PREDATORY BEHAVIOR OF LARVAL SMALL-MOUTHED SALAMANDERS (*AMBYSTOMA TEXANUM*)

SCOTT R. MCWILLIAMS[1] AND MARILYN D. BACHMANN

Department of Animal Ecology,
Iowa State University, Ames, IA 50011, USA

ABSTRACT: The predatory behavior of larval small-mouthed salamanders (*Ambystoma texanum*) was quantitatively studied in the laboratory. A split-plot Latin square design was used to test for differences in behavior between two size classes of larvae foraging on six types of prey. Size-specific differences in foraging behavior were observed. Small larvae had a higher frequency and duration of swimming-affiliated behaviors, while large larvae exhibited more crawling-affiliated behaviors. Shifts in foraging behavior associated with different prey types were not as obvious. Transitions between different sequential pairs of feeding behaviors were never random, regardless of prey type. Larvae showed similarly ordered behavior sequences with *Daphnia*, small isopods, and even when no prey were present. Large isopods and the two size classes of amphipods elicited more complex behavioral sequences, especially for attack sequences. Thus, changes exist in larval foraging behavior in response to prey. These behavioral shifts are responses to general characteristics of the prey (behavior and/or size) and are not species-specific.

Key words: Urodele; *Ambystoma texanum*; Larvae; Foraging; Predation; Behavior; Ontogeny

STUDIES of foraging strategies often involve collecting animals in the field and documenting the types of food eaten by individuals. When this approach is combined with characterizations of the prey available to the predator, indications of preference and selection can be made (Hyslop, 1980; Ivlev, 1961). These types of data have provided valuable information on diet and habitat requirements but have supplied less conclusive results regarding whether predators are seeking or avoiding particular prey types (Maiorana, 1978).

More recently, behavioral ecologists have attempted to identify the mechanisms of predation. This type of research has often involved controlled laboratory studies that provide choices of prey or patches and the recording of the animal's decisions in these environments (Jaeger and Barnard, 1981; Krebs, 1978; Leff and Bachmann, 1986).

Some field studies report anecdotal observations of behavioral sequences involved in larval predation. Hassinger et al. (1970) described variability in prey capture attempts with degree of larval stratification by depth and ontogenetic development for *A. opacum* and *A. tigrinum*. Premetamorphic *A. macrodactylum* and *A. tigrinum* larvae have been observed using short lunges to capture prey (Anderson, 1968). However, these field observations do not separate factors (e.g., water temperature, prey activity and abundance, developmental stage of the larvae) potentially responsible for differences in feeding behavior. Leff (1985) and Leff and Bachmann (1986) provided one of the few studies analyzing feeding behavior of larval salamanders in conditions where access to prey was varied systematically. Little is known regarding possible variation in predatory behaviors with prey type.

Our experiment was designed to determine whether the behavior of larval salamanders varies with prey type. By observing how larvae capture different types of prey, an assessment can be made of the relative costs and benefits associated with foraging on these prey types. The experiment complements a field study undertaken in the same year which documented the diet of larval *Ambystoma texanum* and availability of the prey species (McWilliams, 1986; McWilliams and Bachmann, 1988, 1989).

This study specifically addresses three questions. (1) What are the sequences of behaviors which constitute predation by

[1] PRESENT ADDRESS: Department of Wildlife and Fisheries Biology, University of California, Davis, CA 95616, USA.

larval *Ambystoma texanum*? (2) Do larvae of different sizes vary in predatory behavior? (3) Are unique behavioral sequences used for capturing particular prey types?

MATERIALS AND METHODS

Larvae were collected from a flooded woodland pond at Flaming Prairie Preserve, Louisa County, Iowa (Sec. 29 Port Louisa Twp., T-75N, R-2W) in early May 1984 approximately 10 wk after courtship and oviposition by the adults. Larvae were immediately transported to Iowa State University and placed in 38 l aquaria in an environmental chamber maintained at 16 C, with a 12:12 L:D photoperiod. Approximately 100 larvae were housed in each aquarium. Larvae were fed ad libitum a variety of invertebrates collected from local marshes and acclimated to the laboratory for at least 2 wk prior to being tested.

Individual larvae were given a single prey type and the larva's behavior was serially recorded. Two size classes each of an isopod, amphipod, and cladoceran were used: a *Asellus* sp. ($\bar{x}$ = 3.0 ± 0.7 mm and 1.5 ± 0.3 mm), a *Hyallela* sp. ($\bar{x}$ = 3.1 ± 0.6 mm and 1.4 ± 0.3 mm), and a *Daphnia* sp. ($\bar{x}$ = 2.1 ± 0.7 mm and 0.7 ± 0.3 mm) (all measurements are longest linear distances ±1 SD). All three species of prey are eaten by larvae under natural conditions (McWilliams and Bachmann, 1988) and each exhibits different behavioral and morphological characteristics. In addition, two size classes of larvae were tested to see if any size-specific differences existed. Small larvae were 11–18 mm SVL ($\bar{x}$ = 14.0, SD = 2.1), and large larvae were 21–31 mm SVL ($\bar{x}$ = 26.3, SD = 2.75).

The six prey types and one control with no prey were organized into a 7 × 7 Latin square design, enabling time-of-day (TOD) and day-of-week (DOW) to be blocked. The DOW factor was blocked to control for variation in disturbance between days. The two size classes of larvae were then added to this design as a split-plot component (Cochran and Cox, 1957), providing each larval size class with exposure to each treatment combination. The seven DOW periods corresponded to each day

of the week. The seven TOD periods began with a 0800–0900 h and a 1100–1200 h period with subsequent 1 h time blocks every other hour concluding with a 2100–2200 h time period.

The first four TOD periods were conducted under white light conditions using a 60-W light bulb. The last three TOD periods were conducted under red light conditions using a 60-W light bulb covered with red acetate placed approximately 1 m away from the aquaria. These red light conditions are thought to simulate nighttime conditions since salamanders apparently have low sensitivity to red light (Grusser-Cornehls and Himstedt, 1976).

We randomized the order in which sizes of larvae were tested for the first day. Individual larvae (total n = 98) were tested only once. These larvae were randomly selected from approximately 500 larvae collected in early May 1984.

A single trial consisted of randomly selecting a specific-sized larva which had not been fed for 24 h, and placing it in one side of a 30 × 15 cm glass aquarium filled to a depth of 8 cm with dechlorinated water. One individual of the designated prey species and size to be tested was placed on the opposite side of a removable partition which divided the aquarium in half. Only one prey individual was used in an attempt to elicit an active predatory response (versus passive capture which is potentially similar across prey types).

After a 10 min acclimation period, the partition separating the larva from the prey was removed. Using a Datamyte 1000 recorder (DataMyte Corp., Minnetonka, Minnesota), 12 components of the feeding behavior and activity of the larva (defined in Table 1) were serially recorded (EXIT was recorded only when no feeding was observed). These 12 components were defined initially by watching videotapes of larvae preying on a variety of prey types and represent all common behaviors exhibited by larvae while feeding. Terminology is consistent with, though not exactly the same as, that found in Lindquist and Bachmann (1980) and Leff and Bachmann (1986). Here we delineate two modes of prey capture, STRIKE and LUNGE

(Table 1). STRIKE has been kinematically described for mid-water prey capture by premetamorphic *Ambystoma* larvae (Hoff et al. 1985). LUNGE is associated with capture attempts initiated while the larva is on the substrate typically motionless. This type of prey capture has been kinematically described for aquatic *Ambystoma* adults (Lauder and Shaffer, 1985; Shaffer and Lauder, 1985a,b).

The Datamyte recorded the time a behavioral component occurred, so durations of each of the behaviors in a given trial could be calculated. In addition, the sequences and frequencies of components could be determined for every predatory sequence. The trial ended either 5 min after the larva had captured the prey or after 10 min had elapsed without an encounter between the larva and prey.

Statistical analysis was conducted using Statistical Analysis System (SAS Institute Inc., 1985). Sequence analysis (Chatfield and Lemon, 1970; Lewis and Gower, 1980) was used to compare larvae foraging on different prey types and to compare the foraging behaviors of the two size classes of larvae. Transition matrices were constructed documenting the frequency with which each behavior preceded every other behavior. A total of 10 transition matrices were constructed; one matrix was constructed by pooling across all trials, seven matrices represent larvae foraging on six different prey types and one control (with no prey), and two matrices were constructed by pooling across all trials with either large larvae or small larvae. Each matrix was square and at most 10 by 10 in dimension, because CONSUME, MISS, and EXIT were excluded from the sequence analysis. These three behaviors were excluded because they are sequels to other behaviors rather than independent behaviors. Smaller matrices result when one or more behaviors are not exhibited during a given set of trials.

A chi-square test was performed for each matrix to test whether the matrix was significantly different from one constructed assuming all behaviors were independent. The diagonal of each matrix consisted of all zeros, because only transitions in be-

TABLE 1.—Behavioral components of larval salamander feeding behavior.

READY—motionless; in contact with substrate.
FLOAT—motionless; not in contact with substrate.
SWIM—active movement of tail fin with legs and gills pulled back alongside body.
BRAKE—vertical or horizontal movement, with legs and gills outstretched and no movement of the tail fin.
CRAWL—limbs used in coordination to move body along substrate.
LUNGE—rapid, short distance movement in the direction of prey; initiated by limb movement (see text for details).
STRIKE—rapid, longer distance movement in the direction of prey; initiated by thrust of the tail (see text for details).
SNAP—quick opening and closing of the mouth.
CONSUME—prey in mouth, not visible to observer.
MISS—unsuccessful prey consumption.
GULP—quick movements of the jaw, but mouth stays relatively closed compared to SNAP.
AIR GULP—snout breaks surface of the water and larva snaps air.
EXIT—documents 10 min without predator/prey encounter or 5 min after prey consumption.

haviors were counted. Expected values were calculated for this type of matrix using methods outlined in Lewis and Gower (1980) and Appendix I of Lemon and Chatfield (1971). Simulation studies indicate that if 10 behaviors are used in the analysis, a minimum of 500 behavioral transitions must be recorded and preferably no less than 1000 (Fagen and Young, 1978). All transition matrices used in this study, except for the control matrix with no prey, had more than the prescribed 1000 transitions. The control matrix had 993 total behavioral pairs.

When the chi-square method is used, it is assumed that the probabilities associated with each behavioral occurrence do not change over time (Lemon and Chatfield, 1971). Additionally, because we combine sequential data from more than one individual, we assume that variation between individuals is negligible. Because our data do not conform entirely to these assumptions, the levels of significance associated with the chi-square tests must be viewed as only rough indicators of the major sequential dependencies. Consequently, we have followed Lemon and Chatfield's (1971) suggestion and reject the null
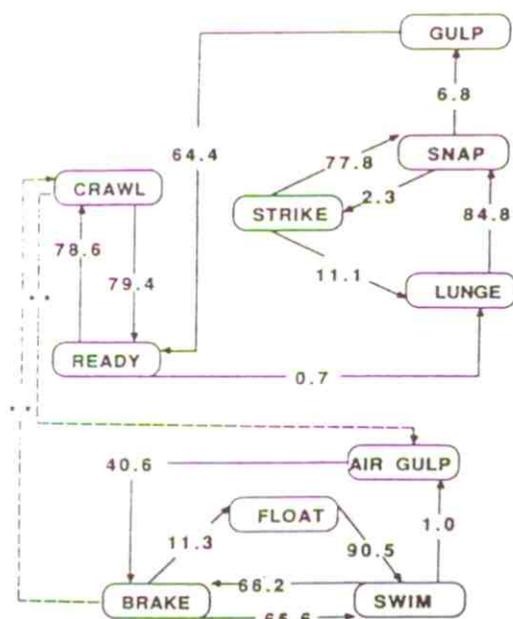
FIG. 1.—Flow diagram illustrating significant transitions (based on the binomial test) for general foraging behavior of larval *A. texanum*. Values are calculated by dividing the number of times the specific transition occurred by the row total for the preceding behavioral component. ** = frequent transitions which integrate the crawling and swimming sequences but which are not significant based on the binomial test.

with respect to TOD and DOW blocks, and prey type and larval size treatments. The duration and frequency values used in the ANOVA were standardized by trial length and the total number of behavioral acts in a given trial, respectively. All values used in the ANOVA were tested for normality and homogeneity of variance and found to conform to the assumptions of ANOVA.

RESULTS

The general foraging behavior of larval *Ambystoma texanum* was obtained by combining data for all prey types and larval sizes. The chi-square value for this transition matrix was significantly larger than expected ($P < 0.001$, df = 71), implying behaviors were not independent of one another. Four of the 10 categories of behavior constituted 95% of the 9873 individual behaviors observed in all 98 trials. READY (27.4%) and CRAWL (29.0%) were the two most frequently occurring behaviors, with SWIM (23.1%) and BRAKE (15.6%) constituting the remaining two predominant components. FLOAT (1.9%) was the only other behavior with greater than 0.5% frequency of occurrence.

Analysis of each transition in the matrix using the binomial test reveals two separate sets of significant behaviors (Fig. 1); one associated with mid-water activity, the other associated with substrate activity. Prey capture attempts always involved SNAP, although SNAP occurs equally as often when prey are not close. LUNGE and STRIKE are also integral components of prey capture, with SNAP following LUNGE or STRIKE at least 75% of the time.

Most of a larva's time during a trial was spent either alternating READY and CRAWL, or BRAKE and SWIM. It was obvious from observing larvae that this stop/start type of activity was the predominant mode of movement whether on the substrate or in mid-water. In particular, it was from this READY or BRAKE position that prey capture was often initiated. These transitions, plus the frequent transition from FLOAT to SWIM, occurred in all transition matrices.

hypothesis only if the test statistic is highly significant ($P < 0.01$). Nevertheless, conclusions based on chi-square analysis in this and similar studies of sequential behavior must be considered tentative when data do not conform entirely to the assumptions that observations are independent and that transition probabilities are constant throughout the behavioral sequences.

The large sample case of the binomial test (Siegel, 1956) was applied to each transition frequency in a given matrix to test whether the deviation of observed from expected frequency was statistically significant. Values used in the calculation of each z score were derived from the equations of Poole (1974).

A split-plot Latin square design analysis of variance (ANOVA) (SAS Institute Inc., 1985) was used to compare the number of transitions in each trial (standardized by trial length), the duration and arcsine transformed frequency of each behavior

AIR GULP was followed significantly more often by BRAKE ($z = 14.41$, df = 1198, $P < 0.01$), and often initiated the transition from substrate activity to swimming; however, the transition from CRAWL to SWIM was not mediated by any significant behavioral transitions (Fig. 1).

Separate chi-square and binomial tests were calculated for transition matrices compiled separately for each prey type and the control with no prey. In all seven cases, the chi-square values were significant ($P < 0.001$, df = 71), implying an ordered sequence of behaviors.

In all seven transition matrices, binomial tests of each transition revealed the same general behavior characterized by alternating transitions between READY and CRAWL, and SWIM and BRAKE, with FLOAT regularly preceding SWIM. Even larvae in a tank with no prey exhibited this basic pattern of behavior [see Appendix in McWilliams (1986) for separate prey type flow diagrams similar to Fig. 1].

Prey capture in all seven treatments consisted of LUNGE followed by SNAP (frequency of this transition ranged from 75–100%: $\bar{x} = 91\%$). Significant transitions ($P < 0.01$) between STRIKE and SNAP were found for larvae feeding on large isopods ($z = 13.04$, df = 1311) and both small amphipods ($z = 8.69$, df = 1559) and large amphipods ($z = 9.30$, df = 1343). This added dimension to the capture attempt for larvae preying on large isopods and small and large amphipods may be a reflection of the added difficulty in capturing these prey types. It was obvious from observing larvae foraging that amphipods were the most difficult of the three prey types to capture due to their quickness and tendency to remain relatively motionless and then burst away when encountered by the larvae. This view is further supported in that both size classes of larvae foraging on small and large amphipods and small larvae foraging on large isopods showed higher frequency of MISS relative to the number of successful captures (Table 2) compared to the other prey types.

In general, salamander larvae feeding on *Daphnia* or small isopods missed ap-

TABLE 2.—Efficiency of prey capture as a function of prey and predator size.

Prey type	No. captured: no. missed	
	Large larvae (21–31 mm SVL)	Small larvae (11–18 mm SVL)
Small *Daphnia*	0.75	0.75
Large *Daphnia*	0.33[b]	1.14
Small Isopoda	0.80	1.00
Large Isopoda	1.57	0.40
Small Amphipoda	0.50	0.67
Large Amphipoda	0.20	0.23

[a] Each value is based on seven salamander larvae.
[b] Low value is due to a single larva that missed six times before finally capturing the prey. If this larva is excluded from the calculation, the ratio becomes 1.00.

proximately once for every successful capture (i.e., values in Table 2 are approximately 1.00). Larvae feeding on amphipods missed at least twice for each successful capture, with large amphipods being the most difficult to catch of all prey types (Table 2). Large isopods were the only prey type to show order of magnitude differences in capture efficiency between larval size classes. Small larvae missed capturing large isopods twice as often as they were successful whereas large larvae were much more efficient at capturing large isopods.

The transition matrices compiled separately for the two larval size classes also had significant chi-square values ($P < 0.001$, df = 71) indicating a non-random sequence of behaviors. SNAP followed STRIKE and LUNGE about equally (approximately 80% frequency) for small larvae, while large larvae utilized LUNGE prior to SNAP more frequently (approximately 89%).

The only significant differences in duration of individual behaviors were for larval size (Table 3). Larger larvae spent significantly more time in CRAWL, SNAP, and GULP and significantly less time in SWIM and BRAKE (Table 4). No significant TOD or DOW changes in predatory behavior were apparent (Table 3). Thus, small and large larvae differ in the extent to which they were active in the water column compared to on the substrate, but both larval size classes are similar in that neither exhibited any diel shifts in foraging behavior.

Significant differences in frequency of individual behaviors were found for both

TABLE 3.—ANOVA table for the split-plot Latin square design analysis with duration of each behavior as the dependent variable.

Source	df		F-statistic for each behavior				
			CRAWL	SNAP	GULP	SWIM	BRAKE
Day-of-week	6		1.25	1.18	1.29	0.99	2.08
Time-of-day	6		0.20	0.43	0.78	0.66	2.44
Prey	6		1.38	0.93	1.97	0.96	1.97
Exp. error A	30	(MSE =	2.39	6.00	0.00092	2.05	0.95)
Larval size	1		9.62*	3.88*	4.76*	5.71*	16.84*
Prey × larvae	6		1.49	1.29	2.20	1.51	0.66
Exp. error B	42	(MSE =	1.83	5.24	0.00085	1.20	1.10)

* $P < 0.05$

larval size and prey type. Larval size trends parallel those found using the duration variable (Table 4). This provides complementary evidence that small larvae are predominantly swimming predators while larger larvae are mostly crawling predators. Large larvae also exhibit significantly more READY and AIR GULP behaviors ($F_{1.42} = 20.4$, $P = 0.0001$; $F_{1.42} = 5.46$, $P = 0.02$, respectively).

Significant differences between prey types were found for frequency of READY, SWIM, BRAKE, and MISS ($F_{6.30} = 3.72$, $P = 0.007$; $F_{6.30} = 4.00$, $P = 0.003$; $F_{6.30} = 2.64$, $P = 0.04$; $F_{6.30} = 2.88$, $P = 0.02$, respectively). Least significant difference (LSD) analysis was used to delineate the prey types responsible for the significant prey type main effects (Table 5), and particularly how the prey treatments differed from the controls with no prey. Larvae feeding on small *Daphnia* or large amphipods had a higher frequency of READY than controls, with all other prey types included in at least one grouping with the control. Larvae feeding on large amphipods showed significantly fewer SWIM behaviors than controls, with the other five prey types always grouped at least once with the controls. Larvae with small isopods had the highest occurrence of SWIM and BRAKE and the smallest frequency of READY; however, these values were not significantly different from the controls for all groupings.

The only significant difference in the number of transitions of behavior in a given trial was for larval size ($F_{1.42} = 4.46$, $P = 0.003$). Small larvae alternated behaviors more often than larger larvae, implying either that they are generally more active foragers or that mid-water activity requires more frequent transitions in behavior.

DISCUSSION

The general behavior exhibited by larvae includes four primary behaviors in two sets. Large larvae on the substrate alternate frequently between READY and CRAWL whereas small larvae active in mid-water alternate frequently between BRAKE and SWIM. However, this division of behaviors by larval size is not exclusive. The transi-

TABLE 4.—Percent duration and percent frequency of individual behaviors for the two size classes of larvae (SVL in parentheses).

Larvae size		Behaviors				
		CRAWL	SNAP	GULP	SWIM	BRAKE
Large (21–31 mm) % duration		21.21	0.40	0.55	5.99	1.61
% frequency		37.01	0.94	1.19	9.90	5.30
Small (11–18 mm) % duration		12.73	0.11	0.12	11.29	10.30
% frequency		24.07	0.21	0.08	25.12	15.83
F-value for % frequency*		17.60	4.98	8.51	51.84	20.20
	P =	0.0001	0.031	0.0056	0.0001	0.0001

* Table 3 contains F-values for differences in percent duration between large and small larvae.

TABLE 5.—Frequency of occurrence of specific behavioral components adjusted for trial length for each of the prey types.

Prey type	Behaviors					
	READY	LSD[*]	SWIM	LSD	BRAKE	LSD
Small *Daphnia*	34.59	A	17.40	B	9.45	B
Large *Daphnia*	35.44	AB	14.39	BC	5.42	B
Small Isopoda	23.67	C	25.67	A	19.18	A
Large Isopoda	32.66	BC	16.80	B	11.83	AB
Small Amphipoda	30.45	BC	19.51	AB	12.16	AB
Large Amphipoda	42.60	A	7.50	C	4.62	B
No prey (control)	27.06	BC	21.31	AB	11.27	AB

[*] Means with the same letters are not significantly different ($P > 0.05$) based on least significant difference (LSD) analysis

tion from substrate to mid-water activity is often accomplished in large larvae by air gulping at the water's surface. Air gulping is thought to enable buoyancy and consequently mid-water foraging (Lannoo and Bachmann, 1984). Leff (1985) also found air gulping was followed most often by floating. The significantly greater number of air gulps by large larvae may result from differences in buoyancy between small and large larvae. That is, small larvae are typically quite active in the water column and may require less air gulping to maintain buoyancy. Large larvae on the other hand apparently require much activity to keep their bodies suspended in the water column. Air gulping may enable large larvae to use less energy while preying in the water column.

Results using duration and frequency of individual behaviors as dependent variables confirm that smaller larvae spend more time in and exhibit more swimming-affiliated behaviors, while larger larvae spend significantly more time crawling. These ontogenetic differences in feeding behavior provide a mechanism to explain why larvae of different sizes captured in the field varied in the proportion of open water active prey (versus benthic prey) found in the diet (McWilliams and Bachmann, 1989). Since small larvae (10–18 mm SVL) swim more, they encounter prey active in the water column (e.g., cladocerans and ostracods) more frequently. This effect on encounter rate may result in small larvae consuming higher proportions of ostracods and cladocerans.

Other researchers have found similar ontogenetic shifts in foraging strategy.

Larval *Ambystoma tigrinum* showed the same ontogenetic differences in foraging behavior in the laboratory (Leff and Bachmann, 1986). Diet studies conducted in the field also have documented this foraging shift in *A. tigrinum* (Collins and Holomuzki, 1984; Dodson and Dodson, 1971) and *A. macrodactylum* larvae (Anderson, 1968).

Age-related differences in foraging behavior may be important as intraspecific niche partitioning mechanisms reducing competition (Polis, 1984). This is unlikely to be true for *A. texanum* because of the synchronous nature of breeding and the consequent homogeneity of larval sizes at any given time (McWilliams and Bachmann, 1988). The age component of niche use by larval salamanders has the potential to be more important in interspecific interactions in which differences in growth rate between species can create large differences in relative sizes of predator and prey among age classes of predators.

No diel shifts in foraging activity were apparent. Leff and Bachmann (1986) found that larval *Ambystoma tigrinum* expanded their feeding times when brought into the laboratory. In the field, larvae fed primarily at night whereas in the laboratory they fed throughout the diel period. Holomuzki (1986) documented changes in larval *A. tigrinum* diel activity in response to predatory beetles in both the field and laboratory. In our study, larval *A. texanum* exhibited no diel shifts in feeding behavior, nor were any diel shifts in diet found under natural conditions (McWilliams, 1986). Petranka (1982, 1983) found that larval *A. texanum* inhabiting streams were

also actively foraging throughout the 24 h period. Thus, unlike *A. tigrinum*, evidence for this type of flexible response in foraging behavior within a single population is lacking for *A. texanum*.

Although larval foraging behavior varies with prey type, little difference in larval behavior was seen in trials with no prey and with the less conspicuous prey types: i.e., the two size classes of *Daphnia* and the small isopod. It may be that larvae in these cases were searching for prey or were simply active in non-foraging behaviors regardless of prey presence.

In summary, size-specific differences in larval foraging strategy were found. The differences are consistent with results of a field study (McWilliams, 1986; McWilliams and Bachmann, 1988, 1989) which showed that small larvae predominantly fed in the open water on crustacea, while large larvae generally fed in contact with the substrate on benthic prey. These ontogenetic differences in behavior potentially influence microhabitat use and consequently encounters with prey. What remains to be demonstrated is whether larvae exhibit preferences for certain prey types and how these preferences interact with encounter rates.

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.

CHATFIELD, C., AND R. E. LEMON. 1970. Analysing sequences of behavioural events. J. Theor. Biol. 29: 427–445.

COCHRAN, W. G., AND G. M. COX. 1957. Experimental Designs, 2nd ed. John Wiley and Sons, New York.

COLLINS, J. P., AND J. R. HOLOMUZKI. 1984. Intra-specific variation in diet within and between trophic morphs in larval tiger salamanders (*Ambystoma tigrinum nebulosum*). Can. J. Zool. 62:168–174.

DODSON, S. I., AND V. E. DODSON. 1971. The diet of *Ambystoma tigrinum* larvae from western Colorado. Copeia 1971:614–624.

FAGEN, R. M., AND D. Y. YOUNG. 1978. Temporal patterns of behaviors: Durations, intervals, latencies, and sequences. Pp. 79–114. *In* P. W. Colgan (Ed.), Quantitative Ethology. John Wiley and Sons, New York.

GRUSSER-CORNEHLS, U., AND W. HIMSTEDT. 1976. The urodele visual system. Pp. 203–266. *In* K. V. Fite (Ed.), The Amphibian Visual System: A Multidisciplinary Approach. Academic Press, New York.

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. Am. 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.

HYSLOP, E. J. 1980. Stomach content analysis—A review of methods and their application. J. Fish Biol. 17:411–429.

IVLEV, V. S. 1961. Experimental Ecology of the Feeding of Fishes. Yale University Press, New Haven.

JAEGER, R. G., AND D. E. BARNARD. 1981. Foraging tactics of a terrestrial salamander: Choice of diet in structurally simple environments. Am. Nat. 117: 639–664.

KREBS, J. R. 1978. Optimal foraging: Decision rules for predators. Pp. 23–63. *In* J. R. Krebs and N. B. Davies (Eds.), Behavioural Ecology, an Evolutionary Approach. Sinauer, Sunderland, Massachusetts.

LANNOO, M. J., 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.

LAUDER, G. V., AND H. B. SHAFFER. 1985. Functional morphology of the feeding mechanism in aquatic ambystomatid salamanders. J. Morphol. 185: 297–326.

LEFF, L. G. 1985. Predatory Behavior and Selective Feeding of Larval Tiger Salamanders (*Ambystoma tigrinum*). M.S. Thesis, Iowa State University, Ames, Iowa.

LEFF, L. G., AND M. D. BACHMANN. 1986. Ontogenetic changes in predatory behavior of larval tiger salamanders (*Ambystoma tigrinum*). Can. J. Zool. 64:1337–1344.

LEMON, R. E., AND C. CHATFIELD. 1971. Organization of song in cardinals. Anim. Behav. 19:1–17.

LEWIS, D. B., AND D. M. GOWER. 1980. Biology of Communication. Blackie and Son Ltd., London.

LINDQUIST, S. B., AND M. D. BACHMANN. 1980. Feeding behavior in the tiger salamander, *Ambystoma tigrinum*. Herpetologica 36:144–158.

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. M.S. Thesis, Iowa State University, Ames, Iowa.

MCWILLIAMS, S. R., 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.

————. 1989. Foraging ecology and prey preference of pond-form larval small-mouthed salamanders. *Ambystoma texanum*. Copeia 1989:In press.

PETRANKA, J. W. 1982. 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.

POLIS, G. A. 1984. Age structure component of niche width and intraspecific resource partitioning. Can age groups function as ecological species? Am. Nat. 123:541–564.

POOLE, T. B. 1974. Detailed analysis of fighting in polecats (Mustelidae) using cine film. J. Zool. 173. 369–393

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

SHAFFER, H. B., AND G. V. LAUDER. 1985a. Aquatic prey capture in ambystomatid salamanders: Patterns of variation in muscle activity. J. Morphol. 183:273–284.

————. 1985b. Patterns of variation on aquatic ambystomatid salamanders: Kinematics of the feeding mechanism. Evolution 39:83–92.

SIEGEL, S. 1956. Nonparametric Statistics for the Behavioral Sciences. McGraw-Hill, New York.

DURATION OF IMMOBILITY IN SALAMANDERS, GENUS *PLETHODON* (CAUDATA: PLETHODONTIDAE)

C. KENNETH DODD, JR.

National Ecology Research Center, U.S. Fish and Wildlife Service,
412 N.E. 16th Avenue, Room 250, Gainesville, FL 32601, USA

ABSTRACT: Immobility is a potentially important antipredator behavior in salamanders, especially for those possessing noxious skin secretions. The duration of immobility in 15 species of terrestrial salamanders (*Plethodon*) varied among species. Most salamanders (78.8%) became immobile when initially contacted under field conditions, and remained immobile from 1–180 s. Immobility duration was inversely correlated with substrate temperature and covaried with air temperature, but snout–vent length (SVL) had no effect on duration. Only immobility times of *Plethodon shenandoah* were significantly different from any other species. Substrate temperature, air temperature, SVL, and species accounted for only a small percentage of the variance ($r^2 = 0.09$). The degree of disturbance received during a predator-prey encounter is probably more important than the subtle effects of temperature and SVL in determining immobility duration.

Key words: Immobility; Death-feigning; Defensive behavior; Salamanders; *Plethodon*

WOODLAND salamanders of the genus *Plethodon* are conspicuous members of terrestrial leaf litter forest communities in North America (Burton and Likens, 1975a; Bury, 1983; Hairston, 1980; Heatwole, 1962; Jaeger, 1979). As such, they play important ecological roles as both predators and prey (Burton and Likens, 1975b; Pough, 1983). Although birds might be "inefficient" predators on salamanders (Jaeger, 1981), vertebrates and invertebrates likely prey upon them opportunistically (Brandon and Huheey, 1975; Brodie et al., 1979). In response, salamanders have evolved a variety of antipredator mechanisms (e.g., Brandon and Huheey, 1981; Brodie, 1977, 1978; Brodie and Howard, 1973; Brodie et al., 1974; DiGiovanni and Brodie, 1981; Dodd and Brodie, 1976; Howard and Brodie, 1973; Wil-