

The Consequences of Metamorphosis on Salamander (*Ambystoma*) Locomotor Performance

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Abstract

*Radical shifts in morphology and ecology of salamanders during metamorphosis affect many aspects of their life history. We quantify the effects of metamorphosis on burst speed and endurance capacity on a large sample of *Ambystoma californiense*. Locomotor performances are highly repeatable within metamorphic stages but change dramatically between larval and postmetamorphic stages. For burst speed, larvae are twice as fast as metamorphosed aquatic animals, and metamorphosed terrestrial salamanders are even slower. However, mean endurance of terrestrial animals is significantly greater than for either aquatic stage. Repeatabilities of burst and of endurance between metamorphic stages are zero, suggesting that they are under separate physiological control. In addition, correlations between burst and endurance, both within and among metamorphic stages, are zero. Metamorphosis seemingly decouples locomotor performance in different environments and promotes increased flexibility for organisms with complex life cycles.*

Introduction

Metamorphosis represents a major and abrupt change in life history, morphology, physiology, and ecology. In amphibians, for example, these changes frequently encompass fundamental changes in diet, respiration, feeding, and locomotion, as well as the physiological requirements associated with life in aquatic and terrestrial environments (Duellman and Trueb 1986; Lauder and Shaffer 1988; Shaffer and Lauder 1988). Amphibian meta-

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morphosis also influences ecology: potential predators and prey change dramatically.

Several recent studies on ectothermal tetrapods have quantified two aspects of locomotor performance: maximal burst (or sprint) speed and endurance capacity. These two types of locomotor performance bracket a wide range of ecological and physiological extremes within which locomotor activities take place (Bennett 1985). Burst speed can be important in predator avoidance, prey capture, some social interactions, and rapid response to environmental conditions. It is based on anaerobic metabolism and recruits fast-twitch muscle fibers. Endurance can be important in sustained, long-distance activity associated with migration, cruising for prey or mates, and so on. It reflects primarily aerobic capabilities and utilizes slow-twitch muscle fibers (Else and Bennett 1987; Garland 1988).

How do burst speed and endurance change when an amphibian metamorphoses from an aquatic larva to a terrestrial juvenile? Does performance before metamorphosis predict (or constrain) locomotor ability after transformation, or is performance in different life-history stages decoupled by the morphological and physiological changes associated with metamorphosis? Does the variance in performance, and thus the "opportunity for selection" (Arnold and Wade 1984), change ontogenetically? We examine these questions by separating locomotor performance into two discrete components: the relationship between burst and endurance within a life-history stage, and changes that occur in performance between stages.

Three possible relationships exist between endurance and burst speed within a life-history stage of an organism. First, the two locomotor performance variables may be positively correlated. In this case, some individuals are physiologically superior "Olympians" (Garland 1988; Hertz, Huey, and Garland 1988). Second, burst speed and endurance may be negatively correlated, suggesting a trade-off, or cost, to superior performance in one mode of locomotion (Garland 1988). This would be the expected outcome if, for example, the total volume of muscle were limited, such that an abnormally large complement of fast-twitch fibers physically limited the slow-twitch component. Finally, burst speed and endurance may be uncorrelated, implying that they are independent physiological systems (Hertz et al. 1988).

Metamorphosis complicates these relationships because the temporal correlations of locomotor performances between life-history stages must be considered. In amphibians with a biphasic life cycle, locomotor mode shifts from undulatory swimming in larval and metamorphosed aquatic individuals (Webb and Blake 1985; Wassersug 1989) to quadrupedal locomotion in metamorphosed terrestrial animals (Edwards 1977). This fundamental change in locomotor mode and in gas transport may completely

decouple performance in different developmental stages. Alternatively, Edwards (1977) has hypothesized that the same kinematic (and presumably neuromuscular) patterns of lateral undulation are used in swimming and running in salamanders, implying a potential for considerable correlation of locomotor performance across metamorphosis.

Here, we focus on the relationship between burst speed and endurance capabilities within and among life-history stages in the California tiger salamander *Ambystoma californiense* (sometimes known as *A. tigrinum californiense*). We quantify the statistical relationship between burst and endurance in a large sample from a single natural population. In so doing, we answer two questions relating physiological performance and the ability to respond to natural selection. First, are burst and endurance physiologically independent parameters within a life-history stage, and therefore capable of independent responses to selection? Second, to what extent is the locomotor capacity of an individual salamander stable across the metamorphic transition? In other words, do individuals with relatively great speed or stamina as larvae have similar relative capabilities after metamorphosis?

Material and Methods

Animals

Our study animals came from a single breeding pond in Solano County, California. California tiger salamanders have a complex life cycle: they start life as aquatic larvae, metamorphose to a terrestrial stage, and subsequently migrate overland to their aquatic breeding sites (Stebbins 1951).

We collected 134 large larval salamanders on April 30, 1988. Larvae were transported to the University of California, Davis, maintained in small groups in 10-gal aquaria, and fed tubifex worms for 4 wk before testing. Larvae were maintained on a natural photoperiod and a fluctuating thermal regime (17°–21°C). Because temperature affects burst speed and endurance in *Ambystoma* (Else and Bennett 1987), we conducted our experiments at 17°C, a typical field temperature for *Ambystoma* (Feder et al. 1982; H. B. Shaffer, personal observation). After metamorphosis, animals were individually housed in plastic shoe boxes (31 cm × 17 cm × 9 cm deep) and were fed *Galaria* larvae and crickets. Experimental animals fasted for 3 d prior to testing because food in the stomach can affect locomotor performance (Garland 1988). About 25% of the animals died during metamorphosis, apparently from drowning, which reduced sample sizes from 134 to 90. Otherwise, all animals survived the entire experiment, grew at or above normal rates in the field, and appeared in perfect health.

Metamorphic Stages

We measured endurance and burst speed in three developmental "stages." We use the term stage to include all three possible combinations of environmental and metamorphic conditions (Lauder and Shaffer 1988; Shaffer and Lauder 1988). The larval stage is by definition aquatic, because larvae are incapable of sustained activity out of the water. The metamorphosed aquatic stage involves newly metamorphosed animals that were tested for aquatic locomotor performance, whereas the metamorphosed terrestrial stage involves newly metamorphosed animals that were tested for terrestrial performance. In comparing larval and metamorphosed aquatic locomotion, we are contrasting the same basic behavior (undulatory swimming) in the same environment; however, the morphology of the animals has changed as a result of metamorphosis (fig. 1). In contrast, when we compare metamorphosed aquatic and terrestrial locomotion, the morphology of the animals is the same, but the environment and the mode of locomotion (swimming to trotting) have changed dramatically.

Variables

Burst speed was measured with a linear racetrack (152 cm long \times 11 cm wide), marked off in 10-cm increments. For aquatic measurements, the racetrack was filled with 2.3 cm of water (enough to completely immerse the tail fin of all animals). For terrestrial measurements, no water was present, but the bottom of the racetrack was lined with moist paper towels. Individuals were placed at one end of the racetrack, allowed to rest for 15 s, and chased as quickly as possible to the other end by gently prodding or pinching their tails. After resting for another 15 s, the salamander was chased back to the starting point. If an animal did not appear to maintain maximal speed over at least a 50-cm segment of the racetrack, it was allowed to rest for a minimum of 15 s and raced again. After a minimum of 2 h, this procedure was repeated, which resulted in four races for each animal in each stage. All burst races were videotaped at 30 frames per second; burst velocity for each 10-cm segment was analyzed with a Panasonic AG-6300 VCR.

Aquatic endurance was measured as the amount of time an individual could remain swimming against a constant flow of 10 cm/s (0.36 km/h) in an underwater flume (flow tank). Our flow tank was constructed in accordance with Vogel and LaBarbera (1978), with a Plexiglas trough (152 cm long \times 19 cm wide \times 23 cm deep). An aircraft fiberglass honeycomb (4.5 cm thick), placed upstream from the testing portion of the flow tank, reduced turbulence and homogenized flow rates. Salamanders were raced in a piece of 10-cm diameter PVC pipe that was cut in half along the long axis and

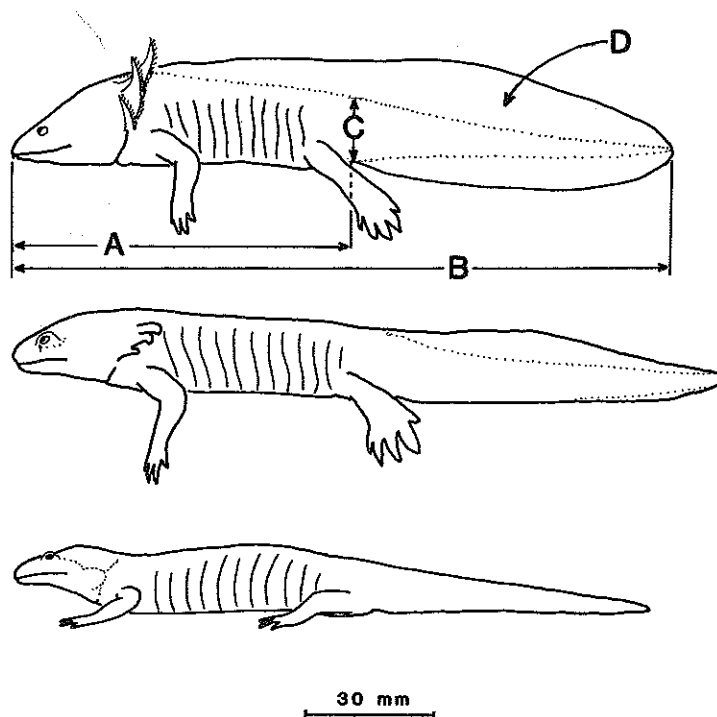


Fig. 1. Three phases in metamorphosis in the tiger salamander, *Ambystoma californiense*. The upper panel shows a larva, the center is an animal in the middle of metamorphosis, and the lower panel is a fully transformed animal. Note the changes in the tail/body fin, the size of the limbs, and the reduction in the head and gills. Measurements taken from larval video images are (A) snout-vent length (SVL), (B) total length, (C) tail muscle height, and (D) tail fin area.

suspended in the flow channel. Preliminary tests on nonexperimental animals indicated that these flow speeds provided aquatic endurance rates of about 8 min. Endurance times in this range index primarily aerobic muscle capacity (Bennett 1985). Individuals were induced to remain swimming by gently tapping their tails. Exhaustion was determined when an individual lost its righting response (Bennett, Garland, and Else 1989).

Terrestrial endurance was measured as the amount of time an individual could remain walking on a constant-speed treadmill at 4.4 cm/s (0.16 km/h). Preliminary tests on nonexperimental animals indicated that this treadmill speed provided terrestrial endurance rates that are representative of aerobic muscular potential. Fatigued salamanders were induced to remain walking by gently tapping their tails. Exhaustion was determined when an individual hit the back of the treadmill three times in a row despite repeated taps on the tail.

Test Schedule

All individuals were tested for both endurance and burst during a continuous, 3-d period. Endurance was always measured first, followed by 24–48 h of rest. Four burst measurements were then collected for each animal.

Morphological Measurements

Profile video images of all individuals were taken immediately after larval endurance tests. Because the larvae used in this experiment were close to metamorphosis and several had actually begun to resorb their tail fins, we collected measurements (fig. 1) that might be correlated with larval performance in a way that was independent of individual physiological differences. Data recorded from larval video images included snout-vent length (SVL, measured from the tip of the snout to the cloaca), total length, tail fin area (measured as the total area of the tail fin just above the tail muscle), and tail muscle height (measured just posterior to the cloaca at the greatest height of the muscle). Larval mass and metamorphosed mass, also measured immediately after the respective endurance tests, were used as covariates to examine the effects of overall size on locomotor performance.

Statistical Analysis

All statistical analyses were conducted with the Statistical Analysis System (SAS 1985). Pearson product-moment correlation coefficients, Spearman rank-order correlations, two-way ANOVAs, and linear regressions were computed in accordance with Sokal and Rohlf (1981) and Siegel (1956). For most analyses of burst speed, we used only the single fastest 20-cm burst from the four trials measured on each individual. However, for the two-way ANOVAs, we treated the four measures of burst as replicated measurements on the same individual to estimate the mean square error. Because the data are balanced, this estimate is justified even though the animals in later trials had slightly slower bursts than in earlier trials. We used log-transformed data in the ANOVAs because the variances of untransformed-stages effects were significantly heteroscedastic (Sokal and Rohlf 1981). To test for inequality of variances, we used the Scheffe-Box procedure, with 10 subsamples of nine individuals for each stage (Sokal and Rohlf 1981).

Locomotor performance is frequently correlated with body mass in other studies (Bennett 1987; Garland 1988; Bennett et al. 1989), producing artifactual correlations in performance that reflect differences in size or mass of individuals. To correct for this, we computed mass-corrected residual

values for all locomotor performance measures and conducted all analyses on both raw and residual scores.

Results

Repeatability

We measured repeatability of endurance and burst speed by racing the same animals two and four times, respectively, and calculating both Spearman rank and Pearson product-moment correlations between scores. (We used these correlations, rather than the intraclass correlation, because the latter is sensitive to changes in the mean and variance [Falconer 1981].) The repeatability of larval endurance, measured for 13 individuals over two consecutive days, was moderate but significant (Pearson product-moment correlation, $r = 0.67$, $P < 0.02$), suggesting that rank order of performance was reproducible over a short time interval (fig. 2). We did not estimate repeatabilities of metamorphosed aquatic or terrestrial endurance; we assume that the larval aquatic values are representative of postmetamorphic performance. However, our unpublished data on these same animals as adults confirm that postmetamorphic endurance repeatabilities are in the range of $r = 0.5$ – 0.7 (C. C. Austin and H. B. Shaffer, unpublished data). Repeatabilities of burst speeds within stages varied from 0.18 to 0.59 (using either raw or

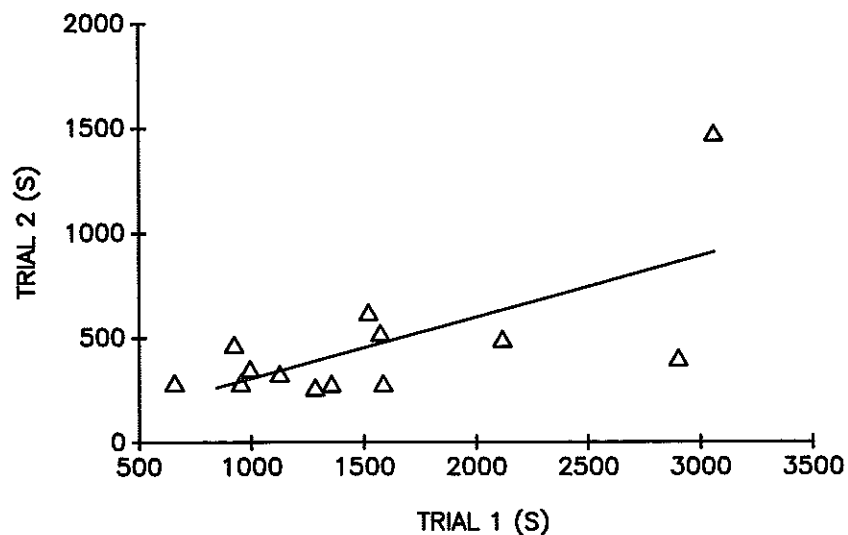


Fig. 2. Repeatability of relative endurance for 13 individual salamanders. The correlation between two trials one day apart is 0.67.

size-corrected values), a range that encompasses other values in reptiles and anurans (Bennett 1987; Huey and Dunham 1987; Garland 1988; Walton 1988; van Berkum et al. 1989).

Size and Morphometric Effects

Locomotor performance of metamorphosed tiger salamanders can be significantly correlated with body mass (Full et al. 1988; Bennett et al. 1989). Because our test animals ranged from 5 to over 11 g (table 1), we assayed for size effects by regressing performance measures on body size.

Within all stages, locomotor performance was independent of body mass (table 2). Even for larval endurance, which approaches a significant regression, only 3% of the variance was related to variation in mass. For the remaining performance measures in all stages, less than 0.5% of the variation

TABLE 1
Summary statistics for all morphological and performance measures

Variable	N	\bar{X}	SD	Minimum	Maximum
Size measurements:					
Larval SVL (mm)	132	49.9	5.39	35.5	62.7
Larval total length (mm)	132	88.0	7.85	61.6	103.9
Larval tail height (mm)	132	7.8	.96	5.3	10.0
Larval fin area (mm ²)	132	186.0	51.92	14.8	347.7
Larval weight (g)	134	7.7	1.26	5.0	11.6
Metamorphosed weight (g) . .	92	7.3	.95	5.0	10.1
Endurance (s):					
Larval aquatic	134	360.1	142.81	103.0	758.0
Metamorphosed aquatic	92	296.4	93.05	130.0	625.0
Metamorphosed terrestrial . . .	93	497.4	291.66	132.0	1,500.0
Burst (cm/s):					
Larval aquatic ^a	134	55.1	13.10	24.0	87.5
Larval aquatic ^b	134	47.7	11.74	21.1	77.0
Metamorphosed aquatic ^a	93	28.5	3.25	21.3	35.4
Metamorphosed aquatic ^b	93	26.3	2.66	10.1	32.0
Metamorphosed terrestrial ^a . .	93	15.5	2.81	10.0	24.0
Metamorphosed terrestrial ^b . .	93	14.4	2.46	9.3	24.0

^a Mean burst speed (cm/s) for the fastest 20-cm interval chosen from any of four replicate races.

^b Mean burst speed (cm/s) of the entire 50–70-cm trial, for the fastest of four replicate races.

TABLE 2
*Regressions of locomotor performance with body mass,
 tail height, and fin area*

Independent Variable	Dependent Variable	N	Slope	Intercept	Probability of Full Model	R ²
Body mass	Larval aquatic endurance	133	18.39	218.7	.06	.026
Body mass	Larval aquatic burst	133	-.74	59.8	.42	.005
Body mass	Metamorphosed aquatic endurance	91	6.88	246.2	.51	.005
Body mass	Metamorphosed aquatic burst	91	.09	27.6	.80	.0007
Body mass	Metamorphosed terrestrial endurance	91	19.32	359.0	.55	.004
Body mass	Metamorphosed terrestrial burst	91	-.07	15.9	.82	.0006
Tail height	Larval aquatic endurance	131	14.80	245.9	.26	.01
Tail height	Larval aquatic burst	131	.39	51.1	.75	.0008
Fin area	Larval aquatic endurance	131	.52	264.5	.03	.035
Fin area	Larval aquatic burst	131	.03	47.8	.12	.018

in performance was related to body-mass variance. (This difference in the relationship between body mass and locomotor performance between our results and those of Bennett et al. [1989] and of Full et al. [1988] probably reflects the more limited size range of animals in our study [see fig. 1 in Bennett et al. 1989].) Fin area and tail muscle height were also essentially independent of locomotor performance (table 2). Fin area and endurance were significantly correlated ($P < 0.03$), but variance in fin area accounted for only 3% of the variance in endurance. For the other three larval analyses, fin morphology accounted for less than 1% of the variance in locomotor performance (table 2). Thus, the initial stages of metamorphosis involved with tail fin loss do not appear to affect locomotor performance in *Ambystoma*

(as opposed to anurans, in which locomotor performance is drastically affected by metamorphosis [Wassersug and Sperry 1977]).

Shifts in Means and Variances among Stages

For both endurance and burst speed, we used a two-way factorial ANOVA to analyze variation among stages, individuals, and their interaction. All three stages differed significantly in average maximal burst speed (table 3). Larval animals had nearly twice the burst speed of metamorphosed aquatic animals, and metamorphosed animals were roughly twice as fast in the water as on land (fig. 3; table 1). Variation among individuals and the individual-by-stage interaction were both significant (table 3). Thus, certain individuals, regardless of their stage, have greater burst speeds than others. In addition, some individuals have very rapid burst speeds in one stage but perform relatively poorly in a different one (fig. 4). Variance among individuals in burst performance also changed across metamorphosis (fig. 4). Larvae were significantly more variable than both metamorphosed aquatic and metamorphosed terrestrial salamanders.

The interpretation of endurance is more complex, because aquatic and terrestrial endurance were measured at different absolute speeds (aquatic endurance for both larvae and metamorphosed animals was measured at 10 cm/s rate of flow, whereas terrestrial endurance was measured at a treadmill

TABLE 3
ANOVA for burst speed

Source	df	Sum of Squares	Mean Square	F Value	Pr > F
Individual ..	89	16,041	180	4.0	.0001
Stage	2	161,476	80,738	486.0	.0001
Individual					
× stage ..	178	29,667	166	3.7	.0001
Error	792	35,403	45		

Note. Stage is a fixed effect; individual is a random effect. Interaction and individual mean squares were tested over the error mean square, whereas the stage effect was tested over the interaction mean square (Sokal and Rohlf 1981). Only individuals that survived for the entire experiment are analyzed, which leaves a virtually balanced design for 90 individuals. A posteriori tests among stage means were conducted with Duncan's multiple range test and Bonferroni *T*-tests for unplanned comparisons (SAS 1985).

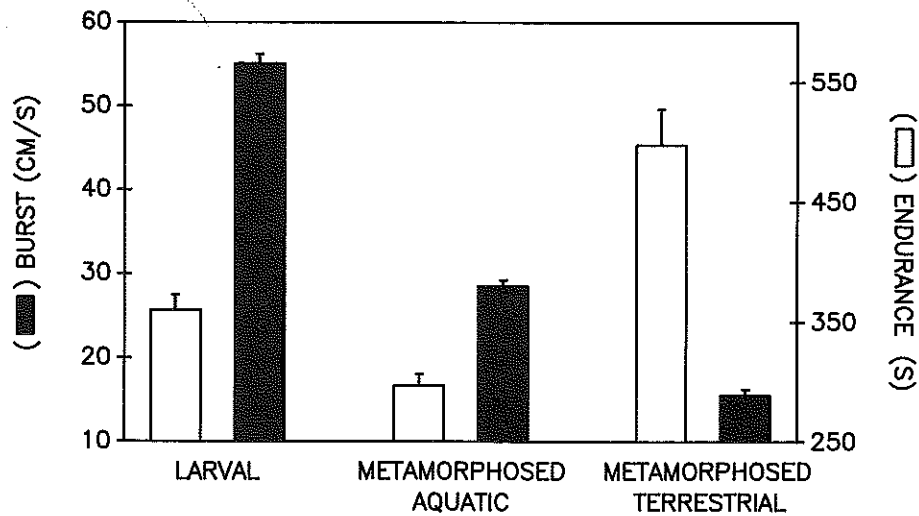


Fig. 3. Mean values of burst speed and endurance for all three metamorphic stages. One standard error of the mean shown above each histogram.

speed of 5 cm/s). The ANOVA for endurance demonstrates a significant effect of variation among the three stages ($P < 0.001$) but no significant variation among individuals (table 4). Mean larval endurance (345 s) and mean metamorphosed aquatic endurance (297 s) did not differ significantly, but endurance of metamorphosed terrestrial animals (496 s) differed significantly from the aquatic endurance values. The variance of metamorphosed terrestrial endurance is significantly greater than that of either larval or aquatic metamorphosed endurance ($P < 0.001$, Scheffe-Box test).

Character Correlations

We analyzed three separate sets of character correlations. First, we examined the correlations between burst and endurance for larval, metamorphosed aquatic, and metamorphosed terrestrial individuals to assess the independence of these two aspects of locomotor performance (the diagonal elements of table 5). Second, we quantified the extent to which an individual's performance in one stage predicts its ability at a different stage for the same performance (table 6). In the third set of correlations, we examined the independence of burst and endurance capabilities in different stages (the off-diagonal elements of table 5).

All Pearson product-moment correlations are nonsignificant (tables 5, 6). Rank-order correlations showed identical patterns. We also recalculated all

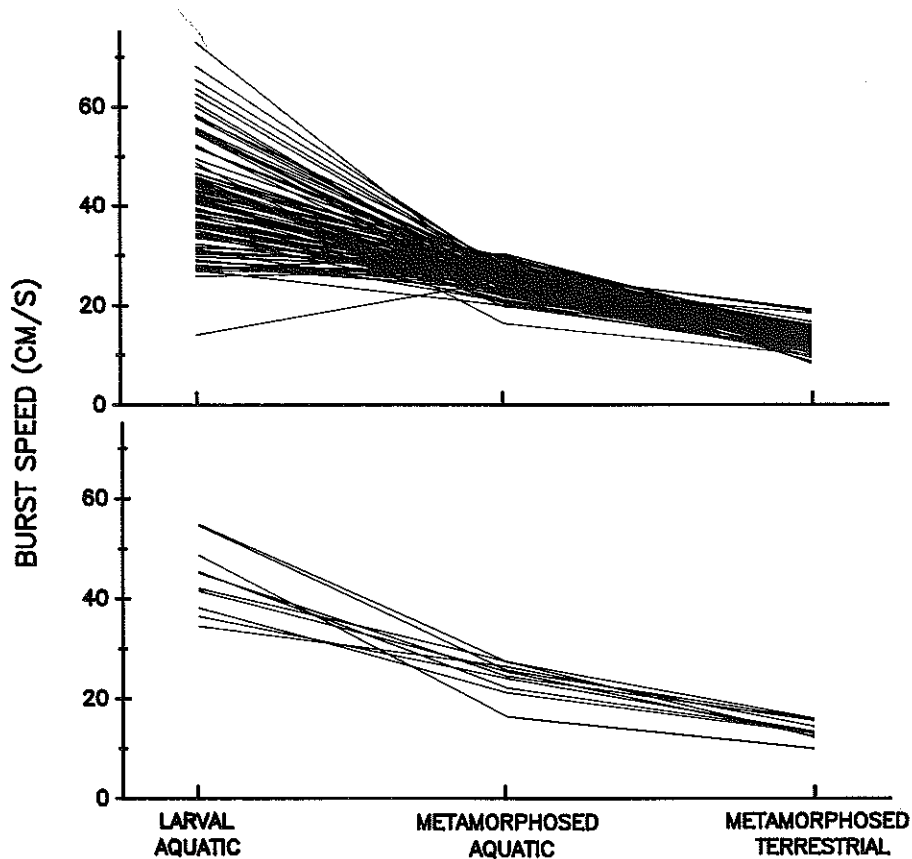


Fig. 4. Burst performance for all individual salamanders in all three stages. The mean value of four replicated races is plotted for each animal; lines connect the three values of each individual. The upper panel shows all 90 individuals, whereas the lower panel shows a random sample of 10 animals. Note that animals shifted their relative positions among stages. Larvae were significantly more variable than both metamorphosed animals ($P < 0.0001$, according to the Scheffe-Box test [Sokal and Rohlf 1981]). A posteriori Bonferroni T-tests confirmed that larvae were significantly more variable than metamorphosed aquatic and terrestrial animals, which were not different from each other.

correlations after removing the effects of body mass; again, all correlations remained zero.

In interpreting these correlations, note that these are robust estimates based on large sample sizes and that all values are very close to zero. Thus, this lack of statistical significance represents biological reality, not limitations of statistical power. The burst speeds used the fastest of four trials, which

TABLE 4
ANOVA for endurance

Source	df	Sum of Squares	Mean Square	F Value	Pr > F
Individual ..	98	3,364,596	37,804	1.03	.4302
Stage	2	1,934,009	967,004	26.32	.0001
Error	178	6,539,868	36,740		

Note. Because this is an unreplicated analysis, we used the unpartitioned error plus interaction total ("remainder" sum of squares, Sokal and Rohlf [1981]) as the error term for both main effects. This is the correct error for testing the (fixed) stage effect in a mixed-model ANOVA; however, the significance test for variation among individuals must assume that there is no individual-by-stage interaction.

eliminated the chance occurrence of a "bad" race that might lower the correlations of performance measures. To further check our results, we also computed the correlations using the fastest mean burst speed for an entire race (as opposed to the fastest 20-cm segment of a race) to see whether this longer sprint might be physiologically linked with endurance. Again, all correlations were nonsignificant and near zero.

TABLE 5
Pearson product-moment correlations between individual burst speed and endurance

	Larval Aquatic Burst	Metamorphosed Aquatic Burst	Metamorphosed Terrestrial Burst
Larval aquatic endurance	-.12	-.14	.02
Metamorphosed aquatic endurance	-.09	-.04	.04
Metamorphosed terrestrial endurance02	-.01	.15

Note. Diagonal elements are correlations of burst and endurance in the same life-history stage; off-diagonal elements are correlations between different life-history stages. All correlations are nonsignificant ($P > 0.15$).

TABLE 6

Pearson product-moment correlations of the same individual performance measured between life-history stages

	Larval Aquatic	Metamorphosed Aquatic	Metamorphosed Terrestrial
Larval aquatic	1	.12	-.02
Metamorphosed aquatic	-.07	1	.02
Metamorphosed terrestrial . .	.09	.14	1

Note. Endurance correlations are above the diagonal; burst speed correlations are below the diagonal. All correlations are nonsignificant ($P > 0.15$).

Discussion

Our experiments focus on three aspects of phenotypic variation in locomotor performance in the salamander *Ambystoma californiense*. First, by analyzing a large sample from a single population, we add to the small but growing literature on variation among individuals in physiological or functional characters in natural populations (for other vertebrate examples, see Bennett [1987]; Huey and Dunham [1987]; Garland [1988]; Lauder and Shaffer [1988]; Shaffer and Lauder [1988]; Huey et al. [1990]). Second, because our experiments extend across metamorphosis, we provide insights into the average consequences of metamorphosis for both burst and endurance. Finally, by following performances of the same individuals across metamorphosis, we provide unique information on phenotypic correlations both across locomotor performances and among metamorphic stages.

Individual and Stage Variation

Our results indicate the presence of significant variation among individuals in burst speed, as well as a significant stage-by-individual interaction (table 3; fig. 4). Although individual variation for endurance was not significant (table 4), this may be due to a lack of repeated-measures design among individuals, rather than to a true lack of individual variation.

Among-individual variation is important, for it implies that the opportunity for selection (Arnold and Wade 1984) exists for burst speed in natural salamander populations. For this opportunity to be realized (and thus to be of evolutionary significance), both genetic control (i.e., heritability) and dif-

ferential fitness for locomotor performance must occur. Although these data are currently unavailable for *Ambystoma*, studies in other vertebrate species confirm that performance is heritable (van Berkum and Tsuji 1987; Garland 1988; Tsuji et al. 1989) and in some cases is related to correlates of fitness (reviewed in Bennett and Huey [1990]).

Metamorphic stages differ dramatically in both burst and endurance performance (tables 3, 4). For burst, all three stages are significantly different; aquatic larvae have more rapid burst capacities than metamorphosed aquatic animals, and metamorphosed terrestrial salamanders are slower yet (table 1). Interestingly, this result goes against a functional prediction based on the differences in viscosity of water and air (see Bramble and Wake 1985), because burst speed of metamorphosed animals in the water is nearly twice that on land (Stevenson, Peterson, and Tsuji [1985] found a similar result for garter snake locomotion). This same general result holds for feeding ability across metamorphosis in the related salamander *Ambystoma tigrinum mavortium*; feeding performance and associated muscle activity patterns are faster in the viscous aquatic environment than in air (Lauder and Shaffer 1988; Shaffer and Lauder 1988). Thus, although the shift between environments profoundly influences behavior and performance, this shift cannot be predicted from simple a priori considerations of the relative viscosities of water and air alone.

The interpretation of changes in endurance across metamorphosis is more difficult for at least two reasons. First, by measuring all animals within a stage at the same speed, we assume that relative power output for all individuals is the same, such that we are measuring an index of relative aerobic capacity. Oxygen consumption and endurance time vary with speed in *A. tigrinum*, and our experiments were conducted in the range of speeds at which endurance time changes most rapidly with speed (0.1–0.2 km/h; see fig. 4 in Full et al. [1988]). If relative power output for animals varies depending on speed, and if this relationship changes ontogenetically, then it could cause a low correlation for endurance that is unrelated to metamorphosis. Second, because we measured aquatic and terrestrial endurance at different speeds, the interpretation of endurance changes depending on whether time or distance traveled is considered. When we use our original measures of time to exhaustion, larval and metamorphosed aquatic endurance are not statistically different, whereas metamorphosed terrestrial endurance increases relative to the previous two by nearly a factor of two (to about 500 s, at a treadmill speed of 5 cm/s). However, if time to exhaustion is converted to total distance traveled, the relationship between aquatic and terrestrial endurance reverses: metamorphosed terrestrial animals can traverse only 21 m before physiological exhaustion,

whereas larval (36 m) and metamorphosed aquatic (30 m) individuals have greater endurance capabilities. To assess which of these represents the biologically most meaningful interpretation requires information from the field on the speeds at which overland migration and long-distance aquatic cruising generally occur.

Evaluations of the ecological significance of ontogenetic shifts in locomotor performance are hindered by the lack of mark-recapture studies on animals of known physiological capabilities. For all three stages, burst performance is almost certainly important for predator avoidance from birds, snakes, invertebrates, or conspecific predation (Wassersug 1989). The importance of burst in prey capture is less clear, given that aquatic suction and terrestrial lingual feeding involve primarily stationary, ambush strategies (Lauder and Shaffer 1985; Shaffer and Lauder 1985*a*, 1985*b*, 1988). However, small larvae of *Ambystoma maculatum* "lunge" in preparation for suction feeding (Hoff, Lannoo, and Wassersug 1985), and burst capacity may be an important component of the lunge.

The decline in burst speed across metamorphosis (larval vs. metamorphosed aquatic performance) and across environments (metamorphosed aquatic vs. terrestrial performance) may represent a real and previously unrecognized "cost" associated with metamorphosis in *Ambystoma*. Larval reproduction (an extreme form of paedomorphosis) has evolved multiple times in the tiger salamander complex (Shaffer 1984), suggesting strong selection for a permanently aquatic life-style. Although several ecological factors have been plausibly implicated as agents of selection favoring aquatic, larval adults (Wilbur and Collins 1973; Sprules 1974; Harris 1987), the decline in locomotor performance on land represents another, potentially important reason to remain in the aquatic habitat.

The ecological importance of endurance is difficult to evaluate because little is known about the importance of endurance capacity in nature. Terrestrial endurance is potentially extremely important because tiger salamanders can migrate large distances (Semlitsch 1983). The treadmill values presented here place upper bounds on endurance capabilities at a single speed; how often these constitute constraints on migrations requires additional data from the field (as in Walton [1988] for the toad *Bufo woodhousei*).

Correlations

Our results demonstrate complete independence of burst and endurance performance within and among life-history stages (tables 5, 6). That is, the burst capabilities of an individual do not predict either burst performance

in a different stage or endurance capabilities in the same or a different phase of the life cycle. This same result was found for metamorphosed aquatic versus metamorphosed terrestrial burst and endurance in the related *Ambystoma tigrinum nebulosum* by Bennett et al. (1989), although those workers had no information on correlations across the developmental transition of metamorphosis.

In a variety of reptilian species, locomotor performances are highly repeatable during ontogeny (Bennett 1987; Huey and Dunham 1987; van Berkum et al. 1989; Huey et al. 1990). This is not the case for *Ambystoma*. The striking lack of correlation in the same performance measure across life-history stages suggests a fundamental difference between vertebrates that undergo metamorphosis and those that do not. The low correlation between aquatic and terrestrial performance makes some sense, given that the shift from swimming to walking undoubtedly involves the differential recruitment of leg muscles. Nevertheless, larval, metamorphosed aquatic, and metamorphosed terrestrial locomotion all rely on lateral undulation (Edwards 1977; Webb and Blake 1985) and as such might be predicted to be highly intercorrelated. The independence of these locomotor modes implies either (1) that muscle activity patterns at the neuromuscular level are different before and after metamorphosis in *Ambystoma*, or (2) that the morphological changes associated with metamorphosis decouple performance capabilities, even though neuromuscular control is stable ontogenetically. Previous work on the feeding system in *A. tigrinum mavortium* supported the latter hypothesis for the shift from suction to lingual feeding (Lauder and Shaffer 1988; Shaffer and Lauder 1988). Distinguishing between these alternatives requires data on muscle activity patterns during locomotion that are unavailable at present.

The low correlation between aquatic and terrestrial locomotion implies that selection for improved larval performance would have virtually no impact on postmetamorphic performance, at least for the two aspects of locomotion measured here. Because their performance is decoupled across metamorphosis, these animals retain the maximal flexibility to respond to different selection regimes in different environments. Of course, for this independence of locomotor physiology to be evolutionarily important, the phenotypic variances and covariances measured in this study must reflect underlying genetic values, because genetic correlations impose limits to independent evolutionary responses (Arnold 1983; Lande and Arnold 1983). We view the genetic basis of performance as an important direction for future functional and physiological studies (see also Bennett 1987; Lauder and Shaffer, in press) that we are currently pursuing with tiger salamanders.

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