Copeia, 1995(1), pp. 1–7

Compensatory Escape Mode Trade-Offs between Swimming Performance and Maneuvering Behavior through Larval Ontogeny of the Wood Frog, *Rana sylvatica*

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We measured variation in swimming performance (sprint velocity, distance swam) and maneuvering behavior (number of turns per sprint and turn angles) across larval ontogeny of the wood frog *Rana sylvatica* to determine what ontogenetic variation existed in the relationship between these two classes of escape mode. Wood frog tadpoles exhibited low probabilities of turning out of a previously straight trajectory and did so at shallower angles during the mid–late larval growth periods when swimming performance was most highly developed (stages 29–37). In contrast, both before and after this period of heavy reliance on locomotor performance (≤ stage 29; ≥ stage 37), tadpoles demonstrated a significantly greater propensity to engage in turning behavior, and maneuvering occurred at sharper angles from a previous escape trajectory. It was also at these times, at the very beginning and end of tadpole development when larvae are presumably most susceptible to predators, that we observed the lowest values for swimming performance variables measured in this study. Thus, developmental variation in performance escape tactics may be coupled with a quantitative change in a maneuvering behavior escape mode. The apparent escape mode switch detected in this study suggests that behavioral mechanisms may compensate for decreased locomotor performance in metamorphic larval amphibians which may otherwise be differentially vulnerable to aquatic predators.

ANTIPREDATORY strategies of larval amphibian may include a suite of sometimes co-occurring mechanisms such as unpalatability to predator species (Formanowicz and Brodie, 1982), habitat niche segregation (Banks and Beebee, 1987; Formanowicz and Bobka, 1989; Tejedo, 1991), attainment of large body size (Travis et al., 1985; Richards and Bull, 1990; Semlitsch, 1990), reduced mobility/activity patterns (Caldwell. et al., 1980), inferring a reduction in encounters with ambush sit-and-wait predators (Morin, 1986; Skelly and Werber, 1990; Tejedo, 1993), and increased locomotor ability or swimming efficiency (Wassersug and Sperry, 1977; Huey 1980; Wassersug and Hoff, 1985). Tadpoles are fast swimmers (Wassersug, 1989; Wilbur and Semlitsch, 1990) with positive, rheotropic, undulatory swimming behavior (Wassersug, 1973; Wassersug and Sperry, 1977) characterized by sharp bursts of speed ("sprints") and quick turns of up to 180° (Wassersug and Hoff, 1985; Wassersug, 1989).

Both swimming velocity and turning ability may be adaptive for predator avoidance (Wassersug and Hoff, 1985; Wilbur and Semlitsch, 1990); the former may enable larval amphibians to outswim predators (Feder, 1983; Wassersug, 1989), and the latter may serve to confuse a pursuing predator (Gatten, et al., 1984; Wassersug, 1989; Domenici and Blake, 1993). Investigators focusing on sprint speed, sustained swimming ability (Wassersug and Sperry, 1977; Huey, 1980), and swimming kinematics (Wassersug and Hoff, 1985) have shown positive relationships between tadpole size and swimming performance through larval development until a metamorphic rearrangement of the body brings about the emergence of drag-producing appendages and absorption of the tail (Cooke, 1974; Wassersug and Sperry, 1977; Huey, 1980). Furthermore, smaller larvae may be easier to consume because of their high susceptibility to gape-limited predators (Brodie and Formaniwicz, 1983; Wilbur et al., 1989; Semlitsch, 1990) and the relative ease/shorter handling time with which they are captured and consumed (Formanowicz, 1986; Caldwell et al., 1980; Semlitsch, 1990). Disproportionately large amounts of metamorphic tadpoles discovered in the stomachs of snakes (Wassersug and Arnold, 1976; Wassersug and Sperry, 1977) have prompted laboratory studies that have confirmed that metamorphic tadpoles are more frequently subjected to lethal predation than are tadpoles at other stages of development (Wassersug and Sperry, 1977). Decreased locomotor ability at these stages appears to be a key factor in high larval mortality, which can reach 96–97% (Herreid and Kinney, 1966; Calef, 1972). The avoidance of the hazards associated with metamorphosis might provide sufficient selective pressure to bring about the rapidity of the metamorphic transition which appears to be the period of highest vulnerability to predators (Szarski, 1957; Williams, 1966; Wassersug and Sperry, 1977) yet is a small portion of larval ontogeny [mean = 15% for 13 species surveyed by Wassersug and Sperry (1977); Wassersug, 1975].

Variation in larval locomotor performance may affect tadpole success and adult fitness in many ways. For example, slower tadpoles clearly experience higher predation rates (Wassersug and Sperry, 1977) and may receive more nonlethal injuries as a result of unsuccessful predation. As a result of injury, these individuals may experience slower growth rates (Wilbur and Semlitsch, 1990), be less able to exploit limited resources (Wilbur and Collins, 1973), and be at a competitive disadvantage with other amphibian larvae (Wilbur, 1977). Likewise, nonlethal injuries that occur as a result of slower sprint speeds may increase predation risks on subsequent encounters (Feder, 1983), increase the time until metamorphosis (Wilbur and Semlitsch, 1990), and lengthen the time that tadpoles are exposed to aquatic predators (Alford and Harris, 1988). The effects of size at metamorphosis are often noted later in terrestrial phases of the anuran life cycle (Travis, 1984; Semlitsch et al., 1988) and, thus, may influence reproductive success and adult fitness. Howard (1980) has shown that size at metamorphosis is correlated with mating success in the wood frog, *Rana sylvatica*.

Relatively little attention has been given to behavioral predation avoidance mechanisms during the actual predator attack and chase scenario, despite the presumed adaptive significance (and theoretical importance) of any such mechanism which might offset ontogenetic variation in vulnerability to predators. Like locomotor performance (swimming speed, acceleration, efficiency) escape mode tactics, behavioral escape modes (utilization of refuges, microhabitat segregation, combative defense, or maneuvering behavior), should be favored by natural selection if individuals employing such strategies differentially survive the larval stages of amphibian ontogeny and later demonstrate increased reproductive fitness. Gatten et al. (1984) have concluded that for Rana and Hyla tadpoles "avoidance of a predator depends on rapid changes in direction. . .and apparently on velocity or acceleration but not on the endurance of the swimming."

This experiment was designed to test and compare the locomotor ability of the larvae of the wood frog *Rana sylvatica* at several key stages of tadpole development. We also quantified and described the maneuvering behavior of the larvae of this anuran during escape locomotion at these same stages. Because of the lack of recent investigations into the maneuvering behavior of anuran larvae, despite acknowledgment of these behaviors as an area of considerable interest (Wassersug, 1973; Wassersug and Sperry, 1977; Wassersug and Hoff, 1985), we measured sprint performance variables (swimming velocity, distance swam) in concert with maneuvering behavior variables (turn angles from a previously straight trajectory and number of turns per continuous sprint) throughout larval development. Here we present an effort to study the patterns in variation of these parameters across larval ontogeny and the relationship between these two classes of escape modes (swimming performance vs maneuvering behavior).

Materials and Methods

Rana sylvatica larvae at stages between 15 and 22 (Gosner, 1960) were collected by dipnetting from natural woodland ponds in Adams County, Ohio. We selected four standardized stages of larval development on the basis of the following distinguishing characteristics: stage 26 (small tadpoles with feeding behavior well established), stage 31 (larger tadpoles with limb buds but no appendages), stage 37 (still larger tadpoles with rear limbs well developed), and stage 43 (emergence of one or both forelimbs).

Eighty tadpoles (approximately between stages 19 and 23 when placed under experimental conditions) were housed in two 190-liter tanks (n = 40 per tank at the start of the experiment) with 70 liters of aged, dechlorinated tap water. Water temperature was maintained at 25.5 ± 1.1 C and a 12L/12D photoperiod was utilized. Tadpoles were fed boiled spinach ad libitum and tank water was replaced every three days. On days when water was changed, the positions

Table 1. Synopsis of Larval *Rana sylvatica* Body Size Measurements Taken from Tadpoles Used in the Locomotor Performance Trials and a Summary of Separate One-Factor ANOVAs Run on SVL and Tail Length (mm). Presented are means for 10 individuals (±1 SD) and results of Scheffe's means separation tests (superscript letter differences indicate statistical significance between stages at the ≤0.001 level).

Stage	26	31	37	43	F-value	*P*-value
SVL	9.56 (0.91)^{a}	12.19 (0.83)^{b}	14.12 (0.85)^{c}	14.36 (1.97)^{c}	32.12	0.0001
Tail	13.03 (1.23)^{a}	20.50 (2.37)^{b}	25.01 (2.44)^{c}	18.09 (3.28)^{b}	41.78	0.0001

of the tanks on the shelf in the environmental chamber were switched to minimize position/light/temperature effects. At this time, both tanks were mixed together and tadpoles were haphazardly reassigned to ensure homogeneity of the laboratory population. In between water changes, waste was removed daily by siphon, and any dead tadpoles were also removed. Developmental stage was scored daily for ≥ 20 individuals; and, when these were judged close to the desired stage, larger samples were taken until it was estimated that ≥ 60% of the tadpoles were ready to be tested. Ten tadpoles were then randomly selected for escape performance tests from these larger samples.

A 140 × 102 × 30 cm plastic box served as the arena for the escape performance tests. A reference grid divided into 2-cm increments was drawn on the bottom of the arena which was filled with approximately 6 cm of aged dechlorinated tap water. All escape performance tests were carried out at approximately the middle of the light phase of the imposed photoperiod. Tests were performed within the environmental chambers that held developing tadpoles to control for temperature effects during trials. During each trial, individual tadpoles were placed in a designated starting area (between 10 and 15 cm of one end of the arena) and allowed to settle for 30 sec. If settled tadpoles were not oriented toward the far end of the arena, they were gently proded with a blunt glass rod until their head was pointing down the long axis of the arena. Once in position to swim the length of the arena, they were allowed to settle again for 30 sec. A sharp flick across the tail with a dissecting needle simulated a predator attack and induced the tadpoles to sprint to apparent maximum velocity. Swimming larvae moving across the measurement reference grid were recorded with a Sony VHS videocamera. This procedure was repeated five times for each tadpole (with a 30 sec rest in between trials) and the best (most linearly complete, > 10 cm) sprint from each was used in subsequent analyses. In an attempt to minimize possible effects of the tank's wall on the variables measured, video records of tadpole sprints in which the animal came within 10 cm of any edge of the sprint arena were not used for calculating performance data or scoring maneuvering behavior. Velocity was calculated (according to $\Delta d/\Delta t$; the camera filmed at 30 frames per second and frames were counted individually), and total distance swam per sprint (in cm) was also recorded. The number of single turns from a previous trajectory were counted, and the angles of the first turn per sprint were measured directly from the monitor screen with a large plastic protractor.

Following each trial, tadpoles were kept temporarily in individually marked finger bowls and measured (SVL and tail in mm) on wet paper towels with calipers to ensure the accurate assignment of size data with individual performance data. After each group of 10 tadpoles was tested, the tadpoles were taken out of the experiment to ensure that no individual was used more than once.

We used analysis of variance techniques after checking our data for normality and homoscedasticity (Sokal and Rohlf, 1981). For all variables quantified, Scheffe's mean separation F-tests were utilized to examine for significant differences among individual stages. Canonical correlation analysis (see Miles and Ricklefs, 1984, for a discussion of this procedure) was used to determine whether the linear combination of maneuvering behavior variables (number of turns, turn angles) was correlated with a linear combination of the performance variables (velocity, distance). This analysis was performed according to the Statistical Analysis Systems CANCORR procedure (Helwig et al., 1979). To examine the general relationship between the two types of variables (swimming performance vs maneuvering behavior), the factors of velocity × distance and number of turns × mean turn angle were plotted as a bivariate model.

Results

Table 1 contains a synopsis of body size measurements recorded from tadpoles employed in the locomotor performance trials in this study

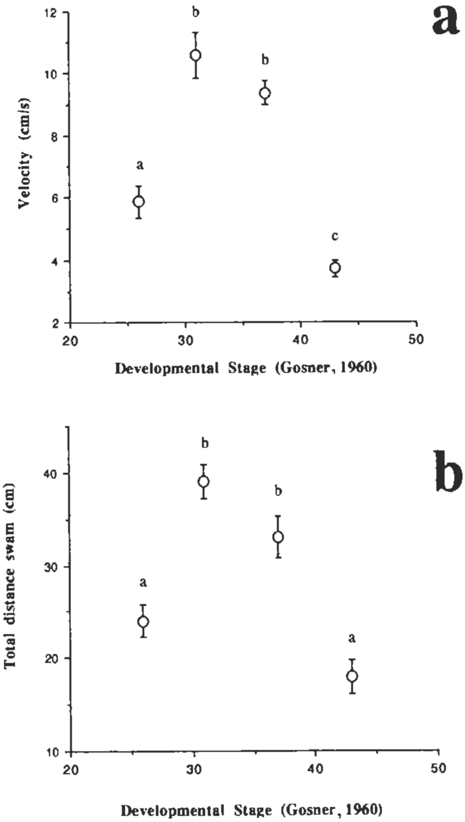

Fig. 1. Larval variation in swimming performance as measured by (a) velocity (cm/sec) and (b) distance swam (cm). Circles represent the means for 10 individuals and error bars are one standard error of the mean.

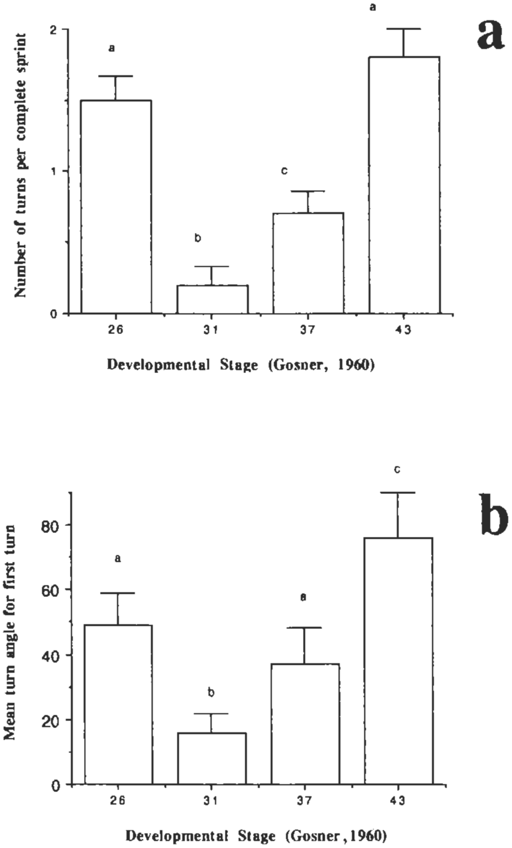

Fig. 2. Larval variation in maneuvering behavior as measured by (a) number of turns per complete sprint and (b) turn angle for the first turn per sprint. Circles represent the means for 10 individuals and error bars are one standard error of the mean.

and a summary of separate one-factor ANOVAs run on SVL and tail length. Nearly identical relationships between stage and swimming performance were observed in sprint velocity (Fig. 1a) and total distance swam (Fig. 1b); and stage had a significant main effect on both variables (Velocity: F = 37.86; df = 3, *P* = 0.0001; Distance: F = 22.05; df = 3, *P* = 0.0001). Both performance variables increased from stage 26 to apparent maximums at stage 31, then decreased through stage 37, and reached final lowest points recorded at stage 43. Stage also had a significant main effect on mean number of turns per sprint (F = 19.71; df = 3, *P* = 0.0001) and mean turn angle for first turn per sprint (F = 7.63; df = 3, *P* = 0.0009). However, in contrast to the swimming performance variables, both maneuvering behavior variables (Fig. 2) showed an inverse pattern of variation through larval development. The probability of turning and angle of evasive turns decreased from stage 26 to 31 and increased incrementally after stage 31, finally reaching a maximum at stage 43.

The canonical correlation indicates that the maneuvering behavior variables and the performance variables were significantly correlated (r = 0.77; F = 7.90; df = 4, 50; *P* = 0.0001). The proportion of variance explained by the first canonical correlate was 94%. The maneuvering behavior variables were positively and moderately correlated with the performance canonical variable. The performance variables were negatively and moderately correlated with velocity and weakly correlated with distance. Velocity contributed most to the first performance canonical variable and the first maneuvering behavior cannonical variable was primarily explained by turn angle (Table 2). Alternatively, by combining variables types (Fig. 3), we found that " increased use of maneuvering behavior" (number of turns × mean turn angle; arbitrary units) progressively declined as "swimming performance" (velocity × distance; arbitrary units) increased.

DISCUSSION

Although we did not undertake to investigate the causality behind relations of body size and locomotor performance, these data are consistent with several other studies, all of which have shown that tadpole size—and, most important, tail size—contributes to swimming performance (Wassersug and Sperry, 1977; Huey, 1980; Wassersug, 1989). Accordingly, we have demonstrated a pattern of ontogenetic body size variation that resembles a similar pattern of developmental variation in swimming performance—measured here in terms of velocity and distance.

Locomotor performance may also be governed by ontogenetic constraints, such as body structure and shape, which have a pronounced effect on swimming kinematics (Wassersug and Hoff, 1985). As mentioned above, size can be a factor in sprint performance. At early stages, *Rana sylvatica* tadpoles are small and swim at significantly slower velocities for significantly shorter distances than they do later at stage 31. Interestingly, these same animals engage in significantly more turns, the latter conducted at sharper angles from original sprint trajectories. This deployment of maneuvering behavior during initial stages of low performance capabilities when body size is also low may be an adaptation aimed at avoiding gape-limited predators that differentially succeed most often in capturing such younger tadpoles (Wilbur et al., 1989; Semlitsch, 1990). Not only do larger tadpoles swim faster, but they also escape invertebrate predation and nonlethal injury with a greater frequency that do smaller tadpoles (Richards and Bull, 1990). Accordingly, we have shown that by stage 31, large-sized *R. sylvatica* tadpoles had grown to larger sizes, were swimming at the highest velocities and for the longest distances recorded in this study, and were less likely to exhibit turning behavior. Under these latter circumstances, when linear locomotor performance is highly developed and presumably sufficient for escaping a predator's attack (and distance is increased between the individual and the predator, possibly to ward off another such attack; Weihs and Webb, 1984), turning tactics as part of an escape trajectory may be unnecessary and so may not be employed by the tadpole in favor of speed and distance alone. The concept is extended further by considering later stages of development in which the drag-producing rear legs appear and the animal is again at a performance disadvantage (Huey, 1980; Wassersug and Hoff, 1985; Wassersug, 1989). Optimality theorists have predicted that a sharply turning prey item may substitute maneuverability for speed when faced with an inert, yet somewhat faster, predator (Howland, 1974; Weihs and Webb, 1984). We argue that, by stages 37–43 (corresponding to a decrease in speed and distance), *R. sylvatica* larvae may employ turning behavior to confuse a pursuing predator that may otherwise be able to close in on a straight escape trajectory when the tadpole's swimming abilities are impaired (see Howland, 1974). Because a dramatic decrease in velocity and swimming distance starting at stage 37 corresponds to an increase in the probability of turning at sharper angles, we suggest that this compensatory maneuvering behavior may be adaptive for escaping predation by behavioral compensation of decreased locomotor performance. Hence, it is at stage 43, when at least one forearm has emerged from underneath the operculum, and the tail has begun to be absorbed by the developing froglet, that number of turns per single sprint and mean turn angle are at their highest. This further underscores the apparent performance—maneuvering behavior trade-off and the degree to which a behavioral escape mode appears to compensate for decreased locomotor performance. In similar studies, it has been shown that gravid lizards (Bauwens and Thoen, 1981) and snakes (Brodie, 1989) behaviorally compensate for mass-induced performance dissadvantages (implying an increase in susceptibility to predators) by decreasing activity patterns and switching to less mobile antipredator tactics. We believe that natural selection may favor a similar escape tactic switch in *R. sylvatica* tadpoles such that behavioral compensation of reduced locomotor performance may be possible.

TABLE 2. CANONICAL CORRELATION ANALYSIS OF PERFORMANCE (VELOCITY, DISTANCE) AND OF MANEUVERING BEHAVIOR (NUMBER OF TURNS, TURN ANGLES). Values under "within" represent correlations between a variable and its first canonical variable. Values for "between" are correlations between a variable and the opposite canonical variable (i.e., velocity vs maneuvering behavior).

	Within	Between
Performance		
Velocity	−0.831	−0.638
Distance	−0.175	−0.134
Behavior		
# Turns	0.672	0.516
Angles	0.970	0.744

We have primarily offered adaptationist interpretations of the ontogenetic variation in swimming performance and maneuvering be-

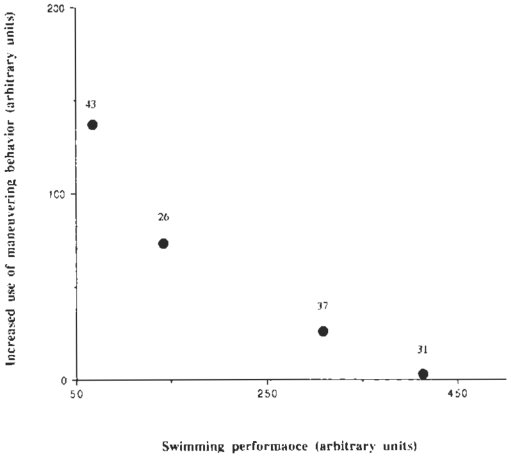

Fig. 3. The relationship between "increased use of of maneuvering behavior" (number of turns × turn angle, arbitrary units) and "swimming performance" (= velocity × distance, arbitrary units). Numbers above each point indicate developmental stage (Gosner, 1960).

havior described here. It has not, however, escaped our attention that an alternative interpretation of the observed patterns is available. A nonadaptationist interpretation of these trends might suggest that increased use of maneuvering behavior is a consequence of the absence of speed alone and is not the result of a behavioral escape mode switch on the part of the animal itself. In accordance with this type of interpretation, turning often and turning sharply may be beneficial at all stages of larval development, but it may only be at early and late stages that tadpoles swim slowly enough to engage in maneuvering behavior. Moreover, larger tadpoles with long tails at intermediate stages of development may be less capable of precise maneuvering because of their high swimming speed and large body size.

Having accounted for 94% of the observed variation with the first canonical correlate and having statistically verified the relationship between behavioral and performance variables, we sought to describe the general relationship between performance and maneuvering behavior across larval ontogeny. When arranged independent of developmental stage, the negative relationship between the prevalence of maneuvering behavior and swimming performance (Fig. 3) demonstrates the degree to which behavior and performance are conceivably interlinked into a compensatory trade-off regime in which selection should favor plasticity in escape modes and the ability to switch back and forth throughout larval development. Experimental verification of the general relationship suggested by our imprecise manipulations of these data will require intrusive laboratory manipulations of swimming performance. With this approach, one may be able to ascertain whether behavioral mechanisms of predator avoidance and escape maneuvering are immediately employed by experimentally handicapped tadpoles—and whether these exhibit differential survivorship with real or simulated predators.

ACKNOWLEDGMENTS

We thank N. Rayner for technical assistance and R. Shaefer for statistical advice. M. Hughes' help with canonical correlation analysis was greatly appreciated. D. H. Claussen, T. M. Rice, and M. S. Finkler provided many helpful comments on earlier drafts of this manuscript.

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Department of Zoology, Miami University, Oxford, Ohio, 45056. Submitted: 20 Dec. 1993. Accepted: 29 April 1994. Section editor: W. J. Matthews.