Growth Rates of Aggressive and Docile Voles, Microtus townsendii

ABSTRACT: Selective dispersal may be necessary to produce population cycles in voles. Dispersing individuals of *Microtus townsendii* are fast-growing, early-maturing voles (Beacham, 1979a). In this note we ask whether aggressive behavior is associated with body growth rates. Docile *M. townsendii* under 50 g had faster growth rates than similar-sized aggressive ones. Dispersal of small fast-growing voles thus leads to selection for aggressive phenotypes in resident *M. townsendii.* This could be the mechanism by which self-regulation is achieved in fluctuating rodent populations.

INTRODUCTION

Chitty (1967) suggested that aggressive voles selected for their threat behavior dominate peak and declining populations because they have been selected for survival under conditions of mutual interference. This change in the proportion of aggressive voles was hypothesized to be the driving mechanism behind population fluctuations (Chitty, 1967). Krebs *et al.* (1973) suggested that selective dispersal of passive voles during the increasing phase of population growth may increase the frequency of aggressive voles in peak and declining populations. Because fast-growing, early-maturing voles disperse from increasing and peak populations (Beacham, 1979b), we compared growth rates of docile and aggressive voles to see if slow growth rates and aggressive behavior are linked.

METHODS

For this analysis, we used the behavioral and growth-rate data of voles from three populations: grids C and E (Krebs *et al.,* 1977) and grid I (LeDuc and Krebs, 1975). Aggressiveness tests were run twice on each vole, and the mean number of boxing and wrestling occurrences in the 10-min bouts were summed for each animal. Voles having three or less "aggressive" occurrences were classified as docile; voles having more than three such occurrences were classified as aggressive. The voles were divided into four weight classes: $<$ 40 g, 40-49 g, 50-59 g, $>$59 g. Very few *Microtus townsendii* less than 40 g were aggressive, and thus we combined voles less than 40 g into a single class. We then did a three-way analysis of covariance with sex, grid and weight class as the three indices, weight as the covariate, and instantaneous relative growth rates as the dependent variable. Growth rates of voles tested behaviorally were calculated as instantaneous rates per day from the weights obtained from biweekly recaptures. Growth rates of pregnant females were excluded. Summer was defined as April to September and winter as October to March.

RESULTS

The highly unbalanced experimental design (Table 1) rendered some statistical tests unreliable, and led us to use nonparametric statistics. Growth rates (corrected for size effects

TABLE 1.—Comparison of growth rates of docile and aggressive *Microtus townsendii.* A + indicates that the growth rate of docile voles was greater than that of aggressive ones; a − indicates the opposite relation. Numbers in parentheses are the number of observations in the docile and aggressive samples, respectively. 0 equals no data for one comparison

	Size class			
	$<$40 g	40-49 g	50-59 g	$>$59 g
		Males		
Winter 1973	0 (11, 0)	+ (8, 4)	− (33, 4)	− (9, 3)
Summer 1974	0 (6, 0)	0 (10, 0)	+ (49, 21)	− (120, 51)
Winter 1974	+ (24, 1)	+ (40, 6)	+ (127, 12)	+ (194, 47)
Summer 1975	0 (0, 0)	0 (3, 0)	0 (42, 0)	− (197, 20)
Winter 1975	0 (0, 0)	0 (3, 0)	0 (16, 0)	0 (34, 0)
		Females		
Winter 1973	+ (29, 8)	+ (3, 8)	0 (0, 0)	0 (0, 0)
Summer 1974	− (28, 5)	+ (56, 30)	+ (63, 28)	− (10, 5)
Winter 1974	0 (18, 0)	+ (90, 8)	− (149, 46)	− (18, 27)
Summer 1975	0 (0, 0)	0 (24, 0)	− (88, 15)	− (70, 45)
Winter 1975	0 (0, 0)	0 (1, 0)	0 (14, 0)	− (18, 5)

by covariance) of docile and aggressive voles were compared by sign test (Mendenhall, 1971, p. 369). A comparison was scored by a "+" when the growth rate of docile voles was faster, and by a "−" when growth rate of the aggressive voles was faster.

When the sexes were pooled, docile voles had faster growth rates than aggressive ones when both groups weighed less than 50 g (7+, 1−, p=.035, one-tailed test) (Table 1). *Microtus townsendii* usually attain sexual maturity and disperse in the 40-49 g class (Beacham, 1979b). There was no significant difference between docile and aggressive voles in the 50-59 g class, but if the voles were over 59 g, docile voles had slower growth rates than aggressive ones, (1+, 7−, p=.035, one-tailed test). Smaller voles that were docile had faster growth rates than similar-sized aggressive voles, but larger docile voles had slower growth rates than aggressive voles.

We calculated a weighted mean growth rate for the size classes by multiplying the covariance-corrected mean growth rate by the sample size, summing over all periods, and dividing by the total sample size for the particular size class and group. Comparisons of mean growth rates obtained in this manner are informative in relative differences only and should be interpreted with caution. By this method, docile voles under 50 g grew 9% faster per day than similar-sized aggressive ones. Similarly, docile voles 50-59 g grew 13% faster per day. Thus docile *Microtus townsendii* under 60 g grow faster than similar-sized aggressive ones.

Growth rates are very low and variable for voles above 59 g and it is impossible to determine from our data whether there is any biologically significant effect of aggressive behavior on growth rate in these larger *Microtus townsendii.*

Discussion

The basic hypothesis underlying this analysis is that dispersal in voles is selective and that dispersers are fast-growing and docile by comparison with residents. Beacham (1979a) provided evidence that the fast-growing, early-maturing voles disperse, and this study follows to show that these fast-growing animals tend to be relatively docile. Krebs *et al.* (1978) found that voles colonizing a removal area—and hence, presumably dispersers—showed more submissive behavior when they fought against resident control animals. However, Myers and Krebs (1971) found that dispersing males from a peak population of *Microtus pennsylvanicus* were more aggressive than resident males. Dispersing voles are usually lighter than resident ones (Myers and Krebs, 1971; Beacham, 1979b). Turner and Iverson (1973) found that larger voles were dominant over smaller ones, so it seems reasonable to suggest that dispersers are usually more docile than residents. Thus dispersal may be the mechanism by which docile voles are removed from the population.

Stenseth (1978) suggested that r-selected voles have rapid growth rates until sexual maturation, after which growth rates rapidly decline to zero. He suggested that K-selected voles continue to grow long after sexual maturation. If r-selected voles are docile and K-selected voles are aggressive, then this study supports Stenseth's (1978) suggestion that until sexual maturation (*i.e.,* 40-50 g in *Microtus townsendii*), docile voles grow faster than aggressive ones.

This study supports the suggestions of Chitty (1967) and Krebs *et al.* (1973) that the proportion of aggressive animals in a vole population may change throughout a population cycle, with selective dispersal of fast-growing, docile voles the mechanism by which this result is achieved. However, it does not demonstrate that changes in behavior are the driving mechanism of the microtine cycle. A comprehensive study of changes in dispersal, growth rate and behavior types during a cycle, and the hereditary basis of these characteristics, may be instrumental in determining the causes of vole population cycles.

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