

Short-, medium-, and long-term repeatability of locomotor performance in the tiger salamander *Ambystoma californiense*

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Summary

Both burst and endurance performance may be crucial determinants of the lifetime fitness of an organism, especially for many amphibians where burst allows for predatory escape and endurance may contribute to migratory ability. However, there are no analyses of the long-term stability of locomotor performance for any amphibian, hindering efforts to extrapolate from single measurements to lifetime performance estimates. We present an analysis of individual repeatability of burst speed and endurance locomotor performance over short (seconds), medium (hours), and long (15 months) time intervals for a large sample of *Ambystoma californiense*. Burst speed is significantly repeatable over all three time intervals. We found a significant tiring effect for burst speeds when measured only seconds apart; apparently several hours are required for complete physiological recovery. Endurance repeatability reaches or approaches statistical significance when measured over periods of several days, but is not repeatable over 15 months. We postulate that both burst and endurance are ecologically important; our results confirm that single measurements of performance may not provide accurate profiles of lifetime locomotor ability. We also present a literature review of locomotor performance repeatability studies for amphibians and squamate reptiles. This review suggests that (1) repeatabilities for amphibians are generally lower than for squamates, and (2) in all cases, repeatability of locomotor performance declines over time. These results emphasize the necessity of multiple measurements over long time intervals to quantify lifetime performance profiles accurately.

Key-words: Ambystomatidae, burst speed, candata, endurance

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Introduction

The repeatability of a trait is always of interest, for it represents the yardstick by which variation among experimental units is measured. However, in physiological or functional studies of organismal performance, repeatability takes on an additional level of importance. As Bennett (1987) has emphasized, two major goals of physiological ecology are understanding the proximate factors that contribute to individual performance, and quantifying the ecological and evolutionary consequences of variation in performance. While these are indeed goals that will serve to unite physiological ecology with the mainstream of evolutionary theory (Bennett 1987), they rely on lifetime fitness estimates, and thus on knowledge of

the repeatability of functional characteristics over an animal's lifetime (van Berkum *et al.* 1989).

Over the past 10 years, the study of locomotor performance in poikilothermic vertebrates has expanded rapidly, and we now have a relatively complete understanding of the relationship between burst and endurance ability and their dependence on temperature, body mass, and internal physiology for several lizard and snake species (Bennet 1987; Garland, Bennett & Daniels 1990a; Garland, Hankins & Huey 1990b). Most of this work has focused on burst and endurance, because burst performance is potentially important in predator avoidance and prey capture, whereas endurance capabilities may be important for sustained locomotor activities such as migration and dispersal. These studies have demonstrated that repeatabilities of locomotor performance are usually high (in the range of 0.40–0.80) over a period of hours or days. A much smaller number of

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Table 1. Literature values of burst and endurance repeatabilities for amphibians, lizards, and snakes. All repeatabilities are Pearson product-moment, or Spearman rank-order correlation coefficients

Taxon	Repeatability	Time period	Citation
<i>Bufo w. fowleri</i>	0.32–0.68 (burst)	1 day	Walton 1988
	0.45 (burst)	2 days	
	0.20–0.24 (endurance)	1 day	
	0.57 (endurance)	2 days	
<i>Bufo boreas</i>	0.63 (endurance)	1 day	Putman & Bennett 1981
<i>Rana pipiens</i>	0.30 (endurance)	1 day	
<i>Ambystoma californiense</i>	0.20–0.67 (burst)	15 s	This study
	0.18–0.49 (burst)	2 h	
	0.15–0.34 (burst)	15 months	
	0.49–0.67 (endurance)	1 day	
	0.08 (endurance)	15 months	
<i>Ctenophorus (Amphibolurus) nuchalis</i>	0.77 (burst)	1 day	Garland 1985
	0.97 (burst)	8 weeks	
<i>Sceloporus merriami</i>	0.56–0.63 (burst) (two populations)	1 year	Huey & Dunham 1987 (see also Huey <i>et al.</i> 1990)
<i>Sceloporus occidentalis</i>	0.84 (burst)	1 day	Garland <i>et al.</i> 1990b
	0.57 (endurance)	1 day	
<i>Sceloporus occidentalis</i>	0.45 (burst)	Few days	van Berkum <i>et al.</i> 1989
	0.06–0.47 (burst)	2–13 months	
	0.65 (endurance)	Few days	
	0.25, 0.80 (endurance)	2–13 months	
<i>Sceloporus occidentalis</i>	0.45 (burst)	5 days	Tsuji <i>et al.</i> 1989
	0.65 (endurance)	5 days	
<i>Thamnophis radix</i>	0.60 (burst)	1 day	Arnold & Bennett 1988
	0.71 (endurance)*	1 day	
	0.55 (endurance)†	1 day	
	0.62 (endurance)‡	1 day	
<i>Thamnophis sirtalis</i>	0.67 (burst)	1 day	Garland <i>et al.</i> 1990a
	0.69 (burst)	1 day	
<i>Thamnophis sirtalis</i>	0.80 (burst)	1 day	Garland 1988
	0.68 (endurance)	1 day	
<i>Thamnophis sirtalis</i>	0.62–0.78 (burst)	1 day	Jayne & Bennett 1990
	0.06–0.65 (burst)	1 year	
	–0.12, 0.18 (burst)	2 years	
	–0.52 (burst)	3 years	
	0.51–0.67 (endurance)	1 day	
	0.22–0.43 (endurance)	1 year	
	0.17, 0.24 (endurance)	2 years	
	0.27 (endurance)	3 years	

* This is the 'mid-distance' speed, defined as the speed of an experiment from the end of the first metre of a race to 2.5 m.

† This is the distance crawled to exhaustion.

‡ This is the duration of a race to exhaustion.

studies indicate that repeatabilities may remain high for months or years (Table 1; also see Bennett 1987; Boake 1989 provides a similar review of the repeatability of behavioural characters).

A full account of repeatability must address both short- and long-term measures, because the performance of an individual may change during the course of ontogeny due to physiological changes, learning, or

both. If locomotor performance is repeatable, then a single measure accurately reflects lifetime performance. However, if locomotor performance is *not* repeatable then either (1) lifetime performance profiles are repeatable but the rank order of individual locomotor ability shifts ontogenetically, or (2) environment factors which change during an individual's lifetime are more important than intrinsic

physiological factors. In either case, if locomotor performance is not repeatable over time then extrapolation of lifetime fitness profiles from a single set of measurements may lead to incorrect conclusions (Arnold 1983; Bennett 1987).

In a previous study, we reported that the repeatability of locomotor performances across metamorphosis in the salamander *Ambystoma californiense* (Gray) is essentially zero (Shaffer, Austin & Huey 1991), and that metamorphosis apparently acts to decouple performance measures in different environments in these amphibians. While these results demonstrate that there is no physiological linkage between burst and endurance across this important transition in the amphibian life cycle, they do not address repeatability *within* either the aquatic or terrestrial phase. We now present a detailed analysis of the repeatability of both burst and endurance performance for these same individuals over short, medium and long time intervals. In particular, we address three questions for the repeatability of locomotor performance. First, are burst and endurance performance equally repeatable over a period of seconds, hours and years? Second, how sensitive are repeatability estimates to the method by which the variable is measured? And third, are there indications of exhaustion or tiring effects, and do they affect repeatability? Because of the sample size in our study (approximately 100 salamanders from a single population), the number of times each animal was measured (20 measurements of burst, five measures of endurance), and the time span of the study (about 1.5 years), we can analyse repeatability in considerably more detail than many previous reports. In addition, this study is the first quantification of long-term repeatability known to us for amphibian (see van Berkum *et al.* 1989; Huey *et al.* 1990; Huey & Dunham 1987, for two species of *Sceloporus* lizards; Jayne & Bennett 1990, for *Thamnophis* garter snakes).

Throughout this report, we consider the repeatability of a character measured at two different times to be the correlation coefficient or a rank-order correlation (Sokal & Rohlf 1981) of the two measurements, rather than the absolute difference between the two values. Traditionally, repeatabilities have been measured as the intraclass correlation (Falconer 1981; Sokal & Rohlf 1981); a measure which increases with the correlation, but decreases if there is a shift in the mean value between trials (van Berkum *et al.* 1989). Whereas both approaches are reasonable, we favour the use of a correlation coefficient in physiological and functional studies where the primary goal is an evolutionary interpretation of performance, rather than a mechanistic one. By using a correlation, a trait will have a high repeatability if the same individuals are consistently the fastest or slowest in a sample, even if the absolute speed of the individuals changes over time. Because

measures of success in ecology and evolution are generally relative, rather than absolute (e.g. Maynard Smith 1989), a correlation correctly indicates the extent to which relative performance is repeatable over time.

Materials and methods

ANIMALS

One hundred and thirty-four larval salamanders were collected from a single breeding pond in Solano County, California on 30 April 1988. Animals were transported to the University of California, Davis, housed in small groups in 10-gallon aquaria and fed tubifex worms. All animals were maintained in a common room on a natural photoperiod with a fluctuating thermal regime (17–21°C). Because temperature affects locomotor performance abilities, we conducted all experiments at 17°C, a typical field temperature for *Ambystoma* (Feder *et al.* 1982; H.B. Shaffer, unpublished observation). Food in the stomach can also affect locomotor performance (Garland & Arnold 1983), so all animals were fasted 3 days prior to experimental testing. Upon completion of the first set of experiments animals were individually housed in plastic shoe boxes (31×17×9 cm deep), fed *Galaria* larvae and crickets, and moved to an environmental control room and maintained at 19°C. Approximately 25% of the animals died during metamorphosis (apparently from drowning), reducing our sample size from 134 to 90. Otherwise, virtually all animals survived the entire 1.5 year experimental period, grew at or above normal rates in the field, and appeared in perfect health. All individuals were hibernated for approximately 10 weeks at 11°C to simulate normal field conditions.

VARIABLES

Burst speed was measured using a linear racetrack (152×11 cm), marked off in 10 cm increments. For aquatic measurements the racetrack was filled with 2.3 cm of water (deep enough to immerse the tail fin of the animals completely). Terrestrial measurements were made using the same racetrack with a moist paper towel substrate. Individuals were removed from their shoe boxes and placed at one end of the racetrack, allowed to rest for 15 s, and then chased as quickly as possible to the opposite end by gently prodding or pinching their tails. After resting for another 15 s individuals were chased back to the starting point. We refer to these as race 1 and race 2, respectively. After a minimum of 2 h this procedure was repeated for race 3 and race 4 (also 15 s apart). We thus have a total of four burst races; two sets (races 1 and 2 and races 3 and 4) 15 s apart within a set, and with at least 2 h between the sets. All burst

Table 2. Locomotor performance mean values. For races 1–4: top value is for mean (cm s^{-1}) of entire race, bottom value is for the fastest 20cm segment of each race. For endurance and body mass, mean values in s and g respectively are shown. Values in parentheses are standard deviation and sample sizes

	Race 1	Race 2	Race 3	Race 4	Endurance	Body mass
Larval aquatic	42.6 (11.4, 122) 48.4 (14.0, 122)	36.7 (9.1, 124) 42.7 (11.6, 124)	38.6 (12.7, 127) 44.0 (14.7, 127)	36.2 (11.8, 126) 41.3 (13.9, 126)	363.4 (145.4, 122)	7.70 (1.3, 122)
Metamorphosed aquatic (1)	24.7 (3.6, 85) 26.6 (3.9, 84)	23.5 (3.7, 86) 25.4 (4.2, 86)	23.2 (3.1, 86) 24.8 (3.6, 83)	23.0 (2.8, 86) 24.8 (3.3, 85)	296.5 (94.5, 85)	7.32 (0.95, 85)
Metamorphosed terrestrial (1)	13.1 (2.2, 85) 14.0 (2.6, 84)	11.8 (2.2, 85) 12.5 (2.6, 85)	13.1 (2.9, 86) 14.1 (3.5, 82)	12.0 (2.8, 86) 12.6 (3.2, 85)	491.3 (278.7, 86)	
Metamorphosed aquatic (2)	24.4 (3.1, 84) 25.9 (3.6, 84)	22.7 (4.3, 84) 25.0 (8.0, 84)	23.7 (3.5, 85) 25.4 (4.2, 85)	22.2 (3.9, 84) 23.7 (4.4, 84)	478.7 (207.7, 81)	30.3 (2.7, 81)
Metamorphosed terrestrial (2)	16.5 (3.8, 83) 17.9 (4.4, 83)	14.9 (3.3, 83) 16.2 (3.8, 83)	17.7 (4.0, 80) 19.2 (4.5, 80)	16.9 (3.9, 79) 18.5 (4.6, 79)	353.6 (115.5, 80)	

races were video taped at 30 frames per second; burst speed for each 10-cm segment was measured using a Panasonic AG-6300 VCR.

Aquatic endurance was measured as the amount of time an individual could remain swimming against a constant flow (10 cm s^{-1} ; 0.36 km h^{-1}) in an underwater flume (flow tank). We used the flow tank to achieve a consistent measure of endurance, even though *Ambystoma* in the field live in quiet pools and ponds with no flow (Stebbins 1951; H.B. Shaffer, unpublished observation). Our underwater flume was constructed following Vogel & LaBarbera (1978).

Terrestrial endurance was measured as the amount of time an individual could remain walking on a constant speed treadmill (4.4 cm s^{-1} ; 0.16 km h^{-1}). Aquatic and terrestrial endurance were measured at three metamorphic stages: larval (aquatic endurance only), newly metamorphosed and 15 months post-metamorphosis. For a more complete description of methods, protocol and calculations of burst and endurance performance see Shaffer *et al.* (1991).

TEST/TIME SCHEDULE

Burst and endurance performance were measured for each animal at three time periods representing five metamorphic/ecological stages. We first measured performance when all animals were aquatic larvae in early May 1988. We measured performance again in mid-July 1988, shortly after all animals had completed metamorphosis. Finally, we examined long-term repeatability by racing each animal again 15 months later in November 1989. At this time, all animals had attained full adult size. For each period all individuals were tested for both endurance and burst performance during a continuous 2–3-day interval. Endurance was always measured first, followed by 24–48h of rest. We then conducted the four races for burst performance (see above). For the post-metamorphic experiments, each animal was

measured for both aquatic and terrestrial performance, yielding a total of five experimental periods for each individual. The exact dates are: larval aquatic (5–7 May 1988), first metamorphosed aquatic (13–15 July 1988), first metamorphosed terrestrial (21–23 July 1988), second metamorphosed aquatic (20–21 November 1989), and second metamorphosed terrestrial (25–26 November 1989).

STATISTICAL ANALYSIS

Pearson product-moment correlation coefficients, Spearman rank-order correlations, paired comparison *t*-tests, and tests for normality were computed with the Statistical Analysis System (SAS 1985). For analyses of burst speed we calculated the single fastest 20cm burst velocity and the mean velocity for the entire race for each of the four burst races per time period. Size-corrected values were computed by regressing performance measures on body size. Raw and size-corrected values gave virtually identical results, and we used raw values in all calculations (see Shaffer *et al.* 1991).

We calculated both Pearson product-moment and Spearman rank-order correlations for all comparisons. Pearson product-moment and Spearman rank-order correlations showed extremely similar values (usually identical to the second decimal place); we only report Pearson product-moment correlations.

Results

MEAN VALUES

We present the mean values for the four burst races, endurance and body mass in Table 2. We also present two different approaches to quantify burst; the mean of the entire race (top value in Table 2) and the fastest 20cm segment of that race (bottom value in Table 2), at each of the five metamorphic stages.

Several trends emerge from these results. First,

Table 3. Short (15s) and medium (2h) repeatability of burst performance and recovery time. The two short-term values are each 15s apart; the medium-term measures are a minimum of 2h apart. In each cell, the top value is the Pearson product-moment correlation for an entire race, and the middle value is the correlation for the fastest 20cm segment of a race. The bottom value shows the *t*-values for a (one-tailed) paired comparison *t*-test comparing the mean of the two races for the fastest 20cm (see text). Values in parentheses are probability levels and sample sizes

	Short term		Medium term	
	Race 1:race 2	Race 3:race 4	Race 1:race 3	Race 2:race 4
Larval	0.55 (0.0001, 121)	0.63 (0.0001, 126)	0.47 (0.0001, 122)	0.38 (0.0001, 123)
aquatic	0.51 (0.0001, 121)	0.60 (0.0001, 126)	0.45 (0.0001, 122)	0.37 (0.0001, 123)
	4.8 (0.0001, 129)	3.4 (0.0005, 134)	2.5 (0.0069, 130)	1.8 (0.0345, 131)
Metamorphosed	0.56 (0.0001, 85)	0.36 (0.0007, 86)	0.32 (0.0032, 85)	0.28 (0.0088, 86)
aquatic (1)	0.53 (0.0001, 84)	0.22 (0.0429, 83)	0.37 (0.0007, 81)	0.18 (0.0968, 85) ^{NS}
	2.4 (0.0090, 92)	-0.45 (0.6750, 91) ^{NS}	4.1 (0.0001, 89)	1.1 (0.1350, 93) ^{NS}
Metamorphosed	0.45 (0.0001, 85)	0.64 (0.0001, 86)	0.45 (0.0001, 85)	0.39 (0.0002, 85)
terrestrial (1)	0.40 (0.0002, 84)	0.58 (0.0001, 81)	0.38 (0.0004, 80)	0.42 (0.0001, 84)
	4.6 (0.0001, 92)	4.7 (0.0001, 89)	-0.64 (0.2400, 88) ^{NS}	0.18 (0.4300, 92) ^{NS}
Metamorphosed	0.31 (0.0040, 84)	0.65 (0.0001, 84)	0.48 (0.0001, 84)	0.49 (0.0001, 83)
aquatic (2)	0.20 (0.0619, 84) ^{NS}	0.63 (0.0001, 84)	0.44 (0.0001, 84)	0.32 (0.0027, 83)
	1.0 (0.1500, 92) ^{NS}	3.8 (0.0002, 90)	1.0 (0.1500, 92) ^{NS}	1.5 (0.0750, 89) ^{NS}
Metamorphosed	0.67 (0.0001, 83)	0.65 (0.0001, 79)	0.48 (0.0001, 80)	0.53 (0.0001, 79)
terrestrial (2)	0.65 (0.0001, 83)	0.60 (0.0001, 79)	0.40 (0.0003, 80)	0.50 (0.0001, 79)
	5.2 (0.0001, 90)	2.2 (0.0150, 87)	-2.9 (0.9975, 88) ^{NS}	-5.0 (0.9999, 86) ^{NS}

^{NS} Not significant.

race 1 is always faster than race 2, and race 3 is faster than race 4, suggesting that there is a consistent tiring effect between races 15s apart. Second, larvae are much faster and have greater endurance than metamorphosed aquatic animals of the same body mass (presumably reflecting larval adaptations to their exclusively aquatic existence). Finally, burst and endurance appear to scale differently with body mass. Over 15 months, body mass increased by a factor of four (from an average of 7.3 to 30.3g). This increase coincides with an increase in mean terrestrial burst speed (paired comparison *t*-test, averaged across all trials, $t = -10.48$, $P < 0.0001$), but no change in aquatic burst performance ($t = 1.52$, $P < 0.13$). Mean endurance showed a different trend; mean aquatic endurance increased (paired $t = -6.77$, $P < 0.0001$), while mean terrestrial endurance decreased ($t = 4.09$, $P < 0.0001$) over time.

BURST

Short-term burst repeatabilities representing a 15-s rest between races 1 and 2, and between races 3 and 4 are shown for all five metamorphic stages (Table 3). Medium-term burst repeatabilities representing a minimum of 2h rest between races 1 and 3, and between 2 and 4 are also shown for all five metamorphic stages (Table 3). In Table 3 the correlations between the values of the mean of the entire race (generally 50–70cm long) and the correlations for the fastest 20cm segment are shown for both short and medium-term repeatabilities. Correlations for the mean of the entire race range from 0.31 to 0.67 for short-term repeatability and 0.28 to 0.53 for medium-

term repeatability. All 20 values, for mean values of an entire race, are highly statistically significant (minimum $P < 0.0088$). Correlations for the fastest 20cm segment of each race range from 0.20 to 0.65 for short-term repeatability and 0.18 to 0.50 for medium-term repeatability, and most (18 out of 20) are statistically significant.

The bottom values in Table 3 are the results from paired comparison *t*-tests (one-tailed). A significant positive *t*-value indicates that the second race of the set was slower, whereas a significant negative *t*-value indicates that the second race was faster than the first. A short-term tiring effect occurs in eight out of 10 cases; races 2 and 4 are significantly slower than races 1 and 3, respectively. However, only three out of 10 of the medium-term comparisons are significantly different suggesting that the 2-h rest between races 1 and 3, and between 2 and 4 is sufficient time to recover burst capabilities (Table 3).

Long-term burst repeatabilities for both metamorphosed aquatic and metamorphosed terrestrial experiments representing a time span of 15 months are presented in Table 4. Burst velocities for each comparable metamorphic stage were calculated in four different ways for the computation of repeatabilities: (1) a mean of all four races was computed from the four means of each entire race, (2) a mean of all four races was computed from the fastest 20cm segment of each race, (3) the fastest of the four races, using the mean of the entire race, and (4) the fastest of the four races, using the fastest 20cm segment of each race (Table 4). When the mean of an entire race is used to calculate long-term burst repeatability, aquatic burst is significantly repeatable ($r = 0.34$ and

Table 4. Long-term (15 months) repeatability of burst performance. In each cell, the top value is calculated over the entire race, and the bottom value is calculated for the fastest 20cm segment of each race. Values are Pearson product-moment correlations, with probability levels and sample sizes in parentheses

	Mean of four races	Fastest of four races
Metamorphosed aquatic	0.34 (0.002, 82) 0.25 (0.022, 85)	0.32 (0.004, 78) 0.26 (0.015, 85)
Metamorphosed terrestrial	0.20 (0.077, 78) ^{NS} 0.31 (0.005, 83)	0.15 (0.205, 72) ^{NS} 0.32 (0.004, 83)

^{NS} Not significant.

0.32) but terrestrial burst is not ($r=0.20$ and 0.15). When the fastest 20cm of each race is used, both aquatic and terrestrial long-term burst are significantly repeatable (Table 4).

ENDURANCE

Medium-term repeatability of endurance representing a 24–48h rest between trials was measured on a random subset of our experimental animals. Medium-term repeatability is statistically significant for the larval aquatic stage ($r=0.67$, $P=0.012$, $n=13$) and approaches significance in the metamorphosed aquatic stage ($r=0.49$, $P=0.144$, $n=10$) and the metamorphosed terrestrial stage ($r=0.53$, $P=0.108$, $n=10$) (Table 5). Whereas these values are not all significant with our relatively small sample sizes, they are consistently in the 0.5 to 0.7 range, and are thus probably indicative of true repeatability values.

Long-term repeatability of endurance over 15 months was non-significant and very close to zero for both metamorphosed aquatic ($r=0.080$, $P=0.535$, $n=62$) and terrestrial ($r=0.081$, $P=0.529$, $n=62$) stages (Table 5).

Discussion

Over the past 10 years, the comparative database on locomotor performance in poikilothermic tetrapods has increased dramatically, especially for squamate reptiles (Table 1); the data we present here (see also Shaffer *et al.* 1991) adds the first large population-level analysis for a urodele. However, before discussing our results in a broader ecological and comparative context, we must emphasize several limitations to this work. First, it is not a field study (although the animals were field collected as larvae), and the laboratory-induced environmental influences on repeatability are unknown. Second, our results reflect the mean values and repeatabilities of a group of animals in the absence of natural selection over a critical period of ontogeny, where mortality is often great. Again, the effects of this are unknown,

although we suspect that both shifts in mean value and repeatabilities may be greater if selection were acting to weed out slower, less fit individuals. Finally, our results are all phenotypic, not genetic. To make inferences about evolutionary significance, we would like to have genetic data on the heritabilities and genetic correlations of locomotor variables to augment our phenotypic values (Arnold 1983; Shaffer *et al.* 1991). Thus, until our ongoing genetic experiments are complete, we must assume that the phenotypic values reported here reflect underlying genetic variances and covariances.

BURST

The ecological significance of burst performance is difficult to assess, given the scarcity of data from natural populations of *A. californiense*. However, burst performance is almost certainly a key component of evading predation from birds, frogs, fishes, turtles, invertebrates and conspecifics (Baldwin 1987; Wassersug 1989). As such, there is probably a premium on maintaining rapid burst abilities throughout an animal's lifetime. Burst performance is less likely to be important in prey capture because aquatic suction and terrestrial lingual feeding in *Ambystoma* involve a relatively static ambush strategy (Lauder & Shaffer 1985; Shaffer & Lauder 1985, 1988).

Over both a period of seconds and hours, burst performance is significantly repeatable in this population of salamanders. Values of repeatability are generally in the range of 0.5, indicating that about 25% of the variance in the second trial is accounted for by variance in the first, regardless of the life-history stage in which burst is measured (Table 3). In addition, there is a short-term tiring effect for salamanders after a 50–70-c burst at maximal speed: 15s later, average speed decreases by up to 5.9 cm s^{-1} (Table 2). Whether this decrease is ecologically relevant to *Ambystoma* is not known, although it may be extremely important for large, active-pursuit predators. However, a 2-h respite is sufficient for

Table 5. Medium (1–2 days) and long (15 months) term repeatability of endurance performance. Values are Pearson product-moment correlations, followed by probability values and sample sizes in parentheses. Long-term repeatability for larvae is not measurable, since all animals metamorphose

	Medium-term	Long-term
Larval aquatic	0.67 (0.012, 13)	—
Metamorphosed aquatic	0.49 (0.144, 10) ^{NS}	0.080 (0.535, 62) ^{NS}
Metamorphosed terrestrial	0.53 (0.108, 10) ^{NS}	0.081 (0.529, 62) ^{NS}

^{NS} Not significant.

complete physiological recovery in most cases (Table 3).

For short- and medium-term experiments, we calculated burst both as the fastest 20cm segment of a race and as the average speed over an entire race, which ranged up to 70cm. Whereas the two measures were always very similar, and led to the same biological conclusions, in 18 of 20 tests the mean of an entire race was slightly more repeatable than the fastest 20cm segment from each race (Table 3). While we feel that ecological significance should be the primary motivation for decisions on how to quantify performance parameters, in the absence of such field data, greater repeatability can be used to decide between differing measures. In this case, our data indicate that the mean burst speed of a longer race is a superior measure to the fastest 20cm segment of each race.

Over a 15-month post-metamorphic period, burst measures generally remained repeatable, although there was a uniform decrease in repeatability compared to short- and medium-term values (Table 4). In addition, long-term repeatabilities were more sensitive to the particular measure of burst performance than were short- and medium-term measures. The long-term repeatabilities of swimming performance are highest when the average of an entire race is used compared to repeatabilities calculated for the fastest 20cm segment, regardless of whether the fastest race of the mean of all four replicates is used. However, the opposite is true for repeatability of terrestrial performance. In addition, there can be large differences in repeatability depending on whether the fastest of four races, or their mean is used. For example, the repeatability of terrestrial running for an entire race is 33% greater when the mean is used rather than the fastest of four trials (Table 4). In general, studies of locomotor performance rely upon the fastest race as the most physiologically relevant measure of maximal burst, even though it may have low repeatability over time (all of the references in Table 1 measure performance in this way). However, ecologically the average burst may be much more relevant than the fastest, because it presumably reflects an individual's normal response to a predator. Because our data are the first known to us that quantitatively examine these different measures of physiological performance, we cannot say which method is generally superior at this time.

ENDURANCE REPEATABILITY

The ecological importance of sustained endurance ability is extremely difficult to evaluate in any organism, because it requires detailed knowledge of courtship, migration, hunting strategies and other activities that may lead to exhaustion. *Ambystoma* have rapid, but frequent, courtship displays (Arnold 1976) and a sedentary ambush prey capture strategy

(see above) which probably do not approach physiological exhaustion. However, tiger salamanders are migratory: adults can move several hundred yards in an evening (Semlitsch 1983), and incidental observations on *A. californiense* suggest that adults and newly metamorphosed sub-adults migrate at least a mile from their breeding ponds (H.B. Shaffer, unpublished observation). Thus, at least in the terrestrial phase, endurance may be an important component of an animal's ability to exploit breeding and aestivation sites.

Comparison of our medium- and long-term repeatability estimates for endurance show a fundamentally different pattern than for burst performance. Once again, for all three life-history stages, endurance appears to be repeatable over a time period of 1 or 2 days (Table 5). Based on small samples (10–13 individuals), our estimates for metamorphosed aquatic and metamorphosed terrestrial repeatability only approach significance at the $0.1 < P < 0.15$ level. However, because these repeatabilities are consistently about 0.5–0.6, and are thus similar in magnitude to burst repeatability, we assume that these values would become significant with larger sample sizes.

We have two measures of long-term endurance repeatability, and in both cases the repeatability values plummet to nearly zero (Table 5). While we cannot say why this pattern occurs, it does suggest that burst and endurance behave very differently in terms of long-term repeatability. When this is added to the different ways in which mean burst and endurance scale with body mass over time (Table 2), it further emphasizes that these two aspects of locomotor performance must be considered separately when designing field experiments on their ecological significance.

COMPARISONS WITH OTHER VALUES

To examine trends in repeatability values for poikilothermic tetrapods, we conducted a literature survey to summarize the currently published repeatability values for amphibians, lizards and snakes for locomotor performance (Table 1, see also Bennett 1987). Our review covers all studies known to us that report *individual* repeatabilities over time. [Bennett (1980) reports changes in mean speeds of groups of several North American lizards over 1 and several days. However, individual data were not reported.]

At present, we still have relatively little broadly comparative information on repeatability of amphibians and squamate reptiles. Several common North American genera are represented by more than one sample [in particular the iguanid *Sceloporus*, the colubrid *Thamnophis*, and the bufonid *Bufo* (Table 1)], but diversity is very low. However, even with this limited sampling, several trends seem to be emerging. First, amphibians in general appear to have

lower repeatabilities than squamates. This may reflect a real biological difference (perhaps amphibians rely on locomotor performance less than squamates, and so are physiologically less capable of sustained, repeatable performance), a difference in the suitability of the experimental apparatus to different organisms (perhaps some amphibians dry out quickly on a treadmill), or both. Tests on additional taxa from both groups, and especially amphibians, will help test this general trend. Second, while most experiments demonstrated significant repeatabilities (virtually all values in Table 1 are statistically significant) the range of repeatability values is moderate, and generally in the 0.5–0.6 range over 1 or 2 days. Third, in the four studies that have measured reasonably long-term repeatability (Garland 1985; Huey & Dunham 1987; Van Berkum *et al.* 1989; Huey *et al.* 1990; Jayne & Bennett 1990; this study), repeatabilities of both burst and endurance generally decline over a long time period. [Arnold & Bennett (1984) also found that the repeatability of antipredator behaviour in *Thamnophis radix* decreased when measured over seconds compared to 1 day and to many days (range $r=0.50-0.76$).] This adds further support to our contention that long-term repeatability must be demonstrated before analyses requiring lifetime performance profiles can be carried out with confidence.

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