

Ontogeny of Aquatic Feeding Performance in the Eastern Newt, *Notophthalmus viridescens* (Salamandridae)

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Ontogenetic changes in feeding performance on four prey types were studied in the eastern newt, *Notophthalmus viridescens*, to test two hypotheses about functional changes in aquatic feeding during development. The hypothesis that the ontogenetic transformation from a unidirectional to bidirectional feeding system results in a decrease in feeding performance is corroborated by comparing the aquatic feeding ability of larvae and efts. Feeding performance in fully transformed and branchiate adults does not support the hypothesis that retention of larval components of hyobranchial morphology in branchiates results in increased aquatic feeding performance.

THE relationship between behavioral performance (the ability of animals to execute behaviors) and the morphological and functional bases of performance has been the subject of increasing discussion in the literature (Emerson, 1978; Emerson and Diehl, 1980; Arnold, 1983). The process of metamorphosis in urodeles involves a dramatic reorganization of skull morphology and function (Duellman and Trueb, 1986) and provides an excellent case study of the relationships among morphology, function, and behavioral performance.

The purpose of this paper is to provide an ontogenetic analysis of feeding performance in the eastern newt (*Notophthalmus viridescens*) to test two functional hypotheses. Our general goal is to test for changes in feeding ability during ontogeny predicted on the basis of previously documented functional and morphological changes that occur during development.

Our first hypothesis is based on the work of Lauder and Shaffer (1986). Larval salamanders possess an aquatic feeding system in which prey are captured by suction (Lauder and Shaffer, 1985): water enters the front of the mouth as pressure drops within the mouth cavity and exits posteriorly through the gill slits. There is thus a unidirectional flow through the mouth cavity. In metamorphosed individuals, the gill slits are closed, and individuals that feed in the water possess bidirectional water flow: water that enters the mouth as prey are captured also exits through the mouth as the jaws close (Lauder and Shaffer, 1986). This ontogenetic transformation from a unidirectional to a bidirectional water-flow system represents a fundamental change in feeding hydrodynamics and design

within a vertebrate species and provides a unique opportunity to examine the relationship between performance and major changes in functional design. Lauder and Shaffer (1986) suggested that the ontogenetic transition from larval to metamorphosed morphology in *Ambystoma* is accompanied by a significant decrease in feeding performance. They indicated that this performance decrease may be due to the change from unidirectional to bidirectional water flow and metamorphic changes in the head muscles and structure of the hyoid. Therefore, we tested the hypothesis that the transformation from a unidirectional to a bidirectional water-flow system during feeding results in a decrease in feeding performance.

Our second hypothesis is based on the work of Reilly (1986, 1987). He has documented ontogenetic changes during metamorphosis in the cranium and hyobranchial apparatus in fully transforming and branchiate *N. viridescens*. Branchiate *N. viridescens* are, in fact, completely metamorphosed except for the variable retention of external gills and ceratobranchials 2-4. Reilly (1987) proposed that, although the retention of gill structures is not necessary for survival in aquatic adult newts, the retention of hyobranchial elements may improve aquatic feeding performance in branchiate newts which remain entirely aquatic. Thus, we tested the hypothesis that the structure of the hyobranchial apparatus affects feeding performance such that postmetamorphic animals that retain more of the hyobranchial apparatus have increased feeding performance relative to individuals that retain only one ceratobranchial (Reilly, 1986, 1987).

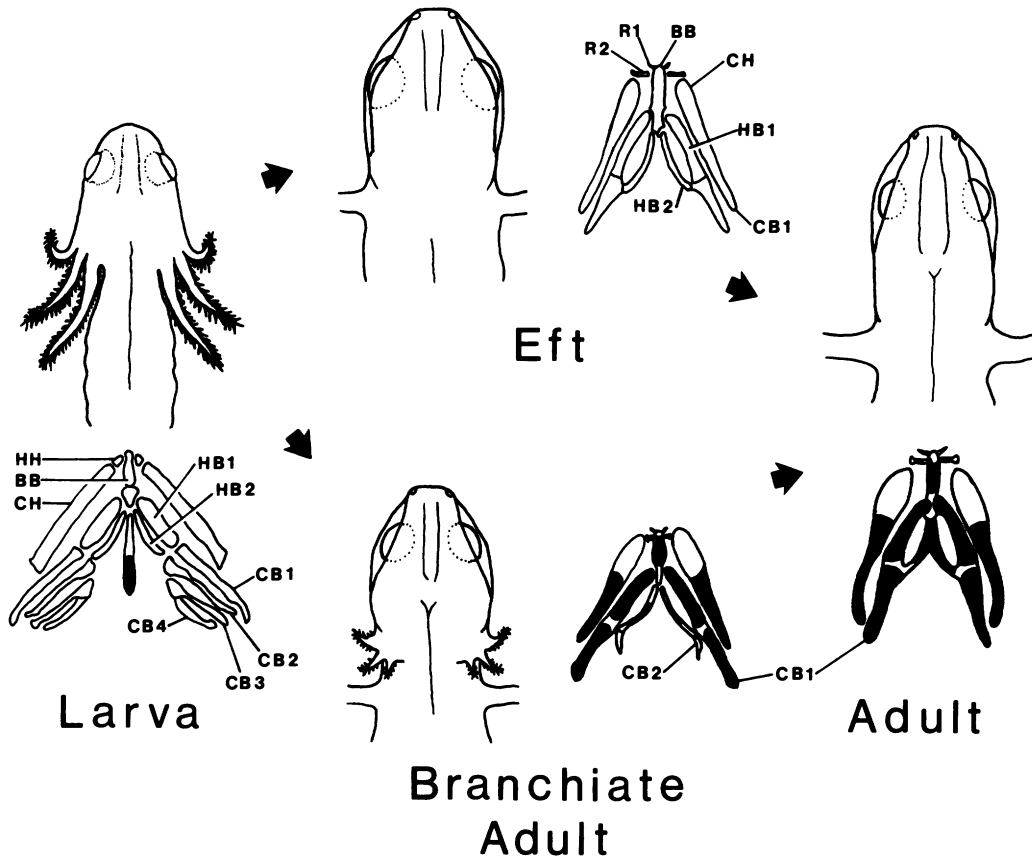


Fig. 1. Ontogeny of head shape and hyobranchial morphology in *Notophthalmus viridescens*. Arrows indicate the two main alternative ontogenetic pathways (Reilly, 1987): larvae (with a unidirectional flow feeding mechanism) may transform into either efts or branchiate adults (both with bidirectional flow feeding systems). Note the retention of external gills and the incompletely transformed hyobranchial apparatus in the branchiate adult stage. Black indicates bone. Abbreviations: BB, basibranchial; CB, ceratobranchial; CH, ceratohyal; HB, hypobranchial; HH, hypohyal; R, radial.

MATERIALS AND METHODS

We test these two hypotheses of performance change during ontogeny using a population of newts in which a variety of well defined morphological stages occur naturally. As documented by Brandon and Bremer (1966) and Reilly (1986, 1987), four morphological stages occur in the water in this population: larvae, efts, fully transformed adults, and 'branchiate' adults (Fig. 1). 'Branchiates' are individuals that retain a variable number of ceratobranchials and external gills following the initial metamorphosis of the skull and skin.

A total of 100 *N. viridescens* were collected during Aug. 1986 from McGuire's Pond, 9.7 km south of Carbondale, Jackson Co., Illinois.

Aquatic feeding performance was tested for larvae and efts (10 each) with one prey type (brown worms, *Lumbriculus* sp.). Feeding performance of branchiate adult and completely transformed adult newts (10 each per prey type) was tested using four prey types: earthworms (*Lumbriculus* sp.), brine shrimp (*Artemia* sp.), and guppies (*Poecilia reticulata*) with and without caudal fins removed. Caudal-cut guppies were used as a prey type of intermediate escape ability between intact guppies and brine shrimp. All newts were kept at 5 C until tested. Newts of each test group were placed in individual finger bowls containing filtered water at ambient temperature for 3 d prior to testing. Paper dividers were used to isolate the newts from each other visually during testing. Each newt and prey type

were put into a finger bowl and the number of feeding attempts and success or failure of each strike were noted. The specific protocol for testing each prey type (and size) was as follows: brown worms: 30 5–10 mm pieces per bowl, 15 min trials; earthworms: 25 5–10 mm pieces per bowl, 30 min trials; brine shrimp: 50 per bowl, 15 min trials; guppies: 5 8–10 mm fish per bowl, 10 min trials. Individual feeding performance was calculated by dividing the number of captures by the number of attempts. A feeding performance of 50% indicates that one half of the feeding attempts resulted in the capture of prey. Performance measures were analyzed as a two-way analysis of variance following Sokal and Rohlf (1981) to test for performance differences between larvae and efts (effect of metamorphic stage), and between branchiate and fully transformed adults (effect of retained ceratobranchials).

Two separate analyses were conducted. The first hypothesis was tested by comparing the feeding performances of larvae and efts of similar size. The major morphological differences in the head between these two ontogenetic stages involve the change from a unidirectional to a bidirectional water-flow system at metamorphosis (Fig. 1). The second hypothesis was tested by comparing the feeding performance of transformed and branchiate adults. Individuals of these two stages are of equivalent size and the major differences between them are in the extent of retention of external gills and the number of ceratobranchials lost through metamorphosis (Fig. 1; Reilly, 1987). Efts and both adult forms have closed gill slits. All specimens were preserved in 10% formalin after testing and snout-vent length (SVL) and degree of gill retention were recorded. The 40 branchiate adults were cleared and double stained for bone and cartilage (Dingerkus and Uhler, 1977), then examined for the retention of ceratobranchials. Voucher specimens have been deposited in the Museum of Natural History, University of Kansas (KU206754–KU206835).

RESULTS

Larvae (mean SVL = 22.6 mm \pm 2.0 SD) and efts (mean SVL = 23.8 mm \pm 2.7 SD) of similar size differed greatly in their ability to capture pieces of brown worms. Larval newts had a mean feeding performance of over 99% (0.992 \pm 0.06 SD) while efts were successful in capturing worms in only 46% (0.46 \pm 0.13 SD) of at-

TABLE 1. ANALYSIS OF VARIANCE SHOWING THE DIFFERENCE IN AQUATIC FEEDING PERFORMANCE IN LARVAE AND EFTS.

Source of variation	Degrees of freedom	Mean square	F	P
Metamorphic stage	1	1.415	163.126	0.0001
Error	18	0.009		

tempts. The result of the ANOVA for metamorphic stage is highly significant (Table 1).

Sample sizes, mean SVL, and mean feeding performance for branchiate and transformed adults are given in Table 2. The two forms showed nearly identical levels of feeding performance on each of the prey types. Both were highly successful at capturing earthworms (89%) and brine shrimp (85%) but were unsuccessful at capturing guppies (<1%). Guppies with the caudal-fin rays removed were intermediate in elusiveness and were also caught equally by both adult forms (26%). The ANOVA comparison of branchiate and transformed adult newts showed no significant difference in feeding performance (Table 3), even when branchiates that retain only one ceratobranchial were removed from the analysis ($P = 0.40$, $df = 1,46$).

Among the 40 branchiate adults 57% had completely transformed hyoids (only ceratobranchial 1 remained, Fig. 1: Adult) and 32% retained ceratobranchials 1 and 2 (Fig. 1: Branchiate). A few specimens retained ceratobranchials 3 (8%) and 4 (3%). Three pairs of rudimentary external gills (Fig. 1) were present in 86% of the branchiates with the remainder retaining one or two small gill nubs. None had open gill slits.

DISCUSSION

Over the last 10 yr, functional morphologists have been increasingly successful in their descriptions of how animals function and in defining explicit biomechanical and physiological differences between individuals and species (Gans, 1974; Goslow, 1985; Shaffer and Lauder, 1985). As a rule, such studies have focused on defining functional and morphological patterns that distinguish species and on relating such patterns to demands imposed by the environment.

An important additional component of re-

TABLE 2. MEAN AQUATIC FEEDING PERFORMANCE OF BRANCHIATE AND FULLY TRANSFORMED ADULT NEWTS FEEDING ON FOUR PREY TYPES.

Stage	Prey type			
	Earthworms	Brine shrimp	Guppies (tails cut)	Guppies
Branchiate	0.888 ± 0.083	0.844 ± 0.097	0.259 ± 0.076	0.006 ± 0.019
(SVL ± SD)	(40.7 ± 4.7)	(40.6 ± 3.5)	(37.0 ± 3.0)	(37.0 ± 0.8)
N	9	8	10	10
Transformed	0.885 ± 0.062	0.850 ± 0.053	0.270 ± 0.124	0.007 ± 0.024
(SVL ± SD)	(42.7 ± 2.8)	(40.5 ± 1.8)	(40.9 ± 3.4)	(39.0 ± 3.5)
N	10	10	10	10

N = sample size.

SVL ± SD = Snout-vent length in mm ± 1 standard deviation.

search in functional morphology, however, relates the structural and functional differences observed within and between species to differences in *performance* (Emerson, 1978; Arnold, 1983; Garland and Arnold, 1983). As discussed by Arnold (1983), measurement of actual animal performance is a fundamental component of any research program that attempts to link evolutionary and biological significance with structural and functional analyses. If measured differences in functional characters between two species have no correlation with differences in behavioral ability or performance, then we must question the utility of such functional analyses. The crucial contribution of measures of animal performance to our understanding of organismal structure and function lies in the link that performance studies provide between measured morphological and functional differences and the actual biological role (Bock and von Wahlert, 1965) played by these features. Our goal has been to test specific hypotheses concerning the ontogenetic relationship between morphology and behavioral performance.

The hypothesis that the transformation from

a unidirectional to a bidirectional water-flow feeding system through metamorphosis results in a decrease in aquatic feeding performance is strongly supported by the significant differences in feeding ability exhibited by larvae and efts. Major morphological changes rapidly occur in cranial and hyobranchial elements during metamorphosis from larva to eft (Reilly, 1986, 1987). The most obvious of these changes are the loss of functional features presumed to be important in unidirectional feeding, such as gill slits, labial folds, and ceratobranchials 2-4. The more than 50% transmetamorphic decrease in aquatic feeding performance in newts is a consequence of some difference in the unidirectional vs bidirectional water-flow feeding system. Lauder and Shaffer (1986) found a similar transmetamorphic change in feeding performance in *Ambystoma tigrinum*, which dropped from 33-0% capture rates using live, intact guppies. A key question is: what functional and/or morphological changes actually cause the drop in feeding performance?

There are at least four ontogenetic changes that could result in reduced feeding performance. First, it might be predicted on the basis of previous research on the biomechanics of aquatic prey capture in salamanders (Lauder and Shaffer, 1985) that retention of more hyobranchial elements would increase suction feeding performance. The hyoid has been shown to be the major cause of the drop in intraoral pressure during feeding and this pressure drop is directly related to feeding performance (Lauder and Shaffer, 1986). The more hyobranchial elements that are retained after metamorphosis, the more negative pressure might be developed in the mouth cavity. However, the results of our second performance comparison between branchiate and adult morphologies in-

TABLE 3. ANALYSIS OF VARIANCE SHOWING NO DIFFERENCE IN AQUATIC FEEDING PERFORMANCE IN BRANCHIATE AND FULLY TRANSFORMED ADULT NEWTS.

Source of variation	Degrees of freedom	Mean square	F	P
Metamorphic stage	1	0.00004	0.006	0.936
Prey type	3	3.660	609.220	0.0001
Interaction	3	0.00006	0.010	0.999
Error	69	0.006		

dicating clearly that the retention of more of the hyobranchial apparatus did not increase feeding performance. The lack of a performance difference in branchiate adults which skeletally differ in ceratobranchial retention indicates that these elements do not contribute to aquatic feeding efficiency.

Second, the mere presence of gill slits in larvae, allowing unidirectional feeding, may be the cause of increased feeding performance. All other factors (e.g., muscle mass, skeletal morphology) being equal, unidirectional flow designs should be more effective at capturing food in the water than bidirectional hydrodynamic designs (Lauder, 1985). Recent research (Lauder and Reilly, 1988) in which the gill slits of axolotls were sutured closed has shown that the experimental production of bidirectional flow caused a significant decrease of feeding performance. Third, movement patterns of the jaws or the electrical activity patterns of the jaw muscles may change through metamorphosis. Fourth, changes in muscle morphology and mass that occur during metamorphosis with the change to terrestrial feeding may be a determining factor in transmetamorphic changes in aquatic feeding performance.

It is as yet not possible to separate out these four interrelated causal factors as determinants of the changes in feeding performance we have documented here. A key objective of future work on this experimental system will be to address the causal basis of these performance changes.

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