

Locomotor performance of hatchling fence lizards (*Sceloporus occidentalis*): quantitative genetics and morphometric correlates

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Summary

We examined heritabilities and correlations among measures of locomotor performance (speed, stamina) and among possible morphometric determinants of performance (hindlimb span, tail length) in families of hatchling lizards (*Sceloporus occidentalis*). We were particularly interested in determining whether these traits were heritable and thus might potentially respond genetically to selection. Moreover, we wished to determine whether speed and stamina are negatively genetically correlated, as suggested by *a priori* physiological and empirical considerations. All four traits appeared to be significantly heritable. Broad-sense heritabilities were 0.33–0.36 for speed, 0.35–0.36 for stamina, 0.45–0.51 for hindlimb span, and 0.46–0.47 for tail length. Contrary to expectations, speed and stamina were not negatively genetically correlated. Hindlimb span and tail length, however, were negatively genetically correlated (but not phenotypically correlated). Hindlimb span and stamina were positively phenotypically correlated. Thus, for example, selection for longer hindlimb span could potentially result in shorter tails, contrary to evolutionary predictions based only on phenotypic correlations.

Keywords: Genetic correlations; heritability; lizards; locomotion; performance; quantitative genetics; *Sceloporus occidentalis*; speed; stamina.

Introduction

Seeing how hereditary evil qualities are, it is fortunate that good health, vigour, and longevity are equally inherited. (C. Darwin, 1868).

The evolutionary response of an individual trait to natural (or sexual) selection depends not only on its heritability, but also on its genetic correlations with other traits that are themselves subject to selection (Falconer, 1981; Arnold, 1987). Thus, selection on one trait can influence evolutionary changes on genetically correlated traits. Consequently, the heritability and genetic correlations of traits are key evolutionary variables (Falconer, 1981; Arnold, 1987); yet they are known for few traits in natural populations (review in Arnold, 1987).

Here we examine the heritabilities and genetic correlations among measures of locomotor performance (speed, stamina) and possible morphometric determinants of performance (hindlimb span, tail length; Garland, 1985) in a population of the iguanid lizard *Sceloporus occidentalis*. Speed and stamina were chosen for analysis because these organismal performance

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traits may influence fitness (Huey and Stevenson, 1979; Arnold, 1983) by affecting feeding success (Greenwald, 1974; but see van Berkum *et al.*, 1989) and escape from predators (Christian and Tracy, 1981; Huey and Hertz, 1984; Webb, 1986; Snell *et al.*, 1988). Moreover, these traits have different physiological bases (Bennett 1980b; Garland, 1984, 1988).

We wished first to determine if speed, stamina, hindlimb span, and tail length were heritable and thus could potentially respond to selection. We wished also to determine if speed and stamina were negatively correlated genetically, such that selection to promote speed might reduce stamina, and vice versa (see Discussion). Physiological and empirical considerations (reviewed in Garland, 1988) suggest that this might be the case. For example, speed and stamina are inversely related among species of lacertid lizards (Huey *et al.*, 1984). In humans, individual athletes may be either excellent sprinters or excellent distance runners, but seldom both (Heinrich, 1985).

We examine the heritability and genetic correlations of locomotion by using a full-sib analysis of hatchling lizards. An earlier and smaller-scale study indicated that speed is heritable in this same population (van Berkum and Tsuji, 1987).

This paper is part of a series dealing with selection on locomotor performance in *Sceloporus occidentalis*. Other papers examine the repeatability of performance over time and among different measurement temperatures (van Berkum *et al.*, 1989) as well as natural selection on performance (Huey *et al.*, in preparation). Our project was inspired by seminal theoretical work by Lande (1979), Lande and Arnold (1983), and Arnold (1983) and by parallel research on garter snakes (Arnold and Bennett, 1988; Garland, 1988; A. F. Bennett and B. C. Jayne, pers. comm.). A comparison of our results with those on garter snakes is of interest because snakes and lizards have different modes of locomotion (Gans, 1986) and ecologies (Seigel *et al.*, 1987).

Materials and methods

Obtaining and incubating eggs

Thirty-three gravid *Sceloporus occidentalis* were collected near Lyle, Klickitat Co., Washington in early June 1985. Within two days of capture, they were measured (mass in g, snout-to-vent length, SVL, in mm), toe-clipped, and housed individually in plastic boxes with damp soil (peat moss and sand), a water dish, and bark. Environmental cycles of light (full-spectrum Vita-lites® and temperature approximated those experienced by lizards in south-central Washington in late spring (12:12 L:D and 34°C:17°C; Tsuji, 1986). Crickets and mealworms, dusted with vitamin supplement (Vionate® and cuttlebone shavings), were provided daily in excess.

Cages were checked for eggs at least twice a day, and females deposited their eggs between 7 and 22 June. Eggs ($n = 483$) were then placed singly in plastic cups with moist vermiculite (Terralite®, grade 3) adjusted to a soil-water potential of -20 kPa (Tracy *et al.*, 1978), and then incubated at 30°C, conditions optimal for incubating eggs of *Sceloporus* (C. R. Tracy, pers. comm.). To eliminate potential among-clutch differences in post-laying environment, which could inflate estimates of heritability, we randomly distributed the cups containing eggs of a clutch into different larger containers that were sealed to minimize water loss (but were opened almost daily to renew oxygen levels), and we shifted the positions of the egg containers every few days. To maintain water potentials, we renewed the incubation media weekly. Eggs quickly absorbed water, so estimates of initial egg mass at laying are confounded by the actual time since laying. We therefore report egg mass taken one week after laying.

Care of hatchlings

Egg cups were checked several times daily, and any new hatchlings were promptly weighed,

measured (snout–vent length (SVL), tail length, hindlimb span (Garland, 1984, 1985)), sexed and toe-clipped (which does not influence speed, Huey *et al.*, unpublished data). Hatching success was 89%; a few of the deaths were accidents in handling. Hatchlings were then transferred to individual plastic cages (18 × 12 × 11 cm, sand substrate, water dish, bark for cover) and placed randomly with respect to clutch in an environmental chamber (conditions as for dams, above). Every week positions of the cages were randomized.

Measurement of locomotor performance

On 8 August 1984, we selected for racing (and reweighed) the 300 hatchlings having the central-most hatching dates (thereby minimizing variation in age): their average (+ SD) age at first race was 12.9 ± 0.05 (range = 12–15) days. Hindlimb span, SVL, and tail length were remeasured about two weeks later. These measurements were used in quantitative genetic tests. Lizards with broken tails were excluded from analyses involving tail length. Consequently, this data set has fewer individuals ($n = 248$) than those for the other three characters ($n = 290$). Because tails were not necessarily broken before the ‘best’ speed or stamina scores, residual speed and residual stamina scores (see data analysis below) were largely unaffected by whether tails were complete or broken (speed: $F = 0.60$; stamina: $F = 2.71$; $p > 0.10$ for both).

We measured speed and stamina of each hatchling on two separate days. We raced (speed or stamina) 75 hatchlings per day; thus, one set of trials took four days. For a given hatchling, sprint speed was measured on day 1 and again on day 6; stamina was measured on days 3 and 8. Days 2, 4, 5 and 7 were rest days. Body temperatures during trials were 34°C, which is near the optimal temperature for sprinting (Bennett, 1980a; van Berkum, 1988).

Sprint speed. Sprint speed was measured by chasing lizards along an electronic ‘racetrack’ (Huey *et al.*, 1981) that was 1 m long and equipped with photoreceptors at 0.1 m intervals (van Berkum *et al.*, 1989). They were raced four times per day with 1 h rest between races. Our measure of maximal speed is the single fastest 0.2 m interval (m/s) from among all eight races. We subjectively judged ‘race quality’ of each run (‘high’ vs ‘low’), following van Berkum and Tsuji (1987). Race quality measures a lizard’s tendency to run continuously down the track.

Stamina. To determine stamina of lizards running on a treadmill, we placed individuals on a rubberized belt moving at a low speed (0.225 km/h) and tapped them lightly when necessary (in van Berkum *et al.*, 1989). Stamina was assessed as the elapsed time (in s) until the hatchling had fallen off the belt several times and had lost its righting response (Huey *et al.*, 1984). The longer of the two trials (on days 3 and 8) estimates maximum stamina (Garland, 1984). We also judged ‘jog quality’ of each run, where high quality indicates that a lizard ran smoothly. Because jog quality and stamina are uncorrelated, we do not report jog quality. Finally, we recorded aggressive behaviors of hatchlings (no aggression vs biting: cf. Arnold and Bennett, 1984; Garland, 1988). However, only 26 lizards measured were aggressive, and only two were aggressive in both trials. Consequently, we do not analyze these data either.

Data analysis

Two performance characters (speed, stamina) were transformed (Sokal and Rohlf, 1981) to achieve the closest approximation to normality: for speed, square; for stamina, inverse square-root. Hindlimb span and tail length were \log_{10} transformed to reduce the dependency of the variance on the mean and to linearize relationships with \log_{10} body size (mass, SVL).

We assumed that newborn lizards were of full-sibs (Arnold, 1981a,b,c; Arnold and Bennett, 1984, 1988; van Berkum and Tsuji, 1987; Garland, 1988). This assumption may result in inflated

heritability estimates if some litter mates were half-sibs (Stearns, 1984). Full-sib data provide an upper bound to parametric narrow-sense heritabilities, because the resulting analyses may be confounded by dominance, and epistasis, non-genetic maternal effects, and common family environment (Arnold, 1981a; Falconer, 1981). Accordingly, other breeding designs will ultimately be necessary for definitive analyses (Falconer, 1981). Nonetheless, full-sib designs represent an important first attempt at genetic analyses (Arnold, 1986).

To reduce the inflation of heritabilities by non-genetic effects, we first screened characters for possible non-genetic maternal effects. For example, maternal size and condition could be affected by nutrition, thermal history or age, rather than by genetic effects. These maternal characteristics could in turn influence hatchling sprint speed, stamina, and morphology by affecting body size or nutrition to the embryo (see Falconer, 1981; Garland, 1988). Therefore, all quantitative genetic analyses were based on residuals computed from multiple regression analyses. First, stepwise multiple regression analyses (for hatchling speed, stamina, hindlimb span, and tail length) were performed with potentially significant covariates (cf. Garland, 1988): egg mass, litter size, hatchling body mass, hatchling sex, hatchling snout-vent length, hatchling age, dam body mass, and dam snout-vent length (Table 1). Speed trials were also examined for behavioral effects by including race quality (above) as a covariate. Second, residuals were calculated for each trait using only significant covariates ($p < 0.05$).

Table 1. Summary statistics of measurements of hatchling lizards ($n = 290$) and dams ($n = 33$). Body mass and age of hatchlings are given for values at time of performance measurements.

Measure (units)	Mean	SD	Range
Body mass (g)	0.62	0.004	0.45–0.85
Snout-vent length (mm)	29.9	0.053	27–32
Age (days)	12.86	0.055	12–15
Egg mass (g)	0.74	0.073	0.57–1.00
Litter size (number of eggs)	12.03	2.734	8–18
Mass of dam after laying (g)	10.23	0.307	7.2–14.5
Snout-vent length of dam (mm)	70.2	0.651	63–77

Quantitative genetic parameters (heritability, genetic and environmental correlations) were calculated and tested for significance using Shaw's (1987) program for restricted maximum likelihood estimation. Although the power of likelihood tests is less than for standard tests using F -ratios (Shaw, 1987), they are the only well-established method for significance testing of genetic and environmental correlations. To permit comparisons with previous studies, however, we (1) report standard least-squares estimates of the genetic parameters (ONEWAY, MANOVA, SPSS-PC+; Norusis, 1986); (2) report estimates of genetic correlations based on correlations among weighted litter means (Arnold, 1981a; Falconer, 1981); and (3) use Bulmer's (1980, p. 84) algorithm to calculate 95% confidence intervals for heritabilities.

To compare variability of characters, we computed approximate coefficients of variation (Garland, 1984, 1988). Specifically, we \log_{10} transformed each character, regressed them on any significant covariates, and compared standard deviations of residuals (multiplied by 2.3026 because transformations were \log_{10} rather than $\log e$).

Heterogeneity of variances among families may indicate underlying effects of major genes and also violates an assumption of least-squares and maximum likelihood tests (Mitchell-Olds and Rutledge, 1986). We therefore tested for homogeneity of variances among families using Cochran's *C* and Bartlett-Box *F* (ONEWAY, SPSS-PC+; Norusis, 1986; Sokal and Rohlf, 1981). We also used Levene's test, an analysis of variance of absolute deviations of each individual's residual value from its corresponding family mean of residual values (Conover *et al.*, 1981).

Results

Repeatability of locomotor performance

Both speed and stamina were significantly repeatable between the two trials (see also van Berkum *et al.*, 1989). Intraclass correlation coefficients were 0.450 and 0.643, respectively ($F = 2.63$, $p << 0.001$, $n = 297$; $F = 4.60$, $p << 0.001$, $n = 295$). Pearson product-moment correlations were also significant (0.453, $p << 0.001$; and 0.655, $p << 0.001$). Overall, speed scores of individuals did not change significantly between trials (paired *t*-test; $t = 1.76$; $p = 0.08$). Stamina scores, on the other hand, increased within individuals between trials by an average of 15.6 s ($t = 3.01$; $p = 0.003$). Log-transformed speed and stamina scores yielded similar results.

Descriptive statistics and scaling

The performance characters (speed, stamina) were much more variable than the morphometric characters (hindlimb span, tail length) (Table 2). Treadmill stamina was considerably more variable than speed (CV = 42.3 versus 13.9%, respectively), as has been noted in several previous studies of reptiles (Garland, 1984, 1985, 1988; Garland and Else, 1987). The relative variability of a character was essentially unchanged after computing residuals (Table 2, standard deviation of residuals).

Table 2. Descriptive statistics of morphometric and performance traits. $n=290$, except for tail length $n=248$.

Character (units)	Mean±SD	Range	CV(%)	SD of Logs (× 2.3026)	SD* of Residuals (× 2.3026)
Speed (m/s)	1.26±0.176	0.38–1.77	13.9	15.5	13.5
Stamina (s)	276±117.2	89–1288	42.3	33.2	32.9
Hindlimb span (mm)	41.7±1.40	37.0–46.0	3.4	3.4	2.3
Tail (mm)	31.0±1.91	25.5–36.0	6.2	6.2	4.8

* Approximately equal to a coefficient of variation; computed by multiplying the standard deviation of \log_{10} residuals by 2.3026 (see Materials and methods).

Coefficients of static allometry, or scaling of the four characters with body size, were calculated by partial regression of \log_{10} transformation of characters on \log_{10} (body mass) and any other appropriate covariates that were not related to size (see next section). The resulting scaling relationships were for speed, $\text{mass}^{0.171+0.135}$ (+95% confidence limits, partial $r^2 = 0.017$, $p = 0.013$);

for hindlimb span, $\text{mass}^{0.192+0.025}$ (partial $r^2 = 0.428$, $p < 0.001$); and for tail, $\text{mass}^{0.263+0.057}$ (partial $r^2 = 0.247$, $p < 0.001$). In contrast to other studies in reptiles (Garland, 1984, 1985, 1988; Garland and Else, 1987), stamina did not vary with body mass either when age was or was not held constant ($\text{mass}^{0.187+0.329}$; partial $r^2 = 0.004$, $p = 0.265$). (We note, however, that the size range (Table 1) is very small.)

Variation among families

Before computing residuals, we first evaluated variation among families on the transformed values. Transformed values of the four characters varied significantly among families (21.5% speed, 20.9% stamina, 46.3% hindlimb span, and 37.8% tail; all $p < 0.0001$). These components of variance very likely are inflated by non-genetic maternal effects, which we attempted to remove by regressing the characters on appropriate covariates (such as body size) and taking residuals. The decrease in the among-family variance after removing the effects of these covariates is described in the following sections.

Correlations among characters

Of the potential covariates (see Materials and methods), female snout–vent length and body mass after egg-laying, egg mass, litter size, and hatchling snout–vent length and body mass (average size during the performance measurements) were significantly positively correlated (Table 3). Larger dams produced not only greater numbers of eggs but also larger eggs and heavier hatchlings, although egg mass was not correlated with litter size. (Larger female garter snakes also produced larger litters and larger offspring (Garland, 1988).) Despite the small range of hatchling ages, hatchling size was correlated with age at performance measurements. Not surprisingly, body length was correlated with body mass. (These correlations may bias estimates of partial regression coefficients (see below; Slinker and Glantz, 1985); however, our objective is to remove as much of the non-genetic maternal or common family environment effects as possible, not to interpret the independent effects of each covariate on the four traits.)

Raw speeds were initially leptokurtic, but the square transformation normalized the

Table 3. Pearson product–moment correlations among potential covariates of traits ($n = 290$). Significant correlations ($p < 0.05$) are **boldface**. All correlations involving snout–vent length (SVL) or mass are based on log-transformed values.

	Body mass	Sex	Age	Egg mass	Litter size	Dam SVL	Dam mass
Hatchlings							
SVL	0.693	0.041	0.162	0.387	0.132	0.197	0.086
Body mass		0.045	0.180	0.439	0.098	0.120	0.251
Sex*			–0.068	0.045	0.076	0.023	0.055
Age				0.298	0.068	–0.071	–0.005
Egg mass					0.069	0.105	0.290
Litter size						0.772	0.713
Dams							
Dam SVL							0.661

* 1 = male, 2 = female.

distribution. In stepwise regression of speed with the possible covariates, race quality (partial $r^2 = 10.8\%$) and log snout–vent length (partial $r^2 = 4.3\%$) were significant predictors (multiple $r^2 = 15.1\%$) of speed (squared). Fast lizards typically had high race quality (i.e., sprinted more continuously) and had longer bodies. Residuals computed from the transformed scores were also normal (Figure 1).

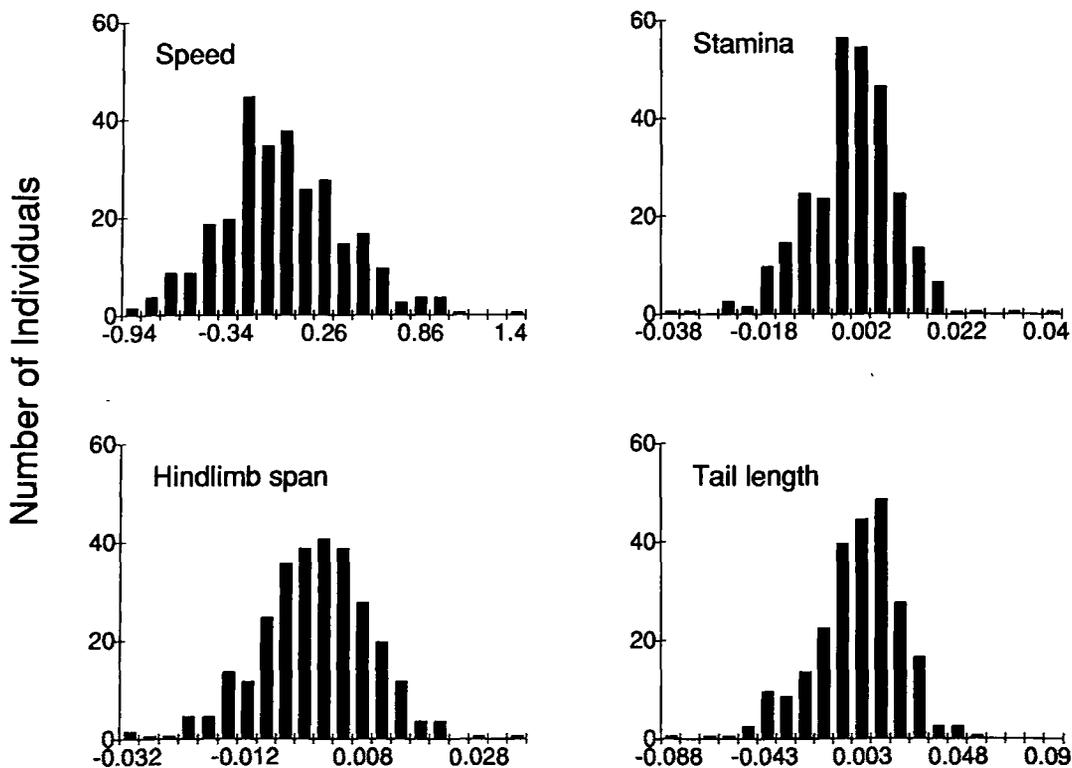


Figure 1. Frequency distributions of residuals computed from transformed scores of performance and morphometric traits.

Raw endurance times were positively skewed and highly leptokurtic ($g_2 = 22.23$). In other words, a few individuals had exceptional stamina. An inverse square-root transformation greatly improved the normality of the distribution stamina, which however remained leptokurtic ($g_2 = 1.66$, $t = 5.81$, $p < 0.01$). Explained variation in endurance times was small but significant (multiple $r^2 = 2.8\%$). Lizards with high stamina were older (partial $r^2 = 1.6\%$) and were from larger dams (partial $r^2 = 1.2\%$). The kurtosis of the distribution became slightly worse when residual values were computed ($g_2 = 1.76$, $t = 6.19$, $p < 0.01$, Fig. 1).

The distribution of hindlimb spans was leptokurtic ($g_2 = 1.11$) and negatively skewed ($g_1 = -0.66$). Log transformation reduced the dependence of the variance on the mean, but slightly increased both kurtosis ($g_2 = 1.32$, $t = 4.63$, $p < 0.01$) and skewness ($g_1 = -0.79$, $t = 5.55$, $p < 0.01$). Several covariates explained significant amounts of variance in log hindlimb span (multiple $r^2 = 55.3\%$): hatchling mass (partial $r^2 = 44.1\%$), log egg mass ($r^2 = 5.4\%$), log hatchling snout–vent length ($r^2 = 2.6\%$), sex ($r^2 = 1.4\%$), age ($r^2 = 1.1$), log dam snout–vent length ($r^2 = 0.7\%$). Thus, hindlimb span was greater in heavier and longer hatchlings, those with

longer body length relative to mass, younger hatchlings irrespective of size, males, hatchlings from longer dams, and hatchlings from larger eggs. The residuals of this character were nearly normal and only slightly leptokurtic ($g_1 = 0.72$, $t = 2.53$, $0.01 < p < 0.02$, Fig. 1).

Tail length was normal ($g_2 = -0.27$, $g_1 = -0.06$). Significant variance in log tail length was explained by log snout-vent length (partial $r^2 = 32.7\%$), log egg mass ($r^2 = 1.8\%$), age ($r^2 = 2.3\%$), and sex (1.1%). Younger males with greater snout-vent length from larger eggs had longer tails. The distribution was also normal after log transformation ($g_2 = -0.21$, $t = -0.70$, $p > 0.40$; $g_1 = -0.22$, $t = -1.41$, $p > 0.10$). The distribution of the residuals was leptokurtic and negatively skewed ($g_2 = 0.95$, $t = 3.07$, $p < 0.01$; $g_1 = -0.60$, $t = 3.84$, $p < 0.01$; Fig. 1).

Among-family variance and heritability

Variation among families was highly significant for all four residual characters: 16.4% speed, 17.5% stamina, 22.8% hindlimb span, 23.1% tail length. Heritabilities (twice these values) ranged from 0.33 for speed to 0.46 for tail length (Table 4). When the effects of race quality on speed are not removed, the heritability for speed increases to 0.40. (Race quality differed significantly among families (ANOVA, $F = 1.77$, $p = 0.009$).

Table 4. Heritabilities (based on residuals from multiple regression equations, see text) calculated first by analysis of variance of among versus within families ($df=32$ 257 except for tail length, $df=32$ 215), and second by restricted maximum likelihood estimation (REML) using a chi-square test for significance ($df=3$ for speed and hindlimb span; $df=4$ for stamina and tail length). Bulmer's 95% confidence limits are also listed.

Character	Heritability	F or χ^2	p	Method
Speed	0.33	2.72	<0.001	ANOVA
	0.36	17.5	<0.001	REML
	0.17<0.39<0.73	–	–	Bulmer
Stamina	0.35	2.85	<0.001	ANOVA
	0.36	22.5	<0.001	REML
	0.16<0.35<0.66	–	–	Bulmer
Hindlimb span	0.45	3.57	<0.001	ANOVA
	0.51	35.2	<0.001	REML
	0.25<0.48<0.80	–	–	Bulmer
Tail length	0.46	3.24	<0.001	ANOVA
	0.47	33.4	<0.001	REML
	0.26<0.52<0.89	–	–	Bulmer

All residual characters, except speed, showed significant heterogeneity of variances among families (endurance: Cochran's $C = 0.105$, $p = 0.019$; Bartlett-Box $F = 1.95$, $p = 0.001$; hindlimb span: $C = 0.17$, $p < 0.01$; $F = 1.45$, $p = 0.052$; tail: $C = 0.12$, $p < 0.01$; $F = 2.18$, $p < 0.01$). However, Levene's tests, which determine if families differ in magnitude of variation, were significant only for stamina (8% heterogeneity among families) and tail length (15% among families). Although the degree to which this heteroscedasity may have biased significance tests of heritabilities for stamina and tail length are uncertain, the magnitude of heritabilities for these traits suggests that true heritabilities should still be significantly greater than zero.

To check for the possible effects of major genes (Mitchell-Olds and Rutledge, 1986), we examined plots and corresponding quadratic regressions of the magnitude of deviation of an individual's residual value from its family mean of residuals versus the family mean of residuals for each trait. Specifically, greater variability for intermediate than for extreme families would suggest effects of major genes (T. Mitchell-Olds, pers. comm.). (Extreme families are those with high absolute deviation of family means from the mean of all residuals, 0.) Variability was similar for extreme and intermediate families for most traits. However, stamina did show differences in variability between extreme and intermediate families. The quadratic term for this trait explained only 3.4% of the variation ($p = 0.002$) with more extreme families being slightly more variable. Overall, our results and those of Garland (1988) do not show evidence of effects of major genes.

Phenotypic, genetic and environmental correlations

Significant phenotypic correlations were found between residual speed and stamina and between residual stamina and tail length ($r = -0.13$, $p = 0.026$; $r = -0.22$, $p = 0.001$; respectively; Table 5). (NB. Because stamina was inversely transformed, the negative sign of this correlation indicates a positive correlation between these traits.) Thus, lizards that were fast also tended to have high stamina; those with longer tails had greater stamina.

Based on maximum likelihood tests, genotypic covariances and thus correlations between traits were significant only for hindlimb span and tail length, which were negatively genetically correlated. The only significant environmental covariance was a positive correlation between

Table 5. Correlations among speed, treadmill endurance, hindlimb span and tail length (based on residuals from multiple regression equations; $n = 290$, except for tail length for which $n = 248$). Phenotypic correlations are standard Pearson product-moment. Genetic correlations are maximum likelihood estimates followed (in parentheses) by least-squares estimates, obtained by partitioning covariance among versus within families, and (2) correlations among weighted litter means (Arnold, 1981a). Environmental correlations are maximum likelihood estimates, followed (in parentheses) by least-squares estimates. For phenotypic and maximum likelihood estimates, significant ($p < 0.05$) results are in **boldface**.

Correlation	Trait		
	Stamina	Hindlimb span	Tail length
Speed			
Phenotypic	-0.130*	0.079	0.034
Genetic	-0.039 (-0.047, -0.083)	0.400 (0.372, 0.255)	<0.001 (-0.147, -0.012)
Environmental	-0.109 (-0.173)	-0.120 (-0.107)	0.054 (0.152)
Stamina			
Phenotypic		0.032	-0.218
Genetic		0.239 (0.230, 0.153)	-0.346 (-0.343, -0.265)
Environmental		-0.109 (-0.100)	-0.147 (-0.136)
Hindlimb			
Phenotypic			0.003
Genetic			-0.638 (-0.653, -0.390)
Environmental			0.585 (0.556)

* Because stamina values were transformed by an inverse square-root function, a negative correlation between stamina and any other trait is actually a positive correlation and vice versa.

hindlimb span and tail length. Because the environmental and genetic correlations for these two traits have opposite signs and magnitudes, the phenotypic correlation is about zero (Table 5).

Discussion

Heritability

Speed appears to be heritable in *Sceloporus occidentalis* and thus could potentially respond to selection. The heritability of speed (0.33–0.39, range of estimates; Table 4) was less than reported in an earlier (smaller-scale) study of lizards from this same population (0.59; van Berkum and Tsuji, 1987). This difference may reflect sampling errors, or the fact that eggs of a given clutch in the previous study were incubated in the same container. Our estimates are also lower than those for newborn garter snakes (0.58, Garland, 1988). However, the confidence limits of all these heritability estimates are broad (0.17–0.89 in the present study) and overlap considerably.

Heritabilities of various indices of sprint performance in racehorses and greyhounds are roughly similar to those reported for lizards. Heritability estimates of race timing or speed in thoroughbred and standardbred horses range from 0.02 to 0.32, whereas those based on other measures of racing ability (such as handicap or earnings) are 0.19 to 0.76 (Hintz, 1980; Langlois, 1980; Ojala and Van Vleck, 1981; Tolley *et al.*, 1983; Gaffney and Cunningham, 1988). Track performance in greyhounds (timing and finishing place) has a heritability of 0.23 (Ryan, 1975).

Because heritabilities in racehorses are based on sire–progeny correlations, heritabilities above 0.3 to 0.4 are thought to be overestimates (Langlois, 1980). Not only are sires selectively bred to mares of similar quality, but also the environment and training of the progeny depends on the worth of the sire. As a result, heritability estimates for horses and greyhounds are potentially confounded by genotype–environment correlations, assortative mating, and high homogeneity of dams in harems (Langlois, 1980; Hill, 1988).

Treadmill endurance had a heritability of 0.35 to 0.36, suggesting that stamina could also respond to selection. Our value for lizards was less than reported for garter snakes (0.70) by Garland (1988), although the confidence intervals of these values overlap considerably.

Considering the morphometric characters, hindlimb span (0.45–0.51) and tail length (0.46–0.47) were more heritable than were the performance characters (0.33–0.36). In animal breeding studies, linear dimensions typically show heritabilities of 70% or higher (Arnold, 1987). In *Sceloporus occidentalis*, hindlimb span and tail length appear to conform roughly to this generalization.

We emphasize that our measures probably overestimate narrow-sense heritabilities because (1) they are actually ‘broad-sense’ heritabilities, and (2) they very likely include some non-genetic maternal effects of common family environments before the eggs were laid. Studies that have examined potential overestimation of narrow-sense heritabilities by full-sib designs report both overestimation and almost no overestimation in natural populations of vertebrates (Boag, 1983; Stearns, 1984; Hailman, 1986; Mousseau and Roff, 1987; Gibbs, 1988). On the other hand, by removing correlations with body size, race quality, and presumed non-genetic effects before estimating heritabilities, we may have inadvertently removed some additive genetic variance. For example, heritability estimates for speed dropped when the effects of race quality (which itself runs in families) were removed.

Genetic correlations

Given that the performance traits appear heritable, do the phenotypic and genetic correlations suggest the response to selection might be modified by selection on other correlated traits? For residual speed and stamina the answer is seemingly no. A positive phenotypic correlation and the

absence of a significant genetic correlation between speed and stamina indicates that a presumed tradeoff between speed and stamina does not exist, at least with respect to whole-animal performance. Positive phenotypic and genetic correlations between speed and stamina were found in garter snakes (Garland, 1988). Nevertheless, a possible genetic tradeoff between speed and stamina in lizards is suggested by the tendency for hindlimb span to be positively genetically correlated with speed but negatively genetically correlated with stamina (Table 5).

Other factors contributing to tradeoffs between speed and stamina may be tradeoffs between having fast or slow fiber types in muscles or between shape differences such as relative size of limbs or other body proportions (MacMahon, 1984). Our removal of the effects of body mass and length on the four traits, however, may have masked the influence of shape on performance. However, factors such as muscle mass or vigor, both of which might be genetically variable, may cause speed and stamina to be positively correlated (Garland, 1988).

The only significant genetic correlation in our study was the negative genetic correlation between residual hindlimb span and tail length. Accordingly, selection for an increase in one trait could lead to a decrease in the other trait. Interestingly, the phenotypic correlation between these traits is virtually zero because of the positive environmental correlation between these traits. Clearly, prediction of evolutionary response based only on a phenotypic analysis would be misleading.

Garland (1985) reported positive phenotypic correlations between residual hindlimb span and tail length in an Australian agamid lizard, but no correlation between these residuals and residual speed or stamina (Garland and Else, 1987). Studies of other species of lizards have found no significant negative phenotypic correlation between individual differences in speed and stamina (Garland and Else, 1987).

Implications

Traits that are major fitness components, and hence have been under strong directional selection for many generations, are expected at equilibrium to have (1) low heritability or (2) moderate to high heritability and be negatively genetically correlated (cf. Falconer, 1981; Mousseau and Roff, 1987). Speed and stamina do not appear to match either of these predictions. (Garland (1988) found that these predictions also do not hold for snakes.) Therefore, these elements of locomotor performance may not have been under strong directional selection, contrary to expectation (Huey and Stevenson, 1979; Arnold, 1983). Measurements of phenotypic selection in this population of lizards (Huey *et al.*, in prep.) are consistent with this interpretation. Alternatively, speed and stamina could be negatively genetically correlated with some other (unmeasured) fitness traits. However, performance of racehorses and greyhounds appears heritable, despite many generations of selection, so either selection is less strong than imagined (Gaffney and Cunningham, 1988; Hill, 1988) or the theory may not apply.

In conclusion, our study suggests that speed and stamina are heritable but are not negatively genetically correlated, despite *a priori* considerations (Garland, 1988; Introduction). Both traits have the potential to respond to selection, and a response of one trait should be largely independent of the other trait. Validation of these patterns will, however, require use of a more sophisticated breeding design (e.g. half-sib).

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