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FOOD LIMITATION AND COMPETITION: A FIELD EXPERIMENT WITH TWO *CARABUS* SPECIES

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SUMMARY

(1) A field experiment was conducted to assess the effects of food limitation and competition on two predatory ground beetles in a southern Appalachian forest.

(2) Food supplementation significantly increased the average body mass of both non-teneral (reproductive) and teneral (prereproductive) *Carabus limbatus* Say adults.

(3) Food supplementation had no effect on the survival of non-teneral *C. limbatus* adults. Food supplementation may have improved the survival of teneral *C. limbatus* adults, although this effect was marginally non-significant.

(4) Increased reproduction by non-teneral *C. limbatus* adults in response to food supplementation was indicated by significantly more abundant and earlier appearing larvae. Recruitment of teneral *C. limbatus* adults was also significantly greater on food supplementation plots.

(5) The activity of both teneral and non-teneral *C. limbatus* adults was significantly lower on food supplementation plots, indicating that much of their normal activity is associated with foraging.

(6) *C. sylvosus* Say received none of the supplemental food available to *C. limbatus*, yet *C. sylvosus* weighed significantly more on food supplementation plots than on control plots. This improved foraging success of *C. sylvosus* is attributed to reduced competition with *C. limbatus* for naturally occurring food.

INTRODUCTION

There are approximately 40 000 species of carabid beetles (Thiele 1977), including some 600 species found in the Appalachian region (Barr 1969). Most carabid species are entomophagous, and some have been implicated as agents in the biological control of insect pests (e.g. Frank 1967). A review of the literature on carabid ecology has led Thiele (1977) to conclude that 'biotic factors such as competition . . . and food supplies probably exert less influence on population dynamics than abiotic factors . . .' This conclusion is based more on successes in correlating species' distributions with microclimatic affinities than on failures to relate carabid population dynamics to food supplies. Several researchers have now implicated food limitation in natural carabid populations, although this work is largely correlative and not experimental.

Murdoch (1966) showed a positive correlation between egg production in *Agonum fuliginosum* and food availability, and found that variation in the density of new adults reflected preceding variation in egg production. Grüm (1971) found that the activity of

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several *Carabus* species was negatively correlated with their degree of satiation, and showed experimentally that the proportion of satiated individuals could be increased through food supplementation. Grüm (1975a) also suggested that the increased activity of hungry beetles exposed them to additional mortality in the form of predation. Heessen (1980) observed a negative correlation between egg production of *Pterostichus oblongopunctatus* and population density. Lenski (1982b) experimentally demonstrated a negative effect of population density on body mass of *Carabus limbatus*, and correlated egg production with body mass. Lenski also hypothesized that the increased body mass of *C. sylvosus* on a clear-cut area was due, at least in part, to reduced numbers of *C. limbatus*. Baars & van Dijk (1984a) analysed yearly trends in the abundances of *Pterostichus versicolor* and *Calathus melanocephalus* and found correlative evidence for density-dependent effects. Baars & van Dijk (1984b) further showed that egg production in these two species was negatively correlated with population density; experimental food supplementation enhanced egg production in both species.

The importance of designed field experiments to the testing of ecological hypotheses has been emphasized by Connell (1975) and others. The purpose of this paper is to present the results of a field experiment designed to test the effects of food supplementation on the survival, reproduction, and activity of *Carabus limbatus* Say, and the effects of reduced interspecific competition on the foraging success of *C. sylvosus* Say.

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 is found usually in forests somewhat warmer than those inhabited by *C. limbatus* (Barr 1969). The two species co-occur in the vicinity of the site for this experiment (Lenski 1982a, b). Adults of both species are large, facilitating marking, and flightless, making it possible to use uncovered barriers for enclosures. Both species are generalist predators, foraging nocturnally on the forest floor.

C. limbatus adults become active and breed in spring, with larval development taking place in spring and summer. New adults, or teneral, emerge in summer, but must overwinter prior to reproduction; teneral are distinguished by their relatively unsclerotized exoskeletons. *C. sylvosus* adults are autumn breeders, with larvae overwintering and maturing in spring. Teneral emerge in late spring, and undergo a summer aestivation before reproducing. Despite these important differences in the life histories of these congeners, there exists considerable temporal overlap in their adult activity (Lenski 1982b). Interspecific competition, if it exists, probably occurs most intensely between non-teneral *C. limbatus* and teneral *C. sylvosus* adults during late spring and early summer. Predatory interactions between these congeners could also be important. For example, I have observed non-teneral *C. limbatus* preying on teneral *C. sylvosus* in pitfall traps.

Study area

This research was conducted in the Highlands Ranger District of the Nantahala National Forest, in the Blue Ridge Mountains of western North Carolina (Macon County). The study area was on the east slope of Little Fodderstack Mountain, at an elevation of about 975 m. This site was chosen for its proximity and similarity to the oak-hickory forest at Rich Mountain South (Lenski 1982a, b); and for its scarcity of exposed bedrock, large

logs, and shrubby undergrowth that could interfere with construction of the enclosures described below.

Experimental design and sampling procedures

I constructed ten 6 × 6 m square enclosures in March 1981. Enclosures consisted of aluminum edging, 15 cm in height, sunk about halfway into the ground. Twenty pitfall traps (Lenski 1982a, b) were evenly spaced along the interior border of all enclosures, such that each trap's rim touched the aluminum edging. This arrangement permitted me to sample repeatedly without trampling the plots.

I paired adjacent enclosures in order to produce a block design that would allow me to partition out variance in response variables due to spatial heterogeneity. After all enclosures were constructed, one of each pair was randomly designated a food supplementation plot, while the other served as a control plot.

Carabus limbatus occurred at natural densities within these enclosures; i.e., beetles were neither added nor removed. *C. sylvosus* were completely absent from Little Fodderstack Mountain. [At the nearby Rich Mountain South, the density of *C. sylvosus* drops off as one moves away from the clear-cut area (R. E. Lenski, unpublished). Although I have hypothesized that competition with *C. limbatus* is an important factor limiting the distribution and abundance of *C. sylvosus* (Lenski 1982b), I do not claim that the presence of *C. limbatus* is the sole factor accounting for the absence of *C. sylvosus* at Little Fodderstack Mountain.] In order to investigate the possible effects of interspecific competition on *C. sylvosus*, it was necessary to add them to the enclosures. Therefore, the first forty *C. sylvosus* that I trapped in the forest at Rich Mountain South (4 June 1981–11 June 1981) were added to the enclosures at Little Fodderstack Mountain. This manipulation did *not* constitute an experimental treatment, because four *C. sylvosus* were randomly assigned to all enclosures.

I sampled all enclosures during four periods from 15 April 1981 to 27 July 1981 (exact dates are shown in Fig. 1). In August, the capture rates for *C. limbatus* and *C. sylvosus* drop off sharply (Lenski 1982b). Each trap was visited daily in order to minimize mortality due to trapping; traps were closed between sampling periods.

My sampling procedures were as follows. (i) *C. limbatus* and *C. sylvosus* adults were removed from the pitfalls in which they were trapped, and placed individually in vials that were marked to indicate the plots on which beetles were captured. Larvae were recorded by plot, then released. (ii) Beetles were brought to the laboratory, and weighed individually on an analytical balance to the nearest mg. (iii) Each beetle was measured to the nearest 0.5 mm and sexed. In *Carabus*, the protarsi of males are noticeably broader than those of females. (iv) Each beetle was checked for a previous mark. If none was present, the beetle was marked by clipping some combination of (usually) two or three tarsal claws, which in conjunction with the beetle's length and sex permitted individual identification. [The marking of beetles in this manner probably had little effect on the foraging success, as mandibles are their primary weapons for prey capture (see Houston 1981; also personal observation.)] Occasionally, a marked beetle was recaptured that could not be unequivocally identified due to additional loss of claws. In such cases, I assumed parsimoniously the individual to be that one which fit the present mark with the least loss of additional claws and/or which had been most recently released on that plot. (v) The beetle was then returned to its individual vial. Two mealworms (*Tenebrio* sp. larvae) were added to each vial containing a *C. limbatus* captured on a food supplementation plot. No mealworms were given to *C. limbatus* caught on control plots nor to any

C. sylvosus. (vi) Two or more hours elapsed to allow the *C. limbatus* taken on food supplementation plots to feed. (vii) Uneaten food was removed from the vials of *C. limbatus* caught on food supplementation plots. (viii) Beetles were returned to the study area prior to nightfall. Each beetle was tossed onto the centre of that plot from which it had been taken.

The order of steps (ii) and (v) insured that increases in body mass by *C. limbatus* adults on food supplementation plots would not be a trivial consequence of having been immediately fed. Note also that steps (v) and (vii) insured that no supplemental food was available to *C. sylvosus* or to *C. limbatus* larvae.

Response variables and statistical analyses

An analysis of variance was performed on the total number of non-teneral individuals taken per plot, and served as a check for equal densities of *Carabus limbatus* on food supplementation and control plots, exclusive of reproduction.

Differences between paired food supplementation and control plots were computed for all other response variables. These difference scores were analysed using *t* tests for paired comparisons. The *t* statistic is calculated as follows:

$$t = |\bar{x}_C - \bar{x}_{FS}| \sqrt{N/S.D.},$$

where \bar{x}_C and \bar{x}_{FS} are the means of control and food supplementation plots, respectively; *N* is the number of paired comparisons (= 5, except as noted below); and S.D. is the standard deviation of the difference scores. This analysis of difference scores reduced the allowable degrees of freedom (from $2N - 2$ to $N - 1$), but enabled me to partition out some of the variance due to spatial heterogeneity.

I observed the response of *C. limbatus* to food supplementation by measuring body mass, activity, survival, and reproduction. Tests of these responses were one-tailed, with the direction of effects predicted by a model of food limitation. Under that model, food supplementation should increase body mass, reduce activity (e.g., Grüm 1971; see also Mitchell 1963; Baars 1979), improve survival, and enhance reproduction. Body mass for each plot represents the average of recaptures only. Body mass, activity, and survival were computed separately for non-teneral and teneral *C. limbatus* adults.

Activity was estimated as follows. For each individual beetle, I obtained days at risk by counting the sampling dates from the day after its first capture to the day after its last capture, inclusive. I also counted the number of recaptures for each beetle. Total days at risk and total recaptures were obtained for each plot by summing over all individuals. The activity index for each plot was simply the ratio of total recaptures to total days at risk. There were two possible errors in computing days at risk. A beetle may have been present before its first capture and/or after its last capture. Or a beetle may have left the enclosed plot but returned between its first and last captures. These biases oppose one another, and both appear small as I usually observed short intervals between successive captures of the same individual.

Survivorship was estimated in a similar manner. Days at risk were obtained as above, except that non-sampling dates were counted as well as sampling dates. Losses were defined to include any beetle not taken during the final 5 days of sampling. The daily loss rate for each plot was equal to losses divided by total days at risk, and daily survival was the difference between this loss rate and one. Losses were overestimated to the extent that some beetles were inactive yet still present on the plots. Moreover, losses include

emigration as well as mortality, although enclosing the plots greatly reduced the former. Hence, estimates of survival are somewhat low.

Activity and survival, as defined above, are proportions, ranging from 0 to 1. I performed an arcsine transformation (i.e., arcsine \sqrt{P}) on these variables prior to statistical testing in order to homogenize variances.

On one control plot, estimates of teneral *C. limbatus* body mass, activity, and survival were based on extremely meagre data; only two teneral were captured and neither was recaptured. I discarded this plot and the corresponding food supplementation plot from my analyses of these variables, reducing the degrees of freedom to 3.

While it would have been desirable to observe directly the egg production of female beetles, the necessary dissections would have interfered with the rest of this experiment. Therefore, in order to quantify the reproductive response of *C. limbatus*, I observed for each plot the number of larval captures and the number of teneral adults. Both were standardized by dividing by the number of non-teneral (reproductive) females captures on a given plot during the first sampling period; larvae began appearing during the second sampling period. Larvae per female may include multiple observations of the same individual since larvae could not be marked. Teneral per female represent individuals, and not total captures. I also noted the median date for larval captures and the median date for teneral appearances for each plot in order to assess the influence of food supplementation on the timing of reproduction.

I observed the response of *C. sylvosus* to reduced demand by *C. limbatus* for naturally occurring food by measuring average body mass, activity, and survival. Tests of these responses were one-tailed, with the direction of the effects predicted by a model of inter-specific competition for limiting food. Under that model, reduced foraging by *C. limbatus* should increase body mass, reduce activity, and improve survival of *C. sylvosus*. I did not observe the numerical response of *C. sylvosus* because this species does not breed until autumn, by which time most individuals had probably escaped.

It should be emphasized that these statistical analyses are conservative. Although hundreds of different beetles were captured (and recaptured and weighed thousands of times), these measurements were pooled and only a single composite 'observation' was generated for each plot for each response variable. The fact that many individuals were repeatedly captured and weighed in no way invalidates my statistical tests because plots and *not* individuals or captures were my units of analysis. That is, my manipulative treatment (food supplementation or not) was *randomized* with respect to plots and not individuals or captures. While it certainly is desirable to maximize one's degrees of freedom, and while this can sometimes be accomplished by analysing events at the level of the biological individual (e.g. Lenski & Service 1982), it is only permissible to the extent that treatments are randomized at that level.

For this reason, the values presented in Tables 2–5 refer to the means of the plots, and not of all individuals or captures. In presenting trends in body mass through time (Figs 2–4), I present means and standard errors based on all captures (including multiple captures per individual and multiple individuals per plot); however, I do not perform statistical tests on these data.

RESULTS

An analysis of variance reveals no significant difference in the total number of non-teneral *Carabus limbatus* individuals captured in control and food supplementation

enclosures, although there was a significant block effect (Table 1). These results indicate that there were no systematic differences in the number of individuals starting on (plus immigrating to) control and food supplementation plots, although some areas in the forest had higher densities of beetles than others. The overall mean number of non-teneral individuals captured per 6×6 m enclosure was 23.2, but not all of these individuals were likely to have been present at any one time. In Fig. 1, I have plotted the average number of *C. limbatus* individuals captured per control enclosure during the four sampling periods indicated.

The average body mass of non-teneral (reproductive) *C. limbatus* recaptures was significantly higher on food supplementation plots than on control plots (Table 2). In Fig. 2, I have plotted the body mass of these non-teneral *C. limbatus* as a function of the number of days since their first capture. It can be seen that body mass immediately increased to peak values in response to food supplementation, indicating that this treatment was rapid and effective in satiating these beetles. It can also be seen that not all of the difference in body mass between control and food supplementation plots was due to increased body mass on food supplementation plots; there was a downward trend in body mass on control plots. This reduction in body mass through time could be due to the effects of capture and handling and/or to natural physiological processes (including egg laying).

TABLE 1. Analysis of variance for total number of non-teneral *Carabus limbatus* individuals captured per enclosure

Source of variation	d.f.	SS	F	P
Treatment	1	3.6	0.37	0.5781
Block	4	320.6	8.14	0.0333
Error	4	39.4	—	—

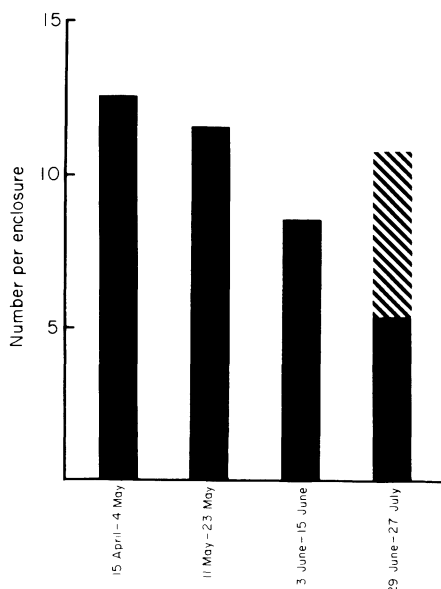


FIG. 1. Average number of *Carabus limbatus* individuals captured per 6×6 m enclosure during the four sampling periods indicated (based on the five controls). Hatching indicates new adults, or teneral.

TABLE 2. Effects of food supplementation on the body mass, activity, and survival of non-teneral *Carabus limbatus*

Response variable	\bar{x}_C	\bar{x}_{FS}	S.D.	<i>t</i>	<i>P</i>
Average mass of recaptures (g)	0.301	0.373	0.009	18.30	<0.0001
Activity (captures/day at risk)	0.496	0.318	—	—	—
Arcsine transformation	0.781	0.599	0.071	5.71	0.0023
Survival (1-losses/day at risk)	0.950	0.945	—	—	—
Arcsine transformation	1.352	1.335	0.050	-0.75*	0.7528

* Negative value indicates difference opposite to anticipated direction.

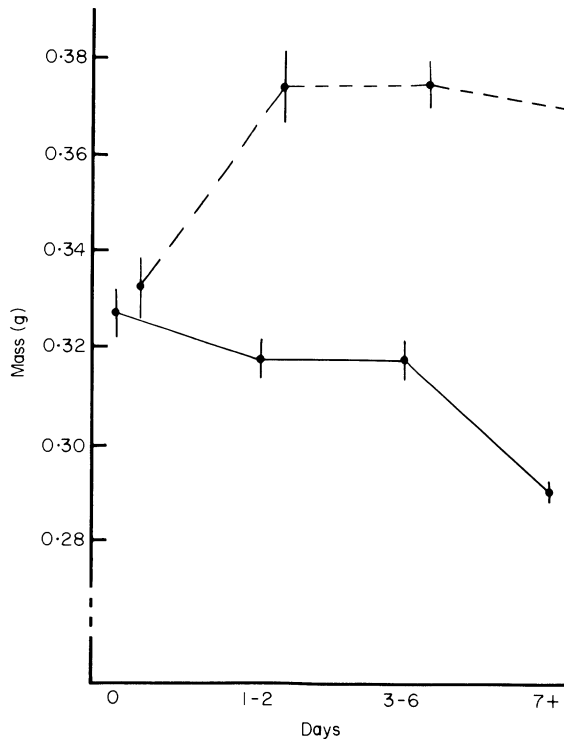


FIG. 2. Mean (± 1 S.E.) body mass of all non-teneral *Carabus limbatus* captures as a function of days since first capture. Solid line indicates control; dashed line indicates food supplementation.

Food supplementation significantly reduced the level of activity of non-teneral *C. limbatus*, by about 35% (Table 2). This result indicates that much of the normal activity of these beetles is associated with foraging, as would be expected if food were a limiting resource.

The survival of non-teneral *C. limbatus* was unaffected by food supplementation (Table 2), indicating that even beetles on control plots had sufficient caloric reserves so that starvation was unlikely. The daily survival rate of about 0.95 corresponds to a daily loss rate of about 0.05; however, these losses include emigration from the enclosures, as well as mortality. A rough estimate of the survival rate exclusive of emigration can be obtained from an examination of Fig. 1, which provides a measure of the relative abundance of non-tenerals at different times. The ratio of non-tenerals in the fourth sampling period to the first sampling period, summed over the five controls, was 0.43; the

mid-points of these two periods were separated by 82 days. Taking the 82nd root of 0.43 yields an estimated daily survival of 0.99, and indicates that most of the losses of non-tenerals were due to emigration and not mortality.

There were significantly more larval captures per female on food supplementation plots than on control plots, by a ratio of 1.77 to 1 (Table 3). The median date of larval captures was significantly earlier on food supplementation plots (Table 3), indicating that females were able to accumulate biomass for egg production more rapidly. Food supplementation also increased the number of new adults (tenerals) per female, by a ratio of 1.64 to 1 (Table 3). Tenerals appeared no earlier, and perhaps later, on food supplementation plots (Table 3).

TABLE 3. Effects of food supplementation on reproduction by *Carabus limbatus*

Response variable	\bar{x}_C	\bar{x}_{FS}	S.D.	<i>t</i>	<i>P</i>
Larval captures per female	1.67	2.95	0.92	3.12	0.0177
Med. date of larvae (June)	11.20	8.40	2.59	2.42	0.0365
Tenerals per female	0.82	1.34	0.14	8.31	0.0006
Med. date of tenerals (July)	14.50	16.50	2.72	-1.65*	0.9125

* Negative value indicates difference opposite to anticipated direction.

TABLE 4. Effects of food supplementation on the body mass, activity, and survival of teneral *Carabus limbatus*

Response variable	\bar{x}_C	\bar{x}_{FS}	S.D.	<i>t</i>	<i>P</i>
Average mass of recaptures (g)	0.226	0.325	0.065	3.08	0.0270
Activity (captures/day at risk)	0.744	0.479	—	—	—
Arcsine transformation	1.048	0.764	0.149	3.81	0.0158
Survival (1-losses/day at risk)	0.810	0.891	—	—	—
Arcsine transformation	1.127	1.252	0.125	2.00	0.0693

Teneral *C. limbatus* also responded significantly to food supplementation (Table 4). In Fig. 3, I have plotted the body mass of these tenerals as a function of the number of days since their first capture. It can be seen that teneral *C. limbatus* on both control and food supplementation plots tended to increase in body mass through time, although this trend was much more pronounced on food supplementation plots.

Food supplementation significantly reduced the level of activity of teneral *C. limbatus*, by about 35% (Table 4). Although this proportion is quite similar to that observed for non-tenerals, the basal level of activity is 50% greater for tenerals, probably corresponding to their lower body mass and greater hunger.

The survival of teneral *C. limbatus* may have been improved by food supplementation, although this effect was marginally non-significant (Table 4). Teneral survival was lower than that of non-tenerals, which may have been due to one or more of the following: (i) greater activity, increasing the likelihood of emigration from the enclosures; (ii) smaller caloric reserves, increasing the possibility of starvation; and (iii) less sclerotization, increasing the risk of predation.

C. sylvosus received none of the supplemental food provided to *C. limbatus*. Yet *C. sylvosus* recaptures weighed significantly more on food supplementation plots than on control plots (Table 5). In Fig. 4, I have plotted the body mass of *C. sylvosus* as a function of the number of days since their release in the experimental enclosures. The increased body mass of *C. sylvosus* on food supplementation plots is not apparent except in those

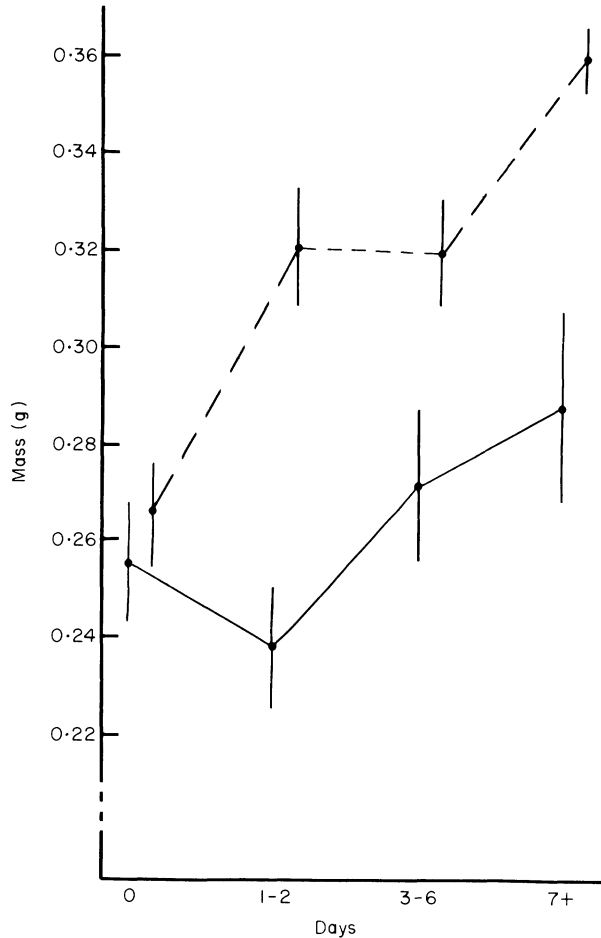


FIG. 3. Mean (± 1 S.E.) body mass of all teneral *Carabus limbatus* captures as a function of days since first capture. Solid line indicates control; dashed line indicates food supplementation.

recaptures 7 and more days after their release, suggesting a gradual increase in body mass. The increased body mass of *C. sylvosus* in response to food supplementation may have been due to the reduced foraging activity by *C. limbatus* for naturally occurring food, or to predation on the more abundant *C. limbatus* larvae.

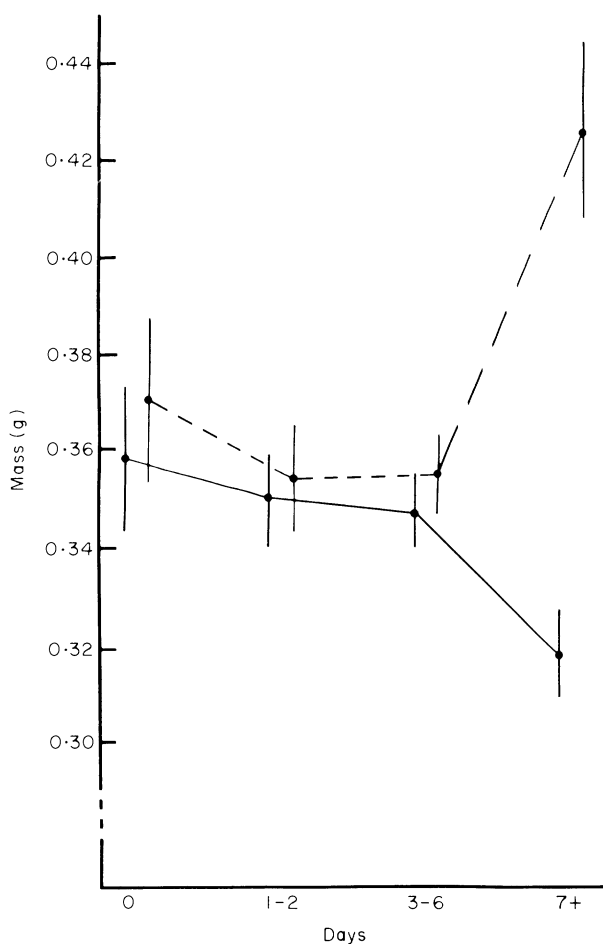
C. sylvosus may have been less active and may have survived better on food supplementation plots, but neither effect was significant (Table 5).

DISCUSSION

The results of this experiment support the hypothesis that food is one factor limiting the population growth of *Carabus limbatus* in this forest habitat. However, demonstration that food availability limits population growth is not sufficient to claim regulation in the sense of density-dependence. As Reynoldson & Bellamy (1971) have pointed out: 'Many populations are likely to respond to an increase in food whether or not competition is occurring because the same amount (or more) may be obtained with less expenditure of

TABLE 5. Indirect effects of supplementing the food available to *Carabus limbatus* on *C. sylvosus*

Response variable	\bar{x}_C	\bar{x}_{FS}	S.D.	<i>t</i>	<i>P</i>
Average mass of recaptures (g)	0.346	0.372	0.019	3.10	0.0181
Activity (captures/day at risk)	0.808	0.727	—	—	—
Arcsine transformation	1.140	1.029	0.252	0.98	0.1902
Survival (1-losses/day at risk)	0.843	0.874	—	—	—
Arcsine transformation	1.168	1.217	0.138	0.79	0.2381

FIG. 4. Mean (± 1 S.E.) body mass of all *Carabus sylvosus* captures as a function of days since release. Solid line indicates control; dashed line indicates food supplementation. *C. sylvosus* received none of the supplemented food.

energy.' Food limitation in the absence of an appreciable density effect has been shown in field experiments with a snail (Eisenberg 1966) and a spider (Wise 1975). What is the evidence that food limitation in these *Carabus* species is influenced by the density of competitors?

The primary evidence for density-dependence was obtained from a previous study in which the densities of *C. limbatus* were experimentally manipulated (Lenski 1982b). The body mass of *C. limbatus* decreased significantly with increasing density in the forest habitat, indicating intraspecific competition. The densities used in this earlier experiment ranged from 0.9 to 3.6 individuals per m²; although chosen to correspond to natural densities in that forest, they were several times higher than the approximately 0.3 individuals per m² at the site of this study (from Fig. 1).

C. sylvosus received none of the supplemented food, yet weighed significantly more on food supplementation plots. This implies a release from interspecific competition resulting from the reduced demand by *C. limbatus* for naturally occurring food. Alternatively, the increased foraging success of *C. sylvosus* on food supplementation plots could represent a predatory response to the increased production of larvae by *C. limbatus*. Although not mutually exclusive, I prefer the former explanation for two reasons. First, the increased densities of *C. limbatus* larvae would seem likely to have only a minor effect on the foraging success of a generalist predator such as *C. sylvosus*. Second, trends in the relative abundance (Lenski 1982a) and foraging success (Lenski 1982b) of these congeners are consistent with a competitive relationship, and could not be readily explained on the basis of a primarily predatory relationship.

There was also some evidence in this study for density-dependence among larvae. Food supplementation increased the production of *C. limbatus* larvae by 77%, while larval resources were not affected. The median date of larval captures was significantly earlier on food supplementation plots. Yet teners appeared no earlier, and perhaps later, suggesting that the headstart of larvae on food supplementation plots was offset by the increased larval densities.

One explanation for the increases in larval production and recruitment of new adults by *C. limbatus* on food supplementation plots is, of course, greater production of eggs by females. Alternatively, these increases could represent reduced cannibalism by the more satiated adults on eggs and/or larvae. I prefer the former explanation because of a strong positive correlation between body mass of and number of eggs carried by female *C. limbatus* (Lenski 1982b). However, Heessen & Brunsting (1981) have shown that cannibalism can be an important factor in the dynamics of carabid populations.

Enclosure experiments have been criticized on the grounds that aspects of the behaviour and ecology of the enclosed population may be altered. While this cannot be denied, favourable aspects of enclosing certain animal populations should also be emphasized. In earlier work with unenclosed 6 × 6 m plots (Lenski 1982b), only 20% ($N = 220$) of the *C. limbatus* released in forest areas were recaptured within 10 days on the same plot. However, the enclosed 6 × 6 m plots in this study resulted in 90% ($N = 132$) of the *C. limbatus* released on control areas being recaptured within 10 days on the same plot. The low rate of recaptures without enclosures would have made improbable the discernment of effects of food supplementation on activity and survival. Moreover, reproduction stimulated by food supplementation would have been scattered over a broader area in the absence of enclosures, making it more difficult to detect though no less real.

Food supplementation significantly reduced the activity of *C. limbatus*, indicating that much of their normal activity was associated with foraging. Greater activity by hungry organisms increases their likelihood of encountering food, and has been observed in numerous animals, including other *Carabus* species (Grüm 1971), the blowfly *Phormia regina* (Browne & Evans 1960), the seed bug *Neacoryphus bicrucis* (Solbreck 1978), and the coelenterate *Hydra littoralis* (Łomnicki & Slobodkin 1966). Were the enclosures not

present, a decline in activity in response to food supplementation would have reduced emigration from the plots, while immigration would have been unaffected. This would create a net flux of beetles onto food supplementation plots, thereby augmenting the increased net reproduction.

Another possible consequence of dispersal is a stabilization of total population size in a temporally and spatially varying environment in which local populations are subject to more or less frequent extinctions (den Boer 1970, 1971, 1979, 1981). Carabid populations are also likely to be stabilized by high survival of reproductive adults between years (van Dijk 1979; Luff 1982). Overlapping of generations has been shown for other *Carabus* species (Grüm 1975b; Houston 1981), and is indicated for *C. limbatus* by the large number of post-reproductive adults still present when new adults were recruited into the population.

Although emigration and immigration are important determinants of local variation in population density, the balance between reproduction and mortality necessarily determines population growth on a broader spatial scale. There was an indication of improved survival of teneral (prereproductive) *C. limbatus* on food supplementation plots, although this effect was marginally non-significant. If real, it may have been due to a reduced risk of predation for these relatively unsclerotized beetles as a consequence of their foraging activity (see Grüm 1971, 1975a). However, I found no evidence for the trade-off between survival and reproduction found by Murdoch (1966) for *Agonum fuliginosum*; survival of non-teneral (reproductive) *C. limbatus* was equal on control plots (lower net reproduction) and food supplementation plots (higher net reproduction). A similar result was found for *Pterostichus versicolor* by Baars & van Dijk (1984b); they concluded that while food was generally sufficient for survival, egg production was often limited.

In conclusion, density-independent factors such as weather (e.g. Baars & van Dijk 1984a) and human disturbance (e.g. Lenski 1982a) undoubtedly play a major role in determining the distribution and abundance of carabid species. But it is also clear that food availability and other potentially density-dependent factors (including predation and parasitism: Heessen 1981; Heessen & Brunsting 1981; Luff 1982) can be of considerable importance to the dynamics of carabid populations.

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