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Body shape, burst speed and escape behavior of larval anurans

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Variation in behavior, morphology and life history traits of larval anurans across predator gradients, and consequences of that variation, have been abundantly studied. Yet the functional link between morphology and burst-swimming speed is largely unknown. We conducted experiments with two divergent species of anurans, *Scaphiopus holbrookii* and *Rana sphenocephala*, to examine how behavior and morphology influence predator vulnerability, and whether tadpole shape is related to burst-swimming performance. *Scaphiopus holbrookii*, a species that typically uses ephemeral pools, was more active, exhibited slower burst speeds, and was more susceptible to predation than *R. sphenocephala*, a species associated with more permanent aquatic sites. Our analysis of morphology and burst speed defined a shared axis of shape variation associated with burst-swimming speed regardless of species. Tadpoles with a deeper tail fin and muscle and a smaller body produced faster speeds. The nature and breadth of the morphology–speed relationship suggests it may represent a generalized ecomorphological paradigm for larval anurans.

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Predators strongly influence the composition of many species assemblages (Paine 1966, Burton et al. 2001, Knapp et al. 2001). In aquatic environments, predators are relatively uncommon in habitats that are short lived (Babbitt et al. 2003). However, prey that inhabit ephemeral pools suffer greater resource competition because predators are not culling the population of prey and resources are often limited (Newman 1987). Furthermore, species inhabiting ephemeral sites have little time available for growth and development. Thus a number of tradeoffs potentially arise for the traits of aquatic organisms across hydroperiod gradients. Species that inhabit short-lived breeding sites must maintain a relatively high feeding rate to facilitate rapid growth, because delaying time to metamorphosis greatly increases the risk of death due to desiccation (Newman 1987). Susceptibility to predation may not be as ecologically important to these species since colonization rates, species richness, and abundance of aquatic predators is low in ephemeral sites compared to longer lasting sites (McPeek 1990, Wellborn et al. 1996, Skelly 1997). Species found in temporary pools tend to be more active, more susceptible to predation, and superior resource competitors compared to species that inhabit perennial sites (Woodward 1983). Species inhabiting more permanent sites tend to exhibit defense strategies that enable them to co-exist with potential predators, which typically result in decreased activity rates and poorer competitive abilities (Woodward 1983, Werner and Anholt 1993, Van Buskirk and Relyea 1998, Wissinger et al. 1999, Laurila 2000, Relyea 2002, Wellborn 2002).

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It is well known that many species exhibit phenotypic plasticity in behavior and morphology in response to predator presence (Lawler 1989, Smith and Van Buskirk 1995, Eklov and Werner 2000, Trussell 2000, Relyea 2001, Richardson 2001a, Van Buskirk 2001, Altwegg 2002, Langerhans and DeWitt 2002, Van Buskirk et al. 2003, Laurila et al. 2004) and these responses are often shown to increase survivorship (McCollum and Van Buskirk 1996, Van Buskirk et al. 1997, Van Buskirk and McCollum 1999, DeWitt and Langerhans 2003, Teplitsky et al. 2005). Higher activity rates in particular affect predator encounter rates through enhanced detection and increased probability of encountering a predator through spatial movement (Lawler 1989, Werner and Anholt 1993, Skelly 1994, Anholt and Werner 1995, Johansson and Rowe 1999, Nicieza 1999, Bryan et al. 2002, Sih and McCarthy 2002, Teplitsky et al. 2003). Burst speed is a trait that is assumed to be correlated with greater survivorship in fish (Webb 1986a, Swain 1992, O'Steen et al. 2002, Langerhans et al. 2004), anurans (Feder 1983, Jung and Jagoe 1995, Watkins 1996, Teplitsky et al. 2005), lizards (Shine 1980, Greene 1988, Miles 2004), caudates (Hileman and Brodie 1994, Storfer 1999), mammals (Wirsing 2003) and damselflies (McPeek et al. 1996). Morphology should have a strong link to swimming speed, as suggested by biomechanical principles and empirical work (Wassersug and Hoff 1985, Wassersug 1989, Liu et al. 1996, Hoff and Wassersug 2000), and thus should play a role in predator escape abilities. While an abundance of research has examined differential survival rates of tadpoles exposed to various predator regimes (Wilbur et al. 1983, Werner and McPeek 1994, Skelly 1997, Dayton and Fitzgerald 2001), very few studies have examined variation in susceptibility to predation within or between anuran species in relation to burst-swimming speed (Watkins 1996), and none have defined a detailed morphological axis that may explain and predict speed. While predator-induced morphologies are well-known in a number of anuran species, several studies have suggested there is no relationship, or only a weak one, between morphology and swimming performance in larval anurans (Van Buskirk and McCollum 2000a, 2000b, Richardson 2001b, 2002).

In this paper we examined susceptibility to predation by dragonfly larvae (*Anax junius* Drury, 1770) of two anuran species, *Scaphiopus holbrookii* Harlan, 1835 (eastern spadefoot toad) and *Rana sphenocephala* Cope, 1886 (southern leopard frog), in relation to activity level, burst speed and morphology. We then examined the potential influence of morphology on burst speed in order to better understand the link between morphology and performance as it relates to increased survivorship. We chose to use *S. holbrookii* and *R. sphenocephala* in our experiments because they co-occur regionally in eastern Texas, USA, and show complete overlap in their temporal breeding periods, but do not utilize the same breeding habitats and are distantly related. *Scaphiopus holbrookii* breed in ephemeral pools from February to May, and metamorphose in approximately 14 to 21 days. *Rana sphenocephala* breed year round in more perennial sites (lasting from several months to year-round) and metamorphose in approximately 45 to 180 days. We collected individuals as eggs to minimize the potential for predator-induced changes in morphology during development. We conducted four main tests: (1) tested for differences in activity between *S. holbrookii* and *R. sphenocephala*; (2) measured differences in susceptibility to predation by recording the species first preyed upon in mixed experimental communities and by comparing the ratio of number of attacks to successful attacks for each species in single prey settings; (3) tested for differences in burst speed and morphology between *S. holbrookii* and *R. sphenocephala* tadpoles; and (4) examined whether morphology could predict burst speed within and among species.

Material and methods

Tadpoles used in our experiments were collected as eggs from the field between on two occasions in May 2000 and March 2002. We collected *S. holbrookii* eggs from a single pond in which several egg masses were laid. *Rana sphenocephala* were collected as eggs from multiple ponds. Eggs and tadpoles were reared in the laboratory and housed in plastic tubs at densities of approximately five tadpoles per liter and fed ground fish food. Tubs were cleaned on a regular basis. An individual tadpole or *A. junius* was used only one time in the experiments described below. Activity and predation experiments were conducted in 2000 and performance trials were conducted in 2002.

Activity

Activity trials were conducted in the laboratory by replicating behavioral assays in which four conspecific tadpoles were placed in a 50 × 15 cm plastic tub with a water depth of approximately 7 cm. Activity was recorded by standing above the tub and recording the number of tadpoles active at a single moment in time. This method does not record activity levels per se rather it provides the proportion of tadpoles moving at each observation (Skelly 1994). All tadpoles were fed 30 min prior to the start of the activity trials and allowed to habituate for 15 minutes prior to our recording of activity. We then calculated the proportion of tadpoles moving per tub and arcsine-square root-transformed the proportional data to meet assumptions of normality for further analysis. Data were analyzed using unpaired t-test to test for differences in activity between the two species. Activity trials were conducted during a single day and were replicated 75 times for each species for a total of 150 tubs and 600 tadpoles.

Predation experiments

Predation experiments were conducted using similar sized *S. holbrookii* tadpoles (20 randomly sampled; total length $\bar{x} = 21.38$ mm, SD = 1.13) and *R. sphenocephala* tadpoles (20 randomly sampled; total length $\bar{x} = 22.13$ mm, SD = 3.06). Tadpoles were placed in pairs (one of each species) in a 50 × 15 cm plastic tub (water depth of approximately 7 cm) with one larval *A. junius*. Experiments were replicated 65 times with no reuse of individual tadpoles or predators. *Anax junius* was used as a predator in these experiments because it occurs in nearly all of the longer lived pools in eastern Texas and is an effective predator on larval anurans. Tubs were continuously monitored until a predation event occurred, at which time the species captured was noted and the experiment terminated for that particular replicate. Trials lacking a successful predation event (n = 8) were excluded from analysis. We used a binomial test to test for differences between the two species in their susceptibility to predatory dragonfly larvae.

To test for differences in number of successful to non-successful attacks between tadpole species, we randomly selected similar-sized tadpoles from a 3-liter tub and placed four conspecific tadpoles in a 50 × 15 cm plastic tub containing one *A. junius* larva. Experiments were replicated 30 times for each species for a total of 60 tubs and 240 tadpoles. Tubs were continuously monitored for 20 minutes during which all unsuccessful and successful attacks by *A. junius* on tadpoles were recorded. Replicates in which *A. junius* did not attack were removed from further analyses (n = 6). We used a Fisher's exact test to compare differences in the number of successful to non-successful attacks between species.

Performance testing

Because larger tadpoles are generally faster swimmers (Wassersug and Sperry 1977, Van Buskirk and McCollum 2000b, Richardson 2001b, 2002, Arendt 2003), better at escaping predator attacks (Caldwell 1982, Brodie and Formanowicz 1983, Crump 1984) and hind limb development has little handicap on swimming abilities until near metamorphosis (Huey 1980, Liu et al. 1996) we chose to use similar sized tadpoles rather than tadpoles of similar Gosner stage (*S. holbrookii*: $\bar{x} = 23.87$ mm, SD = 2.65; *R. sphenocephala:* $\bar{x} = 24.23$ mm, SD = 2.83). Burst speed was measured by individually placing tadpoles in a 100 × 40 cm glass arena (depth approximately 10 cm) with a 1 × 1 cm grid beneath the arena. We used a Sony digital camcorder (30 frames s^{-1}) placed 2.0 m above the arena to film the simulated predation events. Tadpoles were allowed to habituate for one minute. An attack was simulated by probing the tail with a sharp dissecting probe. Each tadpole was filmed from the time at which the predation attempt was simulated until it stopped swimming. We measured burst speed for 30 tadpoles of each species. After each trial tadpoles were removed from the arena and preserved in 10% formalin. We calculated burst speed by measuring the distance traveled by each individual tadpole over a 0.20 s period immediately following the simulated attack and converting the speeds to mm s^{-1}. We excluded cases where tadpoles moved beyond the view of the camera (*S. holbrookii* = 5 and *R. sphenocephala* = 1). Differences in burst speeds between the two species were compared using an independent t-test. Distance was calculated as the distance from the tip of the head at resting position to the tip of the head after 0.20 s. We chose to calculate burst speed during this 0.20 s period as this is likely to be the most critical period for tadpoles to escape attacks from sit and wait predators such as dragonfly naiads that do not chase their prey after the initial attack. One extreme outlier was removed from all analyses (standardized residual value = 3.74).

Morphometrics

Tadpoles from performance tests that were preserved without damage (n = 46; *S. holbrookii* = 22, *R. sphenocephala* = 24) were photographed through a 55-mm telecentric lens. We acquired 13 landmarks from each tadpole image using MorphoSys V. 1.29 software (Meacham 1993). We digitized seven homologous landmarks directly (points 1–7, Fig. 1) and computed six additional points geometrically as follows. Four landmarks were calculated as pairs of points on the tail fin outline perpendicular to a line connecting the tail tip to the midpoint of the base of the tail muscle at 20% and 60% distance from the tip of the tail (points 8–11, Fig. 1). The last two landmarks were calculated as a pair of points on the body outline perpendicular to a line connecting the snout tip to the midpoint of the base of the tail muscle at 33% distance from the snout (points 12–13, Fig. 1). Landmarks were chosen to characterize overall morphology and ensure coverage of functional

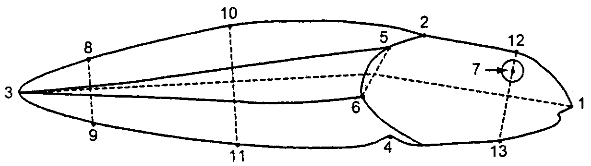

Fig. 1. Landmarks used in morphometric analyses. Consensus configuration (i.e. average of all specimens from both species) depicted. Hypothetical tadpole illustrated.

aspects of shape potentially important for burst-swimming (e.g. depth of the tail fin base, mid-tail fin, tail muscle, and body length).

Landmark coordinates were aligned using generalized least-squares superimposition and used to calculate shape variables (uniform components and partial warps) using tpsRegr software (Rohlf 2000). Uniform shape variation involves global covariation in landmark positions where all landmarks shift together in parallel X or Y directions as a function of some effect in the statistical model. Uniform X variation, for example, would stretch squares into parallelograms and uniform Y variation stretches squares into rectangles. Partial warps are non-uniform components of morphological variation (i.e. localized deformations). These shape variables served as dependent variables in our statistical analyses described below. This method of capturing shape information (geometric morphometrics) facilitates visualization of shape variation (for more information see Rohlf and Marcus 1993, Marcus et al. 1996 and Zelditch et al. 2004). We visualized variation in landmark positions using the thin-plate spline approach, which maps deformations in shape from one object to another using thin-plate splines (Bookstein 1991). Centroid size, the square root of summed, squared distances of all landmarks from their centroid, was used as a covariate in all geometric morphometric analyses. In this study, centroid size was highly correlated with total length ($r \geq 0.99$, $P < 0.0001$ for each species). All statistical analyses were conducted using JMP software (Version 4.0.4, SAS Institute Inc., Cary, NC, USA).

Shape analysis

We investigated two questions involving tadpole shape: 1) do species differ in morphology?, 2) Does morphology predict burst speed? For the first question, morphological data (i.e. 20 partial warps+2 uniform components) were tested for effects attributable to centroid size (covariate) and species using multivariate analysis of covariance (MANCOVA). Heterogeneity of slopes was tested and was not significant. We examined the canonical axis derived from the species term in the MANCOVA to assess the nature of morphological differences among species. We further performed a discriminant function analysis (DFA) to determine the accuracy with which we could assign individuals to the proper species based on shape. To address the second question (are shape and burst speed related?), we first conducted a canonical correlation analysis as a dimension-reducing procedure in order to obtain a morphological index (i.e. linear combination of shape variables) potentially correlated with burst speed, regardless of species. This procedure estimated the relationship between shape and burst speed and generated a canonical axis describing morphological variation potentially associated with burst swimming speed (i.e. an axis reflecting the linear combination of shape variables resulting in the maximal correlation with burst speed). This morphological index was used to examine whether tadpole shape could predict burst speed. We conducted a linear regression examining the relationship between burst speed and the morphological index within each species; we used analysis of covariance (ANCOVA) to evaluate whether slopes differed among species. We initially included centroid size as a covariate in these models, but since it was never significant (all $P > 0.35$), we dropped the term. Morphological differences among species, and variation described by the morphological index, were evaluated by examining the correlations among landmark coordinates and the respective canonical axes, as well as by visualizing morphological variation described by canonical axes using thin-plate spline transformation grids.

Results

Activity, predation and burst speed experiments

The number of *Scaphiopus holbrookii* tadpoles active at any given point was significantly more than *R. sphenocephala* ($t_{74} = 8.80$, $P < 0.001$) with 40% of the tadpoles active ($\bar{x} = 0.39$, $SD = 0.20$) compared to 14% for *R. sphenocephala* tadpoles ($\bar{x} = 0.14$, $SD = 0.15$). Results from pair-wise predation experiments showed that *S. holbrookii* tadpoles were significantly more susceptible to predation than *R. sphenocephala* ($P = 0.0007$), with *S. holbrookii* being the first tadpole captured in 41 of the 56 pair-wise predation trials. There were significant differences in the total number of attacks (non-lethal and lethal) compared to successful attacks (lethal) between the species ($P = 0.019$, Fig. 2) with a ratio of approximately 2:1 (attacks per kill) for *S. holbrookii* and 4:1 for *R. sphenocephala*. Differences in burst-swimming speed between *R. sphenocephala* and *S. holbrookii* tadpoles were highly significant ($t_{51} = 4.60$, $P < 0.0001$). *Rana sphenocephala* tadpoles exhibited faster burst speeds ($\bar{x} = 134$ mm s^{-1}, $SE = 9.89$, $n = 29$) than *S. holbrookii* tadpoles ($\bar{x} = 75$ mm s^{-1}, $SE = 7.74$, $n = 24$, Fig. 3).

Morphometrics

Morphological differences between species were strongly apparent ($F_{22,22} = 62.23$, $P < 0.0001$). Centroid size (covariate) was also significantly correlated with tadpole shape ($F_{22,22} = 4.58$, $P = 0.0004$), indicating multivariate allometry. Species primarily differed in tail tip depth, body length, tail length, tail muscle depth and horizontal position of the eye (Fig. 4, Table 1). Discriminant

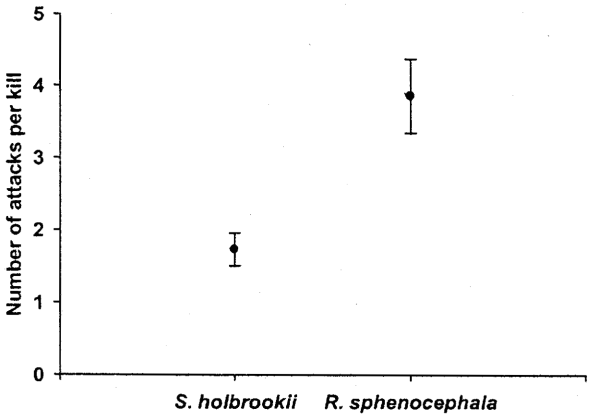

Fig. 2. The mean number of attacks per kill of *S. holbrookii* and *R. sphenocephala* tadpoles from timed predation trials. We only used data in which there was a successful attack upon a tadpole during the timed trial. Thus our estimates are conservative in regards to the ratio of unsuccessful to successful attacks (error bars are ±1 sem). Significantly different at $P = 0.019$.

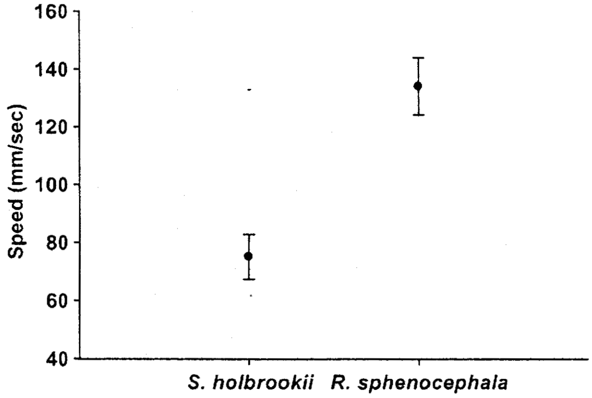

Fig. 3. Mean burst speed for *S. holbrookii* and *R. sphenocephala* (error bars are ±1 sem). Significantly different at $P < 0.0001$.

function analysis was highly significant ($F_{22,23} = 65.05$, $P < 0.0001$) and classified all 46 individual tadpoles to the correct species with a probability of 1.0.

We then used our morphological index to examine the relationship between tadpole shape and burst speed. We found that the morphological index was significantly associated with burst speed in both *R. sphenocephala* ($R^2 = 0.49$, $P = 0.0001$) and *S. holbrookii* ($R^2 = 0.74$, $P < 0.0001$) tadpoles (Fig. 5). ANCOVA revealed that slopes were homogeneous among species (i.e. non-significant interaction term) and that differences in burst speed between species were no longer evident ($P = 0.96$) after controlling for effects of tadpole morphology. Multicollinearity was low (all variance inflation factors < 1.42), indicating that significance tests were not compromised by correlations among factors. These results suggest that the morphological index described functional differences in tadpole shape related to the generation of swimming bursts, and appears largely responsible for differences in burst speed among species. Further support for this conclusion comes from the fact that species exhibited significant differences in morphological index values ($P = 0.0006$), with the faster species (*R. sphenocephala*) exhibiting higher scores (Fig. 5). Thus, it appears that for both species, a relatively deeper tail fin and tail muscle and a smaller body facilitates increased burst-swimming speeds (Fig. 5, Table 1).

Discussion

Our study supports the theory that anurans with relatively short larval periods experience high susceptibility to predators (Woodward 1983, Lawler 1989, Skelly 1994, Dayton and Fitzgerald 2001). As predicted from the hydroperiod gradient theory, *S. holbrookii* were more active, had slower burst speeds, and were more susceptible to predation by *A. junius* larvae than *R. sphenocephala*. On average *S. holbrookii* tadpoles were 2.5 times more active, 50% slower in burst speed and were preyed upon nearly 150% more frequently than *R. sphenocephala* tadpoles. Higher activity increases the probability of encountering sit-and-wait predators and clearly plays a role in the susceptibility of tadpoles to predation, however other morphological and performance factors are also important (Watkins 1997, Van Buskirk 2001, Van Buskirk et al. 2003). *Rana sphenocephala* tadpoles were significantly faster than *S. holbrookii* tadpoles which may either enable them to evade an attack once it is initiated or pull away from the grasp of dragonfly naiads via increased potential to generate thrust causing the tail to rip. If susceptibility to predation were determined entirely by the result of

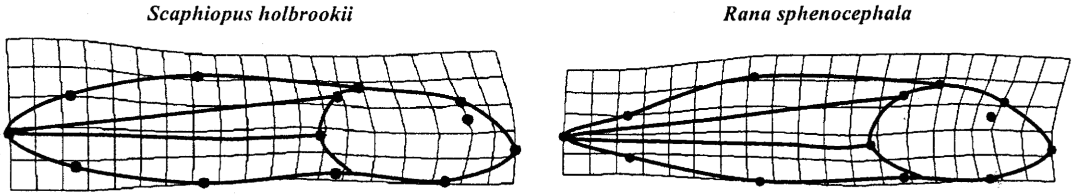

Fig. 4. Thin-plate spline transformations illustrating morphological differences between species. Visualizations were generated with tpsRegr (Rohlf 2000) using landmark coordinates and canonical scores (observed morphological range depicted).

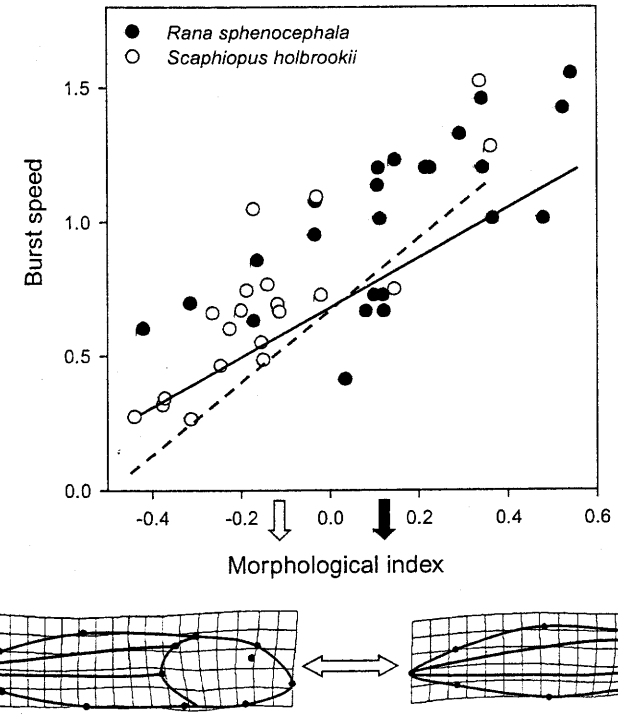

Fig. 5. Relationship between the morphological index (canonical axis, see text) and burst speed for each species (*S. holbrookii*: dashed line, *R. sphenocephala*: solid line). Arrows indicate mean morphological index values for each species (*S. holbrookii*: open arrow, *R. sphenocephala*: filled arrow). Thin-plate spline transformations were generated with tpsRegr (Rohlf 2000) using landmark coordinates and morphological index values (magnified 2 × to more clearly illustrate shape variation).

greater activity leading to increased predatory encounters we would expect a 1:1 ratio of predator attacks to kills (i.e. every attack to be a successful attack); this was not the case in our study. During a predatory strike, *R. sphenocephala* tadpoles were much less likely to be killed than *S. holbrookii* tadpoles. On average it took *A. junius* two attempts to successfully kill *S. holbrookii* tadpoles compared to four attempts for *R. sphenocephala* tadpoles. Moving less (leading to lower predator encounter rates) combined with an increased ability to

Table 1. Pearson correlation between superimposed landmark coordinates and the respective canonical axis. The direction of landmark differences observed in *R. sphenocephala*, relative to *S. holbrookii*, is presented for the species canonical axis. The direction of shifts in landmark positions associated with positive values (i.e. relatively fast tadpoles) is presented for the morphological index. Landmark shifts are only presented for correlation values ≥|0.2|.

Landmark	Species canonical axis	Direction	Speed index	Direction
1X	−0.7076	posterior	−0.4675	posterior
1Y	−0.0634	–	−0.0272	–
2X	0.8915	anterior	0.5639	anterior
2Y	0.5060	dorsal	0.2222	dorsal
3X	−0.7668	posterior	−0.4411	posterior
3Y	−0.0067	–	−0.0581	–
4X	0.6601	anterior	0.1186	–
4Y	−0.2642	ventral	0.0828	–
5X	0.6992	anterior	0.5355	anterior
5Y	0.1906	–	0.1688	–
6X	−0.2128	posterior	−0.2845	posterior
6Y	−0.5069	ventral	−0.2333	ventral
7X	−0.9129	posterior	−0.3910	posterior
7Y	0.2304	ventral	0.0423	–
8X	−0.6625	posterior	−0.3515	posterior
8Y	−0.8949	ventral	−0.4093	ventral
9X	−0.7755	posterior	−0.4416	posterior
9Y	0.8316	dorsal	0.3317	dorsal
10X	0.22996	anterior	0.1653	–
10Y	0.2234	dorsal	0.1196	–
11X	0.0025	–	0.1508	–
11Y	0.2371	dorsal	−0.0540	–
12X	−0.5299	posterior	−0.3662	posterior
12Y	−0.0675	ventral	−0.2089	ventral
13X	−0.4097	posterior	−0.2619	posterior
13Y	0.3468	dorsal	0.4051	dorsal

escape predatory attacks lends support to the hypothesis that *R. sphenocephala* is better adapted at evading and escaping predatory encounters with dragonfly naiads. All of the tadpoles in our study were similar in size and had not been previously exposed to predators, yet *R. sphenocephala* tadpoles were significantly better at escaping predators once an attack had been initiated, indicating that morphological differences and or swimming performance likely influence survivorship.

Increased tail depth has been shown to be a common morphological response in several species of larval anurans when reared with predators (Smith and Van Buskirk 1995, McCollum and Leimberger 1997, Lardner 2000, Relyea and Hoverman 2003, Laurila et al. 2004, Relyea 2004, Teplitsky et al. 2004, 2005, Kishida and Nishimura, 2005) and increases the probability of surviving predation (McCollum and Van Buskirk 1996, Van Buskirk et al. 1997, Van Buskirk and Relyea 1998, Relyea and Hoverman 2003, Teplitsky et al. 2005). The functional role of a deep tail in tadpoles is unclear. Manipulative studies in which surgeries were performed on tadpole tails in order to examine the influence of tail shape on swimming abilities have yielded mixed results. Van Buskirk and McCollum (2000b) manipulated tail depths and lengths of gray treefrog (*Hyla versicolor*) tadpoles and found it took a 50% reduction in tail depth or a 30% reduction in length to significantly decrease maximum swimming speed. Hoff and Wassersug (2000) surgically manipulated bullfrog (*Rana catesbeiana*) tadpole tails and found that reducing tail fin depth in the anterior portion of the tail only slightly reduced speed where as reductions in the posterior region of the tail greatly reduced maximum velocity. Richardson (2002) found that for *R. sphenocephala* tadpoles collected from the field, speed was correlated with long narrow tails. Teplitsky et al. (2005) showed that swimming speed of *Rana dalmatina* tadpoles, reared from eggs, was positively correlated with greater tail muscle depth and length. Our study found that tadpoles with an overall deeper tail and tail muscle and a smaller body, irrespective of species, exhibited faster burst speeds (Fig. 5). Our finding lends support to the hypothesis that traits often observed in predator-induced morphologies may have functional value (increased speed) and play a role in increasing survival during predatory encounters for *S. holbrookii* and *R. sphenocephala*. Furthermore, the observed relationship between morphology and swimming performance (i.e. greater speed associated with greater allocation in thrust-propelling regions) is in accord with biomechanical principles (Webb and Blake 1985, Webb 1986b, Walker 1997) and recent empirical work with fish (Langerhans et al. 2004).

Recent studies have suggested that deeper tails enable tadpoles to escape predation due to non-lethal ripping of the tail fin when tadpoles are grabbed by a predator (Doherty et al. 1998, Van Buskirk et al. 2003). Doherty et al. (1998) showed that tensile strength in tadpole tails is least in regions where attacks are frequent (i.e. tail fin versus muscle). Additional studies have shown that several species exhibit color markings on their tails in regions where an attack will likely result in only a torn tail rather than death (Doherty et al. 1998, Blair and Wassersug 2000, Hoff and Wassersug 2000). While increased burst speed is assumed to be associated with the ability to outright avoid a predatory attack, an alternative hypothesis is that the same morphology that increases speed also facilitates tail ripping via enhanced thrust. Thus, anti-predator morphology might provide at least two advantages in the presence of predators: directing predator strikes toward less dangerous areas (sensu the "lure effect"; Van Buskirk et al. 2003) and providing increased power/thrust to either escape predators outright or facilitate tail ripping once a predator has grabbed hold.

The two species used in the present study were highly morphologically divergent. According to the hydroperiod gradient theory, we expect a relatively competitor-oriented morphology (large body, small tail) in "ephemeral species" and a relatively anti-predator morphology (large tail, small body) in "permanent species" (Relyea 2002, 2004, Relyea and Hoverman 2003). We found that relationship to be true, the ephemeral species (*S. holbrookii*) exhibited a relatively larger body and the permanent species (*R. sphenocephala*) exhibited a deeper tail fin base and tail muscle. Furthermore, we found that tadpole shape was strongly correlated with burst speed irrespective of species and that faster tadpoles within both taxa were shaped more like "permanent" species. Whether the differences in morphology reflect differential demands on overall morphology in alternative habitats or phylogenetic effects is unclear. However, our results indicate that variation in tadpole morphology plays an important role in swimming performance, that these differences likely affect susceptibility to predation, and the observed relationship between morphology and performance is in accordance with expectations based on the hydroperiod gradient theory.

Results from our speed trials and functional morphology analyses provide a basis for future work examining the relationship between burst speed, morphology, habitat use and life history in larval anurans. As observed in this study, we predict that species with a morphology similar to the low end of our morphological index (Fig. 5) will exhibit relatively slow burst speeds; species with morphologies similar to tadpoles at the high end of our morphological index should produce faster burst speeds and be better at escaping predators. While other studies indicate that there are complex interactions between phylogeny, morphology, habitat, growth rate and burst speed among anuran species (Richardson 2001b, 2002, Arendt 2003), our methods revealed a morphological axis that appears functionally related to burst speed within two anuran species. Since our study only examined two species, we were not able to control for many potential phylogenetic effects. However, the fact that we found tadpole shape to be correlated with speed in a similar manner within both species strongly suggests a mechanistic link between morphology and burst speed exists within some, if not many, anurans (Garland and Adolph 1994). Richardson (2002) examined the influence of habitat, family, and morphology on burst speeds of 14 anuran species. Her results showed that there was a significant amount of variation in burst speed among and within both family and habitat groups (habitat groups defined along a predatory axis) and that while the overall evolution of increased burst speed was correlated with shape for some species, size explained most of the variation in swim speed. The two species examined in our study are distantly related, inhabit very different habitats, and yet we found strong evidence for a shared morphological basis for burst speed.

Our results support the theory that behavior and burst-swimming speed play key integrated roles in larval anurans species persistence across a hydroperiod gradient. In addition, our findings suggest a common link between morphology and burst speed in tadpoles: a deep tail and relatively small body increases burst speed in *S. holbrookii* and *R. sphenocephala*, two distantly related and ecologically different species. Owing to its functional relationship with thrust generation, tadpole morphology is likely to play an important role in species persistence across environments that vary in predation regime.

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