

Ontogeny of escape swimming performance in the spotted salamander

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Summary

1. The life stage suffering the highest predation rate is expected to have the highest escape performance unless developmental or functional constraints interfere. Peak aquatic escape performance in ephemeral pond-breeding amphibians is expected to develop early in the larval period, and metamorphosis is expected to reduce or completely disrupt aquatic escape performance. In anurans, exceptionally low escape performance during metamorphosis creates selection favouring rapid metamorphosis – which minimizes the time individuals spend in the vulnerable transition between tadpole and frog.

2. We investigated the development of aquatic escape performance in the spotted salamander, *Ambystoma maculatum* (Shaw, 1802), from embryonic development through metamorphosis. We expected performance to peak early in the larval period as hatchlings face high rates of predation but embryos must first develop escape behaviours. We also tested whether escape performance during metamorphosis was intermediate, as predicted by tail fin resorption, or lower than larvae and adults indicating a major physiological disruption.

3. Escape performance shows a complex ontogeny that is first positively influenced by embryonic and early larval development and then negatively correlated with tail resorption and body size. Escape distance was the only performance metric not affected by life stage. In contrast, both escape velocity and duration showed ontogenetic peaks early in the larval period with the lowest performance found in early embryos and adults and intermediate performance during metamorphosis.

4. This pattern suggests that metamorphosis does not impose a major physiological disruption on escape performance. Because spotted salamanders do not pass through a frog-like ‘ontogenetic performance valley’ during metamorphosis, they may be less subject than anurans to selection favouring rapid metamorphosis.

5. Functional implications of phenotypic variation should be considered in an ontogenetic framework because the relationship between body size and escape performance can be reversed on either side of an ontogenetic performance peak. The assumption that metamorphosis radically disrupts basic functions such as predator evasion does not seem universally warranted and suggests examination of ontogenetic performance trajectories in a diversity of animals with complex life cycles.

Key-words: amphibian development, anti-predator defence mechanism, aquatic locomotion, hatching, life history evolution, metamorphosis, ontogenetic niche shift

Introduction

Amphibian ontogeny has been an unifying research theme for evolutionary ecologists who aim to explain life history evolution with complex size and time-dependent ecological

interactions such as competition, predation and reproduction (e.g. Semlitsch *et al.* 1996; reviewed in Wells 2007). Body size and developmental stage are often used as metrics to gauge the effects of these interactions. A common assumption is that retarded development or smaller body size may decrease an individual's ability to escape predation. However, the relationship between factors that are

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known to change with ontogeny (e.g. size, shape and development) and escape performance is often unpredictable (Ghalambor, Walker & Reznick 2003) and not well studied for many amphibians.

Aquatic escape responses are ubiquitous and often stereotyped behaviours, performed throughout ontogeny in a diversity of aquatic organisms (e.g. Hoff 1987; Williams *et al.* 1996; Domenici & Blake 1997; Wakeling, Kemp & Johnston 1999; Hale *et al.* 2002; Fitzpatrick, Benard & Fordyce 2003; Ward & Azizi 2004; Gibb *et al.* 2006). Larval salamander morphology, in particular, may be specialized for burst swimming (Hoff *et al.* 1989). The outcome of predatory encounters is a major determinant of survival in both predator and prey species. Therefore, morphological and behavioural variation that affects the ontogeny of escape performance will have direct fitness consequences (Arnold 1983; Watkins 1996; Batty & Domenici 2000; Herrel & Gibb 2006; Langerhans 2009). Consequently, escape performance can help gauge the relative impacts of adaptation and constraint associated with life history evolution (Ghalambor, Reznick & Walker 2004; Kaplan & Phillips 2006).

Relatively high locomotor performance in small and young animals has been interpreted as a result of strong selection via predation during early ontogeny (Carrier 1996; Irschick 2003). Amphibian mortality is generally considered to be highest soon after hatching (e.g. Shoop 1974; Wilbur 1980; Werner 1986; Semlitsch 1987; Stangel 1988; however see Petrankska 1985), and this may be largely due to relatively heavy predation (Anderson, Hassinger & Dalrymple 1971). As mortality and predation have been shown to be density dependent (e.g. Stenhouse 1985; Petrankska 1989; Scott 1990; Van Buskirk & Smith 1991) and to decrease with increasing body size (Stenhouse, Hairston & Cobey 1983; Semlitsch 1987; Sih & Moore 1993; Mathis, Murray & Hickman 2003), selection for escape performance may gradually decrease throughout the larval period. However, despite potentially heavy predation, locomotor performance is relatively low in the earliest stages of development prior to the maturation of locomotor struc-

tures (e.g. Stehouwer 1992; Hale 1996, 1999). As a result, it is expected that salamander locomotor performance improves rapidly during the embryonic stage so that it is functional at hatching.

In anurans, the process of metamorphosis directly impairs locomotor performance (Fig. 1a; Wassersug & Sperry 1977; Huey 1980; however, see Walsh, Downie & Monaghan 2008a). This 'ontogenetic performance valley' is the result of a developmental trade-off between the functions of the tail and limbs. The tail contributes to the larval form of axial locomotion but as it is resorbed during metamorphosis, swimming performance declines and eventually disappears. Adult frogs use limb-based locomotion but development of the limbs produces drag that will tend to slow the larval swimming mode (Dudley, King & Wassersug 1991). Simultaneously, the tail may not only interfere with terrestrial hopping by limiting the take-off angle of a jump, but it also has inertia and induces drag during adult (kick) swimming without contributing to thrust production. The result of poor locomotor performance is that anurans are preyed upon most heavily at metamorphic climax (Arnold & Wassersug 1978). This has been considered strong selection favouring decreasing the duration of metamorphosis (Szarski 1957; Williams 1966).

Like frogs, the life histories of most salamanders include a transition from tail-swimming aquatic larvae to adults that rely on the limbs for locomotion (Ashley-Ross & Bechtel 2004; Azizi & Horton 2004). However, the salamander tail is retained through metamorphosis and is used to generate thrust during swimming at all stages of life (Frolich & Biewener 1992; D'Août & Aerts 1999; Azizi & Landberg 2002). Because the tail fin is resorbed during metamorphosis, the capacity for thrust generation during swimming should decrease and locomotor performance is expected to decline as a consequence of this transition (Shaffer, Austin & Huey 1991; Burggren & Just 1992; Wilson 2005). However, our previous study of the larval and adult stages of a plethodontid salamander, *Eurycea*, showed that aspects of performance

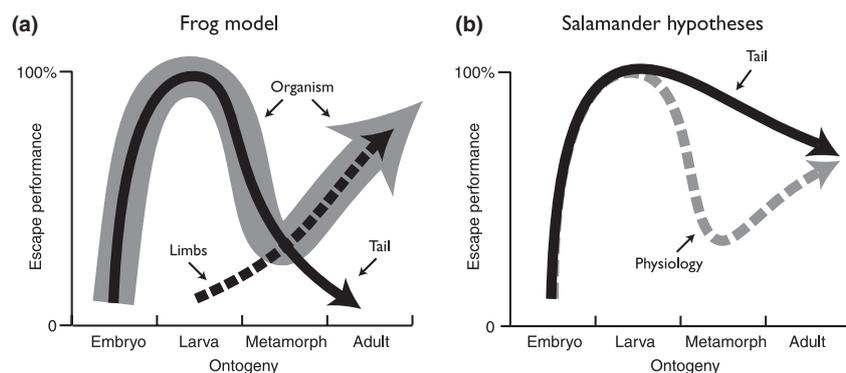


Fig. 1. Ontogenetic models of amphibian escape performance. (a) Previous work has shown that individuals cross an 'ontogenetic performance valley' during metamorphosis as they switch between functional systems (Wassersug & Sperry 1977; Huey 1980). In anurans, this pattern is hypothesized to be from a lack of fully functioning limbs and tail during metamorphosis. However, many other physiological changes occurring during metamorphosis could contribute to poor performance. (b) Salamander escape swimming performance is expected to peak during the larval period and decrease gradually through metamorphosis if it is primarily determined by the size and shape of the tail. Alternately, metamorphosis of respiratory, digestive, sensory and musculo-skeletal systems could impair escape ability.

such as escape distance and duration may remain high after metamorphosis due to kinematic compensation by adults (Azizi & Landberg 2002).

Indirect physiological costs of metamorphosis have also been implicated in the ontogenetic performance valley (Huey 1980). Metamorphosis can be metabolically expensive (e.g. Funkhouser & Mills 1969; Crowder, Nie & Ultsch 1998) and animals may forgo feeding during this period (Deban & Marks 2002). The gut and the hyoid apparatus are restructured, the gills are resorbed, the skin becomes glandular and less permeable to gas exchange, the lateral line system is reduced and blood chemistry changes (Duellman & Trueb 1986). Inefficient respiration, developmental metabolic demands and disrupted sensory systems could all contribute indirectly to decreasing escape performance during metamorphosis.

This study links the ontogeny of body size, tail morphology and escape swimming performance with the complex life history of the spotted salamander (*Ambystoma maculatum*). We take an ontogenetic approach that attempts to explain performance variation in terms of discrete (life stage) and continuous (body size) morphological variation. We test several predictions about escape swimming performance based on the life history of *Ambystoma maculatum*. First, we expect performance to increase with embryonic maturity and peak after normal hatching time – when mortality rates and selective pressure on locomotor ability may be the highest. Next, we test alternative hypotheses about the effect of metamorphosis on escape performance (Fig. 1b). If the physiological costs associated with the process of metamorphosis bear a significant cost to locomotor performance, we expect performance in metamorphosing salamanders to be lower than similarly sized adults and larvae. Alternately, if physiology plays a minor role during metamorphosis, we expect a gradual decline with intermediate performance corresponding to tail fin resorption (Fig. 1b).

Materials and methods

EXPERIMENTAL ANIMALS

Three *Ambystoma maculatum* (Shaw, 1802) egg masses were collected in a vernal pool in Goshen, MA, under a Massachusetts scientific collecting permit (160.02SCRA). In the laboratory, these ~200 eggs were kept at 23 ± 1 °C in a 75-L aquarium filled with aerated water. The water was purified in a reverse-osmosis (RO) system and salts were added to reach physiological osmolarity. Approximately half of the aquarium water was changed daily. As embryos hatched, they were transferred to a 190-L aquarium that contained RO water and an abundance of slate pieces to hide under. Fully metamorphosed salamanders were transferred to a 75-L terrarium and fed 4-week-old crickets (*Acheta domestica*).

During the larval period, salamanders were primarily fed *Tubifex* worms that had been collected from a local trout hatchery. We attempted to satiate the larvae with an abundance of prey items, but a few instances of cannibalization were observed. Only intact animals with less than ~5% of the tail fin missing were filmed. Injured animals were allowed to grow and healed quickly.

The life stage of each individual was assessed based on behaviour (adults crawled out of the water) and external morphology prior to filming (Fig. 2). Embryonic salamanders ($n = 10$) ranged from Harrison stages 37 to 46 (Harrison 1969), had not autonomously hatched from the eggs, possessed balancer organs and lacked hind limbs. Larval salamanders ($n = 40$) had hatched from the egg, possessed large feathery gills, a high tail fin that extended along the dorsum almost to the head and a dark speckled pigmentation pattern. Metamorphosing salamanders ($n = 23$) had a mottled yellow and grey skin colour, reduced gills and a partially resorbed tail fin. Adult salamanders ($n = 15$) had emerged from the water, completely lacked a tail fin and possessed a dark, slate-grey skin colour that became lighter ventrally, with distinct yellow spots and light-coloured metallic flecking along the ventrolateral sides. The term 'adults' in this study refers to the adult external morphology and does not imply that the animals were reproductively mature.

DATA COLLECTION

Salamanders were stimulated to perform escape responses under standardized conditions. The filming arena was filled with fresh, room temperature water to at least two times the tail height of the salamander. Embryonic salamanders were placed into the filming arena while still inside the egg and artificially hatched by gently tearing open the egg membrane with two pairs of forceps. All individuals were allowed to acclimate to the filming arena for 10 min prior to data collection. A tactile stimulus was used to elicit escape responses; a blunted needle perpendicularly oriented to the salamander's long axis was touched to the animal's side between the head and pectoral region. Escape responses were recorded at 500 frames s^{-1} and 1/1000th shutter speed with a Kodak Ekta/Pro high-speed video camera.

One escape response was analysed from each individual for a total of 88 escapes. The cross-sectional experimental design used in this study was motivated by the tendency of individuals to quickly acclimate to the stimulus. Acclimation could significantly alter motivation and thereby confound our interpretation of ontogenetic performance. As a result, the locomotor behaviour studied here did not lend itself to a longitudinal experimental design despite the well-known statistical advantages of such an approach (German 2004).

Salamanders were haphazardly selected from the life stages available. For each individual, we analysed the first complete escape response that occurred at least one body length away from the wall of the filming tank. During the initial 2 months of development, we recorded one individual per day, but as developmental rates declined we sampled the population less frequently so that by the end of data collection, we filmed one individual per week. Immediately following the recording of an escape response, salamanders were overdosed by immersion in a buffered solution of tricaine methanesulfonate (2 g L^{-1}), photographed in lateral view from above for morphometric analysis and preserved in 10% buffered formalin for future study.

MORPHOLOGICAL MEASUREMENTS

Morphometric measurements were made on lateral-view digital photographs using ImageJ software (National Institutes for Health: <http://rsb.info.nih.gov/ij/>). Images were calibrated with a ruler visible in each image ($SE \cong 0.001 \text{ cm}$) before total length, tail height, tail length and tail fin area were measured (Fig. 2). Tail aspect ratio was defined as tail height squared divided by tail area. Normalized tail area was calculated as the square root of tail area divided by total length.

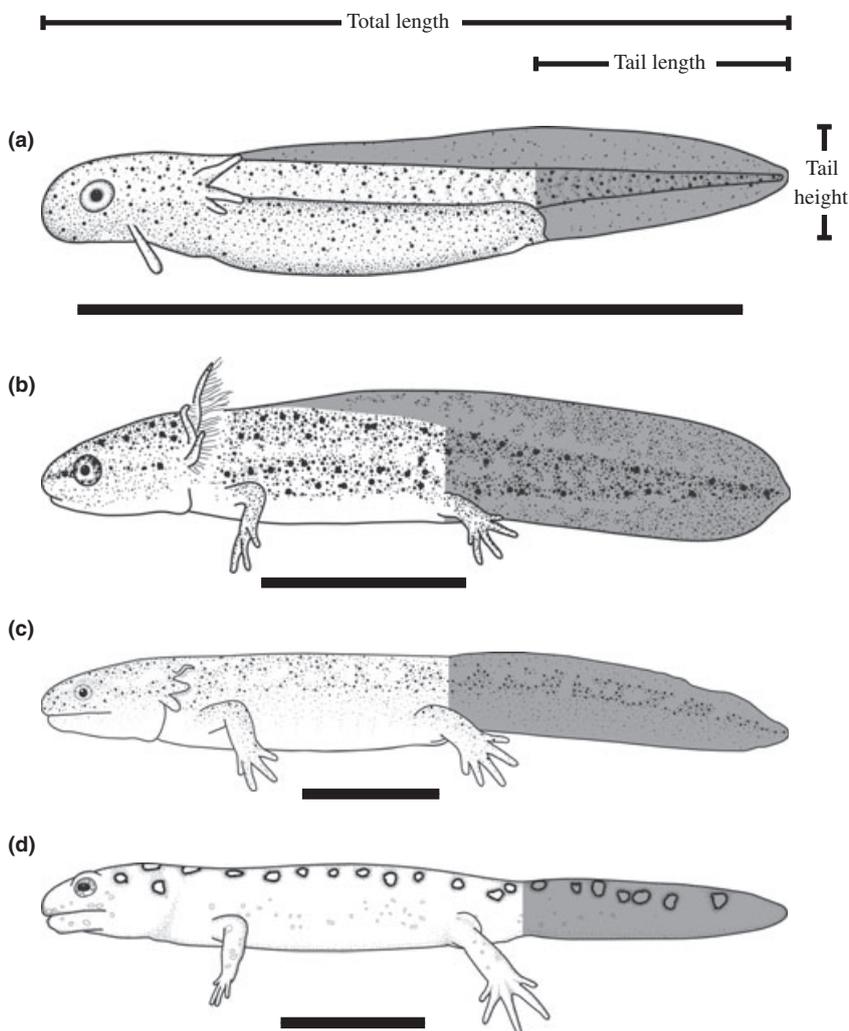


Fig. 2. Life stages of the spotted salamander, *Ambystoma maculatum*: (a) embryonic, (b) larval; (c) metamorphosis; (d) adult. Total length is from the tip of the snout to the tail tip. Tail length is from the cloaca to the tail tip. Tail height is the maximum height perpendicular to the long axis of the tail. Tail area is shaded grey and includes the precaudal part of the tail fin that extends dorsal to the epaxial musculature. Scale bars = 1 cm.

KINEMATIC PARAMETERS

Escape swimming performance variables were calculated as in Azizi & Landberg (2002). We used three video frames from each escape sequence to define the two stages of the escape response and digitized a total of eight points on these three frames to calculate performance parameters. During stage 1, which is the preparatory stage of the escape response, a standing wave of axial bending is generated while the centre of mass of the animal remains relatively still (Domenici & Blake 1997). Stage 1 was defined as beginning the video frame before the onset of movement and ending when maximum axial curvature was reached. Stage 2 is the propulsive phase of the escape response where the wave of axial bending generated during stage 1 travels caudally, generating thrust and translating the animal through the water (Gray 1933; Weiss 1973). Kinematically, stage 2 was defined as beginning at maximum curvature and ending when the crest of the passing wave had propagated off the body. To quantify performance, we digitized points on the tip of the snout, the pectoral girdle and the tail tip at the beginning and end of stage one. We also digitized the position of the snout and pectoral girdle at the end of stage 2.

Escape angles were quantified by calculating the rotation of a line going through the digitized points on the tip of the snout and the pectoral girdle. The initial orientation of the salamander before the escape was defined as 0° . The position of these two digitized points at maximum curvature and the end of stage 2 was used to calculate the

stage 1 and final escape angles respectively. Duration of the escape response was calculated by multiplying the number of frames in each stage by the frame interval (2 ms). We use bending coefficient (one minus the distance from the tail tip to the tip of the snout divided by total length), as our measure of maximum body curvature at the end of stage 1. Bending coefficient therefore increases with body curvature (Azizi & Landberg 2002). Sometimes the tail and the head cross at maximum curvature and the snout-to-tail tip distance is then recorded as negative, which makes the bending coefficient > 1 . Distance travelled during stage 2 was calculated as the linear distance that the pectoral girdle moved from the end of stage 1 to the end of stage 2. Average swimming speed was calculated by dividing this distance by the duration of stage 2.

RECONSTRUCTING ONTOGENY

The goal of this study was to model the ontogeny of escape behaviour with cross-sectional data from a laboratory-reared population. We used a combination of size-based and life stage-based inferences to construct a composite view of ontogenetic change in escape performance. Developmental rates of salamanders vary widely, but through the early larval period, total length predicts developmental state better than age (Brandon 1961; T. Landberg, unpublished data). Therefore, over the first half of our population's size range (0.9–4.0 cm total

length), the data were interpreted as though increases in total length also reflected increases in ontogenetic development.

Metamorphosis naturally occurs across a broad range of total lengths (Wilbur & Collins 1973; Wilbur 1976; Werner 1986). In the size range where metamorphosis occurs (between 4 and 6.5 cm in our data set), animals with identical total lengths may be at different developmental stages and animals at identical stages of development may have different total lengths. To visualize metamorphosis, we constructed life stage means (shown \pm standard deviation and 95% confidence limits in Figs) for the three life stages with overlapping total lengths (the larvae that were greater than 4 cm total length ($n = 12$), all the metamorphosing ($n = 23$) and adult ($n = 15$) animals).

STATISTICAL ANALYSIS

We performed formal statistical analyses on eight kinematic and performance variables. For the six linear variables (stage 1 duration, stage 2 duration, total escape duration, bending coefficient, and velocity and distance travelled during stage 2), we used analysis of covariance (ANCOVA) with life stage (larva, metamorph or adult) as the factor and total length as the covariate. To help reduce the probability of Type-I statistical errors, we used $P = 0.01$ as our alpha level. If ANCOVA results were significant, *post hoc* pairwise comparisons (Tukey HSD) of life stages were performed at the 0.05 alpha level. Regression analysis was used to examine the relationships between performance and morphology. Statistics were calculated using JMP 5.0 (SAS Institute Inc., Cary, NC, USA).

The two remaining variables (stage 1 and final escape angle) were not included in the ANCOVA and were analysed using polar statistics. We pooled all the individuals within the four life stages and used a multisample Watson–Williams test (Batschelet 1981) to test the null hypothesis that there is no difference between life stages in either stage one or final escape angle.

Results

TAIL MORPHOLOGY

Tail morphology of spotted salamanders changes through ontogeny in three distinct ways (Fig. 3). First, tail area increases with total length throughout the embryonic and larval life stages (Fig. 3a). As the tail fin is resorbed during metamorphosis, tail area decreases substantially so that adults have approximately half the tail area of larvae at a given total length (Fig. 3a). Metamorphs have values intermediate between adults and larvae of the same total length.

Next, normalized tail area is a dimensionless measure of tail shape that describes the amount of tail area relative to the total length of the animal. Normalized tail area increases dramatically during early ontogeny, reaching peak values early in the larval period (Fig. 3b). Normalized tail area declines slightly as larvae grow, but then decreases substantially during metamorphosis. Larvae have *c.* 60% greater normalized tail area than similar-sized adults.

Finally, tail aspect ratio, a dimensionless parameter that describes tail length relative to tail area, declines gradually throughout ontogeny (Fig. 3c). Thus, smaller animals at earlier points in ontogeny have greater tail area relative to tail

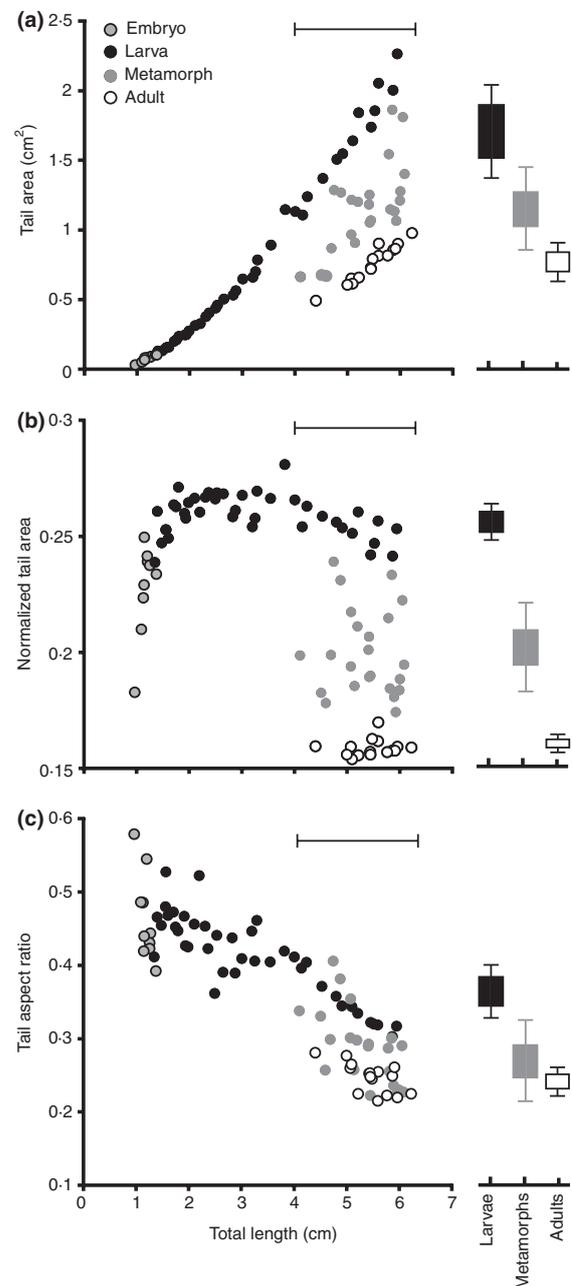


Fig. 3. Tail growth and development of the spotted salamander, *Ambystoma maculatum*. Each point shows tail morphology of a different individual measured just after escape performance was recorded. Embryonic, larval, metamorphosing and adult life stages are represented by differently shaded circles. The bracket above each panel shows the size range (4 cm < total length < 6.5 cm) used to construct life stage means. Boxes represent life stage means \pm 95% confidence limits (on the same Y-axis as the individual data points). Error bars show \pm 1 standard deviation of the mean. (a) Tail area: ontogenetically, tail area increases with total length reaching a maximum during the larval period. Metamorphosis entails resorption of the tail fin and occurs over a range of total lengths in different individuals. (b) Normalized tail area: this dimensionless measure of tail shape is defined as the square root of tail area divided by total length. Higher values indicate greater tail area relative to total length. (c) Tail aspect ratio: this dimensionless measure of tail shape is defined as tail height squared, divided by tail area – therefore higher values indicate greater tail height relative to tail area.

length (high aspect ratios) than larger animals at later stages of development.

ESCAPE RESPONSE

The basic kinematic patterns of the escape response did not vary significantly through ontogeny. Neither escape angles nor bending coefficients differed significantly among life stages. At the end of stage 1 of the escape response, when the animals had reached maximum curvature, the head angle was *c.* 180° away from the initial position (Fig. 4). A multisample Watson–Williams test for angular homogeneity showed no significant effect of life stage on stage 1 angle (Table 1). During stage 2 of the escape response, the animals counter-rotated *c.* 90°, which oriented the animals' final escape angle more or less directly away from the stimulus (Figs 4a,b). A multi-sample Watson–Williams test for angular homogeneity

showed no significant effect of life stage on final escape angle (Table 1). Bending coefficient was used as a measure of axial bending during an escape response. Bending coefficient values were generally high (compared to most fish species) throughout ontogeny, indicating that spotted salamanders were using high body curvature during escape responses (data not shown). There were no distinct ontogenetic trends in bending coefficient and no statistically significant effects of life stage or total length (Table 1).

Escape duration, velocity and distance all change dramatically through ontogeny (Fig. 5). Total escape duration decreases rapidly through the embryonic period and reaches a minimum when the larvae are *c.* 2 cm total length (Fig. 5a). After this size, total escape duration increases with development and total length. Within the three similarly sized life stages, there was a significant and positive effect of size and a significant effect of life stage on total escape duration

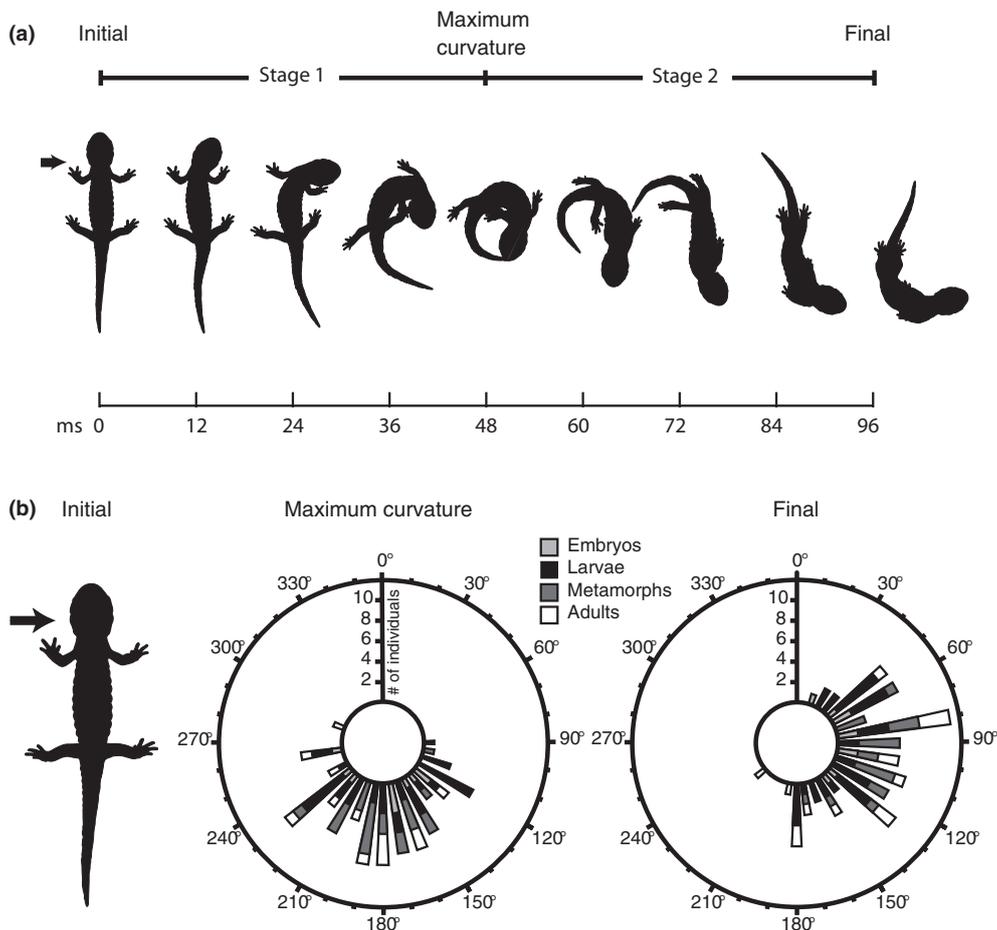


Fig. 4. Escape response kinematics and escape angles of the spotted salamander, *Ambystoma maculatum*. (a) Sequence of illustrations from an escape response of a 5.5-cm long adult. Images are spaced 12 ms apart. Each tick mark on the time scale bar is in the same fixed place relative to the corresponding salamander illustration. (b) Polar stack histograms of escape angles. Escape angles are defined by a line going through the tip of the snout and the pectoral girdle. The four life stages are represented by different shades of grey. The number of individuals with escape angles in 10° bins increases radially. The initial position of each salamander's escape response was standardized to begin at 0° with the stimulus (arrow) coming from the left. Rotation begins clockwise and at the end of stage 1, when the salamanders reach maximum curvature, the anterior portion of the body has rotated *c.* 180°. During stage 2, salamanders counter-rotate *c.* 90° to reach their final escape angle, which is directed away from the stimulus. There is no statistical difference between the mean escape angles of the four life stages at the end of stage 1 or 2 (Watson–Williams test; Table 1).

Table 1. ANCOVA statistics for *Ambystoma maculatum* escape response performance

Parameter	Source	F-ratio	P-value*	Stages differ†
Final angle	Life stage	2.34‡	0.0788	None
Stage 1 angle	Life stage	1.72‡	0.169	None
Stage 2 distance	Life stage	0.73	0.4889	None
Stage 2 distance	Total length	17.3	0.0001	
Stage 2 velocity	Life stage	8.95	0.0005	A < (M,L)
Stage 2 velocity	Total length	9.74	0.0031	
Total escape duration	Life stage	5.31	0.0084	A > (M,L)
Total escape duration	Total length	14.9	0.0004	
Stage 2 duration	Life stage	3.19	0.0505	None
Stage 2 duration	Total length	10.6	0.0021	
Stage 1 duration	Life stage	8.73	0.0006	(A,L) > M
Stage 1 duration	Total length	11.8	0.0013	
Bending coefficient	Life stage	4.44	0.0173	None
Bending coefficient	Total length	0.94	0.3366	

*P-values lower than $\alpha = 0.01$ are shown in bold.

†Life stage differences are based on Tukey *post hoc* tests with $\alpha = 0.05$. Life stages inside brackets are not significantly different; A = adult; M = metamorphs, L = larvae.

‡Polar test statistic equivalent of F-ratio.

(Table 1). Adults have longer escape durations than larvae and metamorphs (Table 1; Fig. 5a). Stages 1 and 2 were similar in duration and contributed *c.* equally to total escape duration throughout ontogeny (Table 1).

Average escape velocity during stage 2 of the escape response also changes dramatically throughout ontogeny (Fig. 5b). The smallest and largest animals in our data have the lowest escape velocities. Escape velocity increases from $\sim 15 \text{ cm s}^{-1}$ in the smallest embryo up to $\sim 55 \text{ cm s}^{-1}$ early in the larval period. Among the three similarly sized life stages, there were significant effects of both total length and life stage on escape velocity (Fig. 5b; Table 1). Larvae and metamorphs are statistically indistinguishable from each other and both have mean escape velocities that are significantly higher than adults (Table 1). Metamorphosing animals had intermediate escape velocities when compared to larvae and adults (Fig 5b) indicating escape velocities declined gradually ontogenetically and did not show an abrupt decline during metamorphosis (i.e. metamorphosing salamanders did not have the lowest velocities).

The distance travelled during stage 2 of the escape response increased similarly with total length across all life stages (Fig. 5c). Among the three similarly sized life stages, there was a strong size effect, but no effect of life stage (Table 1).

Table 2 shows the results of regression analysis between morphology and performance. Total length is significantly correlated with escape distance, velocity and duration. Of the three tail parameters (area, normalized area and aspect ratio), only normalized tail area was significantly correlated with all three performance measured (at $\alpha = 0.01$).

Discussion

PEAK PERFORMANCE DEVELOPMENT

We predicted that the need to develop escape behaviour combined with high predation of early larva would select for

escape swimming performance to increase rapidly in embryos and peak in the early larval period. This prediction was strongly supported for escape velocity and escape duration (Fig 5a,b). Both of these variables had curvilinear relationships with total length that were best fit with second-order polynomials that peak near 2–3 cm total length (Table 2). Relative tail area followed a similar pattern (Fig. 3b).

Embryonic development of performance was rapid compared to large larvae, metamorphs and adults with small increases in total length corresponding to large increases in performance (Fig. 5a,b). Before Harrison stage 37, there is no coordinated escape response, although uncoordinated bending in one direction precedes the development of a complete escape response (Harrison 1969; data not shown). Performance increased rapidly in embryos so that, at room temperature, spotted salamanders take *c.* 1 week for to go from zero performance (stage 36) to near peak values at hatching. This pattern supports the hypothesis that hatchling swimming performance is a target of natural selection because escape behaviours must be fully functional at hatching to survive predators (e.g. Sih & Moore 1993 Warkentin 1995; Gibb, Liu & Swanson 2007).

The rapid performance increase in spotted salamanders is similar to that shown in studies of escape swimming in fishes (several salmonids and a catostomid), in which improvements in performance were coincident with resorption of the external yolk-sac and development of the caudal (tail) fin (Hale 1999; Gibb *et al.* 2006). There are obvious advantages to resorbing a large external yolk-sac; however, the tail fin may generally be more important because halibut, for example, resorb their yolk-sacs long before performance peaks (Gibb *et al.* 2006). Spotted salamander larvae do not have external yolk sacs but they do have internal yolk that is absorbed before and during the hatchling stage (Harrison 1969). Given the rapid development of performance prior to exogenous feeding in young larvae, yolk quantity and quality is likely to be integral to a salamander's ability to increase escape

performance during embryonic and hatchling development by increasing body size, developmental stage and tail fin size.

Studies of escape ability and other anti-predator behaviours often find rapid early development of performance in small or young individuals (Carrier 1996). Survival time with lethal predators increases as embryonic and tadpole development proceeds in the red-eyed tree frog (*Agalychnis*) (Warkentin 1995). Similarly, in a direct-developing frog (*Eleutherodactylus*), a comparison of jumping performance between artificially and normally hatched individuals showed that performance improves rapidly during stages of ontogeny around normal hatching time (Buckley, Michael & Irschick 2005). The locomotor performance of some mammalian species follows a similar pattern. For example, running speed in wild guinea pigs reaches the adult level after only 20 days of development (Trillmich *et al.* 2003). Similarly, young hares were found to accelerate more rapidly than adults (Carrier 1996). This pattern is not limited to locomotor performance. Young rattlesnakes can shake their rattle at higher frequencies than adults as part of their anti-predator repertoire (Moon & Tullis 2006). These studies are consistent with the idea that heavy predation pressures on young individuals coincide with peaks in anti-predator behaviour performance.

A peak in escape swimming performance is consistent with previous studies arguing that changes in muscle architecture, fibre-type development and neuromuscular integration contribute to the sharp increase in performance during early ontogeny (e.g. Gibb *et al.* 2006; Thompson & Kier 2006). The performance peak we predicted based on tail shape (Fig. 1b) and observed (Fig. 5a,b) is consistent with previous studies and a general model of teleost fishes (Hale 1999; Gibb *et al.* 2006). This pattern arises from larval musculoskeletal development and increases in relative tail area followed by negative effects of allometry in adults (e.g. mass increases faster than the ability to produce thrust; Gibb *et al.* 2006). A broader sample of performance curves from organisms with different life histories and predation regimes will help discern how performance peaks evolve.

METAMORPHOSIS

The substantial declines in performance that were previously documented in frogs during metamorphosis (Fig. 1a; Wassersug & Sperry 1977; Huey 1980) were not found in spotted salamanders. Surprisingly, we found no performance differences between larvae and metamorphosing salamanders (Table 1). Metamorphosing salamanders were largely intermediate in performance (Fig. 5), however, providing evidence for the gradual performance decline model (Fig. 1b). This gradual reduction in performance is interpreted as a consequence of changes in tail shape during metamorphosis. As the tail fin is resorbed (Fig. 2), tail depth and the potential to generate thrust are reduced. Given the gradual decline in performance during metamorphosis, we find no evidence suggesting a radical disturbance of escape responses due to metamorphic changes in sensory, metabolic or other physiological systems (Fig. 1b).

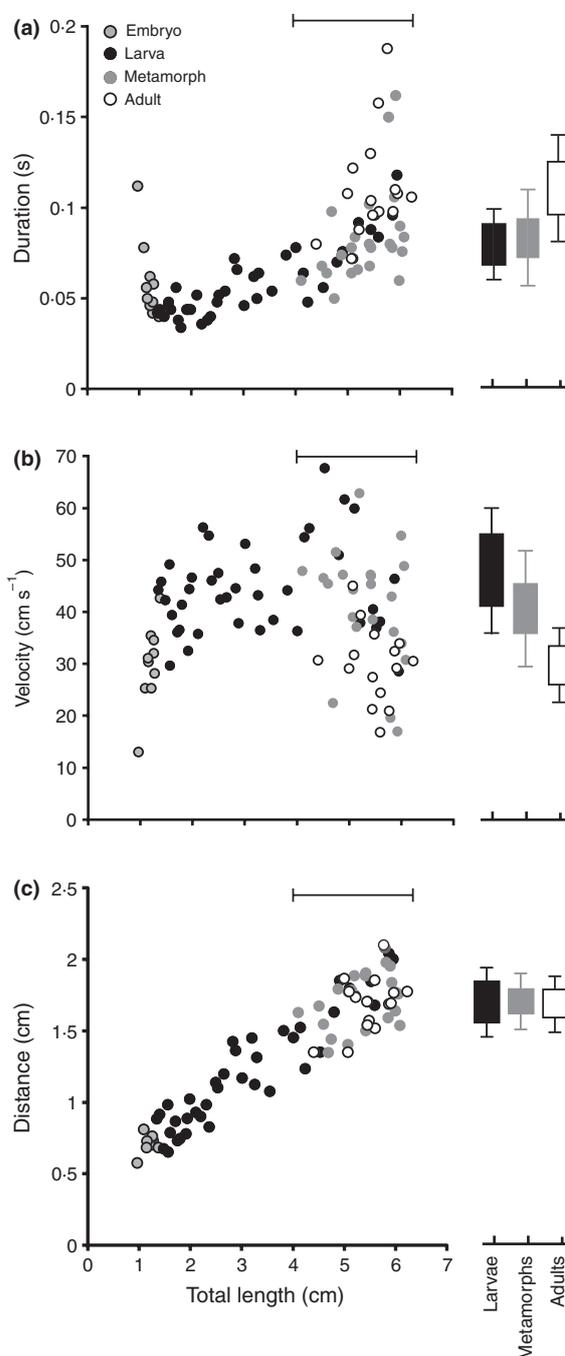


Fig. 5. Escape swimming performance of the spotted salamander, *Ambystoma maculatum*. Symbols are the same as in Fig. 3. (a) Total escape response duration reaches a distinct ontogenetic peak early in the larval period. Metamorphosing salamanders and similar-sized larvae are not statistically different from each other, but both have shorter total escape durations than adults (Table 1). Increasing total length is correlated with longer total escape duration in the three post-embryonic life stages (Table 1). (b) Average swimming velocity during stage two of the escape response increased in embryonic and larval salamanders and then decreased during metamorphosis. Larvae and metamorphosing salamanders are not statistically different, but both have shorter total escape durations than adults (Table 1). Increasing total length is correlated with reduced swim speed in the three post-embryonic life stages (Table 1). (c) Distance travelled during stage two of the escape response (half a swimming stride) increased linearly with total length, but there is no effect of life stage (Table 1).

Table 2. Regression statistics for morphology and escape performance ($n = 88$)

Response (y)	Predictor (x)	Equation	R^2	P -value
Escape distance (cm)	Total length (cm)	$y = 0.46 + 0.023x$	0.87	<0.0001
Escape distance (cm)	Total length (cm)	$y = 0.55 + 0.022x - 0.0002(x - 38.9)^2$	0.88	<0.0001
Escape distance (cm)	Normalized tail area	$y = 2.59 - 5.37x$	0.24	<0.0001
Escape distance (cm)	Tail area (cm ²)	$y = 0.87 + 0.006x$	0.64	<0.0001
Escape distance (cm)	Aspect ratio	$y = 2.64 - 3.58x$	0.63	<0.0001
Duration (s)	Total length (cm)	$y = 0.03 + 0.001x$	0.46	<0.0001
Duration (s)	Total length (cm)	$y = 0.004 + 0.001x + 0.00004(x - 38.9)^2$	0.54	<0.0001
Duration (s)	Normalized tail area	$y = 0.19 - 0.51x$	0.45	<0.0001
Duration (s)	Tail area (cm ²)	$y = 0.055 + 0.0002x$	0.18	<0.0001
Duration (s)	Aspect ratio	$y = 0.15 - 0.21x$	0.45	<0.0001
Velocity (cm s ⁻¹)	Total length (cm)	$y = 39.8 - 0.01x$	0.0002	0.88
Velocity (cm s ⁻¹)	Total length (cm)	$y = 54.8 - 0.19x - 0.02(x - 38.9)^2$	0.24	<0.0001
Velocity (cm s ⁻¹)	Normalized tail area	$y = 12.1 + 121.0x$	0.2	<0.0001
Velocity (cm s ⁻¹)	Tail area (cm ²)	$y = 36.1 + 0.04x$	0.04	0.056
Velocity (cm s ⁻¹)	Aspect ratio	$y = 1.5 + 22.3x$	0.04	0.063

We consider three independent explanations for this pattern. First, salamander metamorphosis involves a far less dramatic transition than anuran metamorphosis and may therefore bear relatively low indirect costs. Second, the indirect costs of metamorphosis may have little effect on escape performance. As escape responses are hard-wired behaviours occurring over a short period of time, they may not completely reflect the increased physiological burden associated with metamorphosis. It is likely that such indirect costs may disproportionately affect endurance locomotion more than anaerobic behaviours such as burst or escape swimming performance (Gibb & Dickson 2002). Third, as other vulnerable life stages have been shown to behaviourally compensate for disadvantageous morphologies (Azizi & Landberg 2002; Irschick *et al.* 2005), metamorphosing spotted salamanders may be performing at a higher percentage of their performance potential. Such compensation is supported by the relatively high performance of metamorphosing salamanders – which was statistically indistinguishable from larvae despite having much less tail area (compare Figs 3b and 5a,b).

Anurans in the process of metamorphosis undergo a rapid transformation from a tadpole that uses the tail for locomotion to a frog that relies on the limbs for propelling itself away from predators (Fig 1a). Metamorphosing anurans often show poor locomotor performance during this radical shift between locomotor modes. This appears to be a consequence of both the tail and the limbs being less-than-fully functional during metamorphosis (Arnold & Wassersug 1978; Huey 1980). Additionally, the tadpole tail may limit the take-off angle for frog-like hopping while the emerging limbs create drag during tadpole-like swimming (Wassersug 1989; Dudley, King & Wassersug 1991; Liu, Wassersug & Kawachi 1996). Reduced locomotor performance during metamorphosis results in high mortality rates for animals at metamorphic climax because individuals at this life stage escape predation less often than similarly sized larvae and adults (Wassersug & Sperry 1977). Consequently, predation on vulnerable metamorphosing individuals is considered an evolutionary selective pressure favouring rapid and synchronized

metamorphosis (Wassersug & Sperry 1977; Crowder, Nie & Ultsch 1998; DeVito *et al.* 1998). A recently discovered exception to this pattern appears in a fully aquatic frog, *Xenopus*, which does not undergo a dramatic performance deficit during metamorphosis (Walsh, Downie and Monaghan 2008a,b). This species is unusual among frogs in its highly derived posture and morphology, unique locomotor kinematics (Hoff & Wassersug 1986) and aquatic preferences.

This observed pattern of relatively high escape performance in metamorphosing salamanders suggests that evolutionary pressure from predators to decrease the duration of salamander metamorphosis may be less than in most anurans. Data on metamorphic duration of salamanders are scarce, but it is generally thought to last longer than the more dramatic transformation of frogs (Norman 1985; Downie, Bryce & Smith 2004). If this relationship is valid, then high metamorphic escape performance relative to that in anurans may contribute to relaxing selection on the duration of salamander metamorphosis.

MORPHOLOGY AND PERFORMANCE

Our results suggest that the normalized tail area is the best predictor of escape swimming performance. Escape performance (velocity and duration) and normalized tail area increased in embryos and hatchlings until the larvae were 2–3 cm long. These ontogenetic peaks early in the larval period suggest a strong link between normalized tail area and two measures of escape performance (compare Figs 3b and 5a,b). The relationship between morphology and performance is supported by the fact that normalized tail area was the only one of the three metrics of tail morphology to show a statistically significant relationship with both escape swimming velocity and escape duration (Table 2). This result is consistent with previous studies of aquatic vertebrate tail fin function (e.g. Hoff & Wassersug 2000; Van Buskirk & McCollum 2000; Dayton *et al.* 2005; Wilson, Kraft & Van Damme 2005; Gibb, Liu & Swanson 2007) and we suggest future researchers consider reporting normalized tail area.

Escape distance increased linearly with salamander total length. Kinematically, escape distance in this paper is equal to one half of a swimming stride (Fig. 4). This linear pattern should not be surprising as previous studies of aquatic locomotion reported approximately constant length-specific stride length with increasing size (e.g. Bainbridge 1958; Videler & Wardle 1991). The surprising result is that large ontogenetic differences in tail morphology do not affect this distance (Fig. 5c). A large sample of young salmonids showed a similar pattern, where different species had a consistent relationship between size and escape distance despite morphological differences (Hale 1999). This metric of aquatic stride length appears shape-neutral; total length maintains a universal relationship with escape distance (stride length), which is not modified by development and tail shape. However, when escape distance is defined with a specified time interval, the number of strides used in a given time may differ and this neutrality may break down.

Our result that size has a negative effect on performance highlights the need to separate the effects of ontogenetic shape change from size effects (captured in the ANCOVA with the life stage factor and the total length covariate). A similar previous study found body size (mass) had positive effects on burst swimming velocity (but negative effects on muscle contraction duration) (Bennett, Garland & Else 1989). However, in that study, increased size and performance were correlated with a relatively longer tail. We also found relatively larger tails contributed to performance, but within spotted salamanders life stages (large larvae, metamorphs and adults), we found negative effects of size on performance (escape duration increased and velocity decreased) (Figs 3 and 5; Table 1).

CONCLUDING REMARKS

Our results highlight a complex relationship between body size, tail shape, developmental stage and locomotor performance. We find that some performance variables may primarily be correlated with body size whereas others additionally depend on life stage (contrast Figs 5a,b with c). We find that ontogenetic changes at the peak of performance alter the relationship between size and performance. On one side of this performance peak, embryos and hatchlings show increased swim speed and decreased escape duration with increasing body size and development (Fig. 5a,b). After performance peaks ontogenetically, increases in body size and development have negative correlations with performance (Fig. 5a,b, Table 1). This result reiterates that understanding links between morphology and performance requires an ontogenetic framework (Arnold 1983). We also find that metamorphosis does not dramatically reduce escape swimming performance in spotted salamanders. Escape performance gradually declined with tail resorption, but a major physiological disruption (as in Fig. 1) was not observed – in fact, metamorphs did better than expected. More information on the forces that shape the duration of metamorphosis (e.g. Orlofsky & Hopkins 2009) as well as the ontogeny of inducible anti-predator defences (e.g. Wilson, Kraft & Van Damme

2005) are needed to complete our understanding of the dynamic forces shaping ontogenetic performance trajectories and life history evolution.

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