
Variation in Locomotor Performance in Demographically Known Populations of the Lizard *Sceloporus merriami*

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Abstract

We examined correlates (sex, size, age) of variation in maximal burst speed (racetrack) and in stamina (time until exhaustion at 0.5 km · h⁻¹) in two populations of the iguanid lizard Sceloporus merriami in Big Bend National Park, Texas. Because these populations were known demographically and were studied in several years, we were able to examine the effects of adult age on performance, the between-year repeatability of individual performance, and environmental correlates of yearly variation in performance. Variation in locomotor capacities was striking. Males were faster than females, and lizards from the Grapevine Hills were faster than those from Boquillas (lower elevation). However, sex and population did not affect stamina. Young adults (1-yr-olds) were slightly faster but had slightly less stamina than did older adults (2-3-yr-olds). Adult size (mass, snout-vent length, hind limb length) had little effect on performance. Average performance varied significantly among years, but stamina varied more than did speed. Stamina was highest in a summer preceded by relatively wet fall and winter. Despite the between-year variation in average performance, individual speed and stamina are both significantly repeatable over at least 1 yr. Neither tail loss nor toe loss affected sprint speed, but body temperature had a marked effect on speed.

Introduction

The ability to sprint quickly or to sustain activity for long periods not only tests an animal's physiological and morphological capacities, but may also

influence how well it captures prey, evades predators, or interacts socially (Huey and Stevenson 1979; Bennett 1980*a*; Arnold 1983; Bennett and Huey 1990). The maximal locomotor performances of animals have received considerable attention, especially regarding two main issues. First, what are the genetical, physiological, and morphological bases of variation in performance (Taylor and Weibel 1981; Bennett, Huey, and John-Alder 1984; Garland 1984, 1985; Huey and Hertz 1984*b*; Bennett 1987; Gleeson and Harrison 1988; Jayne and Bennett 1989*a*, 1989*b*; Tsuji et al. 1989)? Second, what are the ecological and behavioral causes and consequences of that variation (Huey and Stevenson 1979; Shine 1980; Christian and Tracy 1981; Arnold 1983; Huey and Hertz 1984*b*; Snell et al. 1988; Pough 1989; Bennett and Huey 1990)?

In 1984 we began a long-term study of locomotor performance of demographically known populations of the iguanid *Sceloporus merriami*, a small, rock-dwelling lizard found in southwestern Texas and adjacent Coahuila and Chihuahua, Mexico. In each year we measured maximal sprint speed or stamina (or both) of lizards from two populations. Our primary goals were (1) to search for correlates (e.g., sex, age, size, year) of variation in maximal speed and in stamina and (2) to analyze some ecological consequences of that variation. In a previous paper (Huey and Dunham 1987) we examined the between-year (1984–1985) repeatability of sprint speed. Using data gathered between 1984 and 1988, we now address the first goal in detail, that is, determining whether performance varies among years and populations with respect to sex, adult age, size, tail condition, reproductive state of females, and individual identity. We also briefly examine whether patterns of between-year variability in performance correlate with rainfall. Finally, we present experimental data on the effects of body temperature and of tail loss on sprint speed. In a subsequent paper we will analyze the complementary question of whether variation in locomotor performance correlates with survivorship.

We selected *S. merriami* for analyses because two populations of these lizards have been the subject of intensive, long-term studies of their demography, behavior, and ecology (Dunham 1978, 1980, 1981; Ruby and Dunham 1987; Dunham, Grant, and Overall 1989). As a result, knowledge of the general ecology of this species is exceptionally detailed not only at the population level, but at the individual level. Age, reproductive condition, and social status are known for many individuals. We exploit some of this demographic and ecological information in analyses of our physiological data. Because we know each lizard's age, we can determine whether and how age affects locomotor capacities; because all lizards are individually marked, we can determine whether locomotor performance is repeatable through time. The

incorporation of a demographic perspective into physiological studies is overdue.

Material and Methods

Lizards used in these experiments were collected in late June and early July of 1984–1988 (National Park Service permit to A.E.D.) at two sites in Big Bend National Park in southern Texas. The sites are described in detail in Ruby and Dunham (1987) and Dunham et al. (1989). Boquillas (altitude = 560 m) is a narrow limestone (Cretaceous) wash that drains southward into the Rio Grande. The Grapevine Hills sites (II and IV of Dunham 1978, 1980, 1981) are on west- or southwest-facing hillsides of a granitic lacolith (altitude = 1,036 m). These populations, separated by 35 km, are physically isolated by lack of contiguous habitat, have different but overlapping flora, and differ in annual rainfall and temperature (Dunham et al. 1989; see below).

Lizards were collected in the morning from the Grapevine Hills and in the morning or evening from Boquillas and taken to a nearby laboratory. After at least 1 h, we began performance trials. We measured maximal burst speed in every year but 1986, and stamina every year beginning in 1986. Speed and stamina were measured on the first afternoon and following morning, respectively, following capture. Because locomotor performance is highly temperature sensitive (Bennett 1980*a*; Hertz, Huey, and Nevo 1983; Crowley 1985*a*), we measured performance at 33°–34°C, a range chosen to approximate the field body temperature (T_b) of active animals in summer (Grant and Dunham 1988; see table 5). Lizards were not fed during their brief stay in captivity.

Individual lizards at both sites are assigned unique toe clips. For each lizard we recorded toe-clip number, sex, size (body mass in grams, snout-to-vent length [SVL] in millimeters, hind limb length in millimeters), reproductive condition of females (not gravid, developing follicles, gravid, recently oviposited; determined by palpating), tail condition (whole, broken, and regenerating), and length (mm), and noted any visible injuries. Age was determined from capture-recapture records. We presently analyze data only on adults in two age categories: “young” (age 1 yr) or “older” adults (age 2 or 3 yr). Hatchlings and very old lizards (>3 yr, potentially senescing) are uncommon in our samples. To achieve some balance in our analyses of variance, we must therefore exclude data on hatchlings and very old adults.

We raced lizards “blind” with respect to identity and age; however, some young adults can be conspicuously smaller than older adults. We were un-

able to race lizards blind with respect to locality and sex as both the provenance and sex of individuals are morphologically obvious.

Measuring Speed and Stamina

Methods of measuring sprint speed follow Huey and Dunham (1987). In brief, lizards were chased down a 2-m racetrack (rubberized substrate). Photocell stations were positioned at 0.25-m intervals along the track and connected to a computer (Miles and Smith 1987). A sprinting lizard would break the photocell beams, and the interval speeds ($\text{m} \cdot \text{s}^{-1}$) between all photocell stations were automatically recorded. Lizards were raced six times, usually with 1 h rest between trials. The single fastest 0.5-interval among all six trials served as the estimate of maximal speed for each lizard. Methods of measuring stamina follow Huey et al. (1984). Lizards were placed on the moving belt ($0.5 \text{ km} \cdot \text{h}^{-1}$) of a treadmill. The elapsed time (decimal minutes) until the lizard was exhausted (validated by loss of righting response) indexed stamina. Stamina was measured only once.

Effect of Toe Loss

Lizards in population studies are typically identified by unique toe clips (Tinkle 1967; Dunham 1980), and lizards sometimes lose toes naturally, presumably from injuries or encounters with predators. To determine whether toe loss influences sprint speed, we regressed residual speed on number of clipped toes, where the residuals of log speed were obtained from a regression with locality, sex, and cube root of mass as covariates. The average number of toes clipped was 3.5 for Boquillas (range = 2–6), and 3.6 (range = 1–6) for Grapevine. This analysis was conducted for the 1984 and 1985 data sets only.

Effect of Body Temperature

To determine the effect of body temperature on sprint speed, we measured speeds of individual lizards at 28°, 33.5°, and 37°C following general protocols in Hertz et al. (1983). These T_b 's bracket most of the T_b 's experienced by these lizards in nature (Boquillas: median = 32.8°C, Q_1 and Q_3 [lower and upper interquartiles of T_b] = 31.8° and 33.9°C, range = 26.4°–39.5°C; Grapevine Hills: median = 32.3°C, Q_1 and Q_3 = 30.9° and 33.8°C, range = 26.2°–36.6°C; B. Grant, personal communication). Critical thermal limits, used to fix the endpoints for locomotor performance curves, were measured according to the method of Hertz et al. (1983). Speed-versus- T_b data

for each individual were analyzed by means of a modified minimum-polygon algorithm (van Berkum 1986), which allowed us to calculate the temperature ("optimal") at which lizards sprint fastest, the range of temperatures across which lizards can run at 95% and 80% of maximal speed (indices of the degree of thermal specialization), and the relative speeds of lizards at various field activity temperatures (see Hertz et al. 1983).

Effect of Tail Loss

We conducted both descriptive and experimental analyses of whether tail loss influences speed and stamina. First, we compared locomotor performances of two "tail classes" of lizards, those with complete versus those with broken (often partly regenerated) tails. For each area, sex, and age class (young and older adults), we calculated univariate *t*-tests of speed and of stamina between the two tail classes. For each population, we also conducted an ANOVA with age, sex, and tail category as class variables (with two- and three-way interactions). Second, we conducted a repeated-measures experiment (summer 1984) for speed. Lizards with complete tails from an area near the Boquillas site were raced six times and then randomly separated into three groups: control ($n = 6$, tails intact), with $\frac{1}{3}$ length of tail experimentally removed ($n = 6$), and with $\frac{2}{3}$ length of tail removed ($n = 7$). One day later we reraced each lizard six times to determine the effect of tail loss on speed.

Overall Analyses

Prior to analyses we excluded several types of data. If an individual was measured (hence raced) twice in 1 yr, we analyzed its performance in only the first set of trials. Similarly, if an individual was raced in 2 or more yr, we analyzed its performance data only for the last year. These exclusions ensure that data are statistically independent. If an individual was injured (usually a broken tail) during or just before a trial and appeared disabled, it was excluded from analysis. If an individual would not sprint well (i.e., jumped down the track or ran along the wall of the track) or run well (jumped repeatedly when placed on the treadmill), it was excluded. Omissions due to injuries or to poor performance eliminated 17 individuals (3% of the total) for speed and 21 individuals (5% of the total) for stamina. No individual was excluded from the repeatability analyses; however, if an individual was raced in 3 yr, we analyzed repeatability only between the first and second years, thus ensuring independence of data.

The effects on performance of locality, sex, age, and year were analyzed

in four-way ANOVAs. Stamina was log transformed to reduce skewness. F -ratios for locality, sex, and age were estimated with the (effect)-by-year interaction as error terms (year was considered a random effect; see Sokal and Rohlf 1981). Analyses of covariance were performed with log SVL as a covariate. Heterogeneity of slope tests is not reported unless it was significant.

In some correlations between body size and performance, we estimated the residual hind limb length and the residual body mass. Residuals were calculated from least-squares regressions of log hind limb length or log body mass on log SVL, respectively.

Results

General Aspects of Locomotor Performance

The overall frequency distribution for sprint speed (at 32°–34°C) is approximately normally distributed (fig. 1A), with an average speed of 2.10 (SD = 0.355 m · s⁻¹, range = 1.01–3.24 m · s⁻¹, N = 567 individuals; table 1). The distribution for stamina at 0.5 km · h⁻¹ is, however, strongly and positively skewed (fig. 1B). Although most *Sceloporus merriami* become exhausted in a few minutes (\bar{X} = 3.4 min, SD = 1.207, range = 0.9–12.3, N = 432; table 1), a few lizards are exceptional. For example, a 2-yr-old male from Boquillas maintained a speed of 0.5 km · h⁻¹ for 12.3 min, and a 1-yr-old female from Boquillas went 11.5 min. These performances were at least 3.5 times greater than the average for Boquillas lizards or greater than 6 SD above the population mean.

Temporal Repeatability of Speed and of Stamina

Huey and Dunham (1987) reported that speed of individual lizards was repeatable between 1984 and 1985. Additional data (1987 and 1988) support and extend that observation. Speed in the first year of racing explained 24.4% of the variance in speed in the second year ($F[1,81] = 37.00$, $P < 0.001$, $N = 86$), when the effects of sex and locality are controlled in an ANCOVA. No individual was raced successively for 3 yr. Only seven individuals were raced in years 1 and 3, and the speed of these individuals in year 1 did not predict their speed 2 yr later ($r = 0.2$, $P = 0.66$).

An individual's stamina in 1 yr significantly predicted its stamina a year later (ANCOVA, $F[1,65] = 13.65$, $P < 0.001$, $N = 70$), but stamina in year 1 explained only 16.2% of the variance in stamina in year 2. Only 11 individuals had their stamina measured successively for 3 yr. Stamina showed a weak

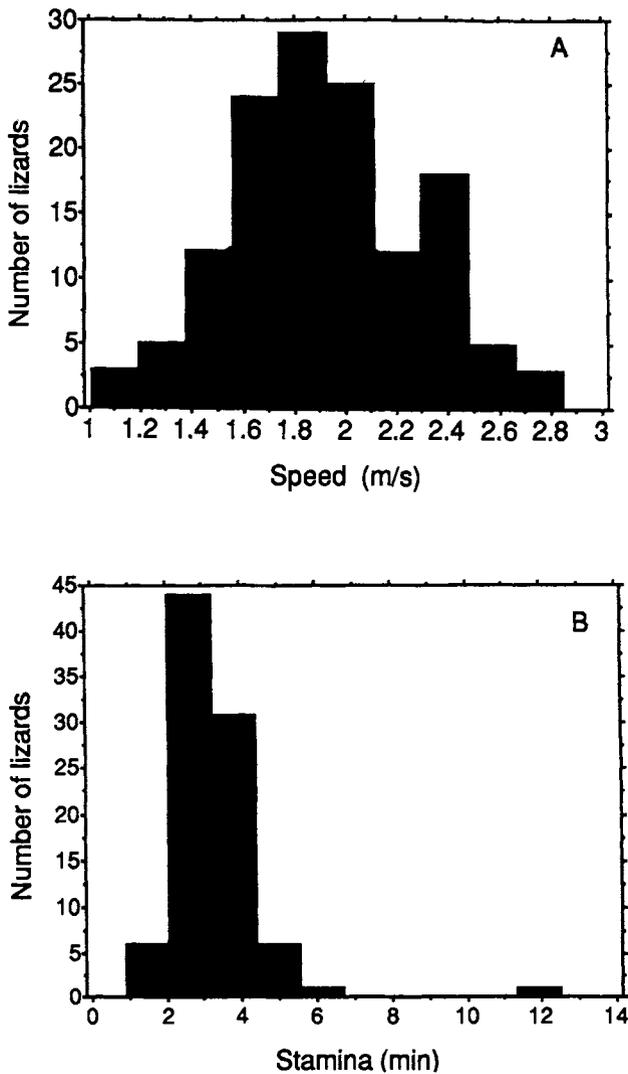


Fig. 1. Locomotor performance of *Sceloporus merriami*. Data for females (ages 1–3) from Boquillas are used as examples. A, Speed ($m \cdot s^{-1}$); B, stamina (time at $0.5 km \cdot h^{-1}$).

tendency to be correlated across 3 yr, but the correlation was insignificant (Kendall coefficient of concordance $W = 0.23$, $P > 0.25$).

Correlates of Performance

Locality. In all 16 sets of paired comparisons (i.e., by population and age class, table 1), Grapevine Hills lizards were faster on average than were Bo-

TABLE 1

Descriptive statistics for performance and size measures of Sceloporus merriami

Group and Year	SVL ^a (mm)	Mass ^a (g)	Hind Limb ^a (mm)	Speed (m · s ⁻¹)	Stamina (min)
Boquillas females:					
Age 1 yr:					
1984	49.2 (1.96, 40)	3.33 (.539, 40)	40.2 (1.59, 12)	1.94 (.381, 32)	...
1985	48.5 (1.57, 37)	3.24 (.534, 37)	39.4 (1.34, 28)	2.11 (.373, 33)	...
1986	49.5 (1.60, 28)	3.34 (.568, 28)	39.7 (1.30, 27)	...	3.15 (.967, 20)
1987	50.5 (1.51, 15)	3.83 (.567, 15)	41.0 (1.66, 14)	1.86 (.272, 23)	4.66 (2.459, 11)
1988	48.6 (2.69, 35)	3.22 (.543, 35)	40.1 (1.57, 31)	1.87 (.319, 35)	3.13 (.942, 32)
Average	49.1 (1.39, 155)	3.33 (.567, 155)	39.9 (1.52, 112)	1.96 (.360, 112)	3.40 (1.430, 63)
Age 2, 3 yr:					
1984	52.6 (.89, 5)	4.08 (.205, 5)	39.0 (..., 1)	1.86 (.181, 5)	...
1985	50.5 (1.41, 8)	3.55 (.592, 8)	40.4 (1.27, 7)	1.81 (.248, 7)	...
1986	50.8 (1.26, 15)	3.40 (.442, 15)	40.1 (1.35, 14)	...	2.75 (.524, 13)
1987	52.0 (1.00, 5)	4.10 (.700, 5)	42.0 (2.35, 5)	1.91 (.303, 5)	3.14 (1.095, 5)
1988	51.8 (1.30, 5)	3.84 (.313, 5)	41.5 (1.73, 4)	1.46 (.281, 5)	3.02 (.363, 5)
Average	51.3 (1.39, 38)	3.67 (.541, 38)	40.6 (1.66, 31)	1.77 (.291, 22)	2.89 (.687, 23)

Boquillas males:

Age 1 yr:	
1984	51.4 (1.52, 38) 3.94 (.467, 38) 42.9 (1.85, 13) 2.12 (.271, 29) ...
1985	51.4 (1.87, 49) 3.90 (.457, 49) 42.6 (1.27, 39) 2.20 (.314, 46) ...
1986	52.1 (1.90, 28) 3.99 (.488, 28) 42.8 (1.57, 27) ...
1987	52.5 (2.07, 13) 4.08 (.468, 13) 43.9 (1.97, 12) 2.00 (.259, 6) 2.97 (.491, 21)
1988	50.5 (2.09, 32) 3.70 (.484, 32) 42.6 (1.65, 30) 1.99 (.289, 31) 3.12 (.948, 6)
Average	51.4 (1.93, 160) 3.90 (.478, 160) 42.8 (1.60, 121) 2.11 (.304, 112) 3.14 (1.231, 29)

Age 2, 3 yr:

1984	54.1 (1.54, 14) 4.54 (.318, 14) 43.7 (2.28, 7) 2.16 (.328, 10) ...
1985	53.3 (1.27, 11) 4.42 (.405, 11) 43.3 (1.03, 6) 2.08 (.287, 11) ...
1986	53.9 (1.29, 20) 4.41 (.409, 20) 43.3 (1.66, 19) ...
1987	54.2 (1.47, 11) 4.45 (.499, 11) 44.1 (1.30, 11) 1.88 (.229, 7) 3.13 (.674, 16)
1988	53.9 (2.02, 10) 4.34 (.538, 10) 43.6 (1.33, 9) 2.02 (.281, 10) 5.35 (3.187, 7)
Average	53.9 (1.48, 66) 4.44 (.420, 66) 43.6 (1.55, 52) 2.05 (.292, 38) 3.31 (.800, 10)

Grapevine Hills females:

Age 1 yr:	
1984	48.4 (1.72, 13) 3.44 (.456, 13) ... 2.15 (.351, 10) ...
1985	49.7 (2.03, 26) 3.82 (.769, 26) 40.4 (1.41, 25) 2.14 (.289, 24) ...
1986	49.0 (4.84, 41) 3.38 (.871, 41) 38.9 (3.44, 41) ...
1987	48.7 (6.32, 25) 3.57 (1.084, 25) 39.5 (4.02, 25) 2.03 (.302, 19) 3.39 (1.133, 36)
1988	48.4 (3.10, 30) 3.28 (.660, 30) 39.6 (1.75, 30) 2.19 (.367, 28) 3.38 (1.269, 19)
Average	48.9 (4.18, 135) 3.48 (.834, 135) 39.5 (2.93, 121) 2.13 (.328, 81) 2.82 (.730, 28)

TABLE 1 (Continued)

Group and Year	SVL ^a (mm)	Mass ^a (g)	Hind Limb ^a (mm)	Speed (m · s ⁻¹)	Stamina (min)
Age 2, 3 yr:					
1984	51.9 (1.49, 14)	4.22 (.625, 14)	...	2.23 (.312, 9)	...
1985	53.3 (1.03, 6)	5.06 (.484, 6)	41.5 (.548, 6)	1.96 (.437, 11)	...
1986	53.7 (1.93, 13)	4.48 (.594, 13)	41.5 (1.198, 13)	...	4.23 (2.392, 10)
1987	52.7 (1.70, 10)	4.25 (.608, 10)	41.0 (2.000, 10)	2.06 (.347, 21)	4.22 (1.027, 7)
1988	53.3 (1.45, 14)	4.37 (.429, 14)	41.4 (.996, 14)	1.86 (.409, 20)	3.53 (1.348, 13)
Average	53.0 (1.68, 57)	4.41 (.478, 57)	41.4 (1.27, 43)	2.01 (.391, 36)	3.92 (1.694, 30)
Grapevine Hills males:					
Age 1 yr:					
1984	52.7 (2.28, 23)	4.21 (.59, 23)	...	2.39 (.336, 19)	...
1985	51.8 (2.65, 29)	4.06 (.703, 29)	43.7 (2.14, 29)	2.31 (.298, 27)	...
1986	53.7 (1.69, 42)	4.29 (.516, 42)	43.9 (1.83, 42)	...	3.23 (.853, 28)
1987	53.1 (1.69, 24)	4.41 (.613, 24)	45.3 (1.42, 24)	2.17 (.217, 17)	4.31 (.934, 16)
1988	49.7 (3.25, 44)	3.45 (.626, 44)	42.3 (2.30, 43)	2.26 (2.261, 42)	3.25 (.740, 43)
Average	52.0 (2.88, 162)	4.03 (.700, 162)	43.6 (2.22, 138)	2.28 (.308, 105)	3.44 (.906, 87)
Age 2, 3 yr:					
1984	55.5 (1.31, 19)	5.02 (.283, 19)	...	2.23 (.312, 9)	...
1985	55.4 (.90, 12)	5.18 (.432, 12)	45.3 (1.82, 12)	2.31 (.437, 11)	...
1986	56.5 (1.34, 22)	5.06 (.330, 22)	45.5 (1.01, 22)	...	3.64 (.809, 15)
1987	56.2 (1.41, 31)	5.15 (.559, 31)	46.4 (1.18, 29)	2.09 (.347, 21)	3.87 (1.348, 21)
1988	55.8 (1.83, 23)	4.96 (.460, 23)	46.2 (2.47, 23)	2.21 (.409, 20)	3.69 (.798, 21)
Average	56.0 (1.46, 107)	5.07 (.440, 107)	45.9 (1.71, 86)	2.19 (.380, 61)	3.74 (1.024, 57)

Note. Values are means (SD, N).

^a Size data include data on a few individuals that were excluded from racing (see Material and Methods).

quillas animals (binomial test, $P < 0.001$). Grapevine lizards were also faster in an ANOVA with locality, sex, and age as class variables ($F[1,3] = 16.71$, $P = 0.02$) and in an ANCOVA with sex, locality, and age class as main effects and SVL as the covariate ($F[1,558] = 29.47$, $P < 0.001$).

The two populations had similar stamina. In 9 of 12 paired comparisons ($P < 0.10$), Grapevine lizards had absolutely greater stamina than did Boquillas animals (table 1). Nevertheless, locality was not significant ($F[1,2] = 0.73$, $P = 0.48$) in an ANOVA with locality, sex, age, and year as main effects.

Sex. Males were faster than females. In 14 of 16 sets of paired comparisons ($P < 0.005$), males were absolutely faster than were females (table 1). Males were significantly faster than females when age class, locality, and year were controlled ($F[1,3] = 66.16$, $P = 0.0039$) or even when SVL was controlled in an ANCOVA ($F[1,558] = 25.91$, $P < 0.0001$). Moreover, males were significantly faster than nongravid females (data in table 3, below).

Males and females had similar stamina. In only 7 of 12 sets of paired comparisons ($P > 0.5$; table 1), males had greater stamina than did females. The similar stamina of males and females was evident also when age class, locality, and year were controlled ($F[1,2] = 3.29$, $P = 0.21$) or when age class, locality, and SVL were controlled in an ANCOVA ($F[1,423] = 0.12$, $P = 0.73$). The equivalent stamina of sexes held even when gravid females were excluded (data on nongravid females in table 3, below).

Age. Older adults (2–3-yr-olds) were slightly slower but may have had slightly greater stamina than did young adults (1-yr-olds). In 11 of 16 paired comparisons ($P > 0.1$), older adults were slower than young adults; however, in 8 of 12 comparisons ($P > 0.1$), older adults had more stamina (table 1). The statistical significance of the effects of age on locomotor performance was, however, marginal. (In part this might reflect small samples of old lizards, especially old females from Boquillas.) The decline in speed of older adults approached significance in a four-way ANOVA ($F[1,3]$, $P = 0.065$). Similarly, the increase in stamina of older adults approached significance in a four-way ANOVA ($F[1,2] = 11.25$, $P = 0.079$). In overall linear regressions for lizards aged 1–3, age had a negative but marginal effect on speed (slope = -0.04 , $P = 0.053$, $N = 567$) and a positive and significant effect on stamina (slope = 0.070 , $P = 0.003$, $N = 432$). Nevertheless, the proportions of variance in performance accounted for by adult age were very small ($r^2 = 0.007$, $r^2 = 0.021$, for speed and stamina, respectively).

Year. Average speed of lizards from the two populations did not vary significantly between 1984 and 1985 (Huey and Dunham 1987). However, in the

larger data set (table 1), both speed ($F[3,542] = 5.93, P < 0.001$) and stamina ($F[2,412] = 4.80, P = 0.009$) varied significantly among years. An area-by-year interaction approached significance for speed ($F[3,542] = 2.46, P = 0.062$) and was significant for stamina ($F[3,412] = 3.17, P = 0.043$). The area-by-year interactions reflect the slightly greater interyear variation for Grapevine than for Boquillas lizards (table 1).

Stamina was relatively more variable among years than was speed (table 1), even though stamina was measured in fewer years. Because stamina is highly skewed (fig. 1B), we used median, not mean, staminal values in these calculations. The percentage difference among years for the eight age, sex, and locality classes (the smallest value as a percentage difference of the largest value) averaged 17.6% for stamina, but only 11.9% for speed.

To determine whether the locomotor performance of animals of different age and sex responded similarly in different years, we computed Kendall coefficients of concordance among years. Speed and stamina in different years were each generally concordant across populations, age, and sex classes (speed: $W = 0.33, P = 0.05$; stamina: $W = 0.52, P < 0.025$). Lizards were usually fastest in 1984 and 1985, slowest in 1987 and 1988. Lizards usually had the greatest stamina in 1987 and the least in 1988.

Body Size. In univariate rank (Spearman) correlations, speed was significantly correlated with residual hind limb length (morphological measurements log transformed; see Material and Methods; $r = 0.21, P < 0.001, N = 426$) and hind limb length ($r = 0.15, P = 0.002, N = 426$), but not with body mass ($r = 0.08, P = 0.07, N = 567$), SVL ($r = 0.07, P = 0.07, N = 567$), or residual mass ($r = 0.01, P = 0.85, N = 567$). Stamina was significantly correlated with hind limb length ($r = 0.20, P < 0.001, N = 416$), body mass ($r = 0.21, P < 0.001, N = 432$), and SVL ($r = 0.20, P < 0.001, N = 432$), but not with residual hind limb length ($r = 0.07, P = 0.17, N = 416$) or residual body mass ($r = 0.06, P = 0.21, N = 432$).

The above patterns are, however, partially confounded by intercorrelations between the size variables and by influences of sex and locality. Therefore, we conducted canonical correlation analyses. These multivariate analyses determine whether a linear combination of the size variables (SVL, body mass, hind limb length) is correlated with a linear combination of performance variables (speed and stamina). To control for locality and sex, we ran separate analyses for four combinations of sex and of locality. These analyses are necessarily restricted to data from 1987 and 1988, years when both speed and stamina were measured.

Size and performance variables were uncorrelated in females (table 2). The canonical correlations were not significant for females from Boquillas

TABLE 2

Canonical correlation analysis of performance (speed, stamina) and of size (SVL, mass, hind limb length, all log transformed)

	Boquillas Females		Boquillas Males		Grapevine Females		Grapevine Males	
	With	Between	With	Between	With	Between	With	Between
Performance:								
Speed	-.97	-.25	.09	.04	.63	.19	-.29	-.11
Stamina	-.36	-.10	.98	.41	.88	.27	.94	.36
Size:								
SVL63	.17	.87	.36	.52	.16	.97	.37
Mass97	.25	.65	.27	.74	.23	.91	.36
Hind limb79	.21	.78	.33	.86	.26	.94	.36

Note. Values under "with" represent correlations between a variable and its first canonical variable. Values for "between" are correlations between a variable (e.g., speed) and the opposite canonical variable (e.g., for size).

($r = 0.26$; Wilks's lambda = 0.93; $df = 6,86$; $P = 0.77$) or those from Grapevine ($r = 0.31$; lambda = 0.89; $df = 6,112$; $P = 0.39$). A canonical redundancy analysis shows that neither canonical variable was a good predictor of the opposite variable: the proportion of explained variance was less than 0.07 in all cases.

Size and performance variables were significantly correlated in males, but the relationships were weak (table 2). Size and stamina were positively correlated, but size and speed were essentially uncorrelated. The canonical correlation was marginally significant for Boquillas males ($r = 0.42$; lambda = 0.77; $df = 6,88$; $P = 0.062$). The three size variables were weakly and positively correlated with the performance variable, which itself was moderately correlated with stamina and very weakly with speed. The proportions of variance explained by the canonical correlate for performance versus that for size were only 0.08 and 0.11, respectively. The canonical correlation was significant for Grapevine males ($r = 0.38$; lambda = 0.85; $df = 6,184$; $P = 0.017$). The three size variables were weakly correlated with the performance variable, which was weakly correlated with stamina. The proportions of variance explained by the canonical correlate for male performance versus size are only 0.07 and 0.13, respectively.

Reproductive State of Females. Females belonging to the four reproductive categories did not differ significantly in speed ($F[3,196] = 0.87$, $P = 0.46$) or in stamina ($F[3,150] = 0.91$, $P = 0.44$) (table 3). Gravid females were only 5% slower than were nongravid females, but even this difference was not significant ($F[1,150] = 1.61$, $P = 0.21$). Gravid and nongravid females were also very similar in stamina ($F[1,137] = 0.14$, $P = 0.71$). Ideally, this analysis should be based on a controlled, repeated-measures design (i.e., individual females when gravid and nongravid).

Toe Loss and Sprint Performance

Sprint speed was unaffected by toe loss (maximum six lost toes). In a regression analysis of data for Boquillas and Grapevine lizards from 1984 to 1985, residual sprint speed (see Material and Methods) was not significantly related to the number of toes lost ($t = -0.917$, $P = 0.87$, $N = 304$).

Tail Loss and Locomotor Performance

Descriptive Analysis. Naturally broken tails did not affect speed or stamina. Animals with complete versus those with broken tails differed significantly in none of the 24 comparisons involving stamina and in only one of those

TABLE 3
Locomotor performance of females at different stages of reproduction

Reproductive State	Boquillas Females				Grapevine Females			
	<i>N</i>	SVL (mm)	Mass (g)	Speed (m · s ⁻¹)	<i>N</i>	SVL (mm)	Mass (g)	Stamina (min)
Not gravid	103	49.2	3.29	2.05	72	48.9	3.15	3.30
With developing follicles	34	49.8	3.79	2.06	9	50.0	3.80	3.50
Gravid	59	51.7	4.40	1.98	77	51.6	4.24	3.34
Recently oviposited . . .	11	49.4	2.97	2.09	2	49.0	2.35	4.41

TABLE 4

Sprint speed ($m \cdot s^{-1}$) before and after experimental removal of part of a lizard's tail

Trial	Fraction of Tail Length Removed		
	0 (control) ^a	1/3	2/3
1 (before)	2.41	2.29	2.53
2 (after)	2.50	2.45	2.56

Note. $N = 6$ in all cases.

^a Tails intact.

involving speed. Moreover, animals with complete tails had higher performance than animals with broken tails in only 12 of 24 ($P = 1.0$) comparisons involving stamina and in only 16 of 24 ($P < 0.1$) involving speed. Analyses of variance (age, sex, locality, and tail-break category as classes) reaffirmed this pattern. Tail-break category had no significant effect on speed ($F[1,553] = 0.12$, $P = 0.73$, $N = 567$) or stamina ($F[1,418] = 0.27$, $P = 0.60$, $N = 432$), and none of the interaction terms involving tail-break category was significant either (all two- and three-way $P > 0.17$).

Tail-Loss Experiment. Our tail-loss experiments confirm the above field patterns: experimental removal of one-third or even two-thirds of the length of a lizard's tail had no conspicuous effect on sprint speed (table 4). The between-trial ($F[1,16] = 1.62$, $P = 0.22$) and treatment effects ($F[2,16] = 0.72$, $P = 0.73$) were minor and not significant.

Speed versus Stamina

Speed and stamina are weakly correlated when all data were pooled ($r = 0.14$, $P = 0.015$). However, in analyses divided by sex and population, only three of the four correlations were positive, and none of the correlations was significant (all $P > 0.11$). (See also the canonical correlation analysis, above.)

Temperature and Sprint Speed

Body temperature had a profound effect on sprint speed (table 5). The estimated optimal temperatures for sprinting for the two populations were

TABLE 5
Descriptive statistics for thermal sensitivity of sprint performance

Population	Thermal Sensitivity of Sprint Speed			Performance at Various T_b 's				
	Critical Thermal Minimum ($^{\circ}\text{C}$)	Optimal Temperature for Sprinting ($^{\circ}\text{C}$)	Critical Thermal Maximum ($^{\circ}\text{C}$)	B_{80}^a	B_{95}^a	Q_1^b	Median T_b^c	Q_3^b
Boquillas	12.9	32.6	41.7	9.9	4.8	.97	.99	.98
Grapevine	14.7	32.7	41.5	9.9	3.8	.93	.96	.98

^a B_{80} and B_{95} are the ranges of T_b over which lizards run at 80% or at 95% or better of maximal speeds.

^b Values are the relative sprint speeds of lizards at Q_1 and Q_3 .

^c Values are relative speeds of lizards at median T_b .

nearly identical and averaged 32.7°C, very close to the median temperatures of field active animals (Boquillas = 32.8°C, Grapevine = 32.3°C). Boquillas ($N = 7$) and Grapevine ($N = 8$) animals also did not differ significantly (both $P > 0.1$) in either lower or upper limits (critical thermal limits), and the pooled averages for these limits were 14.1°C and 41.5°C, respectively.

In most species (Huey et al. 1989), field active animals are normally active at temperatures close to the optimum for sprinting. *Sceloporus merriami* are similar: performance (relative to that at the optimum temperature) for the interquartile field temperatures (i.e., the T_b 's delimiting the central 50% of all T_b records) never dropped below 93%, and performance of lizards at their median field temperature averaged greater than 95%.

Discussion

Until recently, individual variation in physiological capacities has been largely ignored (Bennett 1987; Bennett and Huey 1990). Yet individual variation is a worthy focus of investigation because it can serve as an effective base for studying the mechanistic bases of variation in performance (Garland 1984, 1985; Gleeson and Harrison 1988) and because it may have profound ecological and evolutionary consequences (Arnold 1983; Bennett 1987; Huey and Dunham 1987; Pough 1989; Bennett and Huey 1990; Jayne and Bennett 1990). The study of individual variation can often be enhanced by working with demographically known populations in multiple years. Here we summarize our findings on individual, populational, between-year variation in locomotor performance. We examine first the magnitude of individual variation, then the long-term repeatability of individual performance, and finally some possible correlates of individual performance.

A conspicuous trend is the marked variation among individuals in locomotor performance. Some adults ran three times faster than did others (fig. 1A). Lizards varied even more strikingly in stamina (fig. 1B). In particular, a few individuals showed highly unusual capacities: two "ultramarathoners" had stamina times that were more than six SDs above the mean. The highly skewed distribution for stamina (fig. 1B) is not, however, unusual for reptiles. Distributions of stamina of hatchling fence lizards (*Sceloporus occidentalis*, Tsuji et al. 1989) and of neonate garter snakes (*Thamnophis sirtalis*, Garland 1988) are also highly skewed. The mechanistic bases for the extreme stamina of some individual reptiles is largely unexplored. Perhaps extreme individuals have greatly enhanced cardiovascular capacities (e.g., higher hemoglobin, greater maximum oxygen consumption) or greater muscle mass (Bennett 1980b; Bennett et al. 1984; Garland 1984, 1985).

Repeatability of Performance

The variation in locomotor performance is generally repeatable at several levels:

i) Speed of individual *Sceloporus merriami* is repeatable across temperature (Huey and Dunham 1987); that is, an individual that is relatively fast at one temperature is relatively fast at other temperatures, at least in the normal activity range. This pattern appears general for reptiles (Bennett 1980a, 1987; Huey and Hertz 1984a; Kaufmann and Bennett 1989), and no exception is known.

ii) In the 1984–1985 data for sprint speed (Huey and Dunham 1987), males were consistently faster than were females, Grapevine lizards were consistently faster than were Boquillas lizards (Huey and Dunham 1987), and speed was not significantly different between years. The first two findings were reinforced by data from 1987–1988. However, we now find that speed as well as stamina did vary significantly among years (table 1), but the interyear variation in speed was relatively minor. Variation in stamina was somewhat greater but was unrelated to sex or locality.

iii) Speeds of individual lizards measured in both 1984 and 1985 were significantly repeatable (Huey and Dunham 1987). Data from additional years reinforce that conclusion. Moreover, stamina is also repeatable between years. These correlations are robust despite the fact that *no* individual was deleted from the analysis. Thus, our samples include lizards whose physical condition varied dramatically between years because of injuries, reproductive condition, age, and environmental variation. Locomotor performances did not appear repeatable over 3 yr; however, our samples are very small.

The between-year repeatability of locomotor performance of individuals appears general among reptiles. Stamina and speed of 2-wk-old lizards (*S. occidentalis*) were positively related to their stamina and speed over 1 yr later, even though the lizards had grown by more than 10-fold in body mass during that interval (van Berkum et al. 1989). Speed and stamina are also repeatable between years in growing garter snakes (*T. sirtalis*; Jayne and Bennett 1989b). Speed is also repeatable in greyhounds and in thoroughbred racehorses (see Huey and Dunham 1987). However, speed and stamina are not correlated in larval versus transformed salamanders (*Ambystoma tigrinum*; Shaffer, Austin, and Huey 1991). The long-term repeatability of performance in reptiles encourages further studies of the mechanistic bases of individual variation (Garland 1984, 1985; Bennett 1987; Gleeson and Harrison 1988) as well as the ecological consequences of that variation

(Arnold 1986; Huey and Dunham 1987; Bennett and Huey 1990; Jayne and Bennett 1990).

Interpopulational Differences in Speed

Differences in speed between populations can be analyzed in mechanistic and evolutionary terms. The mechanical reasons for faster speeds of Grapevine lizards are unclear. Grapevine lizards do not have relatively long hind limbs when animals of similar body SVL are compared (table 1), but we could not test this in an ANCOVA because the slopes were heterogeneous.

From an evolutionary perspective, lizard populations from areas with high rates of predation are often fast relative to those from areas with lower rates of predation (Crowley 1985*a*; Snell et al. 1988; Bennett and Huey 1990). We see the opposite pattern here: Grapevine lizards, which have relatively low mortality rates (Dunham et al. 1989), are relatively fast (table 1). Several explanations are possible. First, Boquillas is hotter, drier, and has lower insect densities (Dunham et al. 1989), so perhaps the unexpectedly low speeds of lizards from Boquillas in midsummer reflects greater physical stress. This could be tested by comparing populations during a less stressful season. Second, the limestone rocks at Boquillas are small relative to the granitic boulders at Grapevine, and Grapevine lizards tend to run farther during social and predatory encounters (A. E. Dunham and K. L. Overall, unpublished observations). Third, perhaps mortality rates are simply an unreliable indicator of predation rates in these populations, or high speed does not enhance escape from predators.

Correlations Involving Performance

Size, Sex, Population. Population, sex, and body size (mass, SVL, hind limb length) all influence locomotor performance, but the influence appears small. In fact, in the repeatability analysis for stamina, population, sex, and size accounted for less of the variance than did "individual" identity. In the canonical correlation analyses, size and performance were uncorrelated in females and only weakly correlated in males. Correlations between size measures and performance are apparent only when populations and sexes are lumped.

Body size in other lizards correlates strongly with performance (Huey 1982; Huey and Hertz 1984*b*; Garland 1984, 1985; Snell et al. 1988). Correlations between relative hind limb length and speed are only sometimes significant (Garland 1984, 1985; Miles 1987; Snell et al. 1988; Losos and Sinervo 1989; van Berkum et al. 1989). The weak or absent correlations be-

tween size measures and performance here may well reflect the very small size range of adult *S. merriami* (table 1) relative to that of previously studied lizards.

Age. Shifts in physiological capacities during early ontogeny have been documented for a few species (Pough 1977, 1978, 1989; van Berkum et al. 1989; Jayne and Bennett 1989*b*). However, whether performance shifts as an adult ages is rarely known (Clutton-Brock, Guinness, and Albon 1982), largely because physiological ecologists rarely know the ages of their adult study organisms. By studying performance in a demographically known population, we did know the ages of studied individuals and were able to exploit this information to examine performance in young (1-yr-old) versus older (2–3-yr-old) adults.

Age has marginally significant but very minor effects on performance (table 1); interestingly, age seems to affect speed and stamina in opposite ways. Older lizards lose speed but generally gain stamina (table 1).

Some individuals (especially males) do survive, although very rarely, more than 3 yr. The average cohort generation time for these populations is about 1½ yr (Dunham 1980; Dunham et al. 1989), such that even a 3-yr-old lizard is relatively old. Although our samples of lizards older than 3 yr are small, the age-dependent patterns described above appear to continue. Thus, 4–5-yr-olds were slow, but (except for old Boquillas females, which were very rare) maintained high stamina (R. B. Huey, A. E. Dunham, and K. L. Overall, unpublished data). A senescent decline in sprint speed occurs in greyhounds (Ryan 1975) and humans.

Environmental Correlates of Interyear Variation

Year had significant effects on both speed and stamina, but interyear variation appears more marked for stamina. Does the between-year variation in performance reflect rainfall patterns? Rainfall might influence locomotor performance in complex ways via effects on hydration state (Crowley 1985*b*; Bradshaw 1986; Wilson and Harvel 1989), food abundance and feeding success (Dunham 1978, 1980), or even density-dependent population feedback. Given that data are available for very few years (speed for four years, stamina for 3 yr), any analysis must presently be suggestive at best.

Stamina was highest in 1987, intermediate in 1986, and lowest in 1988 (table 1). In a given year, stamina correlates positively with cumulative rainfall during the previous fall and winter (table 6). Stamina of another iguanid lizard, *Uta stansburiana*, is very sensitive to dehydration state (Wilson and

TABLE 6
Cumulative rainfall (cm) in seasons preceeding performance measurements

Year	Boquillas ^a			Grapevine ^b		
	Fall ^c	Winter ^d	Total	Fall ^c	Winter ^d	Total
1984	7.7	2.0	9.7	5.6	3.3	8.9
1985	9.2	7.6	16.7	9.9	9.1	19.0
1986	8.6	2.4	11.0	16.9	5.9	22.8
1987	16.4	7.2	23.6	17.4	10.3	27.7
1988	6.3	1.7	8.0	5.3	2.6	7.9

^a Data from Rio Grande Village.

^b Data from Panther Junction.

^c Fall = September + October.

^d Winter = November–March.

Harvel 1989). Unfortunately, the hydration state of our lizards in different years is unknown.

Speed was highest in 1984 and 1985, lowest in 1987 and 1988 (table 1). Speed in summer is not obviously associated with rainfall in the previous seasons (table 6). Speed is unaffected by dehydration in *Sceloporus undulatus* (Crowley 1985*b*).

Toe Loss

Even though toes are obviously important in locomotion (by increasing friction and stride length), the loss of only a few toes (maximum six) from toe clipping or from natural injury did not reduce sprint speed in *S. merriami*. In a repeated-measures experiment with hatchling *S. occidentalis*, loss of toes (four) did not affect speed (R. B. Huey, unpublished data). Given that toe clipping is the standard method of individually marking lizards, the findings from these two studies are reassuring. At some point, however, the loss of many toes must affect speed and agility, especially on a complex or vertical substrate.

Tail Loss

Many lizards lose part of their tail during encounters with predators or conspecifics (Arnold 1988). Yet tails are often important to some lizards in burst

locomotion (Snyder 1962), and the loss of a tail usually reduces sprint speed (Arnold 1988). However, in a gecko with a fat tail, tail loss actually increases speed (Daniels 1983). In *S. merriami*, a lizard with a thin tail, tail loss does not affect speed. This pattern holds for lizards both with natural and with experimental tail breaks. The lack of an effect of tail loss in *S. merriami* may reflect the skinny and short (1.4–1.5 times SVL) tails of this species relative to those of other lizards studied.

The extent of natural tail loss did not significantly affect sprint speed in *T. sirtalis* (Jayne and Bennett 1989a). Experimental ablation of the distal two-thirds of the tail reduced speed, but only by 4.5%.

Body Temperature

Body temperature has a profound effect on the sprint speed of *S. merriami*, as it does in other lizards (e.g., Bennett 1980a; Hertz et al. 1983; van Berkum 1985, 1986). The normal body temperatures of most species, including *S. merriami* (table 5), are close to or coincident with temperatures at which they run fastest (but see Huey and Bennett 1987; Huey et al. 1989).

Desert species of lizards often have a relatively high optimal temperature for sprinting and a high critical thermal maximum (see, e.g., Heatwole 1976; Greer 1980; Huey and Bennett 1987). Surprisingly, *S. merriami*, an animal living in a thermally extreme desert for *Sceloporus* (Grant and Dunham 1988), has an optimal sprint temperature (32.6°C) and a critical thermal maximum (41.6°C) that are slightly lower than those of four other species of *Sceloporus* that live in much cooler environments (range of optimal temperatures = 33.3°–35.1°C; range of critical thermal maximum = 42.8°–44.7°C; van Berkum 1985; Crowley 1985a). The relatively low optimal and critical temperatures for *S. merriami* may reflect its origin from a species group (the *couchi-gadovi* group) that probably had its origin in riparian habitats, not deserts (Dunham 1980).

Conclusions

We studied variation in performance in *Sceloporus merriami* because of the background information available on demography and ecology. We wish to emphasize two particular advantages that accrued from studying demographically known populations:

- i) Because recaptured lizards could be uniquely identified, we were able to determine that individual performance is significantly repeatable over periods as long as 1 yr. The temporal repeatability of performance is known in

only a few other populations (Jayne and Bennett 1989*b*; van Berkum et al. 1989), despite the fact that knowing the degree of temporal repeatability is crucial to some physiological (Bennett 1987) and evolutionary analyses (Falconer 1981; Arnold 1986; Huey and Dunham 1987; Bennett and Huey 1990).

ii) Because the age of each individual was known, we were able to discover not only that the effects of adult age on performance were minor, but also that the effects of age on speed appeared opposite to those on stamina. The mechanistic reasons of this unexpected finding are unexplored. Our studies suggest that the ontogenetic dynamics of physiological capacities in natural populations may be more complex than expected from studies of humans and laboratory animals (Shock et al. 1984).

Studies of demographically known populations do, however, have associated disadvantages. Establishing a marked and known-age population is difficult and time consuming. One alternative is collaboration with a demographer who already has a marked population. However, certain physiological experiments (e.g., invasive, terminal, or long-duration ones) may not be possible on such populations, for these would interfere with the demographic patterns themselves. This problem may necessitate either establishing marked populations that are used only for experiments or using noninvasive experiments when possible (Burggren 1987).

Our study also demonstrates the advantages of studying populations in multiple years. Because performance varies among years, a single-year study may not adequately characterize a population's average capacities. Moreover, the existence of between-year variation in performance opens opportunities for analyzing environmental and selective correlates of that variation. Demographers have long appreciated this general point (Tinkle 1979).

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