behavior of *Bufo americanus* tadpoles in response to high densities of micro-organisms. Copeia 1976: 576–578.

VANZOLINI, P. E. 1986. Levantamento herpetológico da área do estado de Rondônia sob a influencia da rodovia BR 364. Assessoria Editorial, Brazilian Conselho Nacional de Desenvolvimento Científico e Technólogico (CNPq), Brasilia, Brasil.

VAZ-FERREIRA, R., AND A. GEHRAU. 1975. Comportamiento epimeletico de la rana comun, *Leptodactylus ocellatus* (L.) (Amphibia, Leptodactylidae). I. Atencion de la cria y actividades alimentarias y agresivas relacionados. Physis 34:1–14.

WALDMAN, B. 1981. Sibling recognition in toad tadpoles: the role of experience. Z. Tierpsychol. 56: 341–358.

———, AND K. ADLER. 1979. Toad tadpoles associate preferentially with siblings. Nature 282:611–613.

WASSERSUG, R. J. 1973. Aspects of social behavior in anuran larvae, p. 273–297. *In:* Evolutionary biology of the anurans. J. L. Vial (ed.). University of Missouri Press, Columbia, Missouri.

———, A. LUM AND MICHAEL J. POTEL. 1981. An analysis of school structure for tadpoles (Anura: Amphibia). Behav. Ecol. Sociobiol. 9:15–22.

WELLS, K. D., AND K. M. BARD. 1988. Parental behavior of an aquatic-breeding tropical frog, *Leptodactylus bolivianus.* J. Herpetol. 22:1–364.

DEPARTMENT OF BIOLOGY, UNIVERSITY OF CALIFORNIA AT LOS ANGELES, LOS ANGELES, CALIFORNIA 90024. Accepted 13 Feb. 1989.

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Foraging Ecology and Prey Preference of Pond-form Larval Small-mouthed Salamanders, *Ambystoma texanum*

SCOTT R. MCWILLIAMS AND MARILYN BACHMANN

Ambystoma texanum larvae inhabiting a flooded woodland pond in southeastern Iowa ate mostly zooplankton when young and then shifted to a predominantly benthic prey diet when older. Larval prey preference also changed during ontogeny—young larvae selected zooplankton whereas older larvae selected benthic prey. Microhabitat selection was relatively more important than gape-limitations in explaining these ontogenetic shifts in foraging strategy. During the diel cycle many _Ambystoma_ larvae shifted between nocturnal zooplankton feeding and diurnal benthic feeding, presumably to avoid diurnal predation and/or track abundant invertebrate populations. Neither _A. texanum_ larvae nor their invertebrate prey exhibited diel shifts in activity. _Ambystoma texanum_ larvae fed throughout the diel period and were secretively active during the day and less secretively active at night. This may be related to ephemeral habitat characteristics unique to flooded woodlands and the life history of _A. texanum._ Prey type and order of ingestion influenced larval digestion rate and their effects cannot be ignored in diet studies. Because of the variability in larval selectivity, and their sensitivity to prey abundance and ontogenetic factors, _A. texanum_ larvae can be classified as facultative specialists.

THE study of foraging strategies involves assessing how a predator directly and indirectly interacts with available prey (Schoener, 1971; Sih, 1987). Predators may adjust their foraging behavior to the energetic demands of growth and to changes in morphology. For example, salamander age classes differ in food niche (Hassinger et al., 1970; Collins and Holomuzki, 1984; Petranka, 1984a; Griffiths, 1985), as do fishes (Werner, 1974, 1984), lizards (Schoener, 1967; Schoener and Gorman, 1968; Simon, 1976), and anurans (Christian, 1982). Moreover, many predators are themselves prey and change foraging tactics to avoid being eaten (Caraco, 1981; Grub and Greenwald, 1982; Werner et al., 1983; Dill and Fraser, 1984). This study documents how small-mouthed salamander (*Ambystoma texanum*) larvae inhabiting ephemeral ponds maintain the intake levels required throughout ontogeny while reducing perceived predation risks.

Ambystoma texanum adults breed in highly ephemeral ponds; accordingly, their larvae have high metabolic rates, rapid growth, and short larval periods (Petranka, 1984b). These metabolic and developmental constraints require high intake rates throughout the larval period. However, vertebrate predators, particularly fish, restrict larval distribution and activity (Petranka, 1983) and place limits on their foraging options.

Prey often shift their activity to avoid predator activity (Stein and Magnuson, 1976; Peckarsky, 1980; Sih, 1982; Holomuzki, 1986; Stangel and Semlitsch, 1987). Some *Ambystoma* larvae shift between nocturnal, pelagic activity and diurnal, substrate hiding (Anderson, 1968; Petranka and Petranka, 1980; Branch and Altig, 1981). Other *Ambystoma* larvae hide diurnally in the substrate and remain associated with the substrate when active at night (Anderson, 1968; Leff and Bachmann, 1986). However, *A. texanum* larvae inhabiting first order streams are diurnally active leaving them vulnerable to fish predation (Petranka, 1983). Furthermore, larvae can flexibly respond to predator pressure (Stangel and Semlitsch, 1987), making diel activity patterns not necessarily species-specific.

Petranka (1982a, 1982b) recognized a pond and stream-breeding race of *A. texanum* that differ in a suite of life history traits, including diel foraging patterns. Petranka (1982a) characterized pond-form larvae as diurnally secretive and nocturnally nonsecretive in contrast to stream-form larvae which were seldom secretive day or night. Petranka (1982a, 1983) hypothesized that selection has favored diurnal secretiveness in pond-form larvae because they can avoid predators without severely compromising foraging rates. This assumes that prey either move in similar diel patterns (Petranka and Petranka, 1980; Branch and Altig, 1981) or are abundant both on the substrate and in the water column. All Iowa populations of *A. texanum* located by us to date are exclusively pond-form and thus, if Petranka's hypothesis is generally correct, should show diurnal shifts between secretive and nonsecretive feeding locations and have little associated changes in prey intake.

The specific objectives of this study included: 1) documenting ontogenetic patterns in diet and prey selectivity of *A. texanum* larvae inhabiting ephemeral ponds, and 2) determining if salamander larvae and their invertebrate prey exhibit diel activity shifts.

METHODS

We collected salamanders and conducted all field work at Flaming Prairie Preserve in Louisa County, Iowa. The preserve has three ponds, the most northerly pond containing more vegetated marsh than open water. We conducted all field work in the flooded woodland at the northern edge of this marsh (see map in McWilliams and Bachmann, 1988).

A canopy of deciduous trees (predominantly red maples [*Acer rubrum*]) covered the study area resulting in a substrate throughout the flooded woodland of leaf litter and fallen branches. The study area contained few aquatic macrophytes. Standing water occurred from ice out until mid-Aug. in 1984, and until mid-June in 1985.

The invertebrate sampling design made it possible to characterize the prey populations potentially available to the salamander larvae. Sampling occurred at three different times-of-day (M = 800–1200 h, A = 1400-1700 h, E = 2100–2400 h), repeated three times each spring (16–20 May, 30 May–4 June, 12–17 June) for 2 yr (1984–85), totaling 18 planned sample periods; however, only 13 periods were actually sampled. We omitted the morning and afternoon times for the first season in 1984 because we captured salamander larvae only during the evening. We also did not sample the third season in 1985 because all larvae had either metamorphosed before or died as the woodland pond dried.

Substrate invertebrates were sampled using an Ekman dredge, open water invertebrates using a stovepipe sampler (Welch, 1948). The Ekman dredge samples were emptied into a 0.5 mm mesh sieve bucket, with the remaining invertebrates and litter transferred to a 1 liter jar and preserved with 10% formalin. The stovepipe sampler (20 cm diameter) was pushed onto the substrate and a 0.5 mm mesh net used to subsample the water contained within the stovepipe (McWilliams, 1986). The composite sample was then placed in 1 liter jars and preserved with 10% formalin. Water depth was measured at each sampling point (maximum water depth was 100 cm and typically was about 30 cm).

The 0.5 mm mesh size used was too large to capture juvenile invertebrates and even adults of some copepod and cladoceran species. This mesh size was still used because prey smaller than 0.5 mm in diameter were rare in the larval diet and because smaller mesh sizes required appreciably more sorting time.

Triplicate Ekman and stovepipe samples were taken at each of the 13 sampling times. Preliminary sampling showed invertebrates were contagiously (patchily) distributed. Using the mean and variance from these preliminary samples and assuming a negative binomial frequency distribution and a standard error of 20%, the appropriate number of samples was calculated following Elliot (1977). Three samples were adequate to estimate isopod, chironomid, ostracod, and cladoceran relative abundance. Three samples were not adequate to estimate copepod and amphipod relative abundance. Since copepods and amphipods were relatively rare components of the larval diet, only three Ekman and three stovepipe samples were collected per sampling time.

A randomly chosen number of paces and a compass bearing were used to locate a given sampling site. One Ekman and one stovepipe sample were taken at each of the three randomly selected sites. No samples were taken whenever salamander larvae could not be captured, and due to drying of the wetland in 1985, stovepipe sampling was not practical during the second season.

In the laboratory, Rose Bengal dye was added to all samples to facilitate finding invertebrates within the leaf debris. Invertebrates were sorted, identified to order, counted, and placed in separate small vials according to taxa. Measurements of length, width, and in some taxa, depth, were made so volumes could be calculated. If a vial contained fewer than 15 individuals, all individuals were measured; vials with greater than 15 individuals were subsampled (McWilliams, 1986).

The actual measurements of the invertebrates were made using a depression slide placed under a compound microscope outfitted with an ocular micrometer. Isopods, amphipods, and cladocerans were assumed to be rectangular (Maiorana, 1978). Chironomids and copepods were assumed to be cylindrical (Burton, 1976). Copepod width measurements were taken at the third thoracic segment to compensate for their tapering body shape. In addition, the two caudal rami were excluded from the length measurements. Ostracods were assumed to be rectangular. Because ostracods were homogeneous in body size, all individuals were pooled across vials, and one subsample of 20 individuals was taken for measurement purposes.

The counts and volumes from each sample were then expressed in terms of area. For the stovepipe sampler, the volume sampled was divided by the water depth to yield an area measure. This standardized the invertebrate abundance data and enabled comparisons between samplers, time-of-day (TOD), and times during the spring (hereafter called "seasons").

Because the Ekman and stovepipe sampled invertebrates differently (McWilliams, 1986), prey relative abundance was taken to equal: only those isopods, chironomids, and amphipods caught in the Ekman; only those copepods and cladocerans caught in the stovepipe; and a sum of the number and volume of ostracods caught in the two samplers. Since the preference analysis (Johnson, 1980) uses ranks instead of actual abundance estimates, changing the way copepod, amphipod, and ostracod relative abundance were calculated (e.g., taking an average of the two samplers or excluding the counts of either sampler) made no difference in the rank order and hence the preference results for these prey types.

An attempt was made to collect 10 salamander larvae during each of the 13 invertebrate sampling periods. Larvae were collected using activity traps, modified lobster traps, and hand nets. Activity traps, plastic gallon jugs with a funnel fastened to the top, were suspended in the water using floats and were designed to capture pelagically active larvae. Only three larvae were captured using this method. Modified lobster traps were made of aluminum window screening shaped into a cylinder with the ends inverted creating funnels. They were designed to capture substrate-active larvae and were placed onto the substrate or pushed into the leaf litter substrate. Approximately 40 larvae were captured using this method.

Sixty-four inactive larvae, many of them sitting on the modified lobster traps, were captured using handnets. An additional eight larvae were captured incidentally in the Ekman samples. These methods generally capture larvae active on or above the substrate and accessible to hand netting. This could bias the stomach analysis towards actively feeding, substrate surface-active individuals.

Captured larvae were immediately placed in separate vials and preserved with 10% formalin. In the laboratory, larvae were blotted dry, weighed, and SVL and snout tail length (STL) measured. The stomach and intestine were removed. The stomach was then separated from the intestine (both large and small portions) and associated prey items were counted separately, and identified to order. Since salamander larvae consume their prey whole, identification of prey type and size is relatively easy. Volume measurements followed the same procedures described above for the invertebrate relative abundance analysis.

A digestion rate experiment was conducted in the laboratory to ascertain whether certain prey types digest more rapidly than others. Larvae were maintained at 17 C in individual half-gallon aquaria. Seven larvae (SVL = 25 ± 2.4 mm) were randomly chosen from the laboratory population and starved for 48 h. Each was then fed a combination of isopods (*Asellus* sp.: 3.0 ± 0.7 mm), amphipods (*Hyallela* sp.: 3.1 ± 0.6 mm), cladocera (*Daphnia* sp.: 2.1 ± 0.7 mm), copepods (0.9 ± 0.3 mm), and chironomids (*Chironomus* sp.: 6.1 ± 2.1 mm).

The feeding procedure involved placing one prey at a time in the aquaria and allowing the larvae to capture the prey item before the next prey was added. We recorded the order in which the six prey were consumed during the 15 min feeding period. Larvae were then randomly assigned to one of three sacrifice times (3 h, 13 h, 24 h), the remaining larva served as a control (i.e., immediately sacrificed). Larvae were placed in formalin for ca 5 min, then their gut contents were immediately removed. We recorded the location of each prey item in the digestive tract and the degree of decomposition.

Statistical analysis system (SAS) was used for all statistical computations (SAS Institute Inc., 1985). Factorial design ANOVA was used to test for year, season, and TOD effects for the diet usage and the invertebrate availability data. Arcsin transformations of all frequency counts were calculated prior to ANOVA tests. Pearson product-moment correlations were used for all tests of association (SAS Institute Inc., 1985).

The preference analysis followed Johnson (1980), using ranks of prey types in place of percentage availability estimates. The ranking procedure is particularly useful when it is difficult to accurately estimate prey populations (Johnson, 1980). Temporary pond invertebrates represent such a population.

All methods used in the prey preference analysis are the same as in Johnson (1980) except ANOVA was used to compare pairs of mean rank differences instead of using the Waller and Duncan (1969) procedure. Rank differences were tested for normality and homogeneity of variance and found to conform to the assumptions of ANOVA. The MANOVA option in SAS (SAS Institute Inc., 1985) was used to test for year, season, and TOD effects in rank differences.

TABLE 1. RELATIVE NUMBERS, VOLUMES, AND FREQUENCY OF PREY FOUND IN 115 *Ambystoma texanum* LARVAE.

	Diet composition		
Prey type	% Number	% Volume	% Stomach with prey
Isopoda	41	54	91
Ostracoda	37	20	91
Cladocera	8	12	51
Chironomidae	3	8	40
Amphipoda	6	5	66
Copepoda	5	2	57

RESULTS

General food habits.—All 115 larvae collected for food habits analysis contained food in their stomachs. A total of nine invertebrate orders comprised the diet; however gastropods, odonates, and coleopterans were found fewer than five times. These three orders were excluded from further diet analysis.

Collectively, isopoda and ostracoda accounted for approx. 75% of the volume and number of prey items found in a given larva (Table 1). An individual larva contained on the average 18.3 (SD = 21.9) ostracods, 15.7 (SD = 13.2) isopods, 5.1 (SD = 15.0) cladocera, 3.4 (SD = 5.6) amphipods, 2.0 (SD = 2.7) copepods, and 1.3 (SD = 3.4) chironomids. The average total volume of food in an individual larva was 18.87 (SD = 18.47) mm^3, with a range of 1.0 mm^3–95.6 mm^3.

The relative importance by volume of copepods, amphipods, and chironomids in the diet was significantly greater in the second year of the study ($F_{1,8} = 10.11$, $P = 0.01$; $F_{1,8} = 11.91$, $P = 0.009$: $F_{1,8} = 35.45$, $P = 0.0003$, respectively). Ostracods generally decreased in diet importance in the second year ($F_{1,8} = 39.6$, $P = 0.0002$). Cladoceran and isopod percent volume did not significantly change between years.

The relative importance by number of amphipods, chironomids, and isopods in the diet

TABLE 2. DIEL CHANGES IN DIET COMPOSITION OF *Ambystoma texanum* LARVAE. n = number of larvae per TOD.

Time-of-day (h)	Prey per larva		Proportion of diet composed of each prey type					
	Average number	Average volume	Isopoda	Amphipoda	Chironomidae	Copepoda	Cladocera	Ostracoda
0800–1200 (n = 30)	16.9	40.3						
% Vol.			72.7	5.3	7.8	1.1	3.6	10.0
% No.			56.9	8.3	2.5	4.0	3.8	23.7
1400–1700 (n = 27)	24.2	91.9						
% Vol.			67.4	3.5	12.6	1.2	7.9	7.9
% No.			53.3	5.6	4.5	3.4	7.8	25.1
2100–2400 (n = 58)	17.3	41.2						
% Vol.			55.3	4.8	7.6	1.8	11.1	18.4
% No.			43.3	5.3	3.0	5.0	6.8	35.3
ANOVA results:	0.77	0.29						
% Vol.: $F_{2,102}$ =			0.38	0.44	1.72	0.05	0.83	0.57
P value =	0.50	0.76	0.70	0.66	0.26	0.95	0.48	0.59
% No.: $F_{2,102}$ =			0.32	0.70	2.83	0.30	0.79	1.59
P value =			0.74	0.53	0.14	0.75	0.50	0.28

was significantly greater in the second year of the study ($F_{1,8} = 26.57, P = 0.0009$; $F_{1,8} = 28.47$, $P = 0.0007$; $F_{1,8} = 28.57$, $P = 0.0007$, respectively). The other three prey types did not show significant annual changes in their relative importance by number in the diet.

Diel changes in food habits.—ANOVA of the stomach contents revealed no significant TOD main effects or TOD interaction effects. The lack of TOD differences in total volume and total number of prey in the stomachs (Table 2) indicates larvae fed throughout the day. Likewise, the relative number or volume of any prey species composing the diet showed no significant TOD changes (Table 2), indicating no diel shift from a nocturnal pelagic foraging strategy to a diurnal benthic foraging strategy. All prey types had significant positive correlations between stomach and intestine contents ($P < 0.0001$, df = 113 in all cases), also indicating larvae ate similar prey types over an extended period of time.

Ontogenetic and seasonal changes in food habits.—Percent volume of all prey taxa in the diet except amphipods and copepods ($F_{2,8} = 3.65$, $P = 0.07$; $F_{2,8} = 1.20$, $P = 0.35$, respectively) changed significantly across seasons. Seasonal trends were order specific (Fig. 1). Isopoda was the only taxon to increase in importance as the seasons progressed ($F_{2,8} = 35.17$, $P = 0.0001$). This increase in isopod importance was associated with a gradual seasonal decline in percent volume for all other taxa except amphipods (ostracods: F = 47.30, $P = 0.0001$; chironomids: F = 18.58, $P = 0.001$; cladocera: F = 8.26, $P = 0.01$; df = 2,8).

The significant year by season interaction for copepods, ostracods, and cladocerans (F = 188.16, $P = 0.0001$; F = 18.54, $P = 0.003$; F = 29.91, $P = 0.0006$, respectively; df = 1,8) results from an unusually large number and larger volume of these prey eaten by larvae in the first season of 1984. The first year of the study was wetter and potentially supplied larger and/or more available populations of these three taxa. However, invertebrate abundance changed significantly only for cladocerans and not for copepods and ostracods across seasons (Fig. 2; $F_{2,31} = 4.74$, $P = 0.02$; F = 2.03, $P = 0.15$; F = 2.16, $P = 0.13$, percent volume respectively). In fact, the abundance of pelagically active invertebrates was generally low throughout the year.

Alternatively, since these first season 1984 larvae averaged 1–2 wk younger than the 1985 first season larvae (Table 3), the results could reflect a more pelagic foraging mode for younger larvae. The seasonal differences in larval size between years obscures ontogenetic effects. By grouping 1984–85 larvae into size classes, the ontogenetic shift from a zooplankton to a

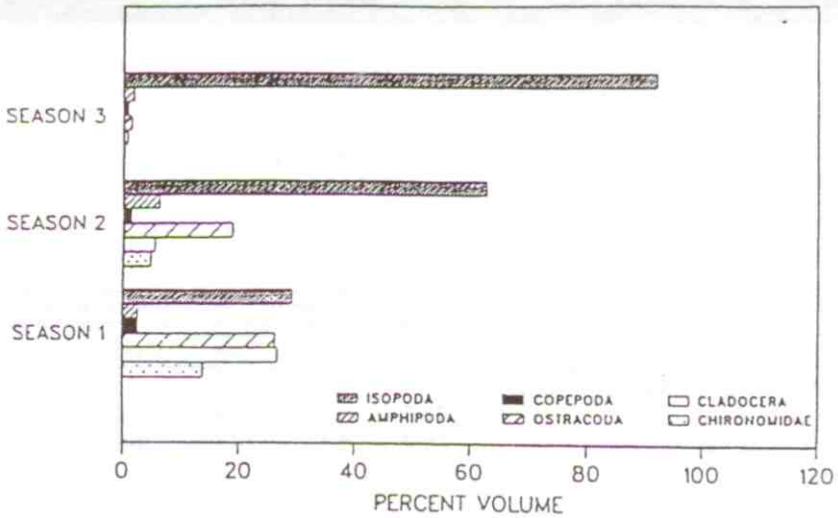

Fig. 1. Seasonal changes in larval diet. Values are relative abundance of prey volume. Seasons: 1 = 16–20 May; 2 = 30 May–4 June; 3 = 12–17 June.

benthic prey diet becomes obvious (Fig. 3). These trends are the same using either percent volume or percent number of prey in the diet (McWilliams and Bachmann, 1988). Cladocerans quickly reduced in diet importance for larvae over 17 mm. Ostracods also were less abundant in older larvae; however, their decline in importance occurs at a larger larval size than for cladocerans. Isopods were the predominant benthic prey type increasing in dietary importance with larval size.

Size-selective predation.—Significant correlations were found between total volume and SVL (r = 0.52, $P = 0.0001$, n = 112), between total volume and larval mass (r = 0.68, $P = 0.0001$, n = 112), and between total number of prey and SVL (r = 0.19, $P = 0.047$, n = 112). The

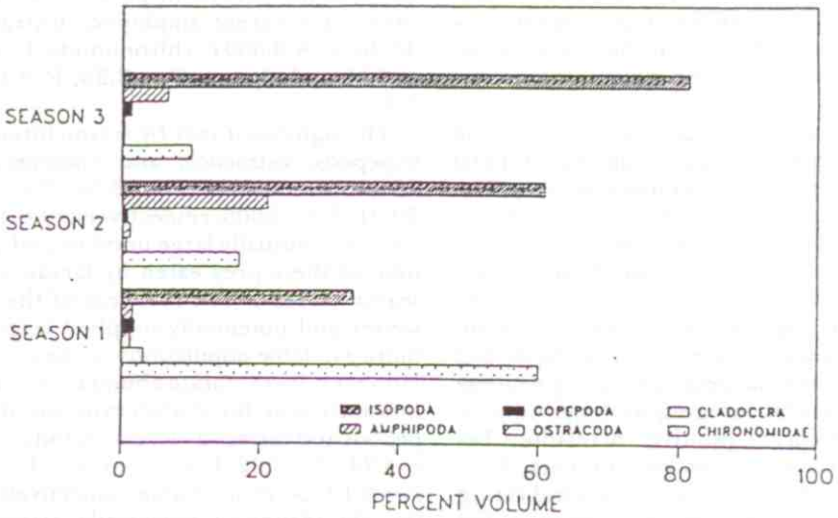

Fig. 2. Seasonal changes in invertebrate abundance. Values are relative abundance of prey volume. Seasons: 1 = 16–20 May; 2 = 30 May–4 June; 3 = 12–17 June.

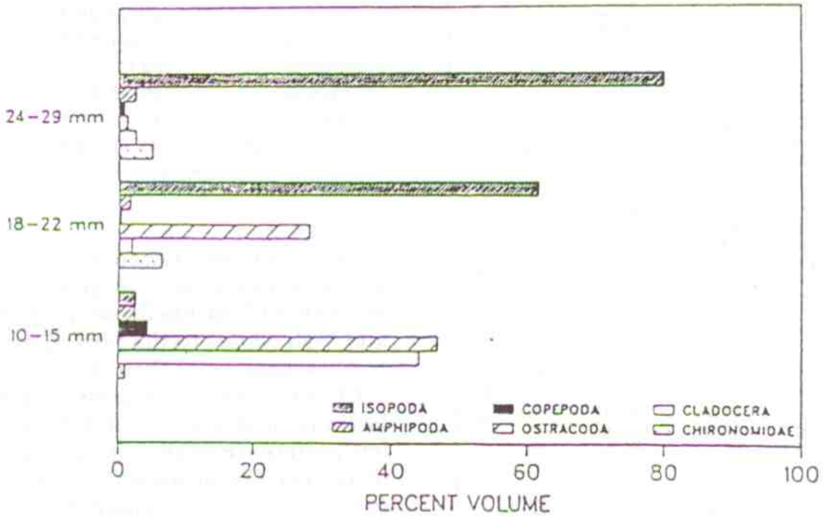

Fig. 3. Ontogenetic changes in larval diet. Larval size is measured as snout-vent length. Values are relative abundance of prey volume.

difference in significance level between correlations using total volume and total number of prey implies that larger larvae were selecting larger sizes of prey rather than eating more of the same sized prey. Average volume of an individual prey type increased significantly for Isopoda, Amphipoda, and Chironomidae across seasons (Table 3), with no significant change in size apparent between seasons or years for Copepoda, Ostracoda, and Cladocera. Average prey size of isopods, amphipods, and chironomids increased across seasons but the increase was not significant (unpubl.).

Digestion rate experiment.—In general, the sequence of prey in the digestive tract corresponded to the sequence in which they were consumed (only three of 42 prey switched position). The control larvae contained only the six prey types offered during the 15 min feeding period; none showed any sign of decomposition.

After 3 h all prey were in the stomach and easily recognizable, with their exterior surfaces showing only a slight fuzziness. By 13 h, the first 1–3 prey consumed were in the intestine and still recognizable though they were 50–80% digested. Prey remaining in the stomach formed a gradient of decomposition, from 0–10% digested in the anterior end of the stomach to 40–60% in the posterior portion.

After 24 h, the first 1–3 prey consumed were indistinguishable. All other prey except the last one eaten were 50–80% digested and found in the intestine or the extreme posterior end of the stomach. In both 24 h treatment larvae the last prey consumed (an isopod and an amphipod) was only 10–30% digested and found in the mid-stomach region.

Prey types differed in their rates of digestion. After 13 h in the gut, amphipods, isopods, and copepods were up to 80% digested whereas cladocerans were unrecognizable. By 24 h all prey types were unrecognizable; however, chironomid heads could always be located. It is important to emphasize that these digestion times ignore position effects. Except for cladocerans, which were unrecognizable by 24 h, the prey consumed last was much less digested. In addition, because larvae were not fed after initially consuming the six prey types, passage rates and digestibility may not be the same when larvae are feeding on a more regular basis.

General prey preference.—The vector of mean differences between ranks of prey usage and availability (Table 4) was significantly different from a vector of zeros ($F_{5,97} = 61.63, P < 0.0001$), indicating prey types were not used in direct accordance with availability.

All mean rank differences except that for Copepoda were significantly different from zero (Table 4). The direction and magnitude of these means indicates whether a prey type was utilized more or less often relative to availability. Usage

TABLE 3. SEASONAL AND ONTOGENETIC CHANGES IN FOOD HABITS OF *Ambystoma texanum* LARVAE. n = number of larvae per season. Seasons: 1 = 16–20 May; 2 = 30 May–4 June; 3 = 12–17 June.

Season	SVL (mm)	Prey per larva (mean ± SD)		Average volume (mm³) of an individual prey type (mean ± SD)					
		Average number	Average volume	Isopoda	Amphipoda	Chironomid	Copepoda	Cladocera	Ostracoda
1									
1984 (n = 25)	11.7 ± 1.9	31.4 ± 16.0	8.9 ± 4.5	.07 ± .13	.18 ± .17	.41 ± .27	.07 ± .07	.59 ± .67	.21 ± .06
1985 (n = 18)	25.6 ± 4.5	48.2 ± 16.1	48.8 ± 22.3	.72 ± .37	.15 ± .08	.91 ± 1.20	.12 ± .06	.22 ± .14	.03 ± .03
2									
1984 (n = 31)	20.5 ± 2.2	33.6 ± 19.6	11.2 ± 5.5	.39 ± .32	.26 ± .21	1.40 ± 2.60	.04 ± .02	.51 ± .54	.19 ± .06
1985 (n = 30)	24.0 ± 3.2	97.3 ± 124.9	17.2 ± 15.9	.96 ± .60	.38 ± .27	2.90 ± 2.70	.06 ± .04	.73 ± .58	.03 ± .01
3									
1984 (n = 11)	27.4 ± 2.1	42.2 ± 15.4	15.7 ± 6.2	.65 ± .42	.33 ± .13	.08 ± .04	.02 ± .03	.47 ± .42	.08 ± .13
Significance of seasonal effects:				<0.01	<0.01	<0.01	>0.10	>0.10	>0.10

TABLE 4. PREFERENCE RANK DIFFERENCES BETWEEN USAGE AND AVAILABILITY. SD are in parentheses. * = rank difference is significantly different from zero ($T_{1,101}$, $P < .001$).

Prey type	Mean % no. rank difference	Mean % vol rank difference
Isopoda	.85 (1.29)*	.45 (1.51)*
Amphipoda	.33 (1.33)*	.41 (1.21)*
Copepoda	−.22 (1.25)	.06 (0.99)
Ostracoda	−1.80 (1.21)*	−1.67 (1.35)*
Cladocera	−.61 (1.27)*	−.70 (1.30)*
Chironomidae	1.45 (1.24)*	1.45 (1.52)*

ranking was subtracted from environmental availability ranking; thus, positive values of the mean result from low (closer to the rank 6) usage and high (closer to the rank 1) availability and imply avoidance of these prey types.

Chironomids, amphipods, and isopods each had a positive mean rank difference, implying less preference or perhaps avoidance for these three taxa. Ostracods and cladocerans were less common in the environment than in the stomach contents, indicating they were preferred. The rank differences varied considerably over TOD, season, and year depending on the specific prey type, with year and season differences accounting for 75% of all the significant ANOVA effects.

Annual, ontogenetic, and diel changes in prey preference.—Isopod rank differences decreased significantly the second summer of the study, from 0.38−−0.49% volume for isopods ($F_{1,7} = 20.69$, $P = 0.003$). Chironomid rank differences also decreased the second summer, from 1.89–1.18% volume, but this decrease was not significant ($F_{1,7} = 2.40$, $P = 0.17$). The percent number of prey showed similar trends. As stated previously, chironomids showed significantly greater increases in percent volume and percent number in the diet in the second summer whereas isopods only increased in percent number. Available prey populations changed in opposite directions—chironomid populations increased in 1985 ($F_{1,31} = 25.5$, $P = 0.0001$), whereas isopod relative abundance decreased from 74.9–32% ($F_{1,31} = 30.8$, $P = 0.0001$) (Fig. 4). Because isopods decreased in availability and increased in usage between years, larvae apparently avoided isopods in 1984 and then preferred them in 1985.

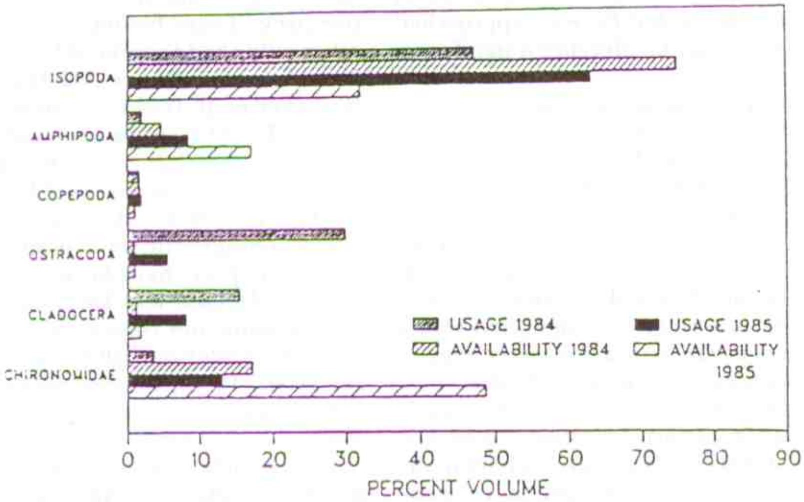

Fig. 4. Yearly changes in prey usage and availability. Values are relative abundance of prey volume.

Isopod rank differences also decreased significantly, from $1.3 - -0.1$, over the three seasons ($F_{2,7} = 15.66$, $P = 0.003$). Changes in isopod usage as opposed to availability produced this decrease in rank differences. Both usage (Fig. 1) and availability (Fig. 2) of chironomids decreased significantly as the seasons progressed ($F_{2,8} = 18.58$, $P = 0.001$; $F_{2,31} = 13.94$, $P = 0.0001$, respectively), resulting in no significant seasonal changes in percent volume or percent number rank differences. Chironomid rank differences were always positive indicating their greater abundance in the environment compared to the diet. The most positive rank differences occurred in season 3 when chironomids were the least frequent prey type in the diet even though they were the second most common prey at this time.

Isopods also showed a significant year by season interaction effect ($F_{1,7} = 41.11$, $P = 0.0004$) due primarily to lower usage and higher availability in the first season of 1984 compared to the first season of 1985. Ontogenetic factors probably caused this first season annual difference since larvae were much smaller in 1984 than in 1985 (Table 3).

Cladoceran percent number rank differences changed significantly between years ($F_{1,7} = 8.34$, $P = 0.02$) with year changes interacting strongly with seasonal effects ($F_{1,7} = 6.84$, $P = 0.03$). Cladoceran environmental abundance also decreased significantly across seasons (Fig. 2). Larvae changed their diet seasonally in 1984, feeding on ostracods and cladocerans in the first season and then feeding predominately on isopods by season 3. This reduction in relative abundance of cladocerans in the diet after the first season (when larvae are smallest), combined with the fact that 1985 first season larvae were older and hence not feeding on cladocerans to the same extent, created the significant year by season interaction effect.

Cladocera was the only prey type to show any significant rank difference changes over TOD ($F_{2,5} = 9.50$, $P = 0.01$). Because the third TOD period in 1984 consisted predominantly (60%) of young, small larvae which fed almost exclusively on ostracods and cladocerans (Fig. 3), the significant TOD effect is mostly a product of an unbalanced sample of larval sizes in each TOD period. Thus, the significant TOD differences reflect ontogenetic shifts in foraging more than diel shifts.

Usage and availability rank differences for amphipods and copepods showed no significant year, season, and year by season interaction effects ($P > 0.05$ in all cases). Relative abundance of amphipods in the environment did change significantly between years ($F_{1,31} = 7.22$, $P = 0.01$) and across seasons ($F_{2,31} = 14.18$, $P = 0.0001$). Copepods were consistently the least common prey type in the diet (of the six prey types used in the analysis) and their relative frequency in the environment did not change significantly between years or seasons.

The percent volume relative abundance of ostracods in the environment did not significantly change between years ($F_{1,31} = 0.02$, $P = 0.89$), whereas abundance in the diet decreased significantly in 1985 compared to 1984. (Percent number showed no significant environmental or dietary changes between years.) As a result of the change in diet abundance a large, negative rank difference (−1.83) occurred in 1984 whereas the rank difference approached zero in 1985 (year rank difference is significant, $F_{1,7} = 6.02$, $P = 0.04$).

In general a significant decrease in the importance of ostracods in the diet occurred as the seasons progressed (Fig. 1), with no significant change in the environmental abundance over this time period (Fig. 2; $F_{2,31} = 2.16$, $P = 0.13$). This decrease in proportion of ostracods eaten did not result in significant seasonal changes in ostracod rank differences. In 1985 the reduction in ostracod consumption across seasons did not occur, with larvae increasing the relative abundance of ostracods in the diet. This seasonal change in diet coincided with a significant increase in ostracod relative abundance ($F_{1,31} = 10.6$, $P = 0.003$). Isopods and amphipods showed similar seasonal changes in environmental abundance probably because these prey types can survive the extensive reduction in water level which occurred in 1985.

Prey preference results using unranked abundance values.—Magnitude differences in percent number and percent volume are obscured by the ranking procedure, possibly removing important information and producing different results. Consequently, we performed the same analyses on arcsin transformed percent number and percent volume values from which the ranked data had been derived. No differences in results were found using the transformed data for isopods, amphipods, cladocerans, copepods, and ostracods.

Chironomid rank and transformed percent analyses produced a number of different significant effects. Whereas chironomid availability estimates were probably accurate (see Methods), the fact that chironomids were consistently the least frequently eaten prey type probably accounts for the difference between the results of the ranked and unranked analyses. Regardless, at least in this study, the use of a ranking method to analyze prey preference (Johnson, 1980) did not make much difference in terms of the significance levels and the results.

Discussion

The diet of *Ambystoma texanum* larvae larger than 15 mm SVL consisted predominantly of isopods and ostracods. There was some indication that smaller larvae ate pelagic prey (ostracods and cladocerans) and then shifted their diet at 15–18 mm SVL and ate benthically-active prey. These findings agree with the only other published account of food habits of pond-form *A. texanum* larvae (Whitaker et al., 1980). Whitaker et al. (1980) found stomachs of 10–14 mm TL (SVL can be approximated by taking 70% of TL) larvae contained 78% by volume *Daphnia*, whereas stomachs of larvae larger than 30 mm TL contained predominantly isopods. Similar ontogenetic shifts in diet, from pelagic to benthic prey, have been found in larval *A. tigrinum* (Dodson and Dodson, 1971; Brophy, 1980; Collins and Holomuzki, 1984), *A. macrodactylum* (Anderson, 1968), *A. opacum* (Hassinger et al., 1970), *Eurycea bislineata* (Petranka, 1984a), and *Notophthalmus viridescens* (Brophy, 1980).

The possible bias caused by sampling larvae active on or above the substrate surface makes the ontogenetic diet shift even more significant. The sampling bias would cause an overemphasis on pelagic prey types in the diet; thus, showing a shift towards benthic feeding would be even more difficult.

Both prey type and the order of ingestion affected digestion rate. In addition, the fullness of the stomach probably alters the passage rate and consequently digestion rate. These results suggest food habits analyses may underestimate cladocerans and potentially overestimate chironomid diet importance. Assuming the differential digestion bias is the same for all larval sizes, it should have negligible effects on ontogenetic comparisons. However, because digestion exceeds 13 h, TOD comparisons will include prey from more than one TOD period.

Licht (1975) found no ontogenetic shifts in the diet of *A. gracile* although large larvae did eat a wider size range of prey items. Branch and Altig (1981) found *A. maculatum* and *A. talpodium* did not shift to a crawling foraging strategy, rather larvae remain pelagic foragers even after limb development. They found older *A. maculatum* larvae increase the depth at which they stratify; however, *A. talpodium* did not show this ontogenetic shift in nocturnal stratification depth.

Why don't all *Ambystoma* larvae exhibit the ontogenetic diet shift characteristic of *A. texanum* larvae in this study? The ontogenetic foraging strategy shift probably results from a combination of prey availability and predator behavior changes due to limb development (Hoff et al., 1985). Small larvae (less than 10 mm SVL) are active swimmers with no ability to crawl (Coghill, 1929). Concurrently, the prey sizes most available to a predominantly swimming predator are often planktonic species. As older larvae develop the ability to crawl, they also become more proficient and agile swimming predators (Hassinger et al., 1970). Encounter rates would then change and ecological factors such as prey abundance (Dodson and Dodson, 1971) or competitive interactions (Anderson, 1968) may determine larval foraging strategies. In our study area benthic prey were more abundant than pelagic prey. Once larvae developed the ability to crawl they could select the benthic microhabitat and exploit this abundant resource.

Another explanation for the ontogenetic shift is that gape limitation excludes prey types (e.g., isopods) when larvae are smaller. Certainly, prey with large variation in size (e.g., isopods and chironomids) are not uniformly susceptible to larval predation. Small larvae could not consume many of the prey found in older larvae (Table 3) due to physical gape-limitations. However, the shift to feeding on more isopods and fewer zooplankton occurred over a relatively small body size range (Fig. 3) and an even smaller mouth size range. Smith and Petranka (1987) found that *A. jeffersonianum* and *A. texanum* populations differ in the extent to which they are gape-limited and suggested prey size availability strongly influences larval intake. At our study site small isopods were available to larvae smaller than 15 mm SVL. Gape-limitations restricted prey intake of larvae but isopods of appropriate size were more available to small larvae than they were used (unpubl.). We conclude that for pond-farm larvae in this study, microhabitat selection better explains the ontogenetic shift in foraging ecology between small (<15 mm SVL) and large larvae.

The total volume and total number of prey in the stomachs did not change over TOD. *Ambystoma texanum* larvae in this study fed throughout the diel period. No diurnal secretive, nonfeeding period was apparent. Anderson and Graham (1967) and Hassinger et al. (1970) have suggested nonfeeding periods allow larvae to avoid predation. As discussed by Petranka (1984b) and Sih (1987), however, it seems unlikely a "fast life-style" species such as *A. texanum* can afford to spend the diurnal period not feeding. Avoiding predators and not feeding need not be mutually exclusive as long as microhabitats providing refuge from predators contain sufficient prey. This seems true for pond-form *A. texanum* larvae in this study which used abundant benthic prey and supports Petranka's (1983) view that reduced benthic prey availability forces stream-form larvae to become diurnally active (and susceptible to fish predators).

The relative abundance of prey in the stomachs did not change significantly over TOD. However, there were still indications that larvae exhibited some diel activity shifts. Cladocerans increased and isopods decreased in percent volume relative abundance during the diel cycle (Table 2). In addition, our own observations of older larvae (>18 mm SVL), and the added difficulty in capturing larvae during the two diurnal TOD sampling periods, suggests larvae were secretively active on or in the leaf litter substrate during most of the daylight hours.

At least two aspects of digestion rate complicate TOD comparisons. First, larvae collected at each time period probably contained prey from each of the other time periods. This would dampen any diel shifts in diet, making it difficult to show statistical differences. Second, prey types had different digestion rates. We still believe the lack of significant TOD differences is a biologically meaningful result. This conclusion is based on the fact that stomach and intestine contents were very similar for individual larvae. Because the digestion rate experiment showed that prey in the gut were in the same order as they were ingested, the similarity between stomach and intestine contents suggests larvae were feeding on similar types of prey throughout the diel period.

Larvae will stratify in the water column and feed on locally abundant pelagic prey. We observed larvae feeding in patches of cladocerans at the study site and captured four larvae during the second TOD period which had between 190 and 580 prey items in their stomachs, over 75% of which were cladocerans. However, given the generally low frequency of this prey item in all other larvae sampled, the occurrence of large numbers of cladocerans in the diet is probably exceptional.

Salamander larvae have been viewed as shifting from a pelagic, nocturnal foraging mode to a benthic, diurnal foraging mode (Branch and Altig, 1981; Petranka and Petranka, 1980). This behavioral shift has been hypothesized as a predator avoidance mechanism (Petranka, 1984a) and/or a prey-tracking mechanism (Anderson and Graham, 1967; Griffiths, 1985).

The prey-tracking hypothesis generally assumes larvae are mirroring the diel rhythms of plankton movement. Thus, larvae feeding throughout the 24 h period would have a diet consisting mainly of plankton. Petranka and Petranka (1980) and Branch and Altig (1981) observed diel shifts in larval activity patterns while stomach contents analysis showed no diel trends in diet. Our results show that *A. texanum* larvae generally ate benthic prey, with no significant nocturnal increase in plankton in the diet. In addition, older larvae (>20 mm SVL) were rarely seen swimming in the water column at any time of day, unlike other *Ambystoma* species (Branch and Altig, 1981; Lannoo, 1982).

This lack of diel foraging strategy shift is adaptive only if sufficient populations of benthic prey exist. The highly ephemeral flooded woodland habitat characteristic of *A. texanum* breeding ponds (Petranka, 1982b; Christiansen, 1981) requires larvae to have extremely rapid growth and metabolic rates (Petranka, 1984b). *Ambystoma texanum* larvae have responded to these physiological constraints by feeding throughout the day and night on prey types which are relatively abundant and easily captured (i.e., isopods and ostracods in our study population). Further research is needed on other pond-form populations to determine larval flexibility given different prey conditions.

The main seasonal and ontogenetic trends consisted of older larvae consuming more isopods and less zooplankton than younger larvae. There was also a seasonal increase in the mean volume and variance of isopods, chironomids, and amphiopods in the diet. Larvae added larger prey sizes to their diet as they grew, but did not drop the smaller prey sizes: this trend has been observed in other *Ambystoma* (Dodson, 1970; Lannoo, 1982) as well as in aquatic predators generally (Zaret, 1980).

In terms of selectivity, salamander larvae have been shown to be generalists, with preferences for particular sizes rather than taxa of prey. Hamilton (1940) found larval newts (*Triturus viridescens*) feed upon the most available prey types and essentially have no preference. However, recent laboratory studies (Ranta and Nuutinen, 1985) have shown larval newts (*T. vulgaris*) are capable of size-selective predation and can affect the size distribution of zooplankton populations. In an earlier study on impacts of salamander larvae on prey community structure, Dodson and Dodson (1971) compared zooplankton abundance in the diet and in the environment, but did not attempt to sample benthic prey availability. In terms of the zooplankton diet, they found preference was based mainly on size rather than on prey type, with greater selectivity for large zooplankton as larvae increased in size.

In this study, *A. texanum* was a selective predator; however, the two most important food items in the larval diet, isopods and ostracods, were selected in markedly different ways. Ostracods were eaten in greater proportion relative to availability regardless of year and season; thus, they were selected. Conversely, isopods generally occurred less frequently in the gut compared to their relative abundance in the environment: thus, they were avoided according to traditional terminology (Johnson, 1980). However, conclusions concerning avoidance and selection of isopods were greatly affected by seasonal and yearly variation. Isopods were selected later in the year, but were avoided when larvae were small (<15 mm SVL). These ontogenetic changes in larval selectivity may reflect underlying changes in prey preference rankings similar to what has been found for bluegill sunfish size classes (Werner et al., 1983).

In conclusion, *A. texanum* larvae fed throughout the day and night and did not exhibit diel shifts in diet. Our observations suggest pond-form *A. texanum* larvae longer than 18 mm SVL were diurnally secretive and nocturnally nonsecretive, but diel activity was restricted predominantly to on or near the substrate. This was probably the result of *A. texanum*'s typical habitat, flooded woodlands, containing low zooplankton populations and relatively high benthic prey availability. *Ambystoma texanum* larvae do share with congenerics ontogenetic shifts in diet—from zooplankton feeders as young larvae, to benthic invertebrate feeders as older larvae—as well as increases in the mean and range of prey sizes selected.

In terms of foraging strategy, *A. texanum* can be classified as a facultative specialist (Jaeger, 1981). Larvae were selective in their choice of prey, with this selection being sensitive to both ontogenetic and invertebrate abundance constraints. Foraging models which assume fixed prey preference may be greatly reducing their applicability to natural populations and must take into account ontogenetic shifts in foraging strategy.

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LITERATURE CITED

Anderson, J. D. 1968. A comparison of the food habits of *Ambystoma macrodactylum sigillatum*, *Ambystoma macrodactylum croceum*, and *Ambystoma tigrinum californiense*. Herpetologica 24:273–284.

———, and R. E. Graham. 1967. Vertical migration and stratification of larval *Ambystoma*. Copeia 1967: 371–374.

Branch, L. C., and R. Altig. 1981. Nocturnal stratification of three species of *Ambystoma* larvae. Copeia 1981:870–873.

Brophy, T. E. 1980. Food habits of sympatric larval *Ambystoma tigrinum* and *Notophthalmus viridescens*. J. Herpetol. 14:1–6.

Burton, T. M. 1976. An analysis of the feeding ecology of the salamanders (Amphibia, Urodela) of the Hubbard Brook Experimental Forest, New Hampshire. *Ibid.* 10:187–204.

Caraco, T. 1981. Energy budgets, risk, and foraging preferences in dark-eyed juncos. Behav. Ecol. Sociobiol. 8:213–217.

Christian, K. A. 1982. Changes in the food niche during postmetamorphic ontogeny of the frog *Pseudacris triseriata*. Copeia 1982:73–80.

Christiansen, J. L. 1981. Population trends among Iowa's amphibians and reptiles. Proc. Iowa Acad. Sci. 88:24–27.

Coghill, G. E. 1929. Anatomy and the problem of behavior. Cambridge University Press, London, England.

Collins, J. P., and J. R. Holomuzki. 1984. Intraspecific variation in diet within and between trophic morphs in larval tiger salamanders (*Ambystoma tigrinum nebulosum*). Can. J. Zool. 62:168–174.

Dill, L. M., and A. H. G. Fraser. 1984. Risk of predation and the feeding behavior of juvenile coho salmon (*Oncorhynchus kisutch*). Behav. Ecol. Sociobiol. 16:65–71.

Dodson, S. I. 1970. Complementary feeding niches sustained by size-selective predation. Limnol. Oceanogr. 15:131–137.

———, and V. E. Dodson. 1971. The diet of *Ambystoma tigrinum* larvae from Western Colorado. Copeia 1971:614–624.

Elliot, J. M. 1977. Some methods for the statistical analysis of samples of benthic invertebrates, 2nd ed. Freshwater Biol. Assoc. Sci. Publ. no. 25.

Griffiths, R. A. 1985. Diel profile of behavior in the smooth newt, *Triturus vulgaris* (L.): an analysis of environmental cues and endogenous timing. Anim. Behav. 33:573–582.

Grubb, T. C., and L. Greenwald. 1982. Sparrows and a brushpile: foraging responses to different combinations of predation risk and energy cost. *Ibid.* 30:637–640.

Hamilton, W. J., Jr. 1940. The feeding habits of larval newts with reference to availability and predilection of food items. Ecology 21:351–356.

Hassinger, D. D., J. D. Anderson and G. H. Dalrymple. 1970. The early life history and ecology of *Ambystoma tigrinum* and *Ambystoma opacum* in New Jersey. Amer. Midl. Nat. 84:474–495.

Hoff, K. S., M. J. Lannoo and R. J. Wassersug. 1985. Kinematics of midwater prey capture by *Ambystoma* (Caudata: Ambystomatidae) larvae. Copeia 1985:247–251.

Holomuzki, J. R. 1986. Predator avoidance and diel patterns of microhabitat use by larval tiger salamanders. Ecology 67:737–748.

Jaeger, R. G. 1981. Diet diversity and clutch size of aquatic and terrestrial salamanders. Oecologia 48: 190–193.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Lannoo, M. J. 1982. Food habits and feeding behavior of tiger salamander larvae (*Ambystoma tigrinum*) in Northwestern Iowa. Unpubl. M.S. thesis, Iowa State University, Ames, Iowa.

———, and M. D. Bachmann. 1984. On flotation and air breathing in *Ambystoma tigrinum* larvae: stimuli for and the relationship between these behaviors. Can. J. Zool. 62:15–18.

Leff, L. G., and M. D. Bachman. 1986. Ontogenetic changes in predatory behavior of larval tiger salamanders (*Ambystoma tigrinum*). *Ibid.* 64:1337–1344.

Licht, L. E. 1975. Growth and food of larval *Ambystoma gracile* from a lowland population in southwestern British Columbia. *Ibid.* 53:1716–1722.

Maiorana, V. C. 1978. Behavior of an unobservable species: diet selection by a salamander. Copeia 1978: 664–672.

McWILLIAMS, S. R. 1986. Foraging behavior and ecology of larval small-mouthed salamanders (*Ambystoma texanum*) in Iowa. Unpubl. M.S. thesis, Iowa State University, Ames, Iowa.

———, AND M. D. BACHMANN. 1988. Using life history and ecology as tools to manage a threatened salamander species. J. Iowa Acad. Sci. 95:66–71.

PECKARSKY, B. L. 1980. Predator-prey interactions between stoneflies and mayflies: behavioral observations. Ecology 61:932–943.

PETRANKA, J. W. 1982a. Ecology and systematics of the small-mouthed salamander (*Ambystoma texanum*) in the east-central United States. Unpubl. Ph.D. dissert., University of Kentucky, Lexington, Kentucky.

———. 1982b. Geographic variation in the mode of reproduction and larval characteristics of the small-mouthed salamander (*Ambystoma texanum*) in the east-central United States. Herpetologica 38:475–485.

———. 1983. Fish predation: a factor affecting the spatial distribution of a stream-breeding salamander. Copeia 1983:624–628.

———. 1984a. Ontogeny of the diet and feeding behavior of *Eurycea bislineata* larvae. J. Herpetol. 18:48–55.

———. 1984b. Incubation, larval growth, and embryonic and larval survivorship of smallmouth salamanders (*Ambystoma texanum*) in streams. Copeia 1984:862–868.

———, AND J. G. PETRANKA. 1980. Selected aspects of the larval ecology of the marbled salamander *Ambystoma opacum* in the southern portion of its range. Amer. Midl. Nat. 104:352–363.

RANTA, E., AND V. NUUTINEN. 1985. Foraging by the smooth newt (*Triturus vulgaris*) on zooplankton: functional responses and diet choice. J. Anim. Ecol. 54:275–293.

SAS INSTITUTE INC. 1985. SAS User's Guide: Statistics, Version 5. SAS Institute Inc., Cary, North Carolina.

SCHOENER, T. W. 1967. The ecological significance of sexual dimorphism in size in the lizard *Anolis conspersus*. Science 155:474–477.

———. 1971. Theory of feeding strategies. Ann. Rev. Ecol. Syst. 11:369–404.

———, AND G. C. GORMAN. 1968. Some niche differences in three Lesser Antillian lizards of the genus *Anolis*. Ecology 49:819–830.

SIH, A. 1982. Foraging strategies and the avoidance of predation by an aquatic insect, *Notonecta hoffmanii*. *Ibid.* 63:786–796.

———. 1987. Predators and prey lifestyles: an evolutionary and ecological overview, p. 203–224. *In:* Predation: direct and indirect impacts on aquatic communities. W. C. Kerfoot and A. Sih (eds.). University Press of New England, Hanover, New Hampshire.

SIMON, C. A. 1976. Size selection of prey by the lizard, *Sceloporus jarrovi*. Amer. Midl. Nat. 96:236–241.

SMITH, C. K., AND J. W. PETRANKA. 1987. Prey size-distributions and size-specific foraging success of *Ambystoma* larvae. Oecologia 71:239–244.

STANGEL, P. W., AND R. D. SEMLITSCH. 1987. Experimental analysis of predation on the diel vertical migrations of a larval salamander. Can. J. Zool. 65: 1554–1558.

STEIN, R. A., AND J. J. MAGNUSON. 1976. Behavioral response of crayfish to a fish predator. Ecology 57: 751–761.

WALLER, R. A., AND D. B. DUNCAN. 1969. A Bayes rule for the symmetric multiple comparisons problem. J. Amer. Stat. Assoc. 64:1484–1503.

WELCH, P. S. 1948. Limnological methods. McGraw-Hill Book Co., New York, New York.

WERNER, E. E. 1974. The fish size, prey size, handling time relation in several sunfishes and some implications. J. Fish. Res. Bd. Can. 31:1531–1536.

WERNER, E. E. 1984. The mechanisms of species interactions and community organization in fish, p. 360–382. *In:* Ecological communities: conceptual issues and the evidence. D. R. Strong, Jr., D. Simberloff, L. G. Abele and A. B. Thistle (eds.). Princeton University Press, Princeton, New Jersey.

WERNER, E. E., G. G. MITTELBACH, D. J. HALL AND J. F. GILLIAM. 1983. Experimental tests of optimal habitat use in fish: the role of relative habitat profitability. Ecology 64:1525–1539.

WHITAKER, J. O., JR., W. W. CUDMORE AND B. A. BROWN. 1980. Foods of larval, subadult and adult smallmouth salamanders, *Ambystoma texanum*, from Vigo County, Indiana. Proc. Indiana Acad. Sci. 90: 461–464.

ZARET, T. M. 1980. Predation and Freshwater Communities. Yale University Press, New Haven, Connecticut.

(SM, MB) DEPARTMENT OF ANIMAL ECOLOGY, IOWA STATE UNIVERSITY, AMES, IOWA 50011. PRESENT ADDRESS (SM): DEPARTMENT OF WILDLIFE AND FISHERIES BIOLOGY, UNIVERSITY OF CALIFORNIA–DAVIS, DAVIS, CALIFORNIA 95616. Accepted 5 Feb. 1989.