

SPECIES PACKING IN *DESMOGNATHUS* SALAMANDERS:
EXPERIMENTAL DEMONSTRATION OF PREDATION
AND COMPETITION

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Our understanding of natural communities is in a state of uncertainty. After a decade or so of virtually complete acceptance, the theory of community organization based on competition and niche partitioning (Hutchinson 1959; MacArthur and Levins 1964, 1967; Cody and Diamond 1975; and many others) has been challenged on a number of grounds. Simberloff (1970, 1980) and others have argued that the assumption of the existence of the organization of communities has been inadequately tested; Hairston et al. (1960), Paine (1966, 1974), Connell (1975), Hairston (1980a), and others have pointed to the evidence that predation is an important organizing force in many communities. Wiens (1977) and Dunham (1980) have provided examples showing that even when evidence exists, competition may be discontinuous in operation. The foregoing statements have reached the status of truisms in recent years, as has the recurring theme that experimentation is necessary to provide the strong inference on which conclusions should be based.

Over the past 15 years, salamanders have provided excellent material for ecological experiments (see, e.g., Jaeger 1971; Wilbur 1972; Hairston 1980b, 1981, 1983; Morin 1983a; Stenhouse et al. 1983; Kleeberger 1984; Southerland 1985). Long-lived animals with unusually stable populations, they conform to the implied assumptions embedded in theories of community organization and of evolution under the influence of interspecific interactions. Many species are abundant enough to provide ample material for experiments, and in some areas, especially the southern Appalachians, multispecies associations among the family Plethodontidae are available for testing hypotheses about the organization of communities and the coevolution of their constituent species.

The genus *Desmognathus* consists of a series of species ranging from aquatic to terrestrial. There are morphological correlates of the ecological distribution. As the species occur farther and farther from surface water, the tail fin and the degree of lateral compression of the tail are lost completely, body form becomes more slender, and most important, size becomes smaller (Dunn 1926; Hairston 1949, 1980a).

In the southern Appalachians, this series is represented in various localities by from three to at least five species. The three species always present are *D. quadramaculatus*, the most aquatic and largest species; *D. monticola*, a stream-bank species sometimes found in the forest; and *D. ochrophaeus*, the smallest and most terrestrial of the three. In some areas, a fourth species, more terrestrial than *D. ochrophaeus*, is found. This is either *D. wrighti*, found at high elevations from southwestern Virginia to the Nantahala Mountains in North Carolina, or *D. aeneus*, found at lower elevations southwest of the Little Tennessee River. Three other species are found at intermediate distances from water in some locations: *D. fuscus*, found from Grandfather Mountain northeast; *D. santeetlah*, found in the Balsam Mountains of North Carolina, the Great Smoky Mountains, and the Unicoi Mountains; and *D. imitator*, confined to the Great Smoky Mountains.

I have pointed out (Hairston 1980a, 1984) that although the genus *Desmognathus* conforms to standard niche-partitioning theory on first examination (Hairston 1949, 1973; Krzysik 1979), it has some characteristics of size relationships and ecological distribution not consistent with the assumption that interspecific competition has molded the community. Assuming that evolution under the influence of competition would proceed in the direction of greater efficiency, it is most reasonable to expect that lungless animals, which must keep their skins moist because a large part of their total respiration is cutaneous, should be larger in more-terrestrial habitats than in aquatic ones. The larger size would prevent the proportionately greater water loss suffered by small individuals. That the opposite is true calls into question the efficiency hypothesis and, through it, the hypothesis that competition has been the important selective force in the evolution of the series of species.

Additional evidence against the importance of competition comes from predictions about the effect on other species when one of the members of the series is absent. For example, in the Black Mountains of North Carolina, *D. monticola* is virtually absent from elevations above 1220 m. Its intermediate position in the series from aquatic to terrestrial would mean that, under the hypothesis of competition, the aquatic species (*D. quadramaculatus*) should be more terrestrial and the terrestrial species (*D. ochrophaeus*) should occur more commonly near streams. Neither of these postulated phenomena occurs. Other predictions predict size adjustments in the presence or absence of putative competitors. These predictions are summarized in table 1. The net result of all of these predictions is that five of eight are not confirmed, thus again forcing us to question the acceptability of interspecific competition as the explanation for the ecological distribution and size relationships in the genus.

In agreement with Tilley (1968) and others, I argued (Hairston 1980a) that predation in streams is the most important interspecific interaction, causing smaller species to be selected for an increasingly terrestrial existence, and I proposed experiments to determine whether competition or predation is the organizing force in the community. Such experiments would also throw light on the evolutionary history of the genus.

Desmognathus is the only genus in the Plethodontidae with such an extensive range of habitats. Two other groups of genera, the tribes Plethodontini and

TABLE 1

PREDICTIONS ABOUT SPECIES ABUNDANCE FOR *Desmognathus* AND THEIR OUTCOMES

PREDICTION	OUTCOME
<i>D. q.</i> should be on stream banks at high elevations, where <i>D. m.</i> is absent.	Not Confirmed
<i>D. q.</i> should be larger at low elevations, where <i>D. m.</i> is present.	Not Confirmed
<i>D. o.</i> should be more terrestrial at low elevations, where <i>D. w.</i> is absent.	Not Confirmed
<i>D. o.</i> should be on stream banks at high elevations, where <i>D. m.</i> is absent.	Not Confirmed
<i>D. o.</i> should be smaller at low elevations, where <i>D. m.</i> is present.	Confirmed
<i>D. o.</i> should be larger at high elevations, where <i>D. w.</i> is present.	Confirmed
<i>D. m.</i> should be larger north of the range of <i>D. q.</i>	Not Confirmed
<i>D. o.</i> should be smaller north of the range of <i>D. w.</i>	Confirmed

NOTE.—Predictions were for levels of *Desmognathus* abundance in the Black Mountains of North Carolina and elsewhere. Predictions were based on the theory of niche partitioning and its morphological correlates (after Hairston 1980a, p. 359). Abbreviations for species: *D. q.*, *Desmognathus quadramaculatus*; *D. m.*, *D. monticola*; *D. o.*, *D. ochrophaeus*; *D. w.*, *D. wrighti*.

Bolitoglossini, have independently become completely terrestrial. Thus, *Desmognathus* provides among its species not only a model of its own evolution, but a miniature model of the history of the Plethodontidae. Further evidence for that assertion comes from the probable origin of the Plethodontidae and their best-known anatomical characteristic, lunglessness. This trait is associated with the mountain-stream habitat, where lungs are not only unnecessary in the highly oxygenated water, but also a disadvantage because they act as floats, an undesirable trait in rocky torrents. All species of Plethodontidae with any obligatory aquatic stage are found in eastern North America, an area in which the original habitat has apparently been preserved since the end of the Paleozoic era. The unique array of species found in the genus *Desmognathus* thus presents two opportunities simultaneously: to investigate the factors determining present ecological distributions; and to obtain evidence on the forces of natural selection that are determining the evolution of the genus and probably have determined the evolution of the other terrestrial Plethodontidae.

In two earlier papers (Hairston 1980a, 1984), I proposed the following experiments. If *D. ochrophaeus* and *D. monticola* compete, removal of *D. ochrophaeus* from replicate plots should result in an increase in the abundance of the larger and somewhat more aquatic *D. monticola*. If, however, *D. monticola* is primarily a predator on *D. ochrophaeus*, removal of the latter should provide no benefit, and indeed might prove detrimental, to *D. monticola* and even to the still larger and more aquatic *D. quadramaculatus*. Removal of *D. monticola* from other plots should result in an increase in the abundance of *D. ochrophaeus* under either hypothesis. *Desmognathus quadramaculatus* should benefit from the removal of *D. monticola* only if the two species compete. If *D. quadramaculatus* is a significant predator on *D. monticola*, removal of the latter should not result in an increase in the abundance of the former.

Any or all of the following three kinds of response might be expected when a competitor is removed: an increase in abundance because of increased reproduc-

tion or immigration; an increase in the proportion of young as a consequence of either more favorable opportunities for reproduction or a reduction in predation on young individuals; or a shift in ecological distribution to occupy the newly vacated area. Changes caused by immigration or by shifts in ecological distribution could be expected to occur fairly rapidly. Those involving reproduction might require as much as the duration of the life cycle. Since *Desmognathus* species do not begin to reproduce until they are 4 yr old (Organ 1961; Tilley 1977), I decided that the proposed experiments should continue for four seasons. The duration of field experiments should be determined in advance, in order to avoid the twin temptations of stopping when the results are favorable and continuing until they are what the investigator expected to find.

METHODS

Location

The experiments were carried out at the Coweeta Hydrologic Laboratory, an experimental forest administered by the U.S. Forest Service. It is located in the Nantahala Mountains approximately 24 km south of Franklin, North Carolina, and covers an elevational range from 678 m to 1592 m. The forest is managed for large-scale studies in which small numbered watersheds are used as replicates in experiments. A weir at the base of each watershed monitors stream flow, and weather data are recorded in a number of locations. There are 11 rain gauges. My experimental plots were located at altitudes ranging from 868 m to 914 m.

Experimental Design

A block design was used, with watersheds serving as blocks. The use of a single stream either would have required placing plots so close together that the treatment on one might have affected adjacent plots or else would have involved an excessive range of altitudes and stream sizes.

The selection of watersheds with adequate numbers of each species was difficult, requiring most of one season of salamander activity. Three watersheds were selected at the end of the summer of 1980: numbers 31, 34, and the confluence of 40 and 41. Three plots were staked out along each stream. One plot was designated for each treatment. Rather than assign these by chance, each treatment was assigned the downstream plot on one stream, the middle plot on another, and the upstream plot on the third. The purpose was to avoid any bias that might have existed with respect to location along the streams. Although allowing for the statistical removal of differences between streams, this design did not allow for the detection of any interactions between streams and treatments.

The Plots

Each plot extended 30 m along the stream, and adjacent plots were separated by at least 30 m. Preliminary observations had shown that for the three species of most interest (*Desmognathus quadramaculatus*, *D. monticola*, and *D. ochrophaeus*), 96%–99% of the specimens were found within 6 m of streams, although

half of the *D. aeneus* specimens were found at greater distances (Hairston 1984). I decided to extend the plots to 7 m from the water. Plots of comparable size had been shown adequate for some experimental manipulations of *Plethodon* (Hairston 1980*b,c*, 1981, 1983). Boundaries of the plots were marked with wooden or bamboo stakes and twine. The liberal use of reflective tape made the boundaries easily visible at night.

Plot Searches

Except for four daytime searches early in the experiments (see below), all observations were made at night, starting with an arbitrary decision that it was dark. This decision was usually made on the basis of observing an active salamander. The time varied from 1945 h EDT (cloudy weather, September) to 2110 h EDT (clear weather, June). Most searches ended by 0100 h EDT, since there was a significant decline in the surface activity of *D. monticola* and *D. ochrophaeus* after midnight. For each specimen seen, whether collected or not, it was estimated by its size as in its first, second, or third year or as a small or large adult. Subsequent measurements of collected specimens showed that the error in assignment between adult and immature stages was 7.9% for *D. monticola* and 8.2% for *D. ochrophaeus*; no such check was available for the other species seen. The distance from the water was also recorded for each specimen. During May and June 1981, four night searches were made of each plot to provide baseline data before any manipulations were begun. The first removals, in July, could not have affected data taken simultaneously, and those observations can legitimately be included in the baseline period. Planned removals continued in August and September 1981 and in May and June 1982. In addition to these night searches, daytime searches were performed in July and August 1981 and in May and June 1982. During the daytime searches, easily moved sticks, stones, and other cover objects were lifted and carefully replaced.

Weather Observations

Weather instruments were set up 1–2 m from the stream before each plot search. Air temperature and relative humidity were measured 2 cm above the ground. Water temperature, soil temperature, and barometric pressure were also recorded after the plot had been searched.

The Change in Protocol

In May and June 1982, it appeared that the removals had caused no demonstrable reduction in the numbers of either *D. ochrophaeus* or *D. monticola*. Figure 1 shows the lack of effect from July 1, 1981, through June 1982. It was clear that, unlike large *Plethodon* species, which were reduced to about 40% of control numbers by six removals per year (Hairston 1984), *Desmognathus* would require more effort to achieve comparable results. In an attempt to estimate what would be needed, I carried out two experiments in intensive removal. On another watershed in Coweeta (no. 32), three new plots were established. They were similar to those in the main experiments, but were 20 m long instead of 30 m. Stakes were set such that each longitudinal quarter could be recorded separately.

This allowed a check to be made on immigration from upstream or downstream. On seven of nine consecutive nights, all *D. monticola* individuals were removed from one plot, and all *D. ochrophaeus* from another; the third plot was searched as a control. There was evidence of a decrease in the number of *D. ochrophaeus* removed, relative to the number counted on the control plot, but *D. monticola* gave no such encouragement, although the numbers were too small for firm conclusions. There was no evidence of immigration into the plots.

A second experiment was conducted to test the hypothesis that *D. ochrophaeus* individuals make frequent brief excursions from refuges to the surface. Three areas of approximately 9 m² were watched successively for 70 min each. All *D. ochrophaeus* salamanders appearing in the area were removed, and the number caught during each 10-min interval was recorded. The pooled results from the three areas show that after both the first interval and the sixth, two salamanders were caught, and three salamanders were captured following each of the other five intervals. There is no evidence of any exhaustion of the pool of individuals below the ground, and no immigration was observed. The total density (19/27 m²) was more than six times as great as observed on any plot.

It was not possible to increase the total effort sufficiently to achieve an effect comparable to that achieved with *Plethodon*, which would have required five or six times as much searching. In order to achieve the required intensity of effort, it was necessary to reduce the size of the plots. The absence of evidence of immigration during these special experiments was encouraging, and the original plots were reduced to one-third their original size, leaving a 10-m stretch of stream and the same 7 m of forest floor on each side. Marker stakes were placed every 2.5 m along the stream and along the outer edges of the plot. These stakes divided the plot into equal quarters; by recording the quarter in which each salamander was found, the possibility of immigration from either upstream or downstream could be monitored.

On each visit, plots were searched three times in succession, thus tripling the effort per unit area. The day searches were dropped and additional night searches substituted, because night searches had been more effective (1.65 times as effective, *D. ochrophaeus*; 1.81 times, *D. monticola*; 3.75 times, *D. quadramaculatus*) and also because repeated day searches would have caused rapid deterioration of the habitat. As before, the academic schedule precluded more than one visit per plot in September.

It was observed that individuals moved very little between searches. This permitted the separate recording of specimens sighted on the first or second search. Thus, individuals not sighted on the first search but seen on the second or third were the only ones included in the total. By comparing the decline in the number of individuals first seen on the second and third searches with the decline in numbers removed from other plots, I established that the method involved no detectable error.

I estimated that the net result of the change in protocol was a fourfold increase in the intensity of effort per unit area, achieved by increasing the average time required of two searchers from 47.6 min to 69.8 min per plot visit. The new schedule meant that no more than three plots could be searched in one night. One

associated benefit was that differences caused by changes in weather between nights were removed statistically as part of block differences, since it was most practical to cover one block per night.

As figure 1 shows, the change in protocol achieved its purpose. For *D. ochrophaeus*, which had yielded more specimens from the removal plots than were seen on the controls during the period of single removals, the new procedure reduced the number of removals to 68.6% of the control counts for the rest of 1982 and to less than half of the control counts in 1983 and 1984. A significant reduction in the *D. monticola* population took a year longer. The numbers removed declined from 115.6% of control counts in 1982 to 70.5% of control counts in 1983 and 49.4% in 1984.

RESULTS: CHANGES IN ABUNDANCE

Effect of Weather on the Number of Salamanders Seen

The analysis of the counts of salamanders seen under different weather conditions showed that air temperature on the plots had a significant effect on the counts of *Desmognathus ochrophaeus*, *D. monticola* (fig. 2), and *D. quadramaculatus*. In addition, the total rainfall for the two weeks prior to a count was correlated with the counts of *D. ochrophaeus*, although the regression was significant only for amounts less than 4.6 cm. Despite the large scatter of points, the high level of significance for the regressions means that a considerable proportion of the total variance in the counts could be removed by using the regressions to correct for the effect of weather. All the coefficients are given in table 2. Figures 3–6 are based on the corrected counts.

The Effect of 'D. monticola' on 'D. ochrophaeus'

The experiments could not give definitive results unless the removal of *D. monticola* resulted in a positive effect on *D. ochrophaeus*, because that result was expected under both competition and predation hypotheses. The most obvious effect, and perhaps the most convincing, is an increase in abundance as a result of the manipulation. Figure 3 shows that the result was achieved. Each point on the graph represents the mean of counts from the three replicate plots for each treatment, the visits to all plots having been made during a short period (3 days to 1 wk). The simplest statistical analysis is that represented in the figure. Comparing the means for one set of visits meets the assumption of independence of observations, and it is these tests that are represented. The mean counts of *D. ochrophaeus* on plots from which *D. monticola* had been removed differed significantly from the means of control plots on eight occasions, all among the last 12 sets of visits (August 1983–September 1984). Block differences were also tested for statistical significance, and were found to be significant no more frequently than chance would lead us to expect. In the more comprehensive tests that follow, blocks were not included.

For this experiment, the results of these direct and simple tests are amply convincing that removing *D. monticola* brought about an increase in the abundance of *D. ochrophaeus*, despite the absence of corrections for multiple tests.

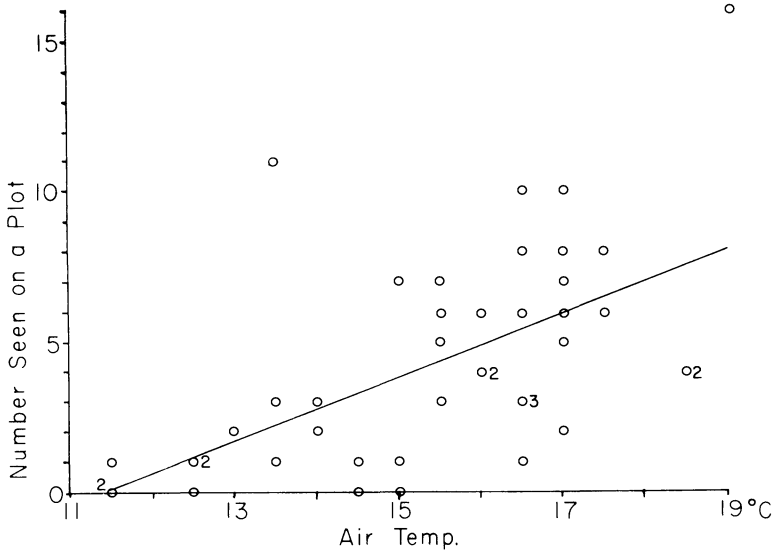


FIG. 2.—The relationship between the air temperature 2 cm above the surface and the number of *D. monticola* salamanders seen on 42 different plot visits. The regression line fits the equation $Y = -12.123 + 1.065X$.

TABLE 2

EFFECT OF AIR TEMPERATURE AND RAINFALL ON THE NUMBER OF *Desmognathus* SALAMANDERS SEEN DURING PLOT SEARCHES

SPECIES	MONTHS	WEATHER FACTOR	COEFFICIENTS	
			<i>a</i>	<i>b</i>
<i>D. ochrophaeus</i>	May, Sept.	Temp.	– 12.098	2.474
	June, July, Aug.	Temp.	– 0.484	1.725
	All	Rain	13.486	3.738
<i>D. monticola</i>	All	Temp.	– 12.123	1.065
<i>D. quadramaculatus</i>	All	Temp.	– 7.936	1.151

NOTE.—The coefficients are those in the equation $Y = a + bX$, where Y is the number of salamanders seen, a is the Y -intercept, b is the slope of regression, and X is degrees Celsius or rainfall in cm.

Such tests, however, discard any summation of effects over a longer period. One would like to know, for example, whether the overall means for 1983 were significantly different. A simple ANOVA using all 27 observations made for each treatment during the year would technically violate the assumption of independence, although the relatively small proportion of all specimens present seen during one visit (see “Change in Protocol,” above) reduces the importance of the violation. There are five periods for which these overall means are important; the first such period is the baseline during May and June 1981, plus the first removal in

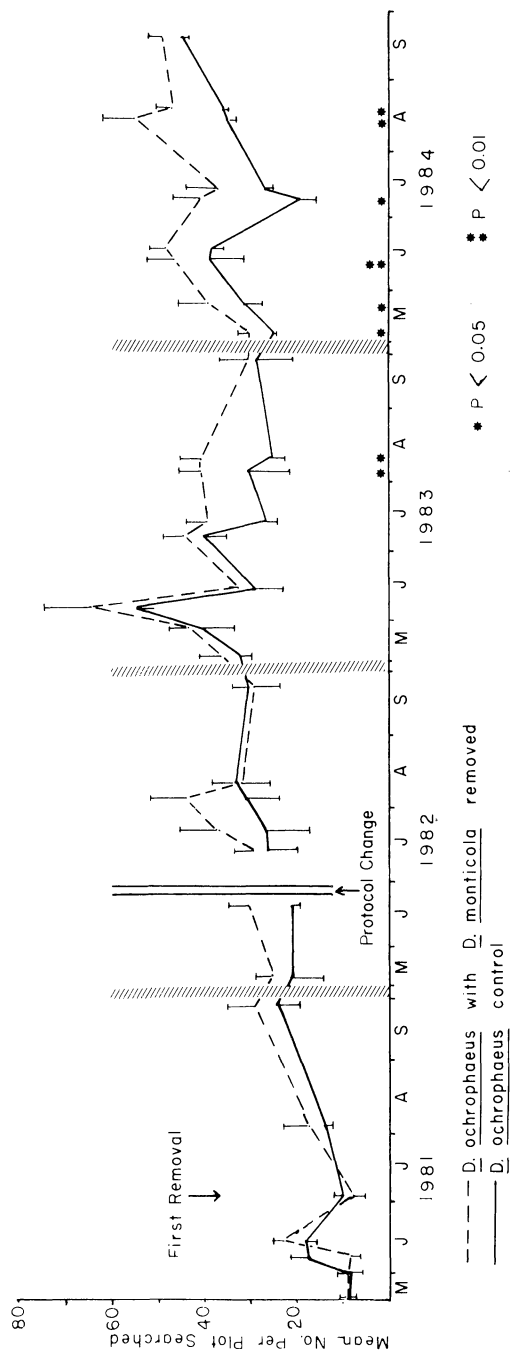


FIG. 3.—The response of the *D. ochrophaeus* population to the removal of *D. monticola*. Vertical bars, 1 SE.

TABLE 3

MEAN NUMBERS OF *D. ochrophaeus* ON CONTROL PLOTS COMPARED WITH MEAN NUMBERS
ON PLOTS FROM WHICH *D. monticola* WAS REMOVED

PERIOD	MEAN DENSITY		ANOVA		REPEATED-MEASURES DESIGN	
	Control	With <i>D.m.</i> Removed	<i>F</i>	<i>P</i>	<i>F</i> _{1,4}	<i>P</i>
Baseline May-July 1981	12.59	11.59	<i>F</i> _{1,28} = 0.18	> .10	0.53	.508
One removal August 1981- June 1982	20.32	25.93	<i>F</i> _{1,22} = 2.63	> .10	4.25	.108
After change in protocol, July-Sept. 1982	29.45	34.66	<i>F</i> _{1,28} = 1.71	> .10	0.45	.541
1983	34.04	41.49	<i>F</i> _{1,52} = 5.33	< .025	2.27	.206
1984	32.96	43.92	<i>F</i> _{1,52} = 17.03	< .001	33.14	.0045

NOTE.—See text for full explanation.

July. Overall means for this period would establish whether there were preexisting differences between the plots designated as controls and those designated for removal of *D. monticola*. The second period of interest is the period of single removals: August and September 1981, and May and June 1982. The remaining three periods are the three years following the change in protocol.

I performed two kinds of analysis on the data. In the first I assumed that the problem of independence of observations was minimal, and I performed a one-way ANOVA covering the whole period of interest. In the second approach I used the repeated-measures design, which is a version of the split-plot analysis. This procedure avoids the problem of independence; the SAS program (Freund and Littell 1981) I used also removes the effect of differences between plots within treatments, and is thus a more conservative test of significance than is the simple ANOVA, since the denominator of *F* is the variance between plots within treatments and carries only 4 degrees of freedom. The results of both analyses are reported in the tables accompanying all the descriptions of the effects of manipulations on the abundance of other species. Table 3 gives the results of the analyses for the effect on *D. ochrophaeus* of removing *D. monticola*. Except for the baseline period, the mean density of *D. ochrophaeus* was greater on the plots from which *D. monticola* was being removed than on the control plots throughout the experiment, but not until 1983 did either statistical test show a significant difference. For that year, ANOVA gives a probability of less than 0.025, but the repeated-measures test does not show significance. For 1984, the two tests show a high level of significance for the difference between the means.

I conclude that *D. monticola* has a definite, negative effect on *D. ochrophaeus*, and that the experimental manipulation was sufficiently powerful to demonstrate the postulated ecological relationships. Whether the effect was one of competition or of predation, however, can be determined only from the results of the reciprocal experiment.

TABLE 4

MEAN NUMBERS OF *D. monticola* ON CONTROL PLOTS COMPARED WITH MEAN NUMBERS
ON PLOTS FROM WHICH *D. ochrophaeus* WAS REMOVED

PERIOD	MEAN DENSITY		ANOVA		REPEATED-MEASURES DESIGN	
	Control	With <i>D.o.</i> Removed	<i>F</i>	<i>P</i>	<i>F</i> _{1,4}	<i>P</i>
Baseline, May– July 1981	2.45	5.24	<i>F</i> _{1,28} = 20.20	< .001	30.31	.005
One removal August 1981– June 1982	7.13	8.84	<i>F</i> _{1,22} = 0.98	> .10	0.75	.434
After change in protocol, July– Sept. 1982	6.80	9.66	<i>F</i> _{1,28} = 4.01	> .05	1.54	.283
1983	5.27	7.15	<i>F</i> _{1,52} = 2.57	> .10	0.66	.461
1984	6.42	7.99	<i>F</i> _{1,52} = 3.26	> .05	0.46	.536

NOTE.—See text for full explanation.

The Effect of 'D. ochrophaeus' on 'D. monticola'

Removing *D. ochrophaeus* should provide the evidence necessary to decide whether the effect of *D. monticola* was competition or predation (results shown in fig. 4 and table 4). It happened that in the assignments of treatments to plots, plots chosen for the removal of *D. ochrophaeus* had higher initial densities of *D. monticola* than did the plots chosen as controls. For three of the five visits during the baseline period, these differences were statistically significant. The significance was confirmed by both ANOVA and the repeated-measures design for the whole period. After the baseline period, the mean number of *D. monticola* on the treated plots converged with the mean on the controls, and no statistically significant differences were detected for the remainder of the experiment. Inasmuch as the removal of *D. ochrophaeus* evidently had a negative effect on the abundance of *D. monticola*, it follows that its presence was originally beneficial to that species. The a priori statement of the interpretation of these results is that *D. monticola* is an effective predator, and that *D. ochrophaeus* is a significant prey item in its diet (Hairston 1980, 1984). If removing *D. ochrophaeus* had not produced a negative effect on *D. monticola*, the two species could possibly be in asymmetrical competition.

The Effect of 'D. ochrophaeus' on 'D. quadramaculatus'

In the two previous papers in which I proposed these experiments (Hairston 1980a, 1984), the hypothesis was advanced that *D. quadramaculatus* might also be a significant predator on *D. ochrophaeus*. In that event, removing the latter should not have a beneficial effect on the former, and "perhaps *D. quadramaculatus* might decline in abundance because of the loss of an important prey item" (Hairston 1984, p. 25). Figure 5 and table 5 reveal the strong possibility that

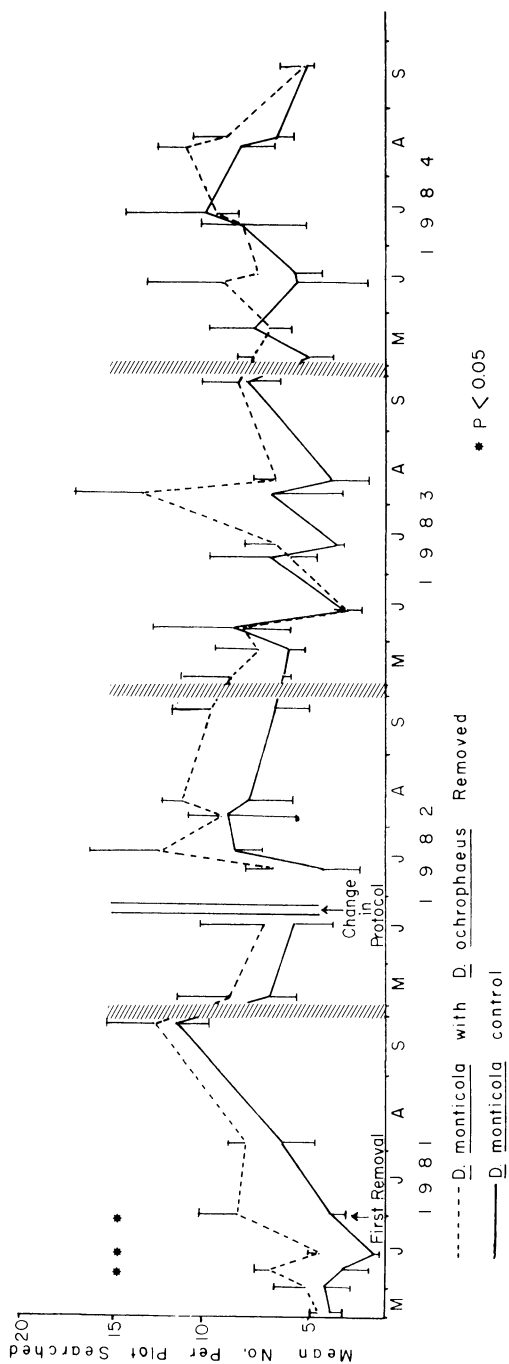


FIG. 4.—The effect on *D. monticola* abundance of the removal of *D. ochrophaeus*. Vertical bars, 1 SE.

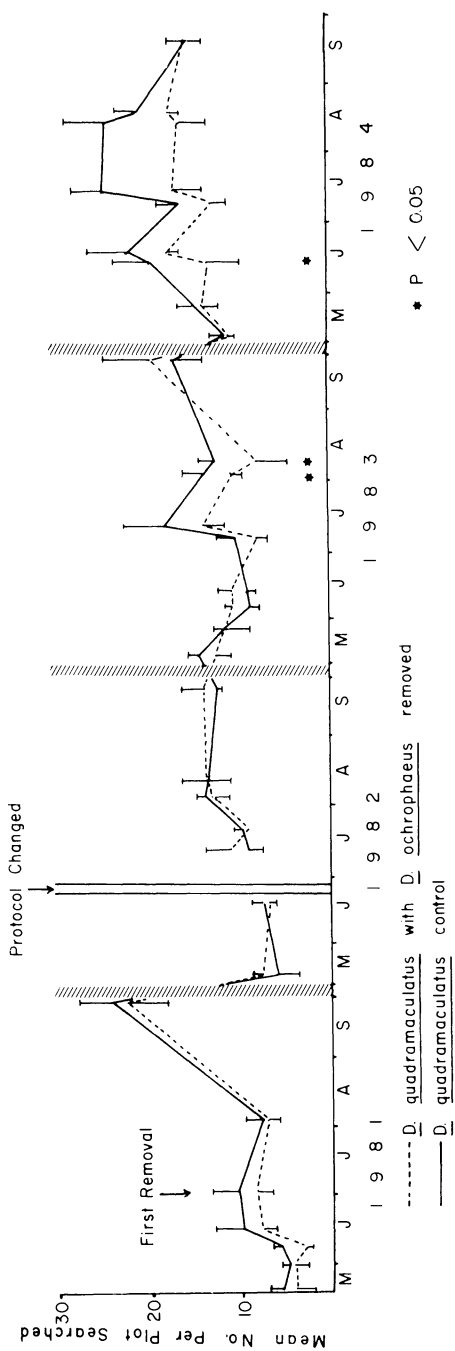


FIG. 5.—The effect on the *D. quadramaculatus* population of *D. ochrophaeus* removal. Vertical bars, 1 SE.

TABLE 5

MEAN NUMBERS OF *D. quadramaculatus* ON CONTROL PLOTS COMPARED WITH MEAN NUMBERS ON PLOTS FROM WHICH *D. ochrophaeus* WAS REMOVED

PERIOD	MEAN DENSITY		ANOVA		REPEATED-MEASURES DESIGN	
	Control	With <i>D.o.</i> Removed	<i>F</i>	<i>P</i>	<i>F</i> _{1,4}	<i>P</i>
Baseline, May– July 1981	7.38	5.46	$F_{1,28} = 2.38$	$> .10$	2.56	.185
One removal August 1981– June 1982	11.44	10.83	$F_{1,22} = 0.03$	$> .10$	0.08	.794
After change in protocol, July– Sept. 1982	12.05	11.66	$F_{1,28} = 0.14$	$> .10$	0.06	.813
1983	12.63	11.58	$F_{1,52} = 0.84$	$> .10$	0.32	.602
1984	18.59	15.34	$F_{1,52} = 7.41$	$< .01$	2.60	.182

NOTE.—See text for full explanation.

such was the case. Any reservation that the reader might feel is caused only by the failure of the conservative version of the repeated-measures design to show that the abundance of *D. quadramaculatus* on control plots differed significantly from that on the plots from which *D. ochrophaeus* was removed in 1984. Like the ANOVA, the repeated-measures design under the complete null hypothesis showed that *D. quadramaculatus* was significantly more abundant on control plots in 1984 than it was on plots from which *D. ochrophaeus* was removed ($F_{1,32} = 13.37, p = .0009$). Thus, the evidence is strong, if not completely conclusive, that *D. ochrophaeus* is an important prey item for *D. quadramaculatus*. Southerland (pers. comm.) has observed a natural example of this predation. That *D. quadramaculatus* did not increase in abundance following the removal of *D. ochrophaeus* is firmly established, and demonstrates that the two species are not competitors.

The Effect of 'D. monticola' on 'D. quadramaculatus'

The foregoing experiments established that *D. ochrophaeus* is an important prey item for *D. monticola*, and very probably for *D. quadramaculatus*. It thus appears possible that those two species compete for food. Removing *D. monticola* should therefore lead to an increase in abundance of *D. quadramaculatus* (results shown in fig. 6 and table 6). During the baseline period, and for the rest of 1981, *D. quadramaculatus* was more abundant on the control plots than on the plots from which *D. monticola* was removed. For the remainder of the experiment, its average abundance was greater on the experimental plots. According to the ANOVA, the difference was significantly greater in 1983 and 1984, although the conservative version of the repeated-measures design failed to show statistical significance. Comparing the mean densities of the two species shows that *D.*

TABLE 6

MEAN NUMBERS OF *D. quadramaculatus* ON CONTROL PLOTS COMPARED WITH MEAN NUMBERS ON PLOTS FROM WHICH *D. monticola* WAS REMOVED

PERIOD	MEAN DENSITY		ANOVA		REPEATED-MEASURES DESIGN	
	Control	With <i>D.m.</i> Removed	<i>F</i>	<i>P</i>	<i>F</i> _{1,4}	<i>P</i>
Baseline, May–June 1981	7.38	6.89	$F_{1,28} = 0.11$	$> .10$	0.10	.767
One removal August 1981–June 1982	11.44	11.62	$F_{1,22} = 0.003$	$> .10$	0.00	.954
After change in protocol, July–Sept. 1982	11.66	14.59	$F_{1,28} = 1.19$	$> .10$	0.49	.524
1983	12.63	15.34	$F_{1,52} = 4.08$	$< .05$	2.61	.181
1984	18.59	22.14	$F_{1,52} = 4.09$	$< .05$	2.05	.225

NOTE.—See text for full explanation.

quadramaculatus is considerably more abundant than *D. monticola* on these plots (tables 4, 6). It is also much larger. Thus, even though they appear to be in competition, removing the less abundant and smaller species would not be expected to show a dramatic effect on the more abundant and larger species. That any effect at all was obtained is evidence of competition between them. Southerland (1985) obtained experimental evidence of a negative effect of *D. quadramaculatus* on *D. monticola*, but Kleeberger (1984) was unable to demonstrate interspecific competition in his experiments manipulating densities and cover objects.

The Effect of the Experiments on 'D. aeneus'

Because the ecological distribution of *D. aeneus* extended well beyond the limit of the experimental plots, it was uncertain whether the manipulations would have a detectable effect on that species. Although no prediction was made for either hypothesis in the two papers proposing the experiments, removing *D. ochrophaeus* or *D. monticola* could have a positive effect on *D. aeneus* only if there was any ecological interaction between that species and either of the larger ones. As for all other species of salamanders, the abundance of *D. aeneus* was recorded for all visits to the plots (results summarized in table 7). Within the area of the plots, *D. aeneus* was much less abundant than the other three species of *Desmognathus*, with an average of a single specimen seen on five plot visits. The manipulations had no detectable effect on the abundance of this species. Either its ecological distribution is sufficiently different from those of the other species for it to avoid deleterious effects from either competition or predation, or these interactions are of negligible importance.

Another characteristic of *D. aeneus* may affect these results: it is apparently less likely to be seen on the surface, even at night, than are the other three

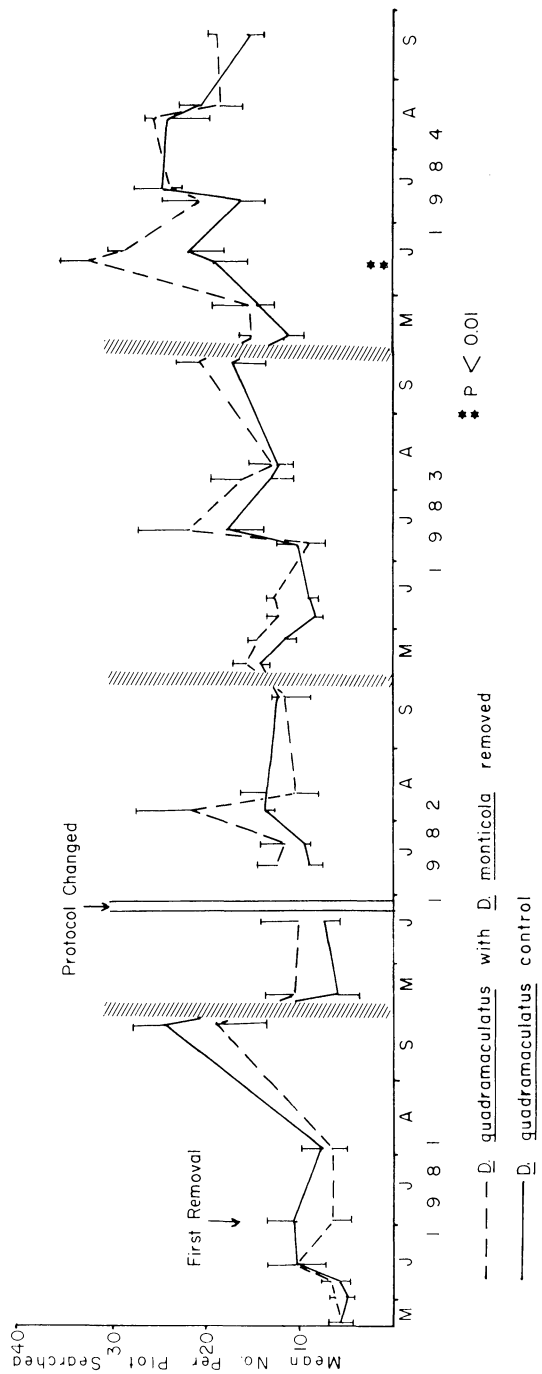


FIG. 6.—The response of the *D. quadramaculatus* population to the removal of *D. monticola*. Vertical bars, 1 SE.

TABLE 7

EFFECT OF THE EXPERIMENTAL MANIPULATIONS ON THE ABUNDANCE OF *D. aeneus*

TREATMENT	BASELINE	SINGLE REMOVALS	REST OF 1982	ALL OF 1983	ALL OF 1984
<i>D. ochrophaeus</i> removed	1	2	6	9	6
<i>D. monticola</i> removed	0	3	2	4	8
Control	1	1	6	7	7
Mean number per plot visit	0.04	0.17	0.31	0.25	0.26

NOTE.—Numbers are totals for all plot visits.

species. Whereas higher numbers of the other species were counted per plot visit at night (see "Methods," above), *D. aeneus* was six times as abundant during the day searches. Thus, the proportion of *D. aeneus* actually recorded was much smaller than that of the other species. Combined with the estimate that at least half of the population was farther from the streams than from the outer edges of the plots, the small proportion seen raises doubts about the accuracy of the experimental results. Still, the claim can be made that *D. aeneus* experienced no major effect from the removal of either *D. ochrophaeus* or *D. monticola*. Since I have observed that both these species are cannibalistic on smaller individuals in captivity, one might expect an effect of predation on *D. aeneus*. Its evident secretiveness, even at night, may be a response to predation.

RESULTS: CHANGES IN AGE STRUCTURE

From elementary considerations of population ecology, one might expect that removing a competitor or a predator would bring about a change in the age distribution of the species under observation. For example, if release from competition causes an increase in reproduction, it would be reasonable to expect that the proportion of young individuals would increase. With appropriate controls, the increase should be detectable. If, however, the species removed is a predator, the response would depend on the part of the population most subject to predation. Ordinarily, one would suppose that predation would affect small individuals more than large ones; if that is true, one would also expect the proportion of young to increase relative to the controls. If all parts of the population are equally susceptible, as when the predator species is much larger than the prey, no change in age structure would be expected to result from removal of the predator.

If the response to the removal of a competitor or a predator species takes the form of a movement into the vacated area, one would not expect the composition of the population to change. Of course, if one age class is especially prone to dispersal, that group should be relatively more abundant in the experimental area.

The results show no consistent effect of the experimental manipulations on the age structures of any of the three species of most interest. No case can be made for any increase in reproduction as the result of the removal of either *D. monticola* or *D. ochrophaeus*. Most of the metamorphosis for all three species occurs during

the summer, and inasmuch as only metamorphosed individuals were recorded, there was a general increase in the proportion of immature individuals during June, July, and August. These changes occurred independently of the experimental treatment, and they will be described elsewhere.

RESULTS: CHANGES IN ECOLOGICAL DISTRIBUTION

The Effect of Seasons

Most descriptions of the ecological distribution of the species of *Desmognathus* have reported single proportions at different distances from streams (Hairston 1949, 1973), but Organ (1961) reported some changes in spring, summer, and fall. Most of my data will be reported elsewhere, but it is not possible to consider the effects of the experimental manipulations without some knowledge of the changes that normally occur during the months when the salamanders are active.

Generally, *Desmognathus* species are found in or near the streams during the cold months, and in the forest during the summer. Table 8 shows that the adults are found farther from water than are the immatures, and that both age classes increase their range of activity during the summer months. Thus, to analyze how the removal of one species affects the ecological distribution of another, the comparison must be limited to one month at a time. Within any month, the relative positions of the species remain much the same, but the absolute positions change so much between months that variances within treatments would negate the effects of the treatments as far as statistical analysis is concerned.

The Effect of 'D. monticola' on 'D. ochrophaeus'

One might expect that a species might respond to the removal of a competitor or a predator by occupying the vacated area. During the early part of these experiments, *D. ochrophaeus* occupied the area vacated by *D. monticola*. For the period of baseline observations, the distribution of *D. ochrophaeus* did not differ significantly among the three control plots ($\chi^2 = 13.58$, 8 df, $P \geq .05$); the distribution also did not differ significantly among the plots selected for experimentation ($\chi^2 = 7.52$, 8 df, $.5 < P < .7$). Pooling the three plots for each treatment and comparing the distributions between the future control and experimental plots shows no significant difference ($\chi^2 = 2.734$, 6 df, $.8 < P < .9$). The same results are obtained when individual plots are compared, whether on the same stream or not. When the three plots of each of the two treatments are matched with each plot of the opposite type, there are nine comparisons that can be made. None shows a statistically significant difference. Thus, any difference observed after the start of removal of *D. monticola* must be the result of the experimental manipulation.

No significant change in distribution was observed until after the effort was intensified in July 1982 (table 9). During July, August, and September, the distribution of *D. ochrophaeus* shifted exactly as if *D. monticola* influenced *D. ochrophaeus* in an ecologically important manner. In all three months, the proportion of *D. ochrophaeus* specimens was significantly greater near streams from which *D. monticola* had been removed than on the control plots.

TABLE 8

SEASONAL CHANGES IN MEAN DISTANCE (METERS) FROM WATER FOR THREE SPECIES OF *Desmognathus*

SPECIES	AGE CLASS	MONTH				
		May	June	July	August	Sept.
<i>D. quadramaculatus</i>	Immature	0.02	0.27	0.55	0.23	0.05
	Adult	0.54	1.03	1.38	1.63	0.20
<i>D. monticola</i>	Immature	0.25	1.74	1.10	2.01	0.22
	Adult	0.37	2.33	1.78	3.05	0.35
<i>D. ochrophaeus</i>	Immature	2.24	2.68	2.85	2.18	2.33
	Adult	2.08	3.18	2.89	3.10	2.79

TABLE 9

DISTRIBUTION OF *D. ochrophaeus* BEFORE AND AFTER THE START OF INTENSIFIED EFFORT TO REMOVE *D. monticola*

MONTH	TREATMENT	METERS FROM STREAM			N	χ^2 (2 df)
		0-2	2-4	4-7		
May	Control	.43	.38	.18	99	1.17 NS
	<i>D. monticola</i> removed	.41	.44	.15	105	
June	Control	.52	.22	.27	79	4.06 NS
	<i>D. monticola</i> removed	.54	.27	.19	115	
July	Control	.34	.30	.36	159	18.79***
	<i>D. monticola</i> removed	.45	.33	.22	204	
August	Control	.24	.41	.34	203	33.00***
	<i>D. monticola</i> removed	.41	.34	.25	231	
Sept.	Control	.20	.39	.41	49	27.34***
	<i>D. monticola</i> removed	.43	.39	.17	69	

NOTE.—The proportion of individuals at different distances from streams is shown for each month of 1982. Effort was intensified in July.

*** $P < .001$.

Superficially, the data for 1983 and 1984 are difficult to reconcile with the results through 1982. In the last half of 1982, but not in 1983 or 1984, I observed the shift of *D. ochrophaeus* toward streams from which *D. monticola* was removed. In fact, during 1983 there was a statistically significant shift in the opposite direction in three of the five months. In 1984, no consistent pattern was detected, and in three of the months, there was no significant difference from the controls. The results for these two years are understandable only if the relationship between *D. monticola* and *D. quadramaculatus* is considered.

The Effect of 'D. ochrophaeus' on 'D. monticola'

The distribution of *D. monticola* was affected more by its own removal than by the removal of *D. ochrophaeus*. During the baseline period and the period of single removals, the distribution of *D. monticola* did not differ significantly among the three treatments. Among the 13 sets of observations after the start of intense

effort, there were six occasions when the distribution on the controls differed significantly from that on the plots from which *D. ochrophaeus* was removed. For two of these occasions, the difference was not easily interpretable. For example, in August 1982, the observed number of specimens was greater than expected in the water and within 0.5 m of it, but also more than 3 m away from the water. At intermediate distances, the numbers were fewer than expected, and the distributions were significantly different ($\chi^2 = 19.11$, 3 df, $P < .001$). This kind of erratic result convinces me that the statistically significant differences were due to factors unrelated to the experimental manipulations.

The Effect of 'D. monticola' on 'D. quadramaculatus'

Because of the size difference between the two species, the removal of *D. monticola* could benefit *D. quadramaculatus* only if they compete. During the period of observations before the intensive removal of *D. monticola*, the distribution of *D. quadramaculatus* did not differ significantly between the control plots and those from which *D. monticola* was to be removed. One would expect any response to involve a shift of *D. quadramaculatus* away from the water onto the stream banks. During the 13 separate months of observation after the start of intense removal of *D. monticola*, the proportion of specimens seen in the water was greater on the control plots on nine occasions; in five instances, this difference was significant. On two other occasions there was no difference, and on the two occasions when the proportion of *D. quadramaculatus* in the water was higher on the experimental plots, the difference was not significant.

The effect of *D. monticola* on the distribution of *D. quadramaculatus* is reminiscent of *D. monticola*'s effect on its abundance. There is a statistically significant shift toward the stream bank, the typical habitat of *D. monticola*, but the difference was not observed in all months. It is as though the competitive relationship between the two species is not intense, or the effect of *D. monticola* is to some extent negated by predation by *D. quadramaculatus*. On one occasion, I observed *D. quadramaculatus* feeding on another large salamander, but the specimen was so mangled that it could not be identified. On another occasion, C. Smith and I saw a *D. quadramaculatus* individual take as prey a large adult *Plethodon glutinosus*. Thus, *D. quadramaculatus* is fully capable of being the effective predator that is postulated.

The Effect of 'D. quadramaculatus' on 'D. ochrophaeus'

The shift of *D. quadramaculatus* toward the habitat of *D. monticola* also moved the population toward that of *D. ochrophaeus*. Most of this shift occurred in May, June, and July 1983, the period when *D. ochrophaeus* stopped its streamward shift in response to the removal of *D. monticola*. I propose that the advent of significant numbers of *D. quadramaculatus* caused the reversal of the apparently unusual change in distribution of *D. ochrophaeus*. If it was advantageous for *D. ochrophaeus* to move toward the stream-bank habitat of *D. monticola* when that species was removed, it was equally advantageous to move back toward the forest when *D. quadramaculatus* replaced *D. monticola* on the stream bank.

DISCUSSION

The most conclusive result of this study is that predation is the predominant interspecific interaction in the *Desmognathus* guild. The experimental evidence is complete for the relationship between *D. monticola* and *D. ochrophaeus*, and follows exactly the hypothetical outcome of the experiments proposed in the two earlier papers (Hairston 1980a, 1984). The alternative, interspecific competition, is eliminated by the failure of the removal of *D. ochrophaeus* to bring about a positive response by *D. monticola*. The conclusion is strengthened by the fact that removing *D. ochrophaeus* actually caused a reduction in the abundance of *D. monticola*, relative to its abundance on the control plots.

The experiments also support predation by *D. quadramaculatus* on *D. ochrophaeus*, since the removal of the latter also reduced the population of the larger species. The reciprocal experiment of removing *D. quadramaculatus* was not performed, and the evidence is not as complete as it is in the case of *D. monticola*.

One of the most interesting aspects of the outcome of the experiments was the significant increase in the abundance of *D. quadramaculatus* where *D. monticola* was removed. Since the latter species is the smaller of the two, this result can only be interpreted as demonstrating the existence of competition. That *D. monticola* was considerably less abundant than *D. quadramaculatus* on these plots provided an unusually stringent test of the relationship.

There is a third outcome that could have been obtained, as Simberloff (1980) and his colleagues (Strong 1983) have frequently insisted. This is the possibility that the species do not affect each other to a detectable degree. This result was also obtained in the case of testing for an effect of *D. ochrophaeus* and *D. monticola* on *D. aeneus*. It is not possible to demonstrate this negative result conclusively because *D. aeneus* has habits that make the experimental technique of searching the surface of the ground at night ineffective for estimating relative densities of the population. Nevertheless, we must accept the evidence as the best available, better than the indirect observations of its ecological distribution and its size relative to the other species, both of which had been interpreted as indicating a competitive system.

For the other species, this third outcome was negated by the rejection of the statistical null hypothesis for all of the experimental combinations. This statement is strengthened by the observation that the null hypothesis was rejected for those years or other time periods that made sense ("common sense," Roughgarden 1983, p. 583) in interpreting the experimental results. Thus, when *D. monticola* was removed, the density of *D. ochrophaeus* on the experimental and control plots differed significantly only during the last two years of the experiment, and most significantly in the last year. On these same plots, the density of *D. quadramaculatus* increased significantly on experimental plots in comparison to control plots during the last two years of the study. When *D. ochrophaeus* was removed, the mean density of *D. quadramaculatus* on control plots was significantly greater than on the experimental ones only in the last year. Finally, the removal of *D. ochrophaeus* reduced the initially higher mean density of *D. monticola* to a density that was not significantly different. The statistically

significant difference occurred only during the baseline period. For none of these experiments was a significant difference obtained that is difficult or impossible to explain.

Monitoring ecological distributions provided data that strengthened the conclusions derived from changes in abundance on the plots. The reciprocal shifts of *D. ochrophaeus* and *D. quadramaculatus* reflect the effects of predation on the former and of competition on the latter. *Desmognathus ochrophaeus* first responded to the removal of *D. monticola* by shifting its distribution toward the streams as soon as the removals began to affect that species. *Desmognathus quadramaculatus* was slower to shift its distribution to occupy the area vacated by the removal of *D. monticola*. When it did so, it apparently put new predatory pressure on *D. ochrophaeus*, which then shifted back to its original position in 1983 and 1984. The foregoing might be considered fanciful explanations were it not for the fact that they are consistent with the changes in numerical abundance. Moreover, the statements are well supported by statistical tests. It is also noteworthy that *D. monticola* did not respond to the removal of *D. ochrophaeus* by any consistent change in its ecological distribution.

In most other natural situations in which both competition and predation have been found to be significant factors, the organisms affected belong to different well-defined trophic levels (for review of marine systems, see Dayton 1984; for terrestrial systems, see Strong 1983; Strong et al. 1984). The other exceptions known to me are also salamander guilds. Wilbur (1972) demonstrated that in Michigan *Ambystoma tigrinum* was an important predator on the competing species, *A. maculatum*, *A. tremblayi*, and *A. laterale*; Stenhouse et al. (1983) showed that *A. opacum* was both an important predator and a competitor of *A. maculatum* in North Carolina; and Morin (1983b) found that competition and predation were important in the ecological relations between *A. tigrinum* and *Notophthalmus viridescens*. This combination of interactions within a guild could only occur among predator species.

The importance of finding both predation and competition within an apparently well-defined guild emphasizes the difficulty of drawing conclusions about interspecific relationships when the evidence consists of an apparent example of niche partitioning. Dayton (1973) provided examples of the misidentification of interactions based on the same kind of information. Without experiments planned specifically to test for the distinction between competition and predation and for the importance of interspecific interactions, the wrong conclusion concerning the *Desmognathus* guild was drawn repeatedly (Hairston 1949, 1973; Organ 1961; Krzysik 1979).

These results have implications for understanding the evolution of the genus. Considering predation in the streams as the most important interspecific interaction, the decrease in size with increasing terrestriality is explained as follows: herpetologists agree that the species most like the common ancestor are large and aquatic or semi-aquatic. Dunn (1926) chose *D. quadramaculatus* as that species; D. Wake (pers. comm.) prefers *D. monticola*. In either case, speciation would leave the smaller of the resulting species under selective pressure to become more terrestrial because of the heavy predation in and near streams. The predictions in table 1 are thus mostly irrelevant.

This evolutionary analysis of the experimental results for *Desmognathus* may also be relevant to the origin of the completely terrestrial Plethodontini and Bolitoglossini. The selective pressure of predation may well have overcome the disadvantage of lunglessness for terrestrial vertebrates, with the interesting result that these forms have been able to extend their distributions far beyond the presumed area of origin in eastern North America.

There is one more feature of this research that merits comment, that is, the preliminary publication of the purpose of the research, and a clear statement of the experimental design (Hairston 1980a, 1984). In those papers, I included the interpretation of each possible outcome of the proposed experiments. This publication before the actual research (the 1984 paper was presented at a symposium in 1981) made the tests of the hypotheses truly a priori. I had previously followed the same procedure in carrying out my experiments on the ecology and evolution of two species of the salamander genus *Plethodon* (Hairston 1973, 1980b,c, 1983). Throughout its existence, ecology has permitted the a posteriori explanation of observations and has thus become discredited, not only by other branches of biology, but within the field as well, as the recent debates demonstrate. Although it is true that not all ecological questions can be solved by an experimental approach, a growing body of literature shows that many conclusions, once thought to be the province of "data dredging," are subject to generally accepted experimental procedures. There is no evidence that the experimental approach is reaching a limit to its usefulness, and until it does it will remain the superior method of solving ecological problems.

SUMMARY

Five years ago, experiments were proposed to determine whether competition or predation is the principal ecological factor in the organization of the community of *Desmognathus* salamanders. The experiments were conducted in the Nantahala Mountains of North Carolina over a four-year period, 1981–1984. There were four species present: *D. quadramaculatus*, the largest and most aquatic; *D. monticola*, the next largest, a stream-bank species; *D. ochrophaeus*, smaller and largely terrestrial; and *D. aeneus*, the smallest and most terrestrial of the four. A block design of replicate plots along streams was used. Removing a smaller species (*D. ochrophaeus*) was expected to cause an increase in the *D. monticola* or *D. quadramaculatus* populations only if competition were the important interaction. Removing *D. monticola* individuals was expected to increase the abundance of *D. ochrophaeus*, whether competition or predation was important, but it would increase *D. quadramaculatus* numbers only in the case of competition. The outcome largely supported the hypothesis that predation is the important organizing force. When *D. ochrophaeus* individuals were removed, the abundance of both larger species decreased significantly, relative to their abundance on control plots. Removing *D. monticola* salamanders led to the expected increase in the abundance of *D. ochrophaeus*, thus completing the predictions of the predation hypothesis. There was a small but statistically significant increase in the numbers of *D. quadramaculatus*, a result that confirmed the existence of competition. I conclude that *D. monticola* and *D. quadramaculatus* compete for food and that *D.*

ochrophaeus is an important item in their diets. The importance of experimentation and prior publication of research designs is stressed.

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