitat quality was assessed and mapped on a scale relevant to vole daily movements. One study was done at the Russell Reservation in Contra Costa County, California (Cockburn and Lidicker 1983, Ost-
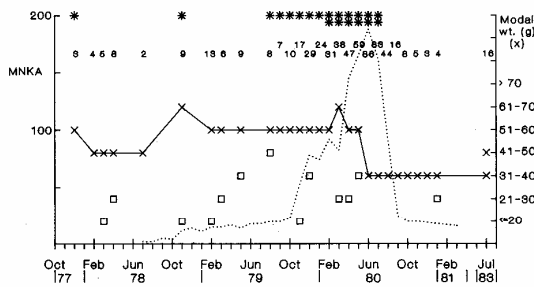
Fig. 7. Modal weight classes of male voles shown in relation to population density (minimum numbers known to be alive = MNKA) at Russell Reservation. Density data from Cockburn and Lidicker, 1983, and Lidicker, 1988. Sample sizes are shown across the top. □ = large cohorts of young producing secondary modes; * = samples containing individuals > 60 g; ** = samples containing individuals > 70 g.

feld et al. 1985), involving a population showing multiannual cycles. The other was a four-year investigation of a relatively stable population at the Bodega Marine Laboratory, Sonoma County, California (Ostfeld and Klosterman 1986). Because these were both live-trapping studies, female weights could not be corrected for pregnancies, and hence our analysis is limited to extra-heavy males.

Russell Reservation

This is an inland site in which the vegetation is dominated by introduced annuals; for details, see Bowen (1982), Cockburn and Lidicker (1983), Heske et al. (1984), Ostfeld et al. (1985). A spectacular peak density of approximately 1000^{-1} ha (Lidicker 1985) occurred in June 1980 (Fig. 7), with smaller peaks occurring in 1976 and 1984. Voles were monitored on four small grids arranged so as to sample different microhabitats in a large grassland from 1976 to March, 1981. Grids 1 and 2 were dominated by the perennial grass *Elymus triticoides* Buckl., Grid 3 by *Conium maculatum* L. (poison hemlock), and various thistles, and Grid 4 was in an annual grassland (for details, see Cockburn and Lid-

Table 5. Reproductive and density measures of habitat quality (grids) at the Russell Reservation, 1978 to 1981; data from Ostfeld et al. 1985.

Criteria	Grid			
	1	2	3	4
Number of individuals recorded	452	462	402	344
Number of recruits	226	236	201	172
Proportion of juveniles**	0.28	0.24	0.16	0.21

**G-Test for heterogeneity among grids; p < 0.01

icker 1983). It is possible to rate Grids 1 and 2 as high quality microhabitats relative to Grids 3 and 4 which can be viewed as "colonizing habitat" (Anderson 1970, 1980, Hansson 1977) or sub-optimal. This ranking is based on average densities, reproductive output, average length of residency, persistence (mean percent of voles captured during a given trap session that were captured again in a subsequent trap session), and numbers of resident adult females (Table 5; Ostfeld et al. 1985). In all these criteria, Grids 1 and 2 scored higher than did Grids 3 and 4.

Fig. 7 shows modal weight classes for males during the 40 months (December, 1977 to March, 1981) for which weight data are available. Using a conservative threshold weight of 60 g, extra-large males occurred in the autumn-winter period of 1977 and 1978, and starting in August, 1979, in every month thereafter through July, 1980. There were none following the population crash and continuing to the end of the study. Males weighing 70 g or more occurred only from February to July, 1980. It is interesting that the modal weight of adult males hardly varied for the 23 month period starting twelve months *before* October, 1979, when the population began to climb to its peak density in June, 1980. Thus, with a four-year density cycle, the pattern of male weight change seems to be one of a high pre-peak and peak year mode, followed by two years of a significantly reduced modal weight. During the peak year breeding season, there is the addition of a few super-heavy individuals. These latter would affect the average weight, but not the mode. This pattern of weight change contrasts with that in the annually cycling Brooks Island population described above, mainly in that extra-heavy males were absent in the post-peak year.

At this point, we examine in detail the activities of the 44 extra-large males (≥ 60 g) that were present in the study population from March through July, 1980. This is the period when the population was growing rapidly to peak numbers and includes the initial stage of the decline. This is also the period when the extra-large males were present in large numbers and occurred on all four grids. All had disappeared by August of that year. Table 6A shows the distribution of these large males on the four grids and also gives the expected distribution assuming the presence of these males is proportional to grid area, density of all adult males, and density of adult females. We were surprised to find that the poorer-habitat grids held 28 (64%) of the large males. In fact, a phenomenal 43% were on Grid 3, and because of this bias the observed distribution across all four grids is significantly non-random ($\chi^2 = 8.00$; p < 0.05). Preference for Grid 3 by extra-large males is probably due to the much better cover present on this grid (poison hemlock and thistle).

The distribution of extra-large males is not statistically different from that of all adult males ($\chi^2 = 2.91$, p > 0.40), although Grid 3 shows an excess of large males. However, extra-large males show a significantly

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Table 6. Distribution of extra-large males relative to habitat, adult male density, and adult female density. Expected numbers assume a distribution proportional to area, male density, and female density for each grid or patch-type. Statistical tests are for comparisons between expected and observed numbers across all four grids or patch-types. Grids and Patch-types 3 and 4 represent the poorer quality habitat types in both study areas.

A. Russell Reservation (peak population in 1980).

	Grid					
	1	2	3	4	X^2	p
Observed numbers (n=44)	9	7	19	9		
Expected numbers						
habitat (area)	11.0	11.0	11.0	11.0	8.00	<0.05
male density	11.0	9.0	13.8	10.2	2.91	>0.40
female density	12.3	13.6	9.6	8.5	13.32	<0.005

B. Bodega Marine Laboratory.

	Patch-type					
	1	2	3	4	X^2	p
Observed numbers (n=10)	5	1	1	3		
Expected numbers						
habitat (area)	4.5	1.8	2.6	1.1	4.51	>0.05
male density	3.8	2.5	2.8	0.9	7.92	<0.05
female density	5.7	2.1	1.8	0.5	14.34	<0.005

different distribution across grids than do adult females ($\chi^2 = 13.32$; p < 0.005). Grids 3 and 4 have more large males than expected and Grids 1 and 2 fewer (Table 6A). We further refined the relationship of large males to adult females by considering next only resident females (recaptured in at least two trapping periods) and secondly only reproductively active resident females (Table 7). For both cases, the distribution of extra-large males deviates significantly from the expected (p < 0.005 and p < 0.025, respectively) in the same direction as for all adult females. This biased distribution is especially marked during the high density situation in May, June, and July, 1980 (p < 0.001 and p < 0.005 for resident and reproductively active resident females, respectively). The same suite of results is achieved if the analysis is further restricted to only those males at least 65 g in weight (n = 27). Grid 2 consistently shows the greatest deficiency of extra-large males, and Grid 3 the greatest excess. We even have one documented instance of a large male's dispersing from Grid 2 to Grid 3. Using data from this same population, Cockburn (1988:111)

showed that males on Grids 3 and 4 show significantly larger percent weight gains than males from the two female-rich grids.

Bodega Marine Laboratory

The data reported here come from a four-year investigation at this coastal location (Ostfeld and Klosterman 1986). Vole densities were remarkably stable, varying only from 76 to 117 per hectare over the entire study. Vegetation on the trapping grid could be easily assigned to seven discrete patch-types (see Ostfeld and Klosterman 1986, for details of species composition and cover characteristics). Five patch-types were extensive enough to be analyzed for quality to voles. Three of these were dominated by a single genus of perennial grass (*Agrostis,* *Holcus,* *Ammophila*); a fourth was characterized by mixed annual grasses and forbs, and the last was dominated by a woody species of lupine (*Lupinus arboreus* Sims). Patch quality was assessed by

Table 7. Distribution of extra-large males relative to that of resident adult females (those ≥ 25 g and captured in at least two trapping periods) at the Russell Reservation totalled over the five-month period March through July, 1980.

	Grid				
	1	2	3	4	Totals
Number of males	9	7	19	9	44
Number of females	98	102	63	46	309
Estimated number of reproductively active females	55.3	63.5	41.4	41.0	201.2

quality of food (except for the lupine patch-type), average vole density, adult female density, persistence rates, per capita reproduction, and emigration/immigration ratios. The highest quality patches by all criteria were those characterized by *Agrostis* and *Holcus*, and these two are combined in the following analysis (Patch-type 1). Substantially poorer quality was shown by the mixed annuals (Patch-type 2), and *Ammophila* (Patch-type 3) areas, with the latter being the poorer of the two. Finally, the lupine patches (Patch-type 4) were found to be the poorest of the five. Eighty-two percent of recaptures were in the same patch-type.

In spite of the relatively low densities occurring on this study site, 10 extra-large males were recorded (1.1% of individuals captured). Relative to area, the large males are distributed randomly, although the highest deviation is shown by Patch-type 4 with an excess of males (Table 6B). Despite the small sample, statistically significant non-randomness is shown relative to adult male distribution and especially adult female occurrences. With respect to adult males, the extra-large individuals are found in excess on Patch-types 1 and 4, thus suggesting a bimodal behavior relative to habitat quality. Patch-type 4 further shows a strong excess of males relative to adult female distribution, while the other three patch-types show slight deficiencies (Table 6B).

The two data sets show similar results, namely, that extra-large males are not found disproportionately in the best quality habitats or associated with the largest numbers of reproductively active females. In fact, they are not even distributed randomly, but are mostly in the poorer habitats (statistically significant only at the Russell Reservation) and where there are the fewest adult females (significant at both sites). This is an extraordinary finding because the Chitty/Krebs model would predict the opposite relationships, that is, large males should have high fitness under high density conditions.

Discussion and conclusions

This research explores the occurrence and fitness consequences of extra-large body size in the California vole, utilizing three different approaches and three independent data sets. In doing this, we test several key assumptions of the Chitty/Krebs model for density regulation in cyclic microtine rodents.

Temporal distribution of extra-large voles

We have found that extra-large body sizes occur in all populations and can occur in any year, although the least likely occurrences are in years following cyclic peak densities. This same pattern was found by Tamarin et al. (1984: fig. 4) for *Microtus pennsylvanicus* in a

situation where densities were high for four years out of five. In our data, large voles are most common in the late winter and spring, which are the most favorable times of the year for growth and survival, and otherwise occur if unusually good conditions prevail (e.g., colonization of empty prime habitat). Among non-cyclic populations, males over 60 g constituted 3.1% of individuals in a population showing chronically high densities (Brooks Island) and 1.1% in a population at consistently moderate numbers (Bodega Marine Laboratory). This difference supports the conclusion that extra-large size is correlated with especially good conditions for growth and survival. Other investigators have similarly reported large body sizes to be associated with periods of greater than usual longevity and/or especially favorable food supplies, rather than with particular densities or demographic phase (Myllymäki 1977 and Ferns 1979, for *Microtus agrestis* L.; Tast 1972, for *M. oeconomus* Pallas). Myllymäki (1977) and Halle and Lehmann (1987) further report that individuals of *M. agrestis* surviving a population crash show slow growth rates and delayed reproductive recrudescence.

Ontogeny of body composition

Our investigations into the ontogeny of body composition (i.e., fat, water, fat-free dry weight) turned out to be much more complex than we had anticipated. Clearly this is an area that deserves further study. We thought that once we understood how body composition changes with size (and age), it should be easy to ask whether extra-large individuals are fatter, no different, or leaner than expected. Fat individuals could be defined as those having regression residuals clearly above the fat on body size regression line, and lean individuals would have residuals well below this line. The same could be done with fat-free dry weight (FFDW), but with reciprocal interpretations.

We found, however, that the normal ontogeny of body composition is quite complex, being influenced profoundly by sex, season, reproductive status, and possibly other unstudied variables. Fig. 1 shows the dimensions of the problem. When fat is regressed against body weight, we find that fat accounts for only 44.8% of the variation in body weight (Table 4), and yet the regression is remarkably linear. Body length proves to be an even poorer covariant with fat ($R^2 = 0.303$; Table 4), and this is probably because of a tendency toward nonlinearity. An analysis of covariance, however, shows that big-bodied voles have a lower (less fat) regression line than do small-bodied individuals.

Body water averaged 72.1% of total body weight and varied only a few percentage points for over 80% of the individuals. Water regressed against body weight or length gave R^2 of 0.99 and 0.84 respectively. It is known, however, that California voles can tolerate some degree of dehydration (Church 1966), so if our

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samples had been taken well into the dry season, we might expect body water to have further complicated body composition.

The Condition Index that we employed requires further comment. We had hoped that this index would correct body weight for body size (length) and hence measure fat content (cf. Lidicker 1973). The index does correlate strongly with fat content, but produces an R^2 only slightly better than for fat against body weight (0.482 vs 0.448). Moreover, the association between the condition index and body weight is so close ($R^2 = 0.96$) that we are forced to conclude that this index carries little information besides body weight. It simply must be that body shape changes regularly with body weight. This would also explain the report by Humiński (1979) that corpulence in *Microtus arvalis* Pallas increases consistently with body length; his "corpulence ratio" is the same as our condition index.

Males and females showed somewhat different body composition relationships (Tables 3, 4), but, for the most part, these could be accounted for by interaction effects with season and reproductive status. The covariance analysis did show that when FFDW was regressed against body length, males had a significantly steeper regression slope than females. Thus males increase their non-fat mass (muscle, bone) faster than females as size increases.

Seasonal influences were shown consistently (Tables 3, 4; Figs. 5, 6). Winter voles, especially males, are less fat than summer individuals for a given weight (y-intercepts different). The reciprocal effect is shown for FFDW; that is, winter voles have the higher y-intercept.

Clear effects of reproductive status are shown on the fat versus body weight regression. Reproductively active females have a lower y-intercept (less fat) than inactive females. For males, inactives are also fatter than active males (at equivalent weights), but because non-reproductive males have a steeper regression slope (not statistically significant), suggesting that they become fatter faster as they grow larger (Fig. 3), their y-intercept is actually lower than for active males. Interestingly, obesity and reproductive activity seem to have a bimodal relationship for males (Fig. 4). Those with very small seminal vesicles are relatively fat as are some of those with the very largest seminal vesicles. In between, fat levels decline. It seems likely that fat reserves are mobilized when puberty is achieved and young males are faced with the demands of establishing themselves socially as adults, greatly increased aggressive interactions, courtship, mating, and possibly dispersal. In an earlier study (Lidicker 1979), reproductively active males were also found to be less fat than inactive ones. Reproductively active females, however, were not leaner, most likely because this earlier study utilized enclosures with abundant food.

Given all of these influences on the development of body composition, what can we conclude about relative obesity in extra-large individuals? Clearly, it is not as simple a question as we had originally thought. Seven females and six males in our sample are in the extra-large category. Among the females, two are lean, three have moderate fat, and two have the largest amount of fat of those in our sample (Fig. 2). All are reproductively active. Both seasons are represented (3 summer, 4 winter; Fig. 1), although seasonal complications are less for females than for males. The six extra-large males are all from the winter sample and all are reproductively competent. Three are very fat and three are very lean (Figs 3, 4). The three lean individuals would represent prototypes of the Chitty/Krebs model large morph. The fat trio, however, has an average seminal vesicle length of 11.7 mm instead of 9.3 mm for the lean group, and includes the largest male (8.8 g heavier than the largest lean male). Therefore, the body composition data do not support either the hypothesis (Chitty/Krebs) that extra-large individuals are mainly composed of bone and muscle (FFDW) or the alternate view that these giants are merely obese.

Spatial distribution of extra-large males

The question of the selective advantage of extra-large individuals at high densities is as critical to the Chitty/Krebs model as is their pattern of temporal occurrences. "Survival" statistics are difficult to interpret primarily because they are measures of persistence on an arbitrarily defined study plot, and may not reflect survival per se. Differential dispersal and imperfect trappabilities confound the meaning of these statistics (e.g., Boonstra and Krebs 1979, and references therein). Our intensive investigations in two quite different areas allowed us to use two preferable measures of fitness, namely, 1) quality of microhabitat being utilized, and 2) association of males with reproductively active females. On both these criteria and on both of our study areas, extra-large males were *not* found in the best habitats nor preferentially associating with reproductively active females as the Chitty/Krebs model would predict. In fact, in both areas extra-large males were not even randomly distributed, but were significantly negatively associated with adult females. With regard to habitat quality, these giant males were randomly distributed on one site (Bodega Marine Lab) and non-randomly associated with the poorer microhabitats on the other (Russell Reservation). Among the poorer habitats, those especially favored by large males are those dominated by relatively tall, dense, and sturdy vegetation (*Conium maculatum*, thistles, *Lupinus arboreus*). This suggests that predator avoidance rather than reproductive prowess or social dominance is of primary importance to extra-large males.

It was because of this apparent tendency of extra-large males to be social "drop-outs" that we termed this the "Big-Wimp Hypothesis" (Lidicker and Ostfeld 1985). We do not mean to imply by this that large size is

not an advantage to males over the usual adult range of sizes (cf. Sheridan and Tamarin 1988). For example, it may well be possible that up to, say, 55 g, body weight is positively associated with social status and reproductive success. What is critical here is that the small percent of males of primary focus and attention in the Chitty/Krebs model is clearly not composed of the super-males predicted by that theory.

Overview

What then is our current view of the large body size phenomenon in cyclic microtines? Considering all the evidence, we feel that extra-large individuals can occur whenever conditions for good growth and survival last long enough for large size to be achieved. Such sustained growth is plausible because *Microtus* species show indeterminant growth (Zullinger et al. 1984). These giant individuals are most often encountered in populations growing to peak densities because this demographic phase is associated with long-lasting favorable conditions, and the high densities at these times simply assure that more large individuals will be caught.

It seems unlikely to us that large morphs represent a genetically distinct type of individual, because 1) they are associated with non-cyclic as well as classically cyclic populations; 2) some are fat and some are not; and 3) we cannot find evidence to support any fitness advantage for these individuals under high density conditions. We find instead that extra-large males occur more often than expected in marginal habitats, and are less than randomly associated with reproductively active females. It is not obvious to us why very large males should behave in this fashion. Some, perhaps, are social subordinates who become fat after they have been forced out of the best locations and have become less actively involved in social activities. Others may be very old individuals who are no longer competitive (possibly the leaner ones). And, it is conceivable that some may have been successful breeders who have little residual reproductive value, and are improving their inclusive fitness by leaving the best habitat patches to their descendants. Certainly, differential allocation of energy to growth (fat) and reproductive activities is a well-known phenomenon (e.g., Kawata 1988 in *Clethrionomys rufocanus* Sundevall; Cothran et al. 1987 in *Odocoileus virginianus* Zimmermann). It is pertinent also that Kawata (1988) failed to find any correlation between male body weights and mating success in his experimental populations subsequent to the period of initial establishment (when relative body weight was critical). Moreover, Hansson and Jaarola (1989) were unable to find any clear advantage of larger size under competitive conditions in *Microtus agrestis*.

Our results point to some obvious and important directions for future research. As they stand, however, we have at least raised the possibility that the extra-large body size syndrome in microtines, rather than being at the core of their demographic machinery, is instead merely an interesting epiphenomenon.

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