REPEATABILITY OF LOCOMOTOR PERFORMANCE IN NATURAL POPULATIONS OF THE LIZARD *SCELOPORUS MERRIAMI*

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Field studies of natural selection are currently undergoing a resurgence (Price et al., 1984; Endler, 1986). Recent theoretical and analytical advances (Lande and Arnold, 1983; Manly, 1985; Arnold and Wade, 1984*a*, 1984*b*) have made these new studies both rigorous and feasible, and criticisms of untested adaptive explanations (Gould and Lewontin, 1979) have made them necessary.

One common approach involves an attempt to correlate interspecific or interpopulational differences in a given trait with environmental gradients, e.g., in predation rate or latitude (Lauder, 1981; Endler, 1986). A second, less common approach involves an attempt to detect the effects of individual differences on one or more components of fitness, e.g., fecundity or survivorship (Lande and Arnold, 1983; Arnold, 1986; Endler, 1986). These and related methods make a key assumption—that measurements of traits are repeatable (Arnold, 1986; Bennett, 1987). For example, the bill size of an individual bird is assumed not to change significantly during the study. This assumption is often valid for morphological traits of adult animals (Falconer, 1981) (but see Smith and Zach, 1979; Price and Grant, 1984). Its validity for organismal "performance" traits, e.g., speed, stamina, or digestive efficiency (Huey and Stevenson, 1979; Arnold, 1983) has to date been established only in the laboratory (review in Bennett [1987]), not in the field. This is unfortunate, as such measures provide a crucial link between "lower-level" (physiological, morphological, biochemical) traits and fitness (Arnold, 1983). Showing that performance traits are repeatable in long-term field studies would encourage attempts to monitor selection on such traits, for only one or a few measurements of performance could adequately characterize an individual's performance. Alternatively, performance would need to be measured multiple times during the course of the study.

Here, we investigate the repeatability of sprint speed in natural populations of a lizard. Sprint speed is a performance trait that may influence fitness via its effects on feeding success (Greenwald, 1974; Webb, 1986), predator avoidance (Shine, 1980; Christian and Tracy, 1981; Huey and Hertz, 1984*b*), and, possibly, social dominance. Sprint speed is significantly repeatable for up to two months in the laboratory (Bennett, 1980, 1987; Garland and Arnold, 1983; Garland, 1985; Garland and Else, 1987; Arnold and Bennett, pers. comm.). Nevertheless, the feasibility of studying natural selection on speed is unclear, because the sprint speed of a lizard may not be a fixed trait in long-term studies: an individual's speed may vary with body size and age (Huey and Hertz, 1982, 1984*b*; Garland, 1985), body temperature (Bennett, 1980; Huey and Hertz, 1984*a*), reproductive condition (Shine, 1980; Bauwens and Thoen, 1981), and injury history (Daniels, 1983), though perhaps not with season (Garland, 1985) or desiccation (Crowley, 1985*b*). These considerations raise an important issue: is sprint speed sufficiently repeatable in nature to render it convenient for field studies of natural selection?

We address two specific questions. First, is the relative speed of an individual repeatable across temperatures? In other words, is the rank order of an individual's speed independent of body temperature? Second, is absolute speed of populations or individuals repeatable in time? If the answer to these questions is yes, then studies of natural selection will be facilitated, because an individual's (or population's) performance can be adequately assessed from a few measurements at a single body temperature.

We studied the repeatability of sprint speed in *Sceloporus merriami* (Iguanidae), a small, diurnal, rock-dwelling, insectivorous lizard that occurs in southwestern Texas and in adjacent areas of Mexico. Populations in Big Bend National Park, Texas are especially well suited for these analyses because their ecology is well known (Dunham, 1978, 1981, 1983). Sprint speed is probably relevant to *Sceloporus merriami,* as these lizards often sprint when capturing prey, escaping predators, and interacting socially. Adult lizards have an average cohort generation time of 1.5 years and a maximum measured lifespan of six years (Dunham, 1981).

MATERIALS AND METHODS

We captured lizards from two populations in Big Bend National Park, Texas, in July 1984 and in July 1985. Boquillas is a hot (elevation 560 m), limestone

TABLE 1. Maximum sprint speeds of adult *Sceloporus merriami* in two populations (Big Bend National Park, Texas) in two years (N = number of individuals). Individuals tested in both years were excluded from the 1984 samples (see text).

Population	Year	Males		Females	
		N	$\bar{x}$ (SE)	N	$\bar{x}$ (SE)
Boquillas	1984	39	2.13 (0.046)	35	1.96 (0.058)
	1985	62	2.17 (0.039)	45	2.01 (0.039)
Grapevine	1984	30	2.37 (0.063)	21	2.18 (0.076)
	1985	41	2.32 (0.052)	31	2.14 (0.048)

feeder canyon of the Rio Grande, whereas Grapevine Hills is less hot (elevation 1036 m; site IV of Dunham, 1981) and is a west-facing, granitic hillside.

Within one day of capture, lizards were transferred to a field-portable environmental chamber (Huey et al., 1984). They were then chased along a 2.3 × 0.2-m racetrack (rubber substrate) (see Huey et al., 1984). Eleven photocell stations were placed at set distances along the track (timed section = 2.0 m) and connected to an Apple II+ computer. The sprinting lizard would break the photocell beams, and elapsed times were converted into speeds (m/sec). Each lizard was tested six times between 9:30 A.M. and 4:00 P.M. (CST), usually with at least a one-hour rest between runs. We selected the fastest speed of each lizard over all 0.5-m sections of the track as the estimate of its maximum speed. In the second year, we raced the lizards "blind" with respect to individual identity. Thus, speeds of these lizards could not have been inadvertently biased by our recognizing fast or slow lizards from the previous year.

Experiment I. — To estimate the repeatability of sprint speed as a function of body temperature, we measured the fastest speed of unmarked adult lizards (11 from a canyon adjacent to the Boquillas site, 10 from near the Grapevine IV site) over four trials at each of three body temperatures (28° and 32°C on day-1, 37°C on day-2) in July 1984, following general procedures of Hertz et al. (1983). The two extreme temperatures bracket 89.7% ($N = 300$) and 96.8% ($N = 282$) of the active body temperatures of these lizards (cloacal temperatures of emergent lizards on clear days, after local sunrise) in summer from Boquillas and Grapevine, respectively, and 32°C approximates their mean activity temperatures (Grant and Dunham, pers. comm.).

Experiment II. — To estimate the repeatability of sprint speed between years, we measured the speeds (32° to 33°C) of individually marked lizards from Boquillas ($N = 97$ in July 1984; $N = 107$ in July 1985) and from the Grapevine Hills ($N = 70$ and $N = 72$, respectively). Of this sample, 42 lizards (23 from Boquillas, 19 from Grapevine) were raced in both years. To ensure independence of data and to enlarge our sample of older lizards, we excluded the speeds for these 42 lizards from the 1984 samples for the interpopulational statistical comparisons. Ongoing demographic studies provided data on body size, sex, age, and reproductive condition for all marked lizards.

We were concerned that our estimates of repeatability might be confounded by effects of body size and age (see Huey and Hertz, 1982). Therefore, we compared (Experiment I) size-corrected relative speeds of each individual at each temperature, where the corrected relative speed was the residual from a regression of the natural logarithm of speed on the natural logarithm of mass (see Huey and Hertz, 1984a). In Experiment II we compared speeds (ln[speed]) using ANCOVA with ln(age in years), ln(mass), and ln(svl) as covariates. None of the interaction terms was significant.

RESULTS

Experiment I. — Absolute speed was significantly affected by body temperature (repeated measures ANOVA, $F_{[2,38]} = 19.3$, $P < 0.001$). Lizards were fastest at 32°C ($\bar{x} \pm$ SE = 2.49 ± 0.062 m/sec) and slower at 28°C (2.17 ± 0.054 m/sec) and at 37°C (2.11 ± 0.090 m/sec). Nevertheless, size-corrected relative speeds of individuals were consistent across temperatures in both populations (Boquillas: Kendall's coefficient of concordance $W = 0.694$, $P < 0.05$; Grapevine: $W = 0.656$, $P < 0.05$). Thus, individuals that were relatively fast at one temperature were relatively fast at other temperatures.

Experiment II. — Average speed of lizards from the two populations was temporally and geographically repeatable (Table 1). Grapevine lizards were faster than those from Boquillas (ANCOVA, $P < 0.001$), males were faster than females ($P < 0.001$) in both populations, and average speeds for 1984 and 1985 were not significantly different ($P > 0.9$). These differences are not an artifact of differences between populations or sexes in body size or age (ANCOVA).

Maximum sprint speeds of individual lizards were repeatable between years in *S. merriami* (Boquillas: intraclass correlation coefficient $t_{intraclass} = 0.627$, $F_{[22,23]} = 4.36$, $P < 0.001$; Grapevine: $t_{intraclass} = 0.562$, $F_{[18,19]} = 3.56$, $P < 0.01$; see Falconer, 1981; Lessels and Boag, 1987). Thus, a lizard that was fast in the summer of 1984 was usually fast the following summer. These patterns reflect consistent individual differences in speed, independent of differences in age, sex, or body size (ANCOVA).

Figure 1 presents a "worst case" from the perspective of demonstrating repeatability, as no lizard was excluded from the analysis. Indeed, Figure 1 includes six females that were gravid in only one of the two years, even though gravidity may reduce sprint speeds of females (Shine, 1980; Bauwens and Thoen, 1981; Garland, 1985). It includes one male that was recovering from an apparent territorial battle or encounter with a predator (fresh scars on his head and torso) in 1984, even though he was very slow for his size that year. Finally, it includes two lizards that were hatchlings in
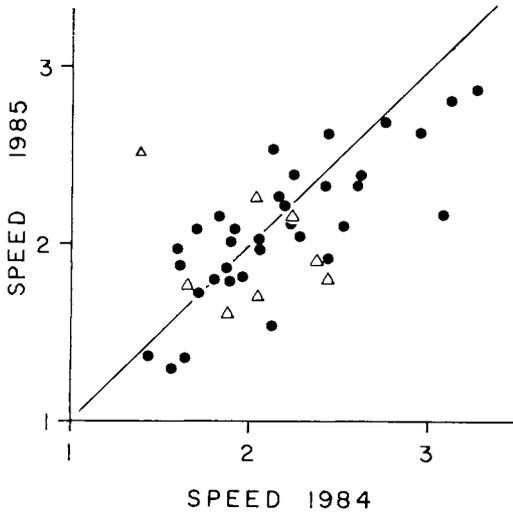
FIG. 1. Maximum speed of individual *Sceloporus merriami* in July 1984 and July 1985. The solid line indicates expected speeds if speed in 1984 exactly coincided with speed in 1985. Triangles represent questionable records (see text).

1984 (one was a female, referred to above), even though hatchlings are slower than yearlings (Huey and Dunham, unpubl.). Deletion of these eight questionable animals (triangles in Fig. 1) increases estimates of repeatability (Boquillas: $t_{intraclass}$ = 0.653; Grapevine: $t_{intraclass}$ = 0.742).

DISCUSSION

Relative sprint speed is independent of body temperature in *S. merriami*. This pattern has now been documented for several lizards (from four families, Bennett, 1980; Huey and Hertz, 1984*a*) and thus appears to be general for lizards. This pattern is also significant for prospective studies of natural selection, for it implies that an estimate of the relative speed of an individual at a single activity temperature adequately predicts its relative speed at other activity temperatures. Were this not the case, the performance of an individual could be assessed only by measuring its performance at several temperatures, a requirement that would complicate field studies and subsequent analyses.

The independence of relative speed and temperature does not mean, however, that temperature should be ignored. Indeed, potential differences among individual lizards or among populations in normal activity temperatures—perhaps because of differences in local microclimate—could confound attempts to study effects of selection on speed. Moreover, body-temperature data may even enhance such studies. For instance, Crowley (1985*b*) compared speeds of *Sceloporus undulatus* from two localities that differed in apparent predation pressure. He found no difference in average speeds of these lizards at their optimal temperature for sprinting. However, because lizards from the high-predation site were more likely to be active at temperatures near the optimum for sprinting than were lizards

from the low-predation site, predicted average speeds of lizards at their normal activity temperatures were faster at the high-predation site.

The between-year repeatability of average speed of populations (Table 1) suggests that "point samples" may adequately characterize the sprint capacities of a population in comparative studies. Nevertheless, we cannot rule out seasonal changes in speed of *S. merriami*: speed changes with season in *S. occidentalis* (Bennett, 1980) but not in *Ctenophorus nuchalis* (Garland, 1985). Stamina does vary seasonally in *Dipsosaurus dorsalis* (John-Alder, 1984) and *C. nuchalis* (Garland, 1985; Garland and Else, 1987).

The between-year repeatability of speeds of individuals within populations is remarkable: one year is a substantial fraction of the cohort generation time (1.5 years) of *S. merriami*, and even includes an overwintering period. Moreover, the repeatability is high despite known between-year changes in reproductive condition and in injury in certain individuals. In fact, even the uncorrected repeatabilities (Fig. 1) are as high or higher than those from most short-term laboratory studies of speed for reptiles (Bennett, 1980; Garland and Arnold, 1983; Garland, 1985; Arnold and Bennett, pers. comm.), slightly higher than those for racehorses and pacers ($t_{intraclass}$ = 0.44, Tolley et al., 1983) and greyhounds ($t_{intraclass}$ = 0.54, Ryan, 1975), and even equivalent to some repeatabilities for morphological traits of birds (Smith and Zach, 1979; Price and Grant, 1984; Smith et al., 1986).

Conclusions

Sprint speed is a repeatable trait in adult *S. merriami*. Lizards that were relatively fast at one body temperature were relatively fast at two other temperatures; intersexual and interpopulational differences in average speed were maintained between years; and individual lizards that were fast one year were still fast when recaptured a year later. However, whether fast hatchlings become fast adults remains to be determined.

This high temporal repeatability of performance should encourage attempts to study selection on sprint speed using either interpopulational (Crowley, 1985*a*) or individual comparisons (Bennett, 1987). Such studies have been proposed (Arnold, 1983, 1986) and are currently in progress (Bennett and Arnold, pers. comm.; Huey et al., unpubl.; Huey and Dunham, unpubl.; Snell, unpubl.). Nevertheless, because the repeatability of locomotor performance is still lower than that for many morphological measurements, the detection of selection may require large samples, strong selection, or both (Lewontin, 1974).

LITERATURE CITED

ARNOLD, S. J. 1983. Morphology, performance and fitness. Amer. Zool. 23:347–361.

———. 1986. Laboratory and field approaches to the study of adaptation, pp. 157–179. *In* M. E. Feder and G. V. Lauder (eds.), Predator-prey Relationships: Perspectives and Approaches from the Study of Lower Vertebrates. Univ. Chicago Press, Chicago, IL.

ARNOLD, S. J., AND M. J. WADE. 1984a. On the measurement of natural and sexual selection: Theory. Evolution 38:709–719.

———. 1984b. On the measurement of natural and sexual selection: Applications. Evolution 38:720–734.

BAUWENS, D., AND C. THOEN. 1981. Escape tactics and vulnerability to predation associated with reproduction in the lizard *Lacerta vivipara*. J. Anim. Ecol. 50:733–743.

BENNETT, A. F. 1980. The thermal dependence of lizard behaviour. Anim. Behav. 28:752–762.

———. 1987. Inter-individual variability: An underutilized resource. *In* M. E. Feder, A. F. Bennett, W. W. Burggren, and R. B. Huey (eds.), New Directions in Ecological Physiology. Cambridge Univ. Press, Cambridge, U.K.

CHRISTIAN, K. A., AND C. R. TRACY. 1981. The effect of the thermal environment on the ability of hatchling Galápagos land iguanas to avoid predation during dispersal. Oecologia 49:218–223.

CROWLEY, S. R. 1985a. Thermal sensitivity of sprint-running in the lizard *Sceloporus undulatus*: Support for a conservative view of thermal physiology. Oecologia 66:219–225.

———. 1985b. Insensitivity to desiccation of sprint running performance in the lizard, *Sceloporus undulatus*. J. Herpetol. 19:171–174.

DANIELS, C. B. 1983. Running: An escape strategy enhanced by autotomy. Herpetologica 39:162–165.

DUNHAM, A. E. 1978. Food availability as a proximate factor influencing individual growth rates in the iguanid lizard *Sceloporus merriami*. Ecology 59:770–778.

———. 1981. Populations in a fluctuating environment: The comparative population ecology of *Sceloporus merriami* and *Urosaurus ornatus*. Misc. Publ. Mus. Zool. Univ. Mich. 158:1–62.

———. 1983. Realized niche overlap, resource abundance, and intensity of interspecific competition, pp. 261–280. *In* R. B. Huey, E. R. Pianka, and T. W. Schoener (eds.), Lizard Ecology: Studies of a Model Organism. Harvard Univ. Press, Cambridge, MA.

ENDLER, J. A. 1986. Natural Selection in the Wild. Princeton Univ. Press, Princeton, NJ.

FALCONER, D. S. 1981. Introduction to Quantitative Genetics, 2nd Ed. Longman, London, U.K.

GARLAND, T., JR. 1985. Ontogenetic and individual variation in size, shape and speed in the Australian agamid lizard *Amphibolurus nuchalis*. J. Zool. London A 297:425–439.

GARLAND, T., JR., AND S. J. ARNOLD. 1983. Effects of a full stomach on locomotory performance of juvenile garter snakes (*Thamnophis elegans*). Copeia 1984:1092–1096.

GARLAND, T., JR., AND P. L. ELSE. 1987. Seasonal, sexual, and individual variation in endurance and activity metabolism in a lizard. Amer. J. Physiol. 247:R806–R815.

GOULD, S. J., AND R. C. LEWONTIN. 1979. The spandrels of San Marco and the panglossian paradigm: A critique of the adaptationist programme. Proc. Roy. Soc. Lond. B 205:581–598.

GREENWALD, O. E. 1974. Thermal dependence of striking and prey capture by gopher snakes. Copeia 1974:141–148.

HERTZ, P. E., R. B. HUEY, AND E. NEVO. 1983. Homage to Santa Anita: Thermal sensitivity of sprint speed in agamid lizards. Evolution 37:1075–1084.

HUEY, R. B., AND P. E. HERTZ. 1982. Effects of body size and slope on sprint speed of a lizard (*Stellio* (*Agama*) *stellio*). J. Exp. Biol. 97:401–409.

———. 1984a. Is a jack-of-all-temperatures a master of none? Evolution 38:441–444.

———. 1984b. Effects of body size and slope on acceleration of a lizard (*Stellio stellio*). J. Exp. Biol. 110:113–123.

HUEY, R. B., A. F. BENNETT, H. B. JOHN-ALDER, AND K. A. NAGY. 1984. Locomotor capacity and foraging behaviour of Kalahari lacertid lizards. Anim. Behav. 32:41–50.

HUEY, R. B., AND R. D. STEVENSON. 1979. Integrating thermal physiology and ecology of ectotherms. Amer. Zool. 19:357–366.

JOHN-ALDER, H. B. 1984. Seasonal variations in activity, aerobic energetic capacities, and plasma thyroid hormones (T3 and T4) in an iguanid lizard. J. Comp. Physiol. B 154:409–419.

LANDE, R., AND S. J. ARNOLD. 1983. The measurement of selection on correlated characters. Evolution 37:1210–1226.

LAUDER, G. V. 1981. Form and function: Structural analysis in evolutionary morphology. Paleobiology 7:430–442.

LESSELS, C. M., AND P. T. BOAG. 1987. Unrepeatable repeatabilities: A common mistake. Auk 104:116–121.

LEWONTIN, R. C. 1974. The Genetic Basis of Evolutionary Change. Columbia Univ. Press, N.Y.

MANLY, F. B. J. 1985. The Statistics of Natural Selection on Animal Populations. Chapman and Hall, N.Y.

PRICE, T. D., AND P. R. GRANT. 1984. Life history traits and natural selection for small body size in a population of Darwin's finches. Evolution 38:483–494.

PRICE, T. D., P. R. GRANT, H. L. GIBBS, AND P. T. BOAG. 1984. Recurrent patterns of natural selection in a population of Darwin's finches. Nature 309:787–789.

RYAN, J. E. 1975. The inheritance of track performance in greyhounds. M.A. Thesis. Trinity College, Dublin, Ireland.

SHINE, R. 1980. "Costs" of reproduction in reptiles. Oecologica 46:92–100.

SMITH, J. N. M., P. ARCESE, AND D. SCHLUTER. 1986. Song sparrows grow and shrink with age. Auk 193:210–212.

SMITH, J. N. M., AND R. ZACH. 1979. Heritability of some morphological characters in a song sparrow population. Evolution 33:460–467.

TOLLEY, E. A., D. R. NOTTER, AND T. J. MARLOWE. 1983. Heritability and repeatability of speed for 2- and 3-year-old standardbred racehorses. J. Anim. Sci. 56:1294–1305.

WEBB, P. W. 1986. Locomotion and predator-prey relationships, pp. 24–41. In M. E. Feder and G. V. Lauder (eds.), Predator-prey Relationships: Perspectives and Approaches from the Study of Lower Vertebrates. Univ. Chicago Press, Chicago, IL.

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EFFECT OF CANNIBALISM ON ALTERNATIVE LIFE HISTORIES IN CHARR

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Cannibalism and other behaviors of fish toward members of their own species should be evolutionarily influenced by degree of genetic relatedness (Hamilton, 1964; Dominey and Blumer, 1984). Precocious stream-resident (hereafter "stream") males of the lacustrine Miyabe char, *Salvelinus malma miyabei*, participate as "streakers" during mating between lake-run (hereafter "lake") males and females (i.e., stream males rush quickly into a pair's territory and release sperm). Due to their small size and subordinate status, stream males are rarely able to pair directly with lake females during a spawning (Maekawa, 1983). A stream male is able to fertilize about 17% of the oviposited eggs by streaking (Maekawa and Onozato, 1986). According to ESS (evolutionarily stable strategy) theory (Maynard Smith, 1982; Gross and Charnov, 1980; Gross, 1982, 1984), a stable equilibrium frequency of the two types of males is possible (Maekawa and Hino, 1986).

Stream males prey on fertilized eggs for energy during or just after spawning, but lake males never do. The question of whether this behavior is cannibalism of stream-male progeny (filial cannibalism), lake-male progeny (heterocannibalism), or random has not been clarified. If the behavior is heterocannibalism, it could affect the evolutionary equilibrium frequency of stream and lake males. In this paper, we characterize the cannibalistic behavior of stream males and extend the model of Gross and Charnov (1980) to include cannibalism in calculating the equilibrium frequencies for alternative life histories of males.

The Model

We propose that the two types of charr have evolved through a mixed ESS (Maekawa and Onozato, 1986), similar to that of bluegill sunfish and coho salmon (Gross, 1984, 1985). We can therefore apply the model of Gross and Charnov (1980) to the charr system. With negative frequency-dependent advantage, the equilib-

rium proportion of males in each life history should be such that the average lifetime fitness of individuals is the same for either life history. Divergence of stream and lake males occurs at about age two (Maekawa and Onozato, 1986). Following the Gross and Charnov (1980) model, at equilibrium

$$\frac{qn \int_{x=2}^{\infty} l_s(x)b_s(x)\, dx}{(1-q)n \int_{x=2}^{\infty} l_l(x)b_l(x)\, dx} = \frac{h}{1-h}, \quad (1)$$

or

$$q = h, \quad (2)$$

where

$l(x)$ = probability an individual is alive at age x

$b(x)$ = number of offspring an individual will produce while at age x

s and l = stream and lake, respectively

n = number of males reaching age two each year

q = proportion of males entering stream life history

$1 - q$ = proportion of males entering lake life history

h = proportion of eggs fertilized by stream males

$1 - h$ = proportion of eggs fertilized by lake males.

This model has been supported by empirical data on sunfish (Gross, 1982) and in preliminary calculations for Dolly Varden in southeastern Alaska (Maekawa and Hino, 1986); it may also apply to coho salmon (Gross, 1985).

If stream males prey on fertilized eggs without regard for parentage, then entering predation into Equation (2) gives