

($t = 0.886$, $P > .5$ and $t = 0.243$, $P > .05$, respectively). In the latter condition the subjects were receiving 21.4 and 22.2 ml, which is more than the 16.5 and 19.9 ml that the control subjects received when their intake was inhibited by the saline counterinjections; however, since these differences in volume are not very large, one more experimental manipulation was undertaken.

For this final test, the vagotomized and control groups were tested under the three experimental conditions as before; however, this time their milk was diluted 1:1 with tap water during the 30-minute meal. Under these conditions the intake of the normal subjects increased only slightly, but the intake of the vagotomized subjects showed a steady increase until, after 4 days, it reached the control level. On the fifth day the animals were tested under baseline conditions to make sure that stabilization had occurred. Then they were tested under two experimental conditions. In one, 0.9 percent saline was infused into their stomachs at a rate equal to half the voluntary consumption. In the second condition, 10 ml of their gastric contents was siphoned off as they drank. The results are presented in Fig. 2. Milk intake by control subjects was affected by both saline infusions and nutrient withdrawal. Vagotomized subjects adjusted their intake only in relation to nutrient withdrawal.

After the behavioral tests were completed the subjects were anesthetized with sodium pentobarbital, the condition of their implants was checked, and the success of the denervation operation was verified by an electrophysiological test involving electrical stimulation of the cervical vagus nerve (6). Finally, the possibility that the vagotomized subjects were not responsive to gastric distension due to an enlargement of their stomachs was investigated. [Such enlargement has been observed in vagotomized subjects kept on solid food (9).] Autopsies showed the stomachs to be of normal size (10).

It appears that gastric distension, one of the signals that control meal size, has no effect on consumption after the vagus nerve is cut. However, gastric nutrient content is still monitored in the normal manner. Clearly, signals conveying information about nutrient content must take another route to the central nervous system.

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7. W. G. Young and J. A. Deutsch, *J. Neurol. Methods* **3**, 377 (1981). Dow Corning Silastic tubing (inner diameter, 1.98 mm) was used to make the gastric cannulas.
8. The infusions were automated. When rats drank milk from one end of a U tube, an electrical circuit at the other end was broken. This activated a relay that turned on an infusion pump equipped with 50-cm² syringe that replenished

the milk in the U tube and a 20-cm² syringe that delivered the infusion. The diameters of these syringes were such that the larger one pumped twice as much fluid per unit time as the smaller one. While the pump was activated the rate of intragastric infusion was 2.2 ml/min.

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10. Three indices of stomach size were collected: surface area, weight, and volume of water required to elevate intragastric pressure to a standard of 30 cm in a water manometer. None of the differences in these values between the control and experimental groups was significant. It is also unlikely that the difference in milk consumption between vagotomized and control rats could be due to differential rates of gastric emptying. While it has been suggested [P. R. McHugh and T. H. Moran, *Am. J. Physiol.* **236**, R-254 (1979)] that rate of gastric emptying could function as a satiety signal, we have shown (3, 4) that satiety is unaffected by occlusion of the pylorus.
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Predatory Salamanders Reverse the Outcome of Competition Among Three Species of Anuran Tadpoles

Abstract. *The outcome of competition among three species of anuran tadpoles in replicated artificial pond communities depends on the density of predatory salamanders present in the community. Predators differentially affect the survival of anuran species to metamorphosis and reverse the pattern of anuran relative abundance resulting from interspecific competition among tadpoles in the absence of predators.*

Theoretical community ecology has been dominated by the assumption that interspecific competition is of paramount importance in the determination of the species composition of most communities (1). In contrast, experimental studies of assemblages of plants and sessile invertebrates have demonstrated that predators may alter the outcome of interspecific competition among their prey (2). Despite the demonstration of an interaction between predation and competition in communities of potentially

space-limited sessile species, the study of the interaction between competition and predation in free-ranging vertebrate prey has been neglected (3) even though descriptive and experimental studies of vertebrates have provided the foundation of arguments for the preeminence of interspecific competition as a mechanism producing patterns of community structure (4). While interspecific competition undoubtedly occurs in some vertebrate communities (5), the effects of variation in intensity of predation on the outcome of competition are usually unknown. Recent reevaluations of earlier descriptive studies of vertebrate communities have also questioned the statistical validity of much of the indirect evidence (for example, character displacement) that has been cited to support the role played by competition in the structuring of communities (6). These studies have suggested that much of the purported pattern in vertebrate communities simply reflects stochastic interspecific variation in morphological attributes usually associated with resource utilization, rather than a systematic partitioning of resources consistent with competition and niche theory.

I have investigated the potential interaction between predation and competition by conducting a community-level experiment on the effects of different

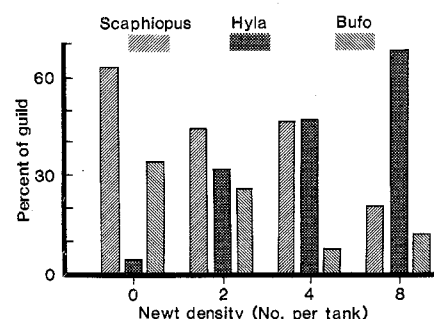


Fig. 1. Summary of the effects of newt density on the mean relative abundance of three species of anurans at metamorphosis. Percentages refer to the mean composition of the tadpole guild over four replicate communities at each level of newt density. Increasing intensity of predation corresponding to increasing newt density leads to a significant reversal in the composition of the tadpole guild (9); $\Lambda = .170$; $P = .02$.

Table 1. The effects of predator density on mean weight [$\pm$ standard error of the mean (S.E.M.)] at metamorphosis and survival to metamorphosis for three species of anurans. Values given are means of population means at each level of newt density. The level of significance of an analysis of variance for the effect of predator density on the population statistics of each species is given on line *P* (see column 1).

Newt density (number per tank)	Mean ($\pm$ S.E.M.) weight at tail resorption (mg)			Survival to metamorphosis (%)		
	<i>S. holbrooki</i>	<i>H. crucifer</i>	<i>B. terrestris</i>	<i>S. holbrooki</i>	<i>H. crucifer</i>	<i>B. terrestris</i>
0	446 $\pm$ 18	49 $\pm$ 5	80 $\pm$ 7	93.3 $\pm$ 1.9	4.0 $\pm$ 2.8	39.6 $\pm$ 11.8
2	552 $\pm$ 51	72 $\pm$ 7	94 $\pm$ 3	57.6 $\pm$ 11.1	27.6 $\pm$ 10.3	23.8 $\pm$ 11.1
4	577 $\pm$ 31	148 $\pm$ 29	88 $\pm$ 2	42.6 $\pm$ 9.1	27.1 $\pm$ 5.5	4.8 $\pm$ 2.8
8	650 $\pm$ 76	211 $\pm$ 32	135 $\pm$ 23	18.0 $\pm$ 8.9	30.3 $\pm$ 7.7	8.0 $\pm$ 5.4
<i>P</i>	.053	.002	.009	.0005	.0086	.0494

intensities of predation by the broken-striped newt, *Notophthalmus viridescens dorsalis*, on the relative abundance at metamorphosis of three species of larval frogs, *Scaphiopus holbrooki*, *Hyla crucifer*, and *Bufo terrestris*. *Notophthalmus* is a generalist predator (7) which co-occurs with these anurans in natural temporary ponds in the Sandhills Region of south-central North Carolina. An experiment with these species of amphibians in replicated artificial ponds has demonstrated that increased density of *Notophthalmus* can generate nonrandom patterns of anuran relative abundance and reverse the pattern of anuran relative abundance that results from interspecific competition among tadpoles in the absence of predators.

During the first 2 weeks of March in 1980, I reconstituted simple replicated temporary pond communities in 16 cylindrical tanks made of galvanized steel and painted with epoxy enamel. The tanks (1.52 m in diameter by 0.61 m) were filled to a depth of 0.51 m with tap water. Each tank additionally received 550 g of dry litter from a *Pinus palustris* savanna, 50 g of Purina Trout Chow as an additional source of nutrients, and a standard volume inoculum of plankton derived from pooled plankton collections from eight natural ponds in the Sandhills. Fifty rooted stems of the aquatic macrophyte *Myriophyllum pinnatum* were planted in the litter of each tank to provide additional cover for the prey. All tanks were covered with lids of fiber glass window screen stapled to hexagonal wooden frames. The lids retained metamorphosing amphibians and prevented the uncontrolled colonization of the tanks by ovipositing frogs and predatory insects.

The intensity of salamander predation was systematically varied by adding none, two, four, or eight *Notophthalmus* to each tank on 22 March, at a sex ratio of 1:1 within tanks. Newts were randomly assigned to tanks according to a randomized block design for variance analysis, and four replicated tank communities were used at each level of *Notophth-*

almus density. Hatchlings of four species of frogs were obtained by collecting eggs and breeding pairs of frogs in the Sandhills. On 27 March, I added 200 *Scaphiopus holbrooki*, 300 *Hyla crucifer*, and 100 *Rana sphenoccephala* as hatchlings to each tank. On 2 May, I added 300 *Bufo terrestris* hatchlings to each tank. Interspecific differences in the number of hatchlings added to each tank reflect differences in the availability of hatchlings. The initial densities of predators and prey fell within the range of variation observed for these species in natural ponds.

Each tank was examined daily for metamorphosing anurans, which were recognized as metamorphs by their forelimbs. All metamorphs were identified to species, counted, towel-dried, and weighed to 1-mg precision. Metamorphs were retained in the laboratory at room temperature without feeding and were again weighed when tail resorption was completed. The dates of collection of the last metamorphs of *Scaphiopus*, *Hyla*, and *Bufo* were 12 May, 28 June, and 15 July, respectively.

The relative abundance of metamorphs of *Scaphiopus*, *Hyla*, and *Bufo* within each tank was used as a measure of tadpole guild composition (8). *Scaphiopus* and *Bufo* were relatively abundant in control tanks without newts, accounting for 62 and 33 percent of the total metamorphs (Fig. 1). In contrast, *Hyla* accounted for only 5 percent of the frogs metamorphosing from the control tanks. This pattern of relative abundance was reversed with increasing newt density. Tanks containing eight newts produced a preponderance of *Hyla* metamorphs (68 percent), while relatively few *Scaphiopus* (20 percent) and *Bufo* (12 percent) metamorphosed. A multivariate analysis of variance of the simultaneous transformed relative abundances of these three species of metamorphs demonstrated the statistical significance ($P = .02$) of this predator-mediated reversal of guild composition (9).

The relative rarity of *Hyla* metamorphs in tanks without newts can be

best explained as a result of interspecific competition with *Scaphiopus* and *Bufo*. The wet weight of an amphibian at metamorphosis is a sensitive measure of the intensity of competition experienced during larval growth; moreover, there is an inverse relation between weight at metamorphosis and the intensity of competition experienced by a given tadpole (10). The fourfold increase in mean *Hyla* weight that accompanied increased predator density (Table 1) suggests that the increased intensity of predation evoked a release from the intense competitive stress manifested by *Hyla* in the absence of predatory newts. This predator-mediated release from competition was significantly correlated with a concomitant reduction in the survival and density of *Scaphiopus* and *Bufo* at higher predator densities. A stepwise multiple regression analysis of the logarithm of mean *Hyla* weight in each replicate as a linear function of the number of metamorphs of *Hyla*, *Scaphiopus*, and *Bufo* collected in each replicate yielded the equation:

$$W = -0.0030 (S) - 0.0018 (B) + 2.4160$$

where *W* is the logarithm of mean *Hyla* weight in milligrams, and *S* and *B* are the respective numbers of *Scaphiopus* and *Bufo* metamorphosing from a replicate (11). This analysis demonstrates that there is a significant negative relation between the final density of *Scaphiopus* and *Bufo* and the weight of *Hyla* at metamorphosis ($P = .0001$, $R^2 = 0.85$). This relation indicates the effect of interspecific competition among tadpoles. *Hyla* weight was not related to the number of metamorphosing conspecifics in this analysis or in a simple product moment correlation analysis ($r = .40$, $P = .11$), which suggests that any intraspecific competitive effects in *Hyla* are being swamped as a result of strong interspecific competition by *Scaphiopus* and *Bufo*. The low survival to metamorphosis of *Hyla* (Table 1) is attributed to the apparent intensity of interspecific competition exerted by *Scaphiopus* and *Bufo* in the absence of newts. Increased

The above results demonstrate that predation and competition can interact to produce deterministic patterns of relative abundance in a guild of vertebrate prey. Furthermore, the outcome of interspecific competition among tadpoles in the absence of predators is not a reliable predictor of tadpole relative abundance when newts are added to the community. *Notophthalmus* can act as a keystone species (13) and prevent the virtual exclusion of competitively inferior species by reducing the survival and density of competitively superior anurans. Any general predictive theory of community ecology must consider the importance of biological interactions among and within trophic levels to account for these results. While descriptive studies of vertebrates may provide only questionable support for the importance of interspecific competition in the structuring of communities, results from controlled experiments can demonstrate that analogs of natural communities may be dramatically structured by interactions among competitors and their predators.

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The two populations of auditory receptor cells, the inner and the outer hair cells, differ morphologically in several important respects (1, 2). Neural innervation patterns of the two cell types also differ; outer hair cells receive only 5 percent of the afferent innervation of the

Although precise functions have been assigned to the two populations of visual receptor cells, the rods and the cones, comparatively little is known regarding the possible differential activity of the

