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Ecology, Volume 63, Issue 5 (Oct., 1982), 1211-1217.

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EFFECTS OF FOREST CUTTING ON TWO *CARABUS* SPECIES: EVIDENCE FOR COMPETITION FOR FOOD¹

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Abstract. I investigated the effects of forest clear-cutting on two predatory beetles. *Carabus limbatus* was numerically dominant in the forest, but its density was significantly reduced on the clear-cut. *C. sylvosus* density was little affected by forest cutting. An enclosure experiment was conducted in order to distinguish between the effects of habitat and density on the foraging success of *C. limbatus*. Individual beetle mass served as an operational measure of foraging success. On the clear-cut, the foraging success of *C. limbatus* was subject to opposing pressures. Lower density of conspecifics tended to improve foraging success, while other attributes of the clear-cut tended to reduce foraging success. *C. sylvosus* is similar to *C. limbatus* in habitat, diet, and temporal activity pattern. *C. sylvosus* foraged significantly more successfully on the clear-cut, where *C. limbatus* was less abundant, than in the forest. I hypothesize that *Carabus* species compete for limiting food in the undisturbed forest, and that clear-cutting ameliorates competition by reducing the numerically dominant *C. limbatus*.

Key words: *Carabus*; clear-cutting; competition; disturbance; food limitation; population regulation; predators.

INTRODUCTION

Hairston et al. (1960) hypothesize that terrestrial predators, as a group, compete for limiting food resources. Carabid beetles, comprising some 40 000 species, are among the dominant predatory arthropods in many terrestrial ecosystems. Yet a review of the literature on carabid ecology leads Thiele (1977: 328) to conclude that: "Biotic factors such as competition . . . and food supplies probably exert less influence on population dynamics than abiotic factors . . ."

To address this conflict, one must recognize that population density is likely to be a poor indicator of food availability for two reasons. First, density is influenced by a plethora of factors in addition to food availability. Second, the response of density to food availability may be obscured by time lags and intervening noise. Hence, it is desirable to have a measure of foraging success which is unequivocally and immediately responsive to food availability, yet indicative of future population growth.

In this study, individual beetle mass served as an operational measure of foraging success. I investigated the effects of forest clear-cutting on the foraging success of *Carabus limbatus* and *C. sylvosus*. Forest and clear-cut differed in many respects, including the relative densities of these congeners. An enclosure experiment was conducted in order to distinguish between the effects of habitat and density on *C. limbatus* foraging success. Hence, there is a natural comparison of *C. limbatus* foraging success between forest and

clear-cut (in which beetle densities varied) and a designed comparison (in which beetle densities were controlled). The possible roles of intraspecific and interspecific competition are discussed in light of the results of the natural and designed experiments.

MATERIALS AND METHODS

Study organisms

Carabus limbatus is common in high-altitude and transition zone forests of the southern Appalachians. *C. sylvosus* is rarer, and typically inhabits forests somewhat warmer than those inhabited by *C. limbatus* (Barr 1969).

C. limbatus adults commence activity in early spring. Larvae are present from midspring to early summer. Teneral first appear in late spring or early summer. Teneral females, and fully sclerotized females known to be new adults, have no mature eggs. Hence, *C. limbatus* adults must overwinter prior to reproduction. Observations on the enlargement of male accessory glands corroborate this conclusion.

Teneral adults of *C. sylvosus* are active from late spring until midsummer, when they disappear rather abruptly. Fully sclerotized adults reappear in late summer or early autumn. Mature eggs and enlarged accessory glands are present only during autumn activity.

Following Thiele's (1977:248) classification of annual rhythms in carabids: *C. limbatus* is one of the "spring breeders which have summer larvae and hibernate as adults," while *C. sylvosus* is a "species with winter larvae, the adults of which emerge in spring and undergo aestivation dormancy prior to reproduction." Nonetheless, there is considerable tem-

¹ Manuscript received 19 March 1981; revised 23 October 1981; accepted 18 November 1981.

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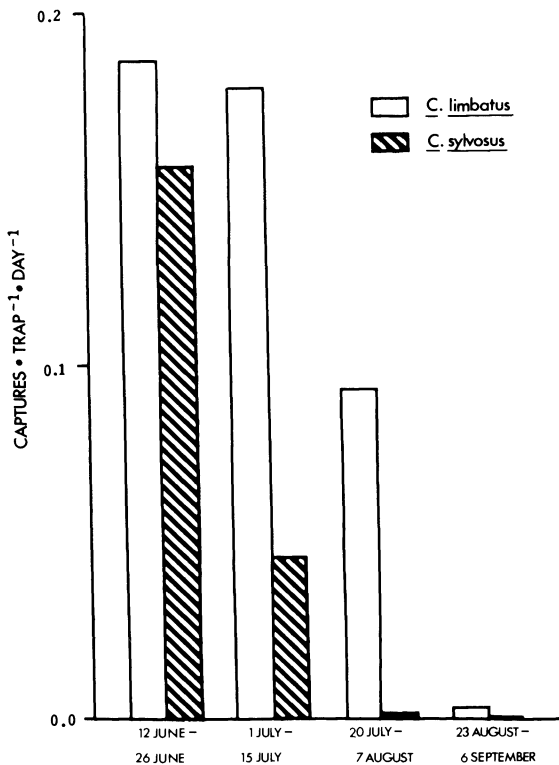


FIG. 1. Temporal overlap in the activity of *Carabus limbatus* and *C. sylvosus* during the course of this study.

poral overlap in the adult activity of these congeners, particularly in late spring and early summer (Fig. 1).

Both species are generalist predators, foraging nocturnally on and near the forest floor. Laboratory feeding experiments suggest considerable dietary overlap, despite some difference in body size. Both species tend to feed on soft-bodied insect larvae, but even the salamander *Plethodon jordani* is readily taken in the lab (R. E. Lenski, personal observation).

Study area

This research was conducted in the Highlands Ranger District of the Nantahala National Forest, in the Blue Ridge Mountains of North Carolina (Macon County). The study area was located on Rich Mountain South, at an elevation of 975 m. During the winter of 1978–1979, 15 ha of forest on the south slope of this mountain were clear-cut.

Before cutting the forest was dominated by chestnut oak (*Quercus prinus*), black oak (*Q. velutina*), and hickories (*Carya* spp.). Flowering dogwood (*Cornus florida*) and the young of the canopy species were important in the understory. Shrubs, tree seedlings, and a diverse assemblage of shade-tolerant herbs and ferns covered a sizeable fraction of the forest floor. Rotting logs, including American chestnut (*Castanea dentata*), were abundant. The adjacent forest, used as a control area, is very similar.

Field-adapted herbs quickly became established on the clear-cut, and tree sprouts proliferated, including especially black locust (*Robinia pseudoacacia*). Horn (1980) and Boring et al. (1981) describe in detail the early vegetational changes that follow clear-cutting in this region. Because all trees were cut, but only merchantable boles removed, there was a large increase in the amount of dead wood present. Due to erosion and reduced deposition, the litter layer of the soil was patchier and generally thinner than in the control forest. McGee (1976) reports soil temperatures in excess of 60°C on clear-cuts in western North Carolina. However, over half the ground was shaded by the end of the second summer after cutting.

Sampling procedures

The basic sampling unit was a pitfall trap, sunk so that the rim was near the interface of humus and litter. The trap was a plastic cup, 11.5 cm deep with a diameter of 9.5 cm at the rim. Within this cup was a smaller cup that could be removed in order to examine the contents of the trap without disrupting the outer cup. In addition, a funnel with a smaller diameter of 3 cm was set into each trap.

I set out 6 × 6 m grids of 16 traps each. Two such plots were located on the clear-cut, and two in the adjacent forest. The four plots formed a rough square, ≈80 m on a side. This distance represents a compromise between minimizing edge effects and maximizing the topographic similarity of clear-cut and forest plots.

Because I was interested in the possibility of intraspecific and interspecific competition, it was important that I minimize the effect of my sampling on population densities. Hence, I decided to live-trap and release, rather than charge my traps with preserving fluid. I visited each trap daily in order to minimize mortality within the traps. Trap mortality during the course of this study was 4% for *Carabus limbatus* and 3% for *C. sylvosus*. I sampled for 64 d between 12 June and 6 September 1980. All pitfalls were closed on days that I did not sample.

Each individual beetle was given a unique mark on its first capture, by clipping some combination of its 12 tarsal claws with microdissection scissors. Usually two or three claws, no two from the same tarsus, were cut. Each individual was further identified by sex; in *Carabus*, the protarsi of males are substantially broader than those of females.

Individual markings permitted an assessment of the degree to which beetles might select one habitat over another. Both species are quite mobile, despite their inability to fly; many individuals were recaptured on plots other than the one on which they had been released. A two-tailed Fisher's exact test was performed on data for each species in order to determine if beetles were more likely to move from forest to clear-cut or vice versa.

The mass of each captured beetle was determined,

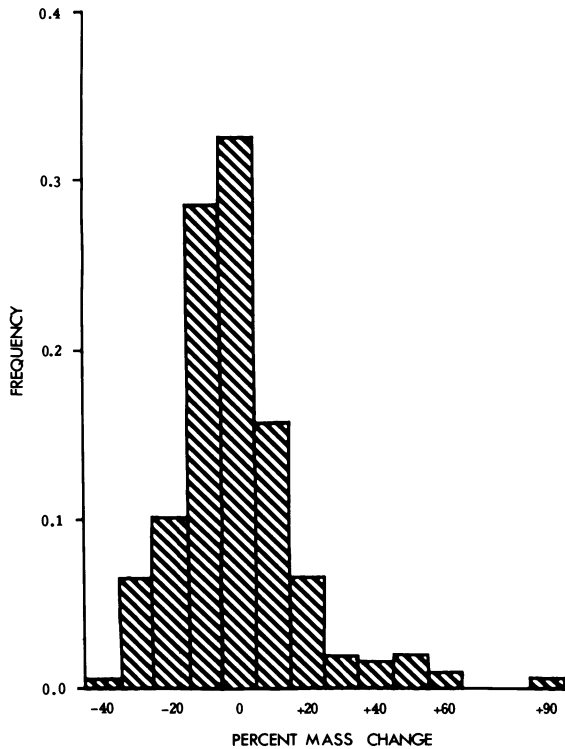


FIG. 2. Percent change in body mass between successive captures of *Carabus* individuals ($N = 196$). Note the positively skewed distribution.

using a portable, 5-g capacity, spring-loaded scale, enclosed within a housing to provide stability and protection from the elements. Masses were determined to the nearest centigram. Changes in mass between successive captures were indicative of the degree to which individuals responded to recent foraging success (Fig. 2). Dissections were performed on 36 egg-bearing *C. limbatus* in order to assess the correlation between individual body mass and potential for population growth.

For all plots, I had data on the proportion of *Carabus* captures represented by *C. limbatus*. I also had an "activity abundance" (captures per trap per day) and a mean individual mass for each species on all plots. Prior to analysis, I performed an arcsine transformation on the proportion and a logarithmic transformation on each species' activity abundance to stabilize variances. Two-tailed t tests were then used to contrast forest and clear-cut plots for each of these variables.

Experimental design

Eighteen small enclosures were constructed to distinguish between the effects of habitat change and density change on *C. limbatus* foraging success. Each enclosure was roughly square, 1.5 m on a side. Aluminum edging was sunk into the ground several

centimetres, and vegetation was cleared from the edges. Six of the enclosures were on the clear-cut (C), six 30–50 m into the forest ($F1$), and six ≈ 100 m into the forest ($F2$). There were five pitfall traps in each enclosure. These pitfalls were open for seven consecutive days, trapping out most or all *Carabus* individuals. Then the pitfalls were closed, and to each enclosure were added two, four, or eight randomly assigned, marked *C. limbatus*. Seven days after these additions the traps were reopened, and for seven more days any remaining *C. limbatus* were caught and weighed on an analytical balance. This experiment began on 6 July and ran through 27 July for one-half the enclosures; for the second half, the experiment began 4 d later.

I observed for each enclosure the proportion recaptured and the mean mass of recaptures. An arcsine transformation was performed on the former in order to stabilize its variance. The variance for each dependent variable was partitioned into that due to habitat, density, habitat \times density interaction, and block effect (i.e., starting date), using analyses of covariance. Habitat and block were treated as nominal (or class) variables. Habitat and block sums of squares were adjusted for density, which was treated as an interval (or continuous) covariable. The habitat and interaction sums of squares were further partitioned into two orthogonal components: $F1$ vs. $F2$, and C vs. $F1 + F2$.

Density vs. activity abundance

Pitfall trapping has been criticized on the grounds that it cannot be used to estimate or compare population densities, since capture rates depend on activity as well as on density (Southwood 1966, but see Baars 1979). However, an activity abundance (captures per trap per day) may be more important than a true density, since the impact of a population on its prey and on competitors is a function of activity as well as density.

I used the number of individuals trapped out of the enclosures described above to obtain density estimates less dependent on activity. (These enclosures were subject to less migration than open plots. However, several individuals released in the enclosures were eventually recovered elsewhere. Hence, densities were overestimated to the extent that these enclosures were "leaky.") Density estimates were analyzed by means of the nonparametric Mann-Whitney U test. Two-tailed comparisons were made for $F1$ vs. $F2$, and C vs. $F1 + F2$, for both *Carabus* species.

RESULTS

Beetle densities

The proportion of *Carabus* captures represented by *C. limbatus* was significantly lower on the clear-cut

TABLE 1. Effects of forest cutting on relative abundance of *Carabus* species.

	Habitat		<i>P</i> *
	Forest	Clear-cut	
Proportion <i>C. limbatus</i>	0.789	0.551	.0129
<i>C. limbatus</i> activity abundance (captures per trap per day)	0.165	0.062	.0870
<i>C. limbatus</i> density (individuals/enclosure)	5.750	0.667	<.05
<i>C. sylvosus</i> activity abundance (captures per trap per day)	0.045	0.049	.7536
<i>C. sylvosus</i> density (individuals/enclosures)	0.333	0.333	NS

* Precise values are not given for Mann-Whitney *U* tests.

than in the forest ($P < .05$). In the forest *C. limbatus* captures outnumbered *C. sylvosus* captures nearly 4 to 1, while on the clear-cut *C. limbatus* captures were only slightly more frequent than *C. sylvosus* captures (Table 1).

This reduction in the dominance of *C. limbatus* on the clear-cut was due primarily to a decrease in *C. limbatus* captures ($P < .1$), and not an increase in *C. sylvosus* captures ($P > .5$). *C. limbatus* captures dropped off >60% from forest to clear-cut, while *C. sylvosus* captures were only slightly more frequent on the clear-cut (Table 1).

The number of beetles trapped out of enclosures over the course of several days provided data for a test of whether trends in capture rates were indicative of trends in true population densities. There were no significant differences between two forest locations ($P > .4$, both species). *C. sylvosus* densities were the same for clear-cut and forest (Table 1). However, *C. limbatus* population density was significantly higher in the forest than on the clear-cut ($P < .05$).

The role of dispersal between forest and clear-cut was analyzed using capture-recapture data. Those beetles that left the plot on which they had been released could be recaptured either on one replicate plot in the same habitat or on one of two plots in the other habitat (Table 2). *C. limbatus* individuals differentially selected the forest habitat ($P < .0001$), while *C. sylvosus* individuals may have selected the clear-cut habitat ($P < .1$).

An operational measure of foraging success

In this study, individual beetle mass served as an operational measure of foraging success. In the lab, hungry beetles may double their mass in a single meal, while beetles that do not feed typically lose a few percent of their body mass per day (R. E. Lenski, *personal observation*). If feeding gains are large, variable, and infrequent relative to metabolic losses, we expect changes in mass between successive captures of the

TABLE 2. Dispersal of *Carabus* species within and between forest and clear-cut habitats.

Release habitat	Capture habitat		<i>P</i>
	Same	Other	
<i>C. limbatus</i>			
Forest	25	15	<.0001
Clear-cut	0	13	
<i>C. sylvosus</i>			
Forest	5	9	.0526
Clear-cut	7	1	

same individual to be positively skewed. Based on the data shown in Fig. 2, percent changes in body mass have a skewness of +1.482. When the number of observations is large, the standard error for the skewness statistic is $\approx \sqrt{6/N}$ (Sokal and Rohlf 1969:137). A two-tailed *t* test indicates that the observed skewness is highly significant ($P < .0001$).

Dissections of 36 egg-bearing *C. limbatus* revealed a positive relationship between individual mass and number of eggs carried ($P < .0001$, $r^2 = .44$, slope = .42 eggs per centigram). The use of average mass as an operational measure of foraging success assumes a causal pathway emanating from food availability, which influences individual body mass, reproductive success, and ultimately population growth.

A natural experiment

C. sylvosus individuals weighed more on the clear-cut than in the forest ($P < .05$), by >15% (Table 3). *C. limbatus* individuals may also have weighed more on the clear-cut ($P < .1$), but by <5%.

Clear-cut and forest differed in many respects, including the density of *C. limbatus*. The increases in foraging success on the clear-cut may represent either a density-independent response to habitat change or a release from competition, or both.

A controlled experiment

An enclosure experiment was conducted in order to distinguish between the effects of habitat and density

TABLE 3. Comparison of body mass (in grams) between forest and clear-cut habitats for *Carabus* species.

Species	Regime	Habitat		<i>P</i>
		Forest	Clear-cut	
Average mass (g)				
<i>C. limbatus</i>	Natural density	0.320	0.334	.0620
<i>C. limbatus</i>	Controlled density*	0.312	0.262	.0040
<i>C. sylvosus</i>	Natural density	0.395	0.462	.0231

* See Table 4.

TABLE 4. Analysis of covariance for average mass of recaptures from *Carabus limbatus* enclosure experiment. Habitats: C = clear-cut; F1 = 30–50 m into forest; F2 = ≈100 m into forest.

Source	df	ss	F	P
Habitat	2	0.01051		
F1 vs. F2	1	0.00003	0.04	.8432
C vs. F1 + F2	1	0.01047	13.15	.0040
Density	1	0.00210	2.63	.1331
Interaction*	2	0.00472		
F1 vs. F2	1	0.00084	1.05	.3276
C vs. F1 + F2	1	0.00388	4.88	.0494
Block (starting date)	1	0.00411	5.16	.0442
Residual	11	0.00876		

* Sum of squares due to heterogeneity of regression slopes among habitats.

on *C. limbatus* foraging success. The analysis of covariance for mean body mass of recaptures (Table 4) indicates a significant habitat effect arising from reduced foraging success on the clear-cut ($P < .01$). The average mass of *C. limbatus* individuals under natural and controlled density regimes are contrasted in Table 3. Note that *C. limbatus* weighed less on the clear-cut only when densities were comparable to the forest. While there was no significant main effect of density on mass ($P > .1$), there was a significant habitat × density interaction ($P < .05$). In the forest there was a significant reduction in mean body mass at higher densities ($P < .05$, Table 5), while there was no such trend on the clear-cut ($P > .4$, Table 6). The absence of a density effect on the clear-cut may indicate a threshold phenomenon; the lowest experimental density (two beetles per enclosure) was much higher than the observed density of *C. limbatus* on the clear-cut (0.67 beetles per enclosure, Table 1).

Low recapture rates are indicative of emigration and/or death. The analysis of covariance for the proportion recaptured (Table 7) shows significant habitat ($P < .05$) and density ($P < .05$) effects. The proportion recaptured declined with increasing density. Recapture rates were lowest on the clear-cut and highest for the forest location most distant from the clear-cut.

DISCUSSION

The foraging success of *Carabus limbatus* on the clear-cut was apparently subject to opposing pres-

TABLE 5. Analysis of covariance for average mass of recaptures from *Carabus limbatus* enclosure experiment: forest enclosures only.

Source	df	ss	F	P
Density	1	0.00538	5.13	.0498
Block (starting date)	1	0.00288	2.75	.1317
Residual	9	0.00944		

TABLE 6. Analysis of covariance for average mass of recaptures from *Carabus limbatus* enclosure experiment: clear-cut enclosures only.

Source	df	ss	F	P
Density	1	0.00060	0.94	.4044
Block (starting date)	1	0.00123	1.93	.2593
Residual	3	0.00192		

ures. The reduced density of conspecifics tended to increase foraging success, while some other attributes of the clear-cut tended to decrease foraging success. Under comparable density conditions, *C. limbatus* foraging success was significantly lower on the clear-cut than in the forest. Under natural density regimes, however, foraging success was at least as great on the clear-cut as in the forest.

The similarity in habitat, diet, and temporal activity of *C. sylvosus* and *C. limbatus* adults suggests that the foraging success of *C. sylvosus* might also be influenced by *C. limbatus* density. *C. sylvosus* weighed significantly more on the clear-cut, where *C. limbatus* was less abundant, than in the forest.

What other evidence is there for food limitation among predatory carabids? Having noted a tendency for satiated beetles to regurgitate the contents of their crops on handling, Grüm (1971) concluded that <15% of the individuals in a natural population of *Carabus arcensis* were satiated. This proportion was increased more than five-fold through food supplementation. In his study of *Agonum fuliginosum*, Murdoch (1966) found that egg production was correlated with food availability, and that variation in the density of new adults reflected preceding variation in egg production and larval density. To date, the only direct evidence for interspecific competition in carabids comes from laboratory experiments conducted at densities many times greater than those observed in nature (Thiele 1977).

TABLE 7. Analysis of covariance for proportion recaptured from *Carabus limbatus* enclosure experiment. Habitats: C = clear-cut; F1 = 30–50 m into forest; F2 = ≈100 m into forest.

Source	df	ss	F	P
Habitat	2	0.72765		
F1 vs. F2	1	0.34555	5.73	.0356
C vs. F1 + F2	1	0.38210	6.34	.0286
Density	1	0.31764	5.27	.0424
Interaction *	2	0.24678		
F1 vs. F2	1	0.17991	2.98	.1121
C vs. F1 + F2	1	0.06687	1.11	.3149
Block (starting date)	1	0.01523	0.25	.6252
Residual	11	0.66338		

* Sum of squares due to heterogeneity of regression slopes among habitats.

I have demonstrated that *C. limbatus* foraging success is influenced by intraspecific competition, and I have suggested that *C. sylvosus* foraging success is subject to interspecific competition. But for neither species have I demonstrated that foraging success limits population density, although I did show a correlation between *C. limbatus* body mass and fecundity.

The importance of designed field experiments to the testing of ecological hypotheses has been expressed elsewhere (e.g., Connell 1975, Hairston 1980). In a forthcoming manuscript, I will discuss the results of an experiment designed to test the following hypotheses. (1) *C. limbatus* and *C. sylvosus* are food limited in the undisturbed forest. Population densities can be increased by supplementing the available food. (2) The food resources of *C. limbatus* and *C. sylvosus* overlap, at least partially. Hence, these congeners compete for a limiting resource. (3) Food limitation hampers the foraging success of individuals, thereby influencing their fecundity, survival, and dispersal. While dispersal may be an important determinant of local variation in population density (e.g., Grüm 1971), reproductive success ultimately controls population size.

Competition for food within and between *Carabus* species in the forest is evidence that supports the hypothesis that terrestrial predators, as a group, are food limited. The lack of competition on the clear-cut cannot be taken as evidence against this hypothesis, since its proponents make it clear that exceptions to food limitation are to be expected for disturbed (Hairston et al. 1960:422) and/or sparse (Slobodkin et al. 1967:109) predator populations.

The results of this study also support the hypothesis that disturbances which ameliorate competition tend to increase species diversity (Dayton 1971, Levin and Paine 1974), provided that disturbances are not of such intensity and/or frequency that species are excluded (Connell 1978). The abundances of *C. limbatus* and *C. sylvosus* were much more even on the clear-cut than in the forest (Lenski, *in press*).

C. limbatus is more abundant than *C. sylvosus* in their preferred forest habitat, but *C. sylvosus* is more tolerant of habitat variation. Such a pattern is to be expected, given evolutionary tradeoffs between habitat specialization and generality. Similar patterns have been documented for competing species belonging to several other taxa, including barnacles (Connell 1961), terrestrial salamanders (Jaeger 1971), and freshwater fish (Werner and Hall 1977).

Predatory carabids have been implicated as important agents in the natural and systematic biological control of insect pests. Even Thiele (1977:328), who maintains that food supplies exert relatively little influence on carabid population dynamics, states that: "... carabids possess a regulatory effect on harmful insects . . ." Operational measures of foraging success (e.g., individual body mass) can be useful in clar-

ifying the relationship between carabid beetles and their food supplies, especially when used in the context of designed field experiments.

ACKNOWLEDGMENTS

Support for this research was provided under a cooperative agreement between the Southeastern Forest Experiment Station of the United States Forest Service, Asheville, North Carolina, and the Highlands Biological Station. Nelson Hairston called my attention to this research opportunity, and offered much advice and encouragement. Richard Bruce kindly enabled me to make full use of the HBS facilities. Nelson Hairston, Janis Antonovics, Elizabeth McMahan, Seth Reice, and JoAnn White read this manuscript and made helpful comments. Two anonymous reviewers and my corresponding editor provided additional constructive criticisms. Madeleine Lenski gave me diversion and free typing. Fellowships from the Morehead and National Science Foundations have supported me during my graduate study.

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