

Performance Consequences of a Trophic Polymorphism: Feeding Behavior in Typical and Cannibal Phenotypes of *Ambystoma tigrinum*

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Aquatic feeding behavior, prey capture performance, and morphological aspects of the feeding mechanism were compared in typical and cannibal phenotypes of *Ambystoma tigrinum melanostictum* to test the hypothesis that the trophic polymorphism affords a performance advantage in feeding. Similar-sized salamanders of the two phenotypes differed morphologically in size of the vomerine tooth patches and head width but not in size of the gape or mass of the hyoid retractor muscles used in suction feeding. Suction feeding and prey handling performance did not differ between the two morphs feeding on live guppies or small conspecific salamanders. However, differences were found in willingness to feed on conspecifics and prey handling performance when feeding on larger salamander larvae. Thus, cannibal morphs possess a significant performance advantage only during predation on large conspecifics. The performance advantage on large prey appears to be a consequence of greater prey handling ability facilitated by the increased size of the vomerine tooth patches.

INTRASPECIFIC morphological differences in vertebrate feeding mechanisms are frequently correlated with intraspecific variation in diet or feeding behavior to explain the ecological advantage of specific morphological traits (Orton, 1954; Liem and Kaufman, 1984; Hoogerhoud, 1986). However, few studies correlating trophic variation with differences in morphology test the performance of the different morphologies in relation to the presumed trophic advantage (Reilly and Lauder, 1988; Smith, 1990; Wainwright et al., 1991). Demonstration of the performance consequences of a polymorphism provides a necessary link between morphological function and its role in partitioning resource use (Emerson and Arnold, 1989; Wainwright, 1991).

Larvae of the tiger salamander, *Ambystoma tigrinum*, are known to exhibit phenotypic polymorphism in trophic morphology (Powers, 1907; Collins et al., 1980; Collins and Holomuzki, 1984). Cannibal morphs have been distinguished morphologically from typical larvae (typical morphs) by possessing larger body size, wider heads, and hypertrophied vomer bones and vomerine teeth. The occurrence of cannibal morphs is associated with high larval densities and cannibal morphs, through their richer diet or perhaps hormonal effects, achieve higher growth rates and earlier metamorphosis than typical morphs (Collins and Cheek, 1983; Lan-

noo and Bachmann, 1984). Thus cannibal morphs are presumed more likely to survive in temporary and unpredictable aquatic habitats.

Underlying the proposed ecological advantage of this trophic polymorphism is the assumption that cannibal morphs are better than typical morphs at capturing and consuming conspecifics (Lannoo and Bachmann, 1984). Dietary studies support this idea because individuals differing in trophic morphology also differ in diet. Typical morphs feed on any prey small enough to capture (including occasional conspecifics), but their diet is mostly small crustaceans and aquatic insects (Holomuzki and Collins, 1987; Collins and Holomuzki, 1984; Lannoo and Bachmann, 1984). Cannibal morphs are not obligate cannibals but macrophagous carnivores in which about 84% of the diet is conspecifics (Collins and Holomuzki, 1984). Therefore, "cannibal" vs "typical" morphs refer to the morphological differences first described by Powers (1907) and a dietary difference in the occurrence of conspecifics in the stomachs of the two morphs.

Paralleling the assumption that cannibal morphs are better at eating conspecifics is the hypothesis that morphological traits expressed in the cannibal morphs confer a performance advantage for eating conspecifics. Increased food intake and higher growth rates in other cannibal species have been explained by can-

nibalistic traits (broader heads and larger mouths) that enable them to feed on larger prey (Heusser, 1976; Crump, 1983). In the cannibal morphs of *A. tigrinum*, several traits may contribute to a performance advantage for large prey. Differences in the size of the head may contribute to a performance advantage for feeding on larger prey by increasing the gape. Hypertrophy of the vomer bone and its teeth, which project ventrally from the palate to oppose the larval tongue, may increase the ability to hold large prey during initial capture and during prey manipulation and transport of prey to the esophagus. In addition, an increase in suction performance due to undocumented differences in the feeding mechanism (such as muscle mass) may contribute to enhanced performance in capturing large prey.

Here we examine morphology of the feeding mechanism and compare aquatic feeding behavior and prey capture performance in typical and cannibal phenotypes of *Ambystoma tigrinum melanostictum* to test the hypothesis that the trophic polymorphism results in a performance advantage during feeding. We first evaluate suction feeding performance and then examine the details of prey manipulation performance. Morphometrics and behavioral testing, using three prey types including small and large conspecifics, demonstrate that cannibal morphs possess a significant performance advantage only during predation on large conspecifics and is not the consequence of suction ability but of increased prey handling ability facilitated by hypertrophied vomer bones and teeth.

MATERIALS AND METHODS

Feeding performance and morphological features were analyzed in typical and cannibal morphs of *A. t. melanostictum* larvae collected near Chadron, Nebraska. Individuals for study were selected from a large series of neotenic larvae to be completely dimorphic for cannibal morph traits and of similar size. Typical morphs had v-shaped heads and narrow, flat vomerine tooth ridges. Cannibal morphs had u-shaped heads and wide, hypertrophied vomerine ridges. Snout-vent lengths (SVL) in the two samples were not significantly different (Table 1). Salamanders were kept in individual 23 × 36 cm plastic trays containing dechlorinated water 4 cm deep. The salamanders, which had been maintained on mealworms for several months, were fed nightcrawlers one week prior to test-

ing and then fasted. Animals were housed and tested in a cold room at 16–17 C.

Individual salamanders feeding on three prey types were videotaped at 60 fields per second using a Panasonic PK-958 camera with a digital time counter superimposed on each video frame using a For-A VTG-33 video timer accurate to 0.01 sec. During feeding trials, each individual tray containing alternately a typical or cannibal morph was placed in vertical view of the video camera. After a 5-min settle-down period, the camera was activated, and one of three prey types (below) was introduced into the tray. The video timer was started with the first feeding attempt, and the trial was terminated after 10 min. Trials in which larvae did not attempt to feed were terminated 10 min after the camera was activated. At the end of each 10-min trial, each individual who had not eaten (whether unwilling or unable to capture the test prey) was offered an earthworm (*Lumbricus* sp.). This was done to test whether they were willing to feed at all, and only trials in which either the test prey or a nightcrawler was eaten were used.

The three prey types (also kept in the cold room) were chosen to test the suction and prey handling abilities of the two morphs. To test suction performance in the two morphs, adult guppies (*Poecilia reticulata*) were used. Previous research (Lauder and Reilly, 1988; Reilly and Lauder, 1989) showed that larval *Ambystoma* readily eat guppies and that they are fast-moving prey that challenge feeding performance by aquatic suction feeding. Guppies have extremely rapid Mauthner-cell-mediated escape response (Eaton, 1984), and larval *Ambystoma* capture guppies only about 50% of the time (Lauder and Reilly, 1988). The guppies were 22 mm ± 2.0 SD in total length which is about two-thirds of the head width of the salamanders being tested. Feeding performance on guppies was tested by introducing 40 fresh live fish into the tray and allowing the salamanders to feed at will.

To quantify feeding performance on guppies, the number of captures and misses per trial were tallied. Salamanders either successfully caught and swallowed the guppies (captures) or failed to suck the prey into the jaws (misses). Mean capture success (captures/attempts) for each morph was calculated and compared using a Mann-Whitney U test (Seigel, 1956).

To further test suction ability and to assess prey manipulation abilities, feeding performance was tested on two larger prey types (small and large conspecifics). Larval *A. tigrinum* were

TABLE 1. MORPHOLOGICAL AND MOTIVATIONAL CHARACTERISTICS OF SAMPLES OF TYPICAL AND CANNIBAL MORPHS OF *Ambystoma tigrinum* USED IN FEEDING TRIALS ON GUPPIES, SMALL SALAMANDERS, AND LARGE SALAMANDERS. Morphological variables are averaged for the subset of each morph willing to feed on each prey type. Percent motivation is the number of individuals of a given morph willing to feed on a given prey type, divided by the number tested times 100. Values are presented as means + SE for distances (mm), masses (grams), or areas (mm²).

Morph	Prey type		
	Guppies	Small salamanders	Large salamanders
Typicals			
N tested	11	11	13
N willing	9	8	6
% motivation	82%	73%	46%
Snout-vent length	117.3 + 2.1	119.8 + 3.2	127.3 + 4.5
Head width	30.6 + 1.1	30.8 + 1.6	34.8 + 2.1
Gape width	30.6 + 1.3	32.5 + 1.7	31.4 + 1.2
Jaw adductor mass	0.431 + 0.09	0.465 + 0.10	0.543 + 0.19
Hyoid retractor mass	0.382 + 0.03	0.393 + 0.04	0.423 + 0.08
Vomer length	5.4 + 0.14	5.5 + 0.15	5.7 + 0.14
Vomer width	0.53 + 0.05	0.55 + 0.05	0.57 + 0.04
Vomerine tooth area	5.3 + 0.4	5.5 + 0.5	5.1 + 0.5
Cannibals			
N tested	9	7	3
N willing	8	7	3
% motivation	89%	100%	100%
Snout-vent length	123.5 + 2.4	126.4 + 2.5	125.4 + 2.5
Head width	35.9 + 0.6* (0.004)	36.0 + 0.7	36.0 + 0.7
Gape width	33.5 + 1.0	34.0 + 1.1	34.7 + 0.3
Jaw adductor mass	0.701 + 0.06* (0.028)*	0.675 + 0.05	0.693 + 0.03
Hyoid retractor mass	0.412 + 0.02	0.451 + 0.02	0.450 + 0.02
Vomer length	6.2 + 0.2* (0.003)	6.4 + 0.2* (0.001)	6.5 + 0.2* (0.02)
Vomer width	2.2 + 0.2* (0.000)	2.4 + 0.2* (0.001)	2.5 + 0.1* (0.02)
Vomerine tooth area	11.3 + 0.6* (0.000)	11.9 + 0.4* (0.001)	12.3 + 0.5* (0.02)

* Probability values <0.05 for Mann-Whitney U Test.

* P is also <0.05 for residuals of jaw adductor mass regressed on SVL.

obtained commercially and sorted into small (SVL = 46.0 mm ± 2.5 SD; HW = 11.5 mm ± 2.3 SD) and large (SVL = 57.2 mm ± 2.9 SD; HW = 14.7 mm ± 3.7 SD) size classes. One week after the guppy trials, both morphs were filmed feeding on small salamanders, and then a week later, trials were repeated using the large salamander prey. No food was provided between trials. In both the small and large prey feeding trials, each salamander was offered three fresh live salamanders as prey. In all cases, individuals unable to capture conspecifics ate nightcrawlers at the end of the trial.

To quantify the performance differences between the two morphs feeding on conspecifics, feeding attempts were placed in two categories: captures and unsuccessful attempts. Captures were those when the prey was caught and in-

gested. This involves holding the prey in the jaws after the initial strike, followed by manipulation of the prey into a longitudinal position in the mouth from whence it is transported into the esophagus and swallowed. To quantify the details of prey manipulation performance, unsuccessful attempts were further categorized as misses, pieces, and holds. Misses occurred when the prey was completely missed (i.e., not touched) during the strike. Pieces occurred when the prey was sucked to or into the mouth but was not successfully grasped by the jaws. Holds occurred when the prey was caught in the jaws but eventually escaped. The duration of each hold was also noted. As in the guppy trials, these measures were tallied from the videotapes of each trial and, when necessary, field-by-field tape advance yielding 1/60 of a second resolution

was used to distinguish between the types of unsuccessful attempts. Percent occurrence (number of occurrences/number of attempts) for each of the four feeding behaviors was calculated for each individual and compared using a Mann-Whitney U test.

Immediately following the performance trials, salamanders were euthanized by overdose of tricaine methanesulphonate and preserved in 10% formalin. From the preserved specimens snout-vent length, head width at the point of jaw articulation, and gape width at the angle of the labial folds were measured to the nearest mm. The vomerine morphology was quantified by measuring length, maximum width, and area of the vomerine tooth patches from video images of the palate of each specimen. In addition, two muscle pairs, the hyoid retractor (rectus cervicis profundus and superficialis), and the jaw adductor (adductor mandibulae internus) muscles were removed. Origins of the jaw adductor muscles were first cut from the skull, squamosal, and quadrate, and then the tendon to the mandible was cut. The hyoid retractor muscles were cut along the second myomere posterior to the urohyal and then pulled anteriorly and removed from their insertions on the hyobranchial apparatus. Care was taken to remove any adhering blood vessels or heart tissue. After the muscle pairs were removed, they were placed in dishes of water. The total bilateral wet mass for each muscle was measured three times to the nearest mg. Each time, muscles were removed from a water dish, gently blotted and weighed. The mean of these three measurements was used in the analysis. The external and palatal measurements and muscle masses for the two morphs were compared using a Mann-Whitney U test using only those individuals willing to feed on a given prey type.

We focused our muscle analysis on the rectus cervicis and adductor mandibulae internus because these are the primary muscles producing the force for hyoid retraction (and thus, negative buccal pressure during suction feeding) and jaw adduction during prey capture and manipulation (Lauder and Shaffer, 1985; Shaffer and Lauder, 1985; Reilly and Lauder, 1989). Because muscle mass is highly correlated with force generating capacity in the cranial muscles of *A. tigrinum* (Lauder and Reilly, 1990), differences in mass of these muscles may reflect differences in amount of suction or jaw strength in the two morphs.

RESULTS

The motivational, morphological, and sample characteristics of typical and cannibal morphs feeding on three prey types are presented in Table 1. Mean morphological measurements are presented for the subset of each sample that was willing to feed on the prey type tested.

Feeding motivation.—Typical and cannibal morphs were equally motivated to capture live guppies. Equal motivation to feed on guppies is indicated by the similar percentage of each morph willing to feed on guppies (82% and 89%) and the similar mean number of attempts (about 24) made by each morph during the 10-min trials.

The percentage of typical morphs willing to attack small conspecifics (73%) was higher than expected based on low rates of cannibalism reported for typical morphs in the field (<1%: Collins and Holomuzki, 1984; Holomuzki and Collins, 1987; and 10%: Lannoo, et al., 1989). Typical morphs that did not attempt to feed on conspecifics spent the entire trial searching for prey, nosed the conspecifics, appeared interested in feeding, but made no attempts to feed until offered an earthworm at the end of the trial. Typical morphs were less motivated to feed on the large conspecifics with only six of 13 individuals willing to attack them (Table 1).

All of the cannibal morphs tested ate conspecifics. Cannibal morphs actively pursued conspecifics as soon as they were introduced into the tray, whereas the typicals generally waited until the prey moved directly in front of them before they pursued them.

Prey capture performance.—Typical and cannibal morphs had similar success in capturing guppies (Table 2). Mean guppy capture success was 60–64%. When feeding on small conspecifics, typical and cannibal morphs had similar numbers of attempts (means of 6.7 and 4.7, respectively) and similar percentages of misses, pieces, holds. In addition, mean capture success (20–29%) was not significantly different but dropped to less than half of that for guppies.

Significant performance differences were found for the two morphs feeding on large conspecifics. Cannibal morphs had a mean capture success about double that of the typicals (33% vs 17%). This difference was not significant at the 0.05 level but could be accepted as signifi-

TABLE 2. MEAN PERCENT OCCURRENCE OF FEEDING BEHAVIORS FOR TYPICAL AND CANNIBAL MORPHS OF *Ambystoma tigrinum* FEEDING ON SMALL AND LARGE TIGER SALAMANDER LARVAE AND GUPPIES. Performance measures are as follows: Captures were when the prey was caught and ingested; unsuccessful attempts are broken down into misses (completely missed the prey), pieces (sucked prey to or into the mouth but missed), and holds (held the prey for a period of time but the prey ultimately escaped); values are the mean occurrence (\pm SE) for each behavior (number of occurrences/total attempts) for each prey type rounded to the nearest percent. Note that percentage of holds was significantly different for the two morphs feeding on large salamanders. Sample sizes are given in Table 1.

Morph	% Misses		% Pieces		% Holds		Mean capture success (%)		
	Small	Large	Small	Large	Small	Large	Guppies	Small	Large
Typicals	61 (10)	50 (12)	9 (4)	14 (5)	10 (6)	19 (10)	64 (5)	20 (12)	17 (17)
Cannibals	56 (7)	50 (17)	9 (4)	17 (17)	6 (5)	0 (0)*	60 (5)	29 (8)	33 (10)

* $P = 0.043$ (Mann-Whitney U Test).

cant at the $P < 0.1$ level. Each of the cannibal morphs captured one of the large salamander prey in an average of 3.7 attempts, but among the typical morphs (which averaged 22.7 attempts), only one was successful. This capture occurred when the prey was startled head-first directly into the predator's mouth during a strike. Except for this apparently abnormal capture, typical morphs lost all large prey that they tried to manipulate in the jaws. Removal of this individual from the analysis results in a significant difference in capture success ($P = 0.01$).

The breakdown of the feeding performance measures (Table 2) indicates the functional differences between the two morphs feeding on large conspecifics. The mean occurrence of holds was significantly different ($P = 0.04$) with cannibal morphs having none and typical morphs holding prey in 19% of attempts. Zero holds vs some holds indicates that, when cannibal morphs get a hold of a prey item, they manage to swallow it, whereas typical morphs usually lose prey held in their jaws. Typical morph holds ranged from 2 sec to 15 min before the prey was lost. In short-duration holds, prey were able to wriggle away. In long-duration holds, the typical morphs that had the prey securely in the jaws tried repeatedly to manipulate and transport the prey in their mouths but were unable to get a better grasp on the prey before losing them. In one case (the 15-min hold), the prey was caught midbody, eventually manipulated to a tail-first position, transported into the mouth about half the body length, and then lost. Cannibal morphs were able to manipulate and swallow any prey regardless of how it was initially held after the strike. Thus, typical morphs were unable to capture the large conspecifics unless they were sucked head first into the

mouth; the main performance advantage of cannibal morphs was in the ability to hold and manipulate large prey. The mean occurrence of misses (as defined) and pieces were similar, and, thus, the two morphs were equally likely to completely or nearly miss large conspecifics.

None of the external morphological measures or muscle masses differed significantly between samples feeding on small or large conspecifics. However, jaw adductor mass and head width were significantly different in the guppy sample (Table 1). Striking differences in the vomerine morphology were found in the cannibal morphs which had vomerine tooth patches significantly greater in length, width, and area for all of the samples. Cannibal morphs had vomerine tooth patches that were about 1 mm longer, 4.5 times wider, and 2.5 times the area (Table 1).

DISCUSSION

Suction feeding performance.—Several results indicate that typical and cannibal morph samples were equal in aquatic suction performance. First, gape width was not different between morphs (Table 1). Differences in mouth shape and size significantly influence water flow during suction feeding (Lauder, 1979, 1983). Given the similarity in mouth shape and size in the two morphs, one would expect little difference in suction feeding ability on the basis of mouth design. Second, the mass of the hyoid retractor muscles (rectus cervicis), which are the major muscles generating negative pressure in the buccal cavity during suction feeding (Lauder and Shaffer, 1985; Reilly and Lauder, 1989), was not different in the two morphs (Table 1). Third, the two morphs did not differ in feeding performance

on elusive prey much smaller than the gape width (guppies and small conspecifics) which suggests that equal volumes of water are sucked into the mouth during feeding. Fourth, the percentage of misses and pieces during feeding on large conspecifics was not significantly different between the two morphs and together accounted for only a third or less of the attempts. Thus, the large salamanders were either missed entirely or pulled into the mouth during the strike and held.

Prey manipulation performance.—Among salamanders, large salamander prey are usually swallowed head first and cannibalistic salamanders can eat conspecifics with head widths as great as their mouth width (Kusano et al., 1985). Because the large conspecific head widths were only 42% of gape width, gape limitation was not a factor affecting prey capture success when the prey was captured head first. However, our performance data indicate that the primary difference between the morphs is in their ability to grasp and manipulate prey that were not sucked head first into the mouth. This suggests the cannibals have some functional advantage in ability to hold prey. Furthermore, larvae of the two morphs that fed on the large conspecifics did not differ in snout-vent length, head width, gape width, or muscle mass. They differed significantly only in morphology of the vomerine ridge and teeth. Thus, hypertrophy of the vomer bone and teeth appears to be the major morphological advantage enabling cannibal morphs to capture and manipulate large conspecifics less than their gape width that are not caught head first. The functional significance of the hypertrophied vomer bone and teeth increases with prey size because of a loss of effectiveness of the maxillary teeth as gape increases to accommodate larger prey.

Phenotypic plasticity, morphometrics, and function.—The inference that greater gape width and head width confer a functional advantage in feeding is problematic for two reasons. First, literature on cannibal morphs states that head width and mouth size are greater in cannibal morphs. Data are available to show that cannibal morphs may have greater head width than typical morphs at a given size (Table 1, guppy sample; figure 1 in Pierce et al., 1983; Lannoo and Bachman, 1984). However, the assertion in the literature that the mouth size of cannibal morphs is greater apparently stems from a state-

ment by Rose and Armentrout (1976) that “the mouth is about 20% wider at the angle of the jaw” although no data, sample sizes, or statistics were presented to support this statement. Our data (Table 1) and that of Pierce et al. (1983) fail to show statistical differences in gape width of large typical and cannibal morphs, and Powers (1907) states that no character is more variable within populations than gape width. It is clear that a detailed morphometric study over a large size range of typical and cannibal morphs with more statistical power is needed to clarify this and other aspects of the trophic polymorphism (such as jaw adductor mass, see below).

The second problem concerns the utility of functional inferences about feeding made from differences in head width. Our data, and functional analyses of aquatic prey capture in salamanders (Lauder and Shaffer, 1985; Lauder and Reilly, 1988), show that head width alone has no discernable functional significance, and the data should not be used as a proxy for functional characteristics of feeding. Studies of polymorphisms should include many kinds of morphometric variables, and special care should be taken when choosing morphological variables from which functional inferences are to be made (Lauder, 1990).

Another difficulty with morphometric analyses of these two morphs is that samples of cannibal morphs with fully expressed cannibal morph traits are compared to samples of purely typical morphs (this study; Pierce et al., 1983) or a mixture of typical morphs and intermediates (Lannoo and Bachmann, 1984). Due to this sampling bias, it is not known whether this is a discrete or continuous polymorphism or how the different traits are correlated. The literature tends to assume that this is a discrete polymorphism, but evidence of intermediates (Lannoo and Bachmann, 1984; Powers, 1907; Reilly and Collins, pers. obs.) indicates that this is more likely a continuous polymorphism.

Furthermore, the expression of the cannibal morph traits appears to be very plastic. Powers (1907) discusses the developmental plasticity of cannibal morph traits both within samples of the same age and through ontogeny. Powers was able to induce cannibal morph traits in typical larvae by raising them on large prey (large *Rana* tadpoles) then have them revert to typical form by switching their food to liver for about three weeks. In addition, he was able to induce typical larvae to develop larger gapes and broader heads simply by raising them in the

dark where they could not see their daphnid prey. He concluded that head width and mouth size were highly variable within populations and that the polymorphism in the vomerine ridge was a functional response to the size of the prey. Our data tend to support this hypothesis. In our samples that fed on conspecifics (Table 1), the only significant difference in the morphs was the hypertrophied vomerine tooth patches in the cannibal morphs, and the performance data (Table 2) suggest that this is the primary morphological trait affording the cannibals a performance advantage on large conspecific prey. In addition, the jaw adductor mass of the guppy sample was significantly greater in the cannibal morphs and larger in the conspecific samples (Table 1), suggesting that bite strength may add a significant advantage in manipulating conspecifics as the prey is secured with the jaws and vomerine teeth.

It is intriguing that cannibal morph traits first emerge in a few of many similar-sized small larvae before the first cannibalistic event occurs (Collins and Cheek, 1983). Thus, the greatest challenge to gape limited feeding in cannibal morphs (i.e., the time when a wider head, if present, is most important), occurs during the first cannibalistic event when the small cannibal morphs eat their first salamander, one that is very similar in size to themselves. After this first conspecific is consumed, the cannibal morphs rapidly grow larger than their cohort typical morphs. After that point, the cannibals feed primarily on the relatively smaller typicals, where the hypertrophied vomerine teeth assume the major role in feeding by enhancing manipulative abilities. Thus, it might be predicted that the gape polymorphism would be greater very early in cannibal morph development when relative prey size is large compared to older individuals. In addition, the vomerine ridge polymorphism would be predicted to increase as the cannibal morphs grow in size and the manipulation of relatively small prey becomes more important. Further research on the developmental, morphometric, and genetic bases of the cannibal morph traits and their plasticity would greatly enhance our understanding of this trophic polymorphism and its evolutionary implications.

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