

Repeatability of individual differences in locomotor performance and body size during early ontogeny of the lizard *Sceloporus occidentalis* (Baird & Girard)

F. H. VAN BERKUM*, R. B. HUEY,
J. S. TSUJI and T. GARLAND, Jr†
Department of Zoology NJ-15, University of
Washington, Seattle, Washington 98195, USA

Abstract. The demonstration of repeatability of relative body size and of locomotor performance in growing lizards is relevant to the functional and genetic basis of these traits as well as to an understanding of how they are influenced by natural selection. Relative locomotor performance of hatchlings was strongly repeatable among body temperatures (28, 33 and 37 °C). We estimated the repeatabilities of individual differences in locomotor performance (speed, stamina) and body size (mass, snout-to-vent length, 'condition' index) for free-ranging lizards (*Sceloporus occidentalis* [Baird & Girard]) over three time intervals between near hatching and 13 months of age, during which time the lizards increased in body mass by an order of magnitude. Relative locomotor performance and body size were significantly repeatable between adjacent censuses, even across the winter hibernation period and over periods of rapid growth. However, these traits (especially body size) were usually not significantly repeatable over long time intervals, in part because of small sample sizes of recaptured animals. Even so, stamina of 2-week-old lizards predicted their stamina over a year later. These patterns generally held even when the confounding effects of body size were controlled. Studies of natural selection on performance and on body size of growing lizards should be restricted to short-term intervals. *Key-words:* Repeatability, thermal biology, locomotion, body size, lizard, natural selection, ontogeny, performance

* Present address: Dr F.H. van Berkum, Department of Ecology and Evolution, State University of New York, Stony Brook, New York 11794, USA.

† Present address: Dr T. Garland, Jr, Department of Zoology, University of Wisconsin, Madison, Wisconsin 53706, USA.

Introduction

Repeatability is an important statistical concept that quantifies the stability of a phenotypic trait within individuals, relative to differences in that trait among individuals (Bulmer, 1980; Falconer, 1981; Lessells & Boag, 1987). If repeated measurements of a given individual are very similar relative to the differences among individuals, then repeatability is high; if measurements within individuals are very different, then repeatability is low.

Repeatability is particularly useful in assessing the gain in precision achieved by making multiple measurements of individuals, in evaluating the precision of a given type of measurement, in establishing the degree of individuality, and in determining the upper bound on heritability (Bennett, 1980, 1987; Bulmer, 1980; Falconer, 1981; Arnold & Bennett, 1984; Wells & Taigen, 1984; Herzog & Burghardt, 1988). Repeatability is also valuable in predicting the ontogenetic consistency of individuals (Tolley, Notter & Marlowe, 1983; Huey & Dunham, 1987) and in placing bounds on the appropriate time limit for studying natural selection on phenotypic traits (*sensu* Huey & Dunham, 1987). Thus, for many analyses of individual variation (Bennett, 1987), estimation of repeatability should be a key first step.

As part of a study of natural selection on speed, stamina, and body size of the lizard *Sceloporus occidentalis* (Baird & Girard) in nature, we here analyse the long-term repeatability of these traits during these lizard's first year of life – a substantial fraction of their ecological lifespan. We also examine the repeatability of locomotor performance measured at different body temperatures, thereby establishing if the relative performance of an individual is stable even at different body temperatures (Bennett, 1980). Locomotor performance and body size are ecologically-relevant traits (Huey & Stevenson, 1979; Arnold, 1983) that potentially influence fitness by affecting feeding success (Greenwald, 1974; Webb, 1986), escape

from predators (Christian & Tracy, 1981; Huey & Hertz, 1984a; Ferguson & Fox, 1984) and social dominance (Rand, 1964; Regal, 1971; Trivers, 1976). Body temperature is a key physiological variable that has a profound influence on all aspects of ectotherm physiology, including locomotion (Dawson, 1975; Bennett, 1980; Avery, Bedford & Newcombe, 1982; Huey, 1982). We address three main issues:

(i) is the relative locomotor performance of an individual stable through time? For example, do individuals with high stamina at birth maintain high stamina later in life? Both speed and stamina of adult lizards are highly repeatable in the laboratory (Bennett, 1987) and in the field (Huey & Dunham, 1987). However, the repeatability of performance during early ontogeny – when lizards are growing rapidly – has not been examined previously.

(ii) Are the relative body size and ‘condition’ index ($\text{mass}^{1/3}/\text{snout-to-vent length}$) of an individual repeatable during early ontogeny? That is, do individuals that are large at hatching also remain relatively large later in life? To our knowledge, the long-term repeatability of body size in natural populations has been documented only in birds (Smith & Zach, 1979; Boag, 1983; Price & Grant, 1984; Smith, Arcese & Schluter, 1986).

(iii) Is the relative locomotor performance of an individual hatchling consistent at different body temperatures? In other words, is an individual that is relatively fast at one body temperature (T_b) also relatively fast at other body temperatures? This appears to be the case in several previous studies, including one of adult *S. occidentalis* (Bennett, 1980; Huey & Hertz, 1984a; Huey & Dunham, 1987).

We have examined the repeatability of performance and size in *S. occidentalis*, a semi-arboreal iguanid lizard that lives in a variety of habitats in western North America from Mexico to Washington state. At our study area in south-central Washington, the lizards are abundant in an open oak-pine forest, where they are active on logs, trees, and under small shrubs. They breed in the late spring, hatchlings are born in July and August and the lizards hibernate from about September (adults) or October (hatchlings) through April. Sexual maturity is not reached until the second or perhaps third year. They are ‘sit-and-wait’ foragers and eat a variety of arthropods.

Materials and methods

Hatchlings used in this study came from the

Tuthill Ranch, Klickitat County, Washington (under permit from the Department of Wildlife). Some (‘lab-reared’, $n = 296$) were raised from eggs laid in the laboratory (summer 1985) and then released on 19 August 1985 (average 23 days of age, range 19 to 28 days) in groups of eight to 10 (randomized with respect to sibship) onto marked sites in a study area near where the dams were originally captured. Methods of obtaining and incubating eggs and of maintaining lab-reared hatchlings are detailed elsewhere (Tsuji *et al.*, in preparation). Several field-reared hatchlings, collected on 22 August 1985, were used in the studies of thermal repeatability of speed ($n = 23$) and of stamina ($n = 18$). A few other field-reared hatchlings ($n = 17$) were collected at this time for baseline estimates of body size and of speed, and these lizards were released on 24 August 1985. Finally, other field-reared hatchlings were captured on the same study area during subsequent recaptures of the lab-reared hatchlings (see below).

Before all sets of racing trials, we noted sex, snout-to-vent length (SVL), body mass, and tail status (complete tail, freshly broken, or regenerating). Subsequently, we calculated a ‘condition’ index, as $\text{mass}^{1/3}/\text{SVL}$, for those individuals possessing a complete, original tail. (This index is frequently used as a measure of condition, e.g. body fatness. However, it does not differentiate between fatness and stockiness and thus the index may be better considered as a general measure of body stockiness.) These data enabled us to examine repeatability of size and condition as well as to check for allometric and sex effects on locomotor performance (see below).

Measuring locomotor performance

Maximal speed was determined by chasing hatchlings along a computerized, 1.2-m racetrack (Huey *et al.*, 1981) with vertical photocell stacks at 0.1-m intervals. Body temperature was maintained at 33–34°C, near the mean activity temperature of these lizards (Tsuji, 1986). At each census, individual lizards were run four times with a one-hour rest between races and an individual’s maximum speed was assessed as the single fastest speed among all 0.2-m intervals. By the August 1986 census, the lizards were nearly adult size; hence the length of the racetrack was increased to 2 m (0.25 m between photocells) for the final census (maximum speed determined among all 0.5-m intervals).

Stamina was indexed as the total time a lizard could maintain station while running slowly on the moving belt (initially at 0.225 km h^{-1} , see below) of a motorized treadmill. At each census we increased the treadmill speed slightly (0.275 km h^{-1} in October 1985, 0.3 km h^{-1} in May 1986, 0.3 km h^{-1} in August 1986) to reflect probable ontogenetic shifts in stamina (Pough, 1983; Garland & Else, 1987). To minimize stress, stamina was measured only once per census or per temperature.

The persons conducting the performance trials could not be the same at all censuses. (For speed, the sequence for the five censuses was FHvB, FHvB, FHvB, RBH, RBH; and for stamina, RBH, RBH, RBH, TG, RBH.) The calculated repeatabilities should thus be underestimates of the true repeatabilities.

Temporal repeatability

Speed and stamina (see below) of the lab-reared hatchlings were initially assessed twice prior to release (8–17 August 1985). Speed was determined first when lizards averaged 13 days old (range 12–15) and then 19 (18–21) days old, whereas stamina was measured when they averaged 16 (15–18) and 21 (20–23) days old.

We recaptured and remeasured hatchlings on three occasions spread over a year (28 September–7 October 1985 = ‘October census’; 20–25 May 1986 = ‘May census’; 23–27 August 1986 = ‘August census’). During each recapture, we also caught some field-reared hatchlings and measured their size and performance. Lizards were probably hibernating for most of the time between the October and May censuses. However, because they did grow during that time (Table 1), they could not have been hibernating full time. By the last recapture hatchlings were about 13 months old.

Between the October and May censuses, about one-third of our study area was cleared for cattle pasture. This contributed to the low recapture rates in 1986.

Thermal repeatability

Speed ($n = 23$ individuals) and then stamina ($n = 20$) were measured at a randomized sequence of body temperatures (33, 28 and 37°C). The two extreme temperatures bound almost all T_b records of active adult lizards at this site, and 33°C

approximates their mean activity temperature (Tsuji, 1986).

Calculating repeatability

Repeatability is traditionally estimated using the intra-class correlation coefficient (Falconer, 1981; Lessells & Boag, 1987). However, this coefficient is inappropriate for growing animals as it is very sensitive to changes in the average values of traits (Bulmer, 1980; Falconer, 1981; C. Janson, personal communication). Accordingly, we estimate temporal repeatability using the *inter*-class correlation coefficient (Pearson’s r). (When repeatability is measured over a single time interval, Pearson’s r is virtually identical to the traditional intra-class correlation coefficient calculated using covariance-corrected values [Curnow, 1961].) Thus we measure whether relative – not absolute – performance and size are temporally stable. Because the measurements did not always appear to be bivariate normal, we report significance levels based on a non-parametric test, Kendall’s tau (C. Janson, personal communication).

We first calculated repeatabilities of two performance measures (sprint speed, stamina) and of three size measures (mass, SVL, condition index). Because body size influences locomotor performance in this species (Tsuji *et al.*, in preparation), significant ‘whole-animal’ repeatabilities of locomotor performance might be measuring primarily the repeatability of body size. Accordingly, we also calculated size-corrected repeatabilities based on residuals of regressions of \ln (performance) versus \ln (SVL) (Huey & Hertz, 1984a).

For the lab-reared lizards, we used the two sets of measurements made in the laboratory before field release, to compute an initial ‘in lab’ repeatability. Then, to calculate repeatabilities between laboratory and field, we selected the higher of two laboratory performance measurements and the final size measurement as the laboratory base line. Because a broken tail may influence locomotor performance (E.N. Arnold, 1987), we calculated whole-animal repeatabilities twice (once only for lizards with complete tails and once for all lizards). However, we excluded lizards with broken tails from repeatabilities involving the body size measurements or size-corrected performances.

We computed separate repeatabilities for males, females, lab-reared, and field-reared lizards. However, these repeatabilities were always homogeneous (Sokal & Rohlf, 1981, pp. 588–589) and were similar in magnitude to the pooled repeatabilities (i.e. all animals combined), so we report only pooled repeatabilities.

Results*Patterns of temporal change*

Between the initial (age about 2 weeks, early August 1985) and final censuses (age about 13 months, August 1986), the lizards doubled in length and increased in body mass by an order of magnitude (Table 1). Most of this growth occurred between the last two censuses (May to August 1986). Males and females were not significantly different in size until the last census, when males were slightly longer and heavier on average than females (Table 1).

During their first summer, field-reared hatchlings averaged slightly longer and heavier than lab-reared hatchlings (Table 1). Whether this reflects older age or better rearing conditions of field-reared hatchling cannot be determined. In any case, differences in size disappeared by the end of the winter hibernation.

Average speed increased by about 50% during the study. Males and females had similar speeds in all but the last census, when males were slightly

faster than females. This difference in speed holds even when the effects of body size are removed (ANCOVA, SVL as covariate, $P < 0.001$). Lab- and field-reared lizards had similar speeds in most censuses (Table 1).

Because treadmill-speed was adjusted as the lizards aged (see materials and methods), the average increase in stamina during the first year of life cannot be determined. However, males and females had similar stamina throughout the study, and field-reared lizards had slightly higher stamina than lab-reared lizards (ANCOVA, SVL as covariate, $P < 0.05$) until the final census.

Repeatability of performance and of size

For the two initial laboratory trials (see materials and methods), both speed ($r = 0.45$, $P < 0.001$, $n = 298$) and stamina ($r = 0.65$, $P < 0.001$, $n = 295$) were significantly repeatable. These values, taken only a few days apart, may be interpreted as measures of how accurately we can quantify individual differences at a single time near

Table 1. Locomotor performance and body size of *S. occidentalis* at several censuses. Units \bar{X} ($\pm 95\%$ CI, sample size in parenthesis) are for SVL = snout-to-vent length (mm), mass (g), speed (m s^{-1}) and stamina (s). Only lizards that were recaptured at least once and that had complete tails are included.

| | Census | | | |
|---|------------------|------------------|-----------------|-----------------|
| | August 1985 | October 1985 | May 1986 | August 1986 |
| Speed (m s^{-1}) | | | | |
| Males | 1.27 (0.041, 65) | 1.55 (0.050, 60) | 1.66 (0.085,45) | 2.07 (0.105,37) |
| Females | 1.28 (0.049, 62) | 1.53 (0.049, 62) | 1.69 (0.068,46) | 1.75 (0.115,39) |
| Lab-reared | 1.27 (0.032,112) | 1.54 (0.037,102) | 1.56 (0.080,22) | 2.04 (0.297,11) |
| Field-reared | 1.35 (0.118, 15) | 1.56 (0.098, 20) | 1.71 (0.064,69) | 1.88 (0.088,65) |
| All | 1.28 (0.031,127) | 1.54 (0.035,122) | 1.67 (0.053,91) | 1.90 (0.085,76) |
| Stamina (s) | | | | |
| Males | 258 (19.5, 58) | 301 (33.2, 54) | 184 (16.4,45) | 267 (25.1,37) |
| Females | 305 (47.7, 53) | 299 (27.3, 55) | 185 (14.3,46) | 265 (40.0,39) |
| Lab-reared | 281 (25.0,111) | 289 (18.2,101) | 163 (20.3,22) | 285 (51.2,11) |
| Field-reared | – (– 0) | 453 (167.1, 8) | 191 (12.3,69) | 262 (26.3,65) |
| All | 281 (25.0,111) | 300 (21.1,109) | 184 (10.6,91) | 266 (23.3,76) |
| Snout-to-vent length (mm) | | | | |
| Males | 30.2 (0.294, 64) | 34.1 (0.429, 72) | 38.3 (0.599,30) | 63.7 (1.08,22) |
| Females | 30.0 (0.278, 62) | 34.1 (0.467, 77) | 39.0 (0.908,27) | 61.3 (1.20,20) |
| Lab-reared | 29.9 (0.156,111) | 33.5 (0.281,101) | 38.4 (0.893,22) | 64.5 (1.54,11) |
| Field-reared | 31.3 (1.16, 15) | 35.4 (0.639, 48) | 38.8 (0.671,35) | 62.6 (1.07,31) |
| All | 30.1 (0.201,126) | 34.1 (0.314,149) | 38.6 (0.523,57) | 62.6 (0.85,42) |
| Mass (g) | | | | |
| Males | 0.75 (0.030, 64) | 1.23 (0.053, 72) | 1.72 (0.067,45) | 8.20 (0.372,37) |
| Females | 0.74 (0.28, 62) | 1.26 (0.070, 77) | 1.83 (0.113,46) | 7.49 (0.439,39) |
| Lab-reared | 0.74 (0.018,111) | 1.15 (0.032,101) | 1.69 (0.111,22) | 7.58 (0.836,11) |
| Field-reared | 0.81 (0.109, 15) | 1.45 (0.098, 48) | 1.80 (0.080,69) | 7.87 (0.323,65) |
| All | 0.75 (0.020,126) | 1.24 (0.004,149) | 1.77 (0.066,91) | 7.84 (0.294,76) |

Table 2. Correlation matrix of repeatabilities (Pearson's r) for speed of all lizards (above diagonal) and for stamina (below diagonal) for *S. occidentalis* at different censuses. Within each triangle, the top coefficients are calculated only for lizards with complete tails, the middle are calculated for lizards with incomplete tails and the bottom ones are the size-corrected coefficients for lizards with complete tails. Numbers in parentheses represent significance level and sample size, respectively. Repeatabilities in boldface are significant at $P < 0.05$ (based on Kendall values, see text).

| | Laboratory | Field | | |
|--------------|--------------------------|--------------------------|-------------------------|-------------------------|
| | August 1985 | October 1985 | May 1986 | August 1986 |
| August 1985 | – | 0.33 (0.001, 117) | 0.25 (0.126, 25) | 0.40 (0.096, 12) |
| | – | 0.31 (0.004, 132) | 0.29 (0.080, 27) | 0.46 (0.080, 13) |
| | – | 0.37 (0.001, 116) | 0.23 (0.280, 25) | 0.38 (0.066, 12) |
| October 1985 | 0.20 (0.001, 101) | – | 0.48 (0.008, 21) | –0.07 (0.326, 10) |
| | 0.22 (0.001, 114) | – | 0.46 (0.008, 24) | –0.24 (0.110, 13) |
| | 0.37 (0.001, 100) | – | 0.47 (0.035, 21) | –0.06 (0.394, 10) |
| May 1986 | 0.27 (0.148, 22) | 0.38 (0.048, 21) | – | 0.19 (0.009, 69) |
| | 0.29 (0.098, 24) | 0.32 (0.166, 24) | – | 0.23 (0.007, 72) |
| | 0.25 (0.102, 22) | 0.25 (0.263, 21) | – | 0.18 (0.002, 69) |
| August 1986 | 0.78 (0.005, 11) | 0.72 (0.141, 10) | 0.27 (0.012, 69) | – |
| | 0.72 (0.037, 12) | 0.66 (0.088, 13) | 0.28 (0.005, 72) | – |
| | 0.77 (0.005, 11) | 0.80 (0.090, 10) | 0.31 (0.013, 69) | – |

hatching. For the subsequent comparisons involving adjacent pairs of censuses (August to October 1985, October 1985 to May 1986, May to August 1986), speed and stamina (Table 2) as well as measures of body size and condition index (Table 3) were usually significantly repeatable, and the associated probabilities were almost always less than 0.01. Thus, locomotor performance and especially body size (and condition) are temporally stable traits in growing lizards, at least over short-time intervals.

The repeatabilities and associated significance levels for locomotor performance did not change substantially when the potentially confounding effects of body size (SVL) were removed (lowest coefficients in Table 2), indicating that the whole-animal repeatabilities were not merely an artifact of the ontogenetic allometry of locomotor performance (Huey & Hertz, 1984b; Garland & Else, 1987; Avery *et al.*, 1987). Similarly, tail loss had little

impact on repeatabilities of locomotor performance (Table 2).

When locomotor performance was compared between non-adjacent censuses (e.g. between August 1985 and May 1986), repeatabilities were usually positive; but the associated probability levels usually only approached significance (Table 2). Because these non-adjacent coefficients were generally of the same magnitude as those between adjacent censuses, this marginal significance may be a function of greatly reduced sample sizes (see Table 2), which in turn results from high natural mortality of hatchling lizards and from habitat destruction (see materials and methods). Stamina was the most consistently repeatable trait; indeed, stamina was significantly repeatable between the first and last censuses (almost 13 months apart). Speed was also generally repeatable but the probability levels were marginal for non-adjacent censuses.

Table 3. Correlation matrix of repeatabilities for SVL (above diagonal, top), mass (above diagonal, bottom), and 'condition' index (below diagonal). Numbers and symbols as per Table 2. All coefficients calculated only for lizards with complete tails.

| | Laboratory | Field | | |
|--------------|--------------------------|--------------------------|-------------------------|-------------------------|
| | August 1985 | October 1985 | May 1986 | August 1986 |
| August 1985 | – | 0.60 (0.001, 118) | 0.18 (0.159, 25) | –0.10 (0.371, 13) |
| | – | 0.60 (0.001, 118) | 0.24 (0.107, 25) | –0.17 (0.334, 13) |
| October 1985 | 0.50 (0.001, 118) | – | 0.77 (0.001, 91) | 0.32 (0.010, 46) |
| | | | 0.82 (0.001, 92) | 0.32 (0.013, 46) |
| May 1986 | 0.27 (0.131, 25) | 0.78 (0.001, 91) | – | 0.43 (0.001, 72) |
| | | | | 0.43 (0.001, 72) |
| August 1986 | –0.13 (0.313, 13) | 0.30 (0.031, 46) | 0.39 (0.001, 72) | – |

Over short time intervals (i.e. adjacent censuses), the size measures (mass, SVL, condition index) were highly repeatable (Table 3). Surprisingly, however, size measures were not always repeatable over long time intervals; and both the magnitude and the significance of repeatability decreased with time. In fact, the size (SVL, mass or condition index) of a lizard at 2 weeks of age did not predict its size at 13 months of age. Nevertheless, size at 2 months did predict size at 13 months (Table 3), suggesting that the growth of a lizard in its first summer may have an important impact on its size as an adult.

Repeatability of performance across temperatures

Body temperature influences sprint speed and stamina. Average ($\pm 95\%$ CI) sprint speeds at 28, 34 and 37 °C are 1.10 ± 0.099 , 1.24 ± 0.089 and 1.17 ± 0.104 m s⁻¹, respectively. Comparable values for stamina are 287 ± 59.7 , 315 ± 46.1 and 395 ± 92.9 s, respectively.

Lizards that have high performance at one body temperature have high performance at other temperatures (Table 4). The rank orders of individuals with respect to both speed and stamina are highly concordant across all three temperatures (Kendall coefficients of concordance, $W = 0.737$, $P < 0.001$; $W = 0.845$, $P < 0.001$, respectively). Both 'individuals', and 'body temperatures' have highly significant effects ($P < 0.001$, two-way ANOVA, mixed model, no interaction) on speed and on stamina. When the variance attributable to the fixed effect (body temperature) is removed, 'individuals' account for 64.5 and 70.2% of the variance in speed and in stamina, respectively (Sokal & Rohlf, 1981).

Discussion

We measured the locomotor performance and body size of lizards at intervals from shortly after

Table 4. Correlation coefficients for speed (above diagonal, $n = 23$) and for stamina (below diagonal, $n = 20$) of hatchling *Sceloporus occidentalis* measured at three body temperatures. All P (one-tail) < 0.001 , $n = 23$ (speed), 20 (stamina).

| Body temperature (°C) | Body temperature (°C) | | |
|-----------------------|-----------------------|------|------|
| | 28 | 33 | 37 |
| 28 | – | 0.62 | 0.66 |
| 33 | 0.77 | – | 0.68 |
| 37 | 0.85 | 0.76 | – |

birth to about 13 months of age and we also determined the effect of body temperature on locomotor performance. Using these data we calculated the repeatabilities of performance and of body size. Here we discuss the patterns and implications of these measures.

Temporal repeatabilities

Is the relative locomotor performance of an individual stable during early ontogeny? When repeatabilities were calculated between pairs of adjacent censuses (Table 2), both speed and stamina of hatchlings were moderately and significantly repeatable. In fact, speed and stamina were significantly repeatable even over hibernation (about 7 months long) and also between 10 and 13 months of age, when the lizards more than tripled in mass. These patterns were generally robust even when the potentially confounding effects of body size are removed (Table 2). However, when repeatabilities were calculated between non-adjacent censuses, speed and stamina were usually positively-repeatable but the associated probability levels were only sometimes significant. This marginal significance may reflect reduced sample sizes caused by high natural mortality (Huey, unpublished) and by the destruction of part of the study area (above). Speed and stamina are significantly repeatable over a full year in adult *Sceloporus merriami* (Stejneger) from Big Bend National Park, Texas (Huey & Dunham, 1987). Speed, distance capacity, and stamina are also significantly repeatable from year to year in garter snakes (*Thamnophis sirtalis* (Linnaeus), A.F. Bennett & B.C. Jayne, personal communication).

Repeatabilities for body size were generally higher than those for locomotor performance for adjacent intervals but were lower than those for performance for non-adjacent censuses, indicating that the long-term repeatability of body size is low for growing lizards. Thus, for example, size at 2 weeks of age did not predict size at 13 months of age (Table 3), although size at 2 months did predict size at 13 months. Whether the low long-term repeatability of body size reflects an inverse relationship between growth and initial size or simply a major environmental effect is unknown. Both factors are likely to be involved. Food level profoundly influences growth rate in *Sceloporus* (Dunham, 1978). Food level, and especially thermal preference, influence growth rate of *S. occidentalis* in the laboratory (Sinervo, 1988); and,

in *S. occidentalis* from southern California, relative growth rate in the laboratory is inversely proportional to hatchling size for the first month of life (Sinervo, 1988). In any case, our results imply that adult size may not be predictable from hatchling size.

The only other published studies of long-term repeatabilities of body sizes in natural populations of vertebrates of which we are aware concern birds. Birds differ fundamentally from lizards in that the former exhibit determinate growth and show much smaller changes in size following fledging than the order of magnitude change in mass shown by *S. occidentalis* (Table 1). Nevertheless, the short-term repeatabilities (adjacent censuses) that we report for SVL, mass and condition index (0.39–0.82, Table 3) of *S. occidentalis* fall within the range of values reported for birds. For body weight and various linear body and beak dimensions, Smith & Zach (1979) report repeatabilities of 0.42 to 0.81, Boag (1983) calculated repeatabilities of 0.55 to 0.98 and Price & Grant (1984) report intraclass correlations of 0.63 to 0.98. (Note that these repeatabilities were based on recaptures that were dispersed in time and thus are not strictly comparable with our data, which were gathered in discrete censuses.) In all of the above studies of birds, repeatabilities of body mass tend to be lower than those of linear dimensions, presumably because body weight is subject to short-term fluctuations not experienced by linear body dimensions. However, somewhat surprisingly such a trend is not apparent in our data (Table 3).

Implications for responses to natural selection

Speed, stamina, and body size appear to be heritable in hatchling *S. occidentalis* from the present study population (van Berkum & Tsuji, 1987). Thus these traits, as measured on hatchlings, have the potential to show a genetic response to selection (Falconer, 1981). However, would directional selection only on hatchlings, e.g. for increased speed (or size), result in a correlated increase in speed (or size) of yearling or adult lizards? This could occur if speed (or size) at one age was positively genetically correlated with speed (or size) at another age (Falconer, 1981; S.J. Arnold, 1987). Body size measures are in fact genetically correlated during ontogeny in laboratory rodents (Atchley & Rutledge, 1980; Cheverud, Rutledge & Atchley 1983; Riska, Atchley & Rutledge, 1984) and in birds in nature (Price & Grant, 1984),

indicating, at least for these species, that directional selection at one age would lead to some correlated responses at other ages.

However, in *S. occidentalis* the phenotypic correlations between hatching and 13 months of age are low and often insignificant (Tables 2, 3). Does this necessarily imply that selection on hatchlings would not lead to a correlated response in yearlings or in adults? Several quantitative genetic analyses of body size of laboratory and of domesticated mammals demonstrate that phenotypic correlations tend to decrease as the time between measurements increases (references in Atchley, 1984). For example, the phenotypic correlation between 14- and 28-day body masses of rats is 0.79, whereas that for 14- and 189-day masses is only 0.35 (Cheverud, *et al.*, 1983; see also Riska *et al.*, 1984 for data on mice). However, phenotypic correlations can differ from genetic correlations, even in sign (Atchley & Rutledge, 1980; Falconer, 1981; S.J. Arnold, 1987). Therefore, the observed low phenotypic correlations between hatching and 13-month sprint speed, stamina and body size in fence lizards are unreliable predictors both of genetic correlations through time and of possible correlated responses to selection.

Thermal repeatability

The relative speed or stamina of an individual is very consistent across temperatures (Table 4) spanning most of the normal range of activity temperatures of these lizards (Tsuji, 1986). Thus, lizards that have high locomotor performance at one temperature have high locomotor performance at others. Comparable results have been obtained in previous studies of lizards (Bennett, 1980; Huey & Hertz, 1984a; Huey & Dunham, 1987), including a study of adult *S. occidentalis* (Bennett, 1980). Thus, we find no evidence, at least from phenotypic comparisons (see Huey & Hertz, 1984a), that a 'jack-of-all-temperatures' is a master of none. The significance of this general finding for field studies of natural selection are evaluated by Huey & Dunham (1987).

Concluding remarks

Locomotor performance and body size were repeatable traits in growing lizards but repeatabilities were generally significant only for adjacent census periods. Body size in particular has low long-term repeatability. Such a finding is certainly

not unexpected on intuitive grounds and is consistent with previous quantitative genetic analyses, both theoretical and empirical. In any case our findings have important implications for field studies of natural selection during early ontogeny of lizards. Because repeatabilities are at best only weakly or marginally significant for long-time intervals (e.g. one year), we recommend that the length of inter-capture intervals should be kept short – certainly less than one year. However, for adult lizards speed and stamina seem to have relatively high stability even over a full year (Huey & Dunham, 1987, unpublished data), suggesting that inter-capture intervals can be longer for adults than for hatchlings. Finally, our results encourage studies that attempt to determine the mechanistic and genetic bases of individual variation in performance and size and its ecological consequences (Wells & Taigen, 1984; Bennett, 1987; Garland & Else, 1987; van Berkum & Tsuji, 1987; Garland, 1988).

Acknowledgments

This research was inspired by many productive discussions with S.J. Arnold and A.F. Bennett. We are deeply indebted to the Tuthill family, especially to Betty Tuthill and the late Philip Tuthill, for permission to conduct these studies on their ranch. Without their support this project would not have been possible. We also acknowledge Richard Hedges for his extraordinary help in the lab and field and also for data entry. S. Adolph, S. Crowley, S. O'Steen and J.R. Sayce provided able assistance in the field; and C. Janson provided valuable statistical advice. This research was supported by National Science Foundation grant BSR-8415855 to R.B. Huey.

References

- Arnold, E.N. (1987) Caudal autotomy as a defense. In *Biology of the Reptilia*, Vol. 16. Ecology B (Defense and Life History) (ed. C. Gans & R.B. Huey), pp. 235–273. A.R. Liss, Inc., New York.
- Arnold, S.J. (1983) Morphology, performance and fitness. *American Zoologist*, **23**, 347–361.
- Arnold, S.J. (1987) Genetic correlation and the evolution of physiology. In *New Directions in Ecological Physiology* (ed. M.E. Feder, A.F. Bennett, W. Burggren & R.B. Huey), pp. 189–215. Cambridge University Press, Cambridge.
- Arnold, S.J. & Bennett, A.F. (1984) Behavioural variation in natural populations. III. Antipredator displays in the garter snake *Thamnophis radix*. *Animal Behaviour*, **32**, 1108–1118.
- Atchley, W.R. (1984) Ontogeny, timing of development, and genetic variance-covariance structure. *American Naturalist*, **123**, 519–540.
- Atchley, W.R. & Rutledge, J.J. (1980) Genetic components of size and shape. I. Dynamics of components of phenotypic variability and covariability during ontogeny in the laboratory rat. *Evolution*, **34**, 1161–1173.
- Avery, R.A., Bedford, J.D. & Newcombe, C.P. (1982) The role of thermoregulation in lizard biology: predatory efficiency in a temperate diurnal basker. *Behavioral Ecology & Sociobiology*, **11**, 261–267.
- Avery, R.A., Mueller, C.F., Jones, S.M., Smith, J.A. & Bond, D.J. (1987) Speeds and movement patterns of European lacertid lizards: a comparative study. *Journal of Herpetology*, **21**, 324–329.
- Bennett, A.F. (1980) The thermal dependence of lizard behaviour. *Animal Behaviour*, **28**, 752–762.
- Bennett, A.F. (1987) Inter-individual variability: an underutilized resource. In *New Directions in Ecological Physiology* (ed. M.E. Feder, A.F. Bennett, W. Burggren & R.B. Huey), pp. 147–169. Cambridge University Press, Cambridge.
- Boag, P.T. (1983) The heritability of external morphology in Darwin's ground finches (*Geospiza*) on Isla Daphne Major, Galapagos. *Evolution*, **37**, 877–894.
- Bulmer, M.G. (1980) *The Mathematical Theory of Quantitative Genetics*. Clarendon Press, Oxford.
- Christian, K.A. & Tracy, C.R. (1981) The effect of the thermal environment on the ability of hatchling Galapagos land iguanas to avoid predation during dispersal. *Oecologia*, **49**, 218–223.
- Cheverud, J.M., Rutledge, J.J. & Atchley, W.R. (1983) Quantitative genetics of development: genetic correlations among age-specific trait values and the evolution of ontogeny. *Evolution*, **37**, 895–905.
- Curnow, R.N. (1961) The estimation of repeatability and heritability from records subject to culling. *Biometrics*, **17**, 553–566.
- Dawson, W.R. (1975) On the physiological significance of preferred body temperature of reptiles. In *Perspectives in Biophysical Ecology*, Vol. 12 (ed. D.M. Gates & R.B. Schmerl), pp. 443–473. Springer-Verlag, New York.
- Dunham, A.E. (1978) Food availability as a proximate factor influencing individual growth rates in the iguanid lizard *Sceloporus merriami*. *Ecology*, **52**, 770–778.
- Falconer, D.S. (1981) *Introduction to Quantitative Genetics*. 2nd edn. Longman, London.
- Ferguson, G.W. & Fox, S.F. (1984) Annual variation of survival advantage of large juvenile side-blotched lizards, *Uta stansburiana*: its causes and evolutionary significance. *Evolution*, **38**, 342–349.
- Garland, T., Jr (1988) Genetic basis of activity metabolism. I. Inheritance of speed, stamina, and antipredator displays in the garter snake *Thamnophis sirtalis*. *Evolution*, **42**, 335–350.
- Garland, T., Jr & Else, P.L. (1987) Seasonal, sexual, and individual variation in endurance and activity metabolism in lizards. *American Journal of Physiology*, **252** (Regulatory, Integrative and Comparative Physiology, **21**), R439–R449.
- Greenwald, O.E. (1974) Thermal dependence of striking and prey capture by gopher snakes. *Copeia*, **1974**, 141–148.

- Herzog, H.H., Jr & Burghardt, G.M. (1988) Development of antipredator responses in snakes: III. Long-term stability of litter and individual differences. *Ethology*, **77**, 250–258.
- Huey, R.B. (1982) Temperature, physiology, and the ecology of reptiles. In *Biology of the Reptilia*, Vol. 12, Physiology (C) (ed. C. Gans & F.H. Pough), pp. 25–91. Academic Press, London.
- Huey, R.B. & Dunham, A.E. (1987) Repeatability of locomotor performance in natural populations of the lizard *Sceloporus merriami*. *Evolution*, **41**, 1116–1120.
- Huey, R.B. & Hertz, P.E. (1984a) Is a jack-of-all-temperatures a master of none? *Evolution*, **38**, 441–444.
- Huey, R.B. & Hertz, P.E. (1984b) Effects of body size and slope on acceleration of a lizard (*Stellio stellio*). *Journal of Experimental Biology*, **110**, 113–123.
- Huey, R.B. & Stevenson, R.D. (1979) Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. *American Zoologist*, **19**, 357–366.
- Huey, R.B., Schneider, W., Erie, G.L. & Stevenson, R.D. (1981) A field-portable racetrack and timer for measuring acceleration and speed of small cursorial animals. *Experientia*, **37**, 1356–1357.
- Lessells, C.M. & Boag, P.T. (1987) Unrepeatable repeatabilities: a common mistake. *Auk*, **104**, 116–121.
- Pough, F.H. (1983) Amphibians and reptiles as low-energy systems. In *Behavioral Energetics: the Cost of Survival in Vertebrates* (ed. W.P. Aspey & S. Lustick), pp. 141–188. Ohio State University Press, Columbus.
- Price, T.D. & Grant, P.R. (1984) Life history traits and natural selection for small body size in a population of Darwin's finches. *Evolution*, **38**, 483–494.
- Rand, A.S. (1964) Inverse relationship between temperature and shyness in the lizard *Anolis lineatopus*. *Ecology*, **45**, 863–864.
- Regal, P.J. (1971) Long term studies with operant conditioning techniques of temperature regulation patterns in reptiles. *Journal de Physiologie*, **653**, 403–406.
- Riska, B., Atchley, W.R. & Rutledge, J.J. (1984) A genetic analysis of targeted growth in mice. *Genetics*, **107**, 79–101.
- Sinervo, B. (1988) *The evolution of growth rate in Sceloporus lizards: maternal, environmental, behavioral, and genetic aspects*. Unpublished PhD thesis, University of Washington.
- Smith, J.N.M. & Zach, R. (1979) Heritability of some morphological characters in a song sparrow population. *Evolution*, **33**, 460–467.
- Smith, J.N.M., Arcese, P. & Schluter, D. (1986) Song sparrows grow and shrink with age. *Auk*, **103**, 210–212.
- Sokal, R.R. & Rohlf, E.J. (1981) *Biometry*. W.H. Freeman and Co., San Francisco.
- Tolley, E.A., Notter, D.R. & Marlowe, T.J. (1983) Heritability and repeatability of speed for 2- and 3-year-old standardbred racehorses. *Journal of Animal Science*, **56**, 1294–1305.
- Trivers, R.L. (1976) Sexual selection and resource-accumulating ability in *Anolis garmani*. *Evolution*, **30**, 253–267.
- Tsuji, J.S. (1986) *Metabolic adaptations to temperature in lizards of the genus Sceloporus from different latitudes*. Unpublished PhD thesis, University of Washington.
- van Berkum, F.H. & Tsuji, J.S. (1987) Inter-familial differences in sprint speed of hatchling *Sceloporus occidentalis*. *Journal of Zoology*, **212**, 511–519.
- Webb, P.W. (1986) Locomotion and predator-prey relationships. In *Predator-Prey Relationships: Perspectives and Approaches from the Study of Lower Vertebrates* (ed. M.E. Feder & G.V. Lauder), pp. 24–41. University of Chicago Press, Chicago.
- Wells, K.D. & Taigen, T.L. (1984) Reproductive behavior and aerobic capacities of male American toads (*Bufo americanus*): is behavior constrained by physiology. *Herpetologica*, **40**, 292–298.

Received 18 February 1988; revised 28 July 1988; accepted 1 August 1988