Quantitative Genetics of Locomotor Speed and Endurance in the Lizard *Lacerta vivipara*

Gabriele Sorci[1,*]
John G. Swallow[2]
Theodore Garland, Jr.[2]
Jean Clobert[1]
[1]Laboratoire d'Ecologie, Centre National de la Recherche Scientifique—URA 258, Université Pierre et Marie Curie, Paris, France; [2]Department of Zoology, 430 Lincoln Drive, University of Wisconsin, Madison, Wisconsin 53706

Accepted 1/9/95

Abstract

We used quantitative genetic analyses to test the hypothesis of a trade-off between locomotor speed and endurance in a population of the European lizard Lacerta vivipara, *which is the subject of long-term demographic studies. We estimated the heritability of maximal sprint speed, treadmill endurance, and tail length, a morphometric trait that may affect locomotor performance, as well as phenotypic, genetic, and environmental correlations between these traits. Gravid females were captured in the field and held in the laboratory under standardized conditions until giving birth; traits were then measured on their offspring. Prior to genetic analyses, we used multiple regressions to remove the effects of such covariates as body size (mass and snout-vent length), dam age, and length of time dams were held in captivity prior to parturition. When we examined the residual characters, heritability was low and statistically nonsignificant for speed but relatively high for both endurance (0.46) and tail length (0.51). None of the phenotypic, genetic, or environmental correlations between traits was statistically significant. Thus, we found no evidence for a trade-off between speed and endurance; these results are consistent with those reported in two previous studies of squamate reptiles (the garter snake* Thamnophis sirtalis *and the fence lizard* Sceloporus occidentalis*). The lack of a negative genetic correlation between speed and endurance suggests that these aspects of locomotor abilities are relatively free to evolve independently, such that natural selection could increase both speed and endurance. However, the species studied to date have low to moderate capacities for speed and endurance, as compared with other squamates. Physiologically based trade-offs—for example, those caused by the composition of muscle fiber types—should be more likely to exist in species that have high capacities for speed and/or endurance.*

---

[*] To whom all correspondence should be sent at Laboratoire d'Ecologie, CNRS—URS 258, Université Pierre et Marie Curie, Bat. A., 7éme étage, 7 quai St. Bernard, Case 237, F-75252 Paris Cedex 05, France. E-mail: gsorci@smv.jussieu.fr.

Physiological Zoology 68(4):698–720. 1995. 0031-935X/95/6804-9451$02.00

Introduction

Natural selection leading to adaptation is widely acknowledged as a major cause, probably *the* major cause, of evolutionary change at the phenotypic level. Yet natural selection is not omnipotent. Instead, "constraints" or "trade-offs" may, in part, determine the course of evolution. Many discussions of the importance of constraints and trade-offs are available. In a recent treatise on life-history evolution, for example, Roff (1992, p. 9) states that "no creature can do all things: it is bound by constraints of its genetic architecture, its history, biophysical and biomechanical factors, and its life-style."

Examples of constraints are well known to ecological and evolutionary physiologists. Patterns of bioenergetic allocation provide some of the most obvious examples. Energy available from foraging, digestion, and assimilation can be allocated among such conflicting demands as maintenance, storage, growth, and reproduction. If the total amount of available energy is limited, then increasing allocation to one of these components will necessitate decreasing allocation to one or more of the others (see, e.g., Sibly and Calow 1986; Calow 1987). In general, this energetic trade-off should constrain the joint evolution of such energy-related traits as resting metabolic rates, growth rates, and reproductive output.

Constraints on adaptive phenotypic evolution can be studied in many different ways (see, e.g., references in Rose, Service, and Hutchinson [1987], Arnold [1992], Roff [1992], Sih [1992], Stearns [1992], Garland and Carter [1994], Moore and Boake [1994], Orzack and Sober [1994], and Wainwright and Reilly 1994). Optimality models, for examples, can be used to predict the phenotype that should yield highest fitness. Interspecific comparative studies, on the other hand, can indicate which phenotypes have actually evolved, and whether they are associated with the predicted (from adaptationist arguments) environmental features (Harvey and Pagel [1991], Garland and Adolph [1994, and references therein]; but see Leroi, Rose, and Lauder [1994]).

Quantitative genetic analyses provide another set of tools for studying evolutionary constraints and trade-offs (Arnold 1987, 1992; Falconer 1989; Brodie and Garland 1993; Boake 1994). In contrast to interspecific studies, which indicate how a character has evolved in the past, quantitative genetic studies indicate how a character could evolve in the future. The field of quantitative genetics begins with the premise that aspects of the phenotype are determined by both genetic and environmental effects, and that it is possible to partition (in a statistical sense) variation among individuals within a population into genetic and environmental components (components reflecting genotype-by-environment interactions can also be estimated). These genetic and environmental components can be further partitioned into components representing, for example, additive, dominance, and epistatic (interactions across loci) effects of genes, pre- and postnatal maternal effects, and effects of other environmental factors, such as variation in temperature during development and growth. Through their emphases on partitioning phenotypic variances and covariances into genetic and environmental components, quantitative genetic methods are also well suited to addressing questions about the correlated evolution of two or more phenotypic traits. Correlated evolution, either positive or negative, is a primary manifestation of constraints and trade-offs.

Quantitative genetics can be both descriptive and predictive. For example, the equation used to describe the predicted change in the phenotypic mean value of a single quantitative character across one generation is

$$\mathrm{R} = h^2 s, \tag{1}$$

where R is the response to selection (i.e., genetic evolution), h^2 is the narrow-sense heritability (ratio of additive genetic to total phenotypic variation), and s is the selection differential (the difference in the phenotypic mean of the entire population before selection and the subset actually selected to breed). Natural selection, however, does not act on single traits, but rather on multiple traits simultaneously. The usual equation for predicting the response to selection (either natural or artificial) of the means of multiple traits is

$$\Delta\bar{\mathbf{z}} = \mathbf{G}\mathbf{P}^{-1}\mathbf{s}, \tag{2}$$

where $\bar{\mathbf{z}}$ is the vector of predicted responses to selection for the phenotypic mean of a series of characters, **G** is the additive genetic variance-covariance matrix, **P** is the phenotypic variance-covariance matrix, and **s** is the vector of selection differentials for each of the series of traits (Lande 1979; Lande and Arnold 1983; Arnold 1987; Brodie and Garland 1993; Boake 1994). An alternative formulation of this equation is

$$\Delta\bar{\mathbf{z}} = \mathbf{G}\mathbf{b}, \tag{3}$$

where **b** is the vector of partial regression coefficients of relative fitness on all characters in the analysis. Consideration of either of the foregoing multivariate equations indicates that the mean values of phenotypic characters will evolve not only because of selection acting directly on them but also because of selection acting on correlated traits.

Measurement of genetic correlations is one way to evidence the potential for trade-offs and constraints among characters (Arnold 1987, 1992; Garland 1988, 1994*b;* Rose 1991; Roff 1992; Stearns 1992; Brodie and Garland 1993).

Estimation of genetic correlations can also be used to test a priori hypotheses. For instance, physiological considerations led Garland (1988) to the expectation of a negative correlation between locomotor speed and endurance. The biophysical and biomechanical properties of vertebrate skeletal muscles differ between "fast-twitch" and "slow-twitch" fiber types (Gleeson and Harrison 1986; Esbjörnsson et al. 1993; Rivero et al. 1993). In overly simple terms, fast-twitch fibers should enhance speed, as they have relatively rapid contraction rates. However, fast-twitch fibers are also less resistant to fatigue than are slow-twitch fibers, which can only contract less rapidly. Indeed, the proportion of muscle fiber types has been shown to predict endurance capacity in horses (Rivero et al. 1993), and anaerobic performance is correlated with the proportion of fast contractile skeletal muscle fibers in humans (Esbjörnsson et al. 1993). Thus, one might expect individuals with a high proportion of fast-twitch fibers to have maximal sprint running speeds but relatively low endurance, whereas individuals with a high proportion of slow-twitch fibers should have high endurance and low speed (Esbjörnsson et al. [1993] and references therein; Rivero et al. [1993] and references therein). To the extent that the proportion of fiber types is a genetically determined trait (Bouchard and Malina [1983*a,* 1983*b*]; Bouchard and Lortie [1984]; Nakamura et al. [1993] and references therein), one should expect a negative genetic correlation between speed and endurance.

Contrary to the predictions outlined in the preceding paragraph, previous studies of two species of garter snake (*Thamnophis:* Garland 1988, 1994*b;* Brodie 1989, 1993; Brodie and Garland 1993) and of a fence lizard (*Sceloporus occidentalis:* Tsuji et al. 1989) found no evidence for a negative genetic correlation between locomotor speed and endurance. Although no comparable data are yet available for mammals, an interspecific comparative study also found no evidence for a negative correlation between maximal sprint running speed and maximal aerobic speed, the latter being one index of stamina (Garland, Geiser, and Baudinette 1988).

The simple connection of the composition of muscle fiber types with speed and endurance outlined above is not the only factor that could lead to a correlation, possibly a trade-off, between speed and endurance. Locomotor mode, for example, might affect relationships between various aspects of locomotor abilities. Garter snakes are limbless and are active foragers, whereas fence lizards are sit-and-wait foragers, which typically employ short sprints to capture insect prey and to escape from predators. Many other locomotor and foraging modes are represented within extant squamate reptiles (references in Garland and Losos [1994]). Before concluding that a lack of negative genetic correlation between locomotor speed and endurance is a general feature of squamate locomotion, it is important to obtain data from representative species exhibiting other modes of locomotion.

The aim of the present study was, therefore, to test the hypothesis of a genetic trade-off between speed and endurance in a species of lacertid lizard, *Lacerta vivipara,* as well as between locomotor performances and one possible morphometric determinant of these traits, tail length (Tsuji et al. [1989]; references in Garland and Losos [1994]). Lacertid lizards are only distantly related to fence lizards and other iguanine lizards; ancestors of these two lineages diverged about 190 million yr ago (systematic and paleontological references in Garland [1994*a*]). Like most other lacertid lizards, *L. vivipara* is an active forager (references in Vitt and Pianka [1994]), whereas *S. occidentalis* (Tsuji et al. 1989) is a sit-and-wait forager. As well, its mode of locomotion is fairly different from that of either *S. occidentalis* or garter snakes.

Material and Methods

In July 1993, we captured 107 gravid female *Lacerta vivipara* at a study site in southern France (Mont Lozère, 44°30′ N, 3°45′ E). This population has been the subject of a long-term study since 1986, so all of the females were known individuals with unique toe clips (Clobert et al. 1994). At capture, we recorded snout-vent length (SVL), total length, and body mass. Dams were then maintained in a laboratory at the field site under standardized conditions until they gave birth (average rearing duration mean ± SD = 26.4 ± 6.42 d, range 5–37). Females were housed in plastic terraria with damp soil, a shelter constructed from one-half of a plastic drinking cup, and water ad lib. They were exposed to a natural photoperiod and to incandescent lamps for heat for 6 h per day. During this period, each dam was fed at one of three different rates (because they were also part of another experiment): one *Pyralis farinalis* (Lepidoptera) larva per day, one per week, or one per 2 wk. This difference in feeding rate had the potential to cause differences among dams, which would in turn affect their offspring, that is, an environmental maternal effect. Such differences among dams would inflate estimates of h^2 and of genetic correlations, which in the present study are based on partitioning variance within and among families of full siblings. Correlations of offspring phenotypes with feeding rate were therefore removed statistically prior to estimation of quantitative genetic parameters (see below).

Terraria were checked twice daily for birth. Each postpartum dam was weighed and then released at her capture site. Any hatchlings were measured (SVL, total length; tail length was determined by subtraction), weighed, and marked by toe clipping within 1 d of birth. Because of the small size of limbs at birth (cf. Tsuji et al. 1989), we could not measure leg length without harming hatchlings. Offspring sex was determined by counting the number of ventral scales, from photographs of each hatchling (Lecomte, Clobert, and Massot 1992). When 5 d old, juveniles were also released at the capture site of their mothers.

Measurement of Locomotor Performance

Sprint Speed. At 2 d of age, we measured maximal sprint speed of the offspring using standard techniques (see, e.g., Garland 1985; Huey et al. 1990). Lizards were chased along a racetrack equipped with photoreceptors at 0.10-m intervals. The racetrack was 1.1 m long, 0.05 m wide, and 0.15 m high, and had a cork substrate; for structural reason the racetrack had two small (1.5 cm width) wooden bars connecting the walls at their tops. Individuals were placed in front of the first photoreceptor, induced to run at apparently top speed by tapping their tails with a small stick (diameter 3 mm), and stimulated each time their speed slowed (range = 0–13 stimuli, mean ± SD = 4.2 ± 1.83, were required to chase individuals along the entire length of the track; see next paragraph). Each individual was raced twice in 1 d, with at least a 1-h rest between trials. We considered maximal speed as the fastest 0.2-m interval attained during either trial (Tsuji et al. 1989). One person conducted all speed trials. All trials were performed at 30°C, which is near the mean body temperature of *L. vivipara* when active in the field (Van Damme, Bauwens, and Verheyen 1990) but about 4°C below the optimal temperature for sprint performance of adult *L. vivipara* from a Belgian population (Bauwens et al., in press).

Sprint speed is generally considered to represent an organismal trait that integrates morphology, physiology, and potentially behavior (reviews in Garland [1994*a*, 1994*b*]; Garland and Losos [1994]). We were primarily interested in variation in apparent maximal sprint running speed as an indicator of underlying morphological and physiological factors. Therefore, in an attempt to reduce the effects of possible variation in inclination to run, we recorded the number of stimuli needed to induce each lizard to run the entire length of the racetrack and used this number as a covariate in statistical analyses (see below).

Endurance. Endurance was also measured according to standard techniques (Garland [1984, 1988, 1994*a,* 1994*b*]; references in Garland and Losos [1994]) by running lizards on a motorized treadmill with a rubberized belt moving at a low speed (0.15 km/h). Lizards were placed on the treadmill and motivated to walk by light tapping on the tail with a small paint brush (bristle area about 10 mm wide). Endurance was measured as the time until the individuals did not maintain belt speed in response to 10 consecutive taps given at a rate of 2–3 taps/s (Garland 1984, 1988, 1994*a*); these final taps were delivered with an index finger. We performed one trial on each of 2 consecutive days (days 3 and 4), and we used the longer trial as an indicator of maximum endurance capacity. One person conducted all endurance trials.

Data Analysis

Sprint speed and tail length were approximately normally distributed and were not transformed prior to statistical analyses. Endurance was positively skewed (as is commonly found in studies of snakes, lizards, and house mice: see, e.g., Garland 1988; Tsuji et al. 1989; Huey et al. 1990; Friedman, Garland, and Dohm 1992) and leptokurtic; however, a double logarithmic transformation approximated normality.

Quantitative genetic analyses were performed according to both the least-squares method (Falconer 1989) and restricted maximum likelihood (REML; Shaw 1987). The latter has several advantages over least-squares estimation; in particular, it provides reliable parameter estimates even with unbalanced designs and it allows statistical tests of significance of genetic correlations.

Resemblances among sibling lizards may arise from the effects of shared genes, from genetic and nongenetic maternal effects, or from influences of a common environment after hatching. Maternal or postnatal common-environment effects, if present, can inflate estimates of such quantitative genetic parameters as h^2 and genetic correlations. In an attempt to reduce maternal effects, we performed a stepwise multiple regression analysis of each variable (sprint speed, log-log endurance, tail length) on a set of possible covariates (dam mass at capture, dam mass after parturition, litter size, dam age, dam SVL, number of days dams spent in captivity prior to parturition, dam feeding treatment [using two dummy variables to identify the three feeding treatments], squared z-transformed dam age, squared z-transformed rearing duration: table 1) and computed residuals for each model using only significant ($P < 0.05$) covariates, except in cases where some linear terms were forced into the model because the corresponding squared term was also significant. Body size is another factor that may affect both tail length and locomotor performance (larger individuals generally are both faster and have higher

TABLE 1

Summary statistics of offspring and dam measurements

	Mean	SD	Minimum–Maximum	*N*
Offspring SVL (mm)	21.30	.872	17–23	537
Offspring body mass (g)	.189	.021	.086–.244	539
Dam SVL (mm)	65.29	3.277	58–74	107
Dam mass at capture (g)	5.27	.925	3.16–7.58	107
Dam mass after parturition (g)	3.06	.543	1.19–4.52	106
Dam age (yr)	2.87	1.282	2–10	107
Litter size (no. of eggs)	5.67	1.344	3–10	107

endurance: see, e.g., Garland [1984, 1985, 1988, 1994*a*]; Tsuji et al. [1989]; review in Garland and Losos [1994]). As we were primarily interested in measures of locomotor performances that represented individual differences in size-independent performance ability, and as offspring size may also be affected by maternal and common-environment effects, we also included offspring SVL and offspring mass as potential covariates in the multiple regression analyses (see Sinervo and Huey [1990] for an experimental study of size-independent performance). By removing the effects of size we may also have removed some genetic covariance between size and the dependent variable, for example, sprint speed, thus arriving at an underestimation of the magnitude of genetic effects on that trait (Garland 1988; Tsuji et al. 1989).

Finally, for sprint speed, we used two different regression models. In the first one we used the same covariates as for endurance. In the second one we also included number of stimuli and squared z-transformed number of stimuli as covariates, in an attempt to control for effects of variation in inclination to run. The residuals of the latter model should therefore correspond more to a "physiological" measure of speed. However, behavior, including responses to stimuli, can be seen as a "filter" between natural selection and performance (Garland 1994*b*). In other words, natural selection is likely to act on "realized" speed, the result of the interaction between the organismal physiological capacity and its particular behavior (cf. Bauwens et al., in press). Thus, our measure of speed uncorrected for stimuli might be more "ecologically relevant."

All quantitative analyses were then performed on the residuals of the stepwise regression. The residuals for each character were approximately normally distributed (fig. 1).

For purposes of the present analyses, we assumed that all offspring of a female are full siblings. No data are actually available on the *L. vivipara* mating system; however, even in the presence of multiple paternity, esti-

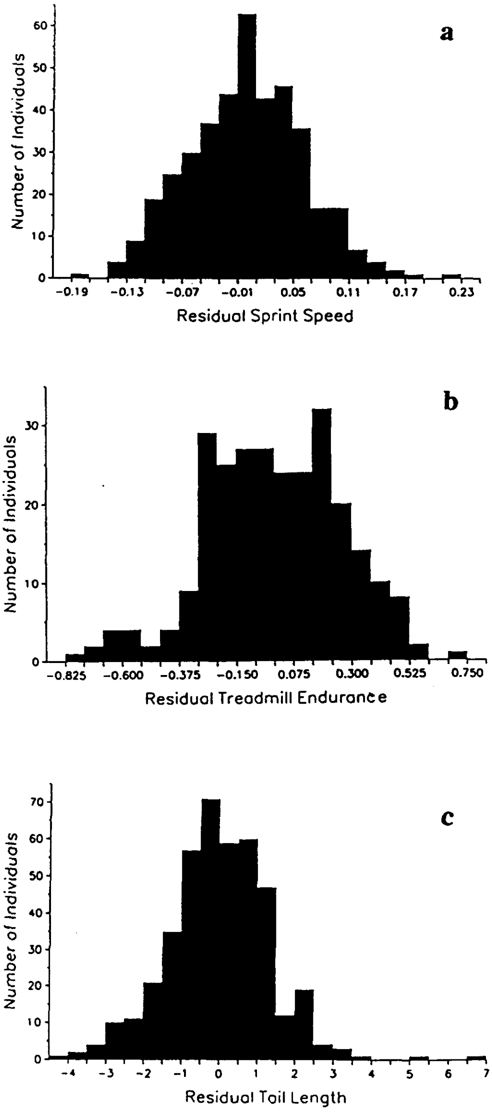

Fig. 1. Frequency distribution of the residuals computed from multiple regressions for speed (a), *endurance* (b), *and tail length* (c). *These residuals were used for estimates of quantitative genetic parameters.*

mates assuming all sibs to be full sibs are conservative, in the sense of underestimating genetic effects. Indeed, the presence of half-sib groups reduces the phenotypic resemblance among offspring within a family, given that their average relatedness is only 0.25, whereas full sibs share 50% of their genes on average, and h^2s and genetic correlations estimated on full-sib analyses are the among-family variance multiplied by the inverse of the relatedness within families.

We compared variability of traits by computing approximate coefficients of variation (CVs; Garland 1984, 1988; Tsuji et al. 1989). These CVs were computed by regressing each $\log_{10}$-transformed trait on any significant covariates and computing the standard deviation of residuals (multiplied by 2.3026 because traits were $\log_{10}$ rather than $\log_e$ transformed). Heterogeneity of variances among families was tested by Levene's test (references in Garland [1988]; Tsuji et al. [1989]). All descriptive statistics, Pearson product-moment correlations, ANOVAs, and multiple regressions have been performed with SAS (SAS 1990) or SPSS/PC+ (Norusis 1988).

Results

Repeatability of Locomotor Performance

A total of 513 and 275 individuals were tested for sprint speed and treadmill endurance, respectively. For logistical reasons, some individuals (127 for sprint speed; 24 for endurance) were tested only once. Repeatabilities were therefore computed for the subsets of 386 and 251 individuals. The Pearson product-moment correlation between sprint speed in trial 1 and trial 2 was 0.492 ($N = 386$, $P < 0.001$); for log-log endurance the value was 0.842 ($N = 251$, $P < 0.001$) (fig. 2).

A paired *t*-test indicated that sprint speed was slightly but significantly lower in trial 2 (mean in trial 1 ± SD = 0.349 ± 0.0791 m/s, mean in trial 2 = 0.336 ± 0.0832 m/s; $N = 386$, $t = 2.21$, $P = 0.028$). Endurance times in trial 2 were also significantly lower than in trial 1 (for raw values, mean time in trial 1 ± SD = 6.7 ± 6.85 min, mean time in trial 2 = 5.8 ± 6.46 min; $N = 251$, $t = 3.22$, $P = 0.001$; for log-log values, mean in trial 1 = 0.217 ± 0.0862, mean in trial 2 = 0.200 ± 0.0897: $t = 5.55$, $P < 0.001$). About two-thirds of the individuals (166 of 251) exhibited longer endurance times in trial 1. It was interesting that the best-performing individual ran for 49.4 min in trial 1 and 65.8 min in trial 2—a truly exceptional performer.

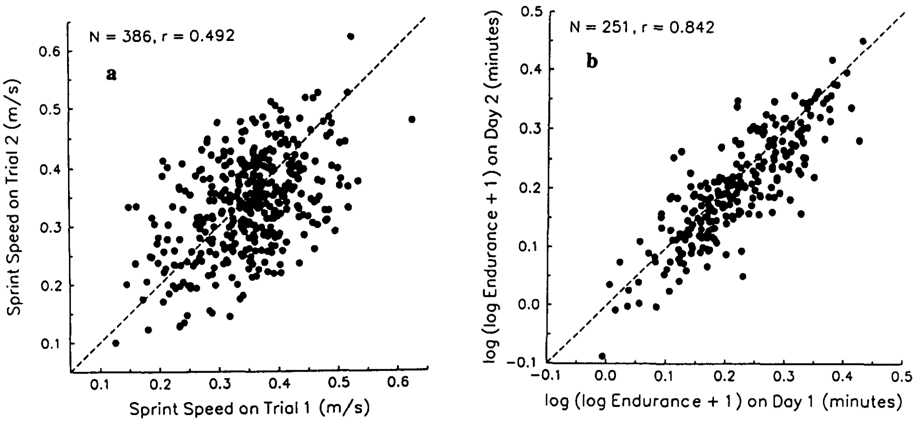

*Fig. 2. Repeatability of sprint speed (*a*) and endurance (*b*). Repeatability was measured as a Pearson product-moment correlation between the first trial and the second trial. The broken line has a slope of one, which would indicate perfect repeatability.*

Descriptive Statistics and Scaling

Table 2 shows the descriptive statistics of maximal speed, endurance, and tail length. Endurance was much more variable than the other characters, and this difference persisted after removing the effect of the covariates (table 2, "SD of Residuals").

We calculated coefficients of static allometry for the three traits (speed, endurance, and tail length) as the slope of the regression of log-transformed traits on log body mass. These coefficients (± SE) are, for speed, $\text{mass}^{0.51+0.092}$ ($r^2 = 0.057$, $P < 0.001$), for endurance, $\text{mass}^{1.59+0.409}$ ($r^2 = 0.052$, $P < 0.001$), and for tail length, $\text{mass}^{0.37+0.023}$ ($r^2 = 0.33$, $P < 0.001$).

TABLE 2

Descriptive statistics for locomotor performance and tail length

	Mean	SD	CV (%)	SD of Residuals[a]
Maximal speed (m/s)	.364	.0794	21.8	23.0
Endurance (min)	7.78	7.753	99.7	71.9
Tail length (mm)	23.30	1.673	7.2	2.8

[a] See text.

Variation among Families

All three characters varied significantly among families. When we examined the raw values, family membership explained 15% of the total interindividual variation in sprint speed, 37.6% in endurance, and 43.4% in tail length (one-way ANOVA, all $P < 0.001$).

Attempts to Reduce Maternal Effects and Computing Residuals

We used two different stepwise multiple regression models to compute speed residuals. When the number of stimuli was excluded as a covariate, offspring mass and the squared dam rearing duration were significant predictors of sprint speed (table 3). When the number of stimuli was added to the regression model, speed was significantly correlated with stimuli, squared number of stimuli, offspring body mass, sex, and squared dam rear-

TABLE 3
Stepwise multiple regression models used to compute residuals of locomotor performance and tail length

Dependent Variable	Independent Variable	Partial r^2	P
Speed[a]	Offspring mass	.073	<.001
	Dam rearing duration^2	.028	<.001
Speed	Stimuli	.327	<.001
	Stimuli^2	.009	.016
	Offspring mass	.043	<.001
	Sex	.014	.002
	Dam rearing duration^2	.007	.032
Endurance	Dam rearing duration	.080	<.001
	Offspring mass	.085	<.001
	Dam SVL	.036	.002
	Dam age	.019	.020
	Feeding treatment	.017	.029
Tail length	Offspring mass	.295	<.001
	Sex	.040	<.001
	Dam rearing duration	.027	<.001
	Dam mass at parturition	.017	.001

[a] This model did not include stimuli as a covariate.

ing duration (table 3). Log-log endurance times were significantly predicted by the number of days dams spent in the lab, body mass, dam SVL, dam age, and one of the dummy variables describing dam feeding treatment (table 3). Finally, tail length was correlated with body mass, sex, number of days dams spent in the lab, and dam mass at parturition (table 3).

Heritability

When we examined the residual characters, variation among families was only marginally significant for speed and nonsignificant for stimuli-corrected speed, whereas it was highly significant for endurance and for tail length (one-way ANOVA: speed $F_{99,306} = 1.308$, $P = 0.044$; stimuli-corrected speed $F_{99,306} = 1.172$, $P = 0.157$; endurance $F_{58,211} = 2.385$, $P < 0.001$; tail length $F_{98,320} = 2.443$, $P < 0.001$). The corresponding h^2s are reported in table 4, which also reports the REML estimates.

Levene's test for homogeneity of variance showed that for all characters variances were heterogeneous among families (all $P < 0.001$). This heteroscedasticity could reflect the action of major genes in the determination of these traits (Mitchell-Olds and Rutledge 1986). In other words, if a major-gene effect exists we should expect higher variance in the families with intermediate mean value than in the extreme families. To test for the existence of major-gene effects, we plotted the deviation of an individual trait value from its family mean value versus the corresponding family mean; we

TABLE 4

Heritabilities calculated by least-squares methods (ANOVA) and by REML estimation

Trait (No. of Families, No. of Individuals)	h^2		P	
	ANOVA	REML	ANOVA	REML
Speed (100, 406)	.141	.116	.044	>.10
Stimuli-corrected speed (100, 406)	.081	.046	.157	>.50
Endurance (59, 270)	.465	.461	<.001	<.001
Tail length (99, 419)	.509	.515	<.001	<.001

Note. Heritabilities are based on residuals from multiple regressions; see Material and Methods.

also performed a regression with a linear and a quadratic term. A significant quadratic term should indicate that families with intermediate values are more variable than are families with extreme values. The quadratic term was significant only for speed ($P = 0.006$); however, the variance explained by the quadratic term was only 1.9%.

Phenotypic, Genetic, and Environmental Correlations

Of all the phenotypic, genetic, and environmental correlations, only two were statistically significant: the phenotypic and the environmental correlations between speed and stimuli-corrected speed (table 5). Speed and endurance were not significantly correlated either phenotypically or genetically (fig. 3). However, note that the REML estimate was high ($r_G = -0.872$) (table 5). This high but nonsignificant correlation is very likely due to a large standard error of the estimate.

Discussion

Genetic Variability of Locomotor Performance

Our results indicate that both treadmill endurance and relative tail length have relatively high h^2s, whereas sprint speed showed a low and statistically insignificant h^2, at least when a measure of inclination to run was statistically removed. In almost all previous studies of reptiles, locomotor performances have also been shown to be heritable (Van Berkum and Tsuji 1987; Garland 1988; Brodie 1989, 1993; Tsuji et al. 1989; Jayne and Bennett 1990*a;* but see Bauwens et al. 1987). Tsuji et al. (1989) also reported tail length to be heritable in fence lizards.

The general finding of relatively high h^2s for aspects of locomotor performances in natural populations is somewhat surprising. Traits that are relatively closely related to Darwinian fitness are expected generally to have low additive genetic variation, as natural selection tends to reduce it through fixation of favorable alleles and elimination of unfavorable ones (Fisher 1930). The finding that life-history traits typically exhibit lower h^2s than do behavioral, physiological, or morphological traits agrees with this theory (Gustaffson 1986; Mousseau and Roff 1987; Roff and Mousseau 1987). Therefore, traits that have been exposed to strong selection pressures (as locomotor speed and endurance are generally thought to be) might also be expected to show relatively low h^2s (Garland 1994*b*). Another argument leading to an expectation of low h^2 for locomotor performances is that they are composite whole-organism traits, resulting from the interaction of many

TABLE 5

Phenotypic, genetic, and environmental correlations for residual speed, residual stimuli-corrected speed, residual endurance, and residual tail length

Trait and Correlation	Trait: Stimuli-Corrected Speed	Endurance	Tail Length
Speed:			
Phenotypic	.819*** (406)	.081 (208)	.046 (399)
Genetic	.740, .816 (100)	−.239, −.053 (56)	−.044, .021 (99)
Environmental	.832***, .824	.230, .139	.090, .062
Stimuli-corrected speed:			
Phenotypic		.014 (208)	.073 (399)
Genetic		−.872, −.208 (56)	−.033, .068 (99)
Environmental		.247, .077	.117, .088
Endurance:			
Phenotypic			−.014 (226)
Genetic			.108, −.011 (56)
Environmental			−.129, −.017

Note. Phenotypic correlations are Pearson product-moment correlations. Genetic correlations are REML estimates, followed by correlations among weight litter means (Arnold 1981). Environmental correlations are REML estimates, followed by least-squares estimates (Falconer 1989). Significance tests for genetic and environmental correlations were attempted only for the REML estimates, by comparing the likelihood of the full model with the likelihood of a model with the corresponding parameter constrained to be zero (Shaw 1987). Sample sizes are given in parentheses, as number of individuals or number of families.

*** $P < 0.001$.

lower-level traits (e.g., enzyme activities), and therefore subject to multiple sources of environmental variance (see Price and Schluter 1991).

Any or all of the foregoing considerations could account for the low h^2 observed for sprint speed. One direct consequence of this low genetic variation is that selection pressures acting on sprint speed should modify it only slowly, because the response to selection is the product of the selection differential times h^2 (see Introduction). Most of the among-individual phenotypic variance observed for sprint speed (CV = 21%) is, therefore, caused by environmental or nonadditive genetic factors. This interpretation is consistent with previous studies of this population of *Lacerta vivipara*, which

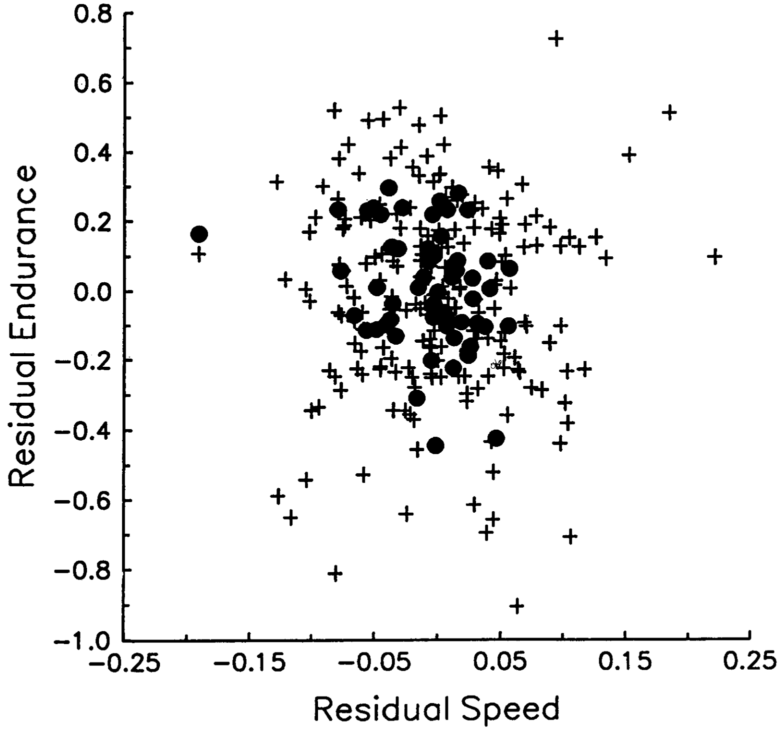

Fig. 3. Phenotypic correlation between residual stimuli-corrected speed and residual endurance (N = *208,* r = *0.081,* P > *0.20). Solid circles, family means* (N = *56,* r = *−0.208,* P > *0.10).*

showed that sprint speed responded significantly to the environment experienced by the mothers while they were held in the laboratory during their gestation (Sorci, Massot, and Clobert 1994; G. Sorci and J. Clobert, unpublished manuscript). Thus, sprint speed is a phenotypically plastic trait. It is interesting that sprint speed has also been reported not to be heritable in another population of *L. vivipara* from northern Belgium (Bauwens et al. 1987).

Endurance showed a relatively high h^2. Does this mean that past selection acting on this trait was not as strong as expected? This explanation is possible, but so are others. Although selection tends to reduce additive genetic variance, mutation tends to restore it. As noted before, locomotor performances are composite traits that potentially can accumulate mutations occurring in all loci that affect a large number of lower-level morphological and biochemical traits (as well as behavior, if inclination to run accounts for some of the variation, as in the case of speed in the present study and Tsuji et al. [1989]). Therefore, if selection pressures are relatively weak and the overall mutation rate is high, we should expect the mutation-selection balance to be reached at relatively high values of h^2 (Lande 1975; Lynch 1985). Another possibility is that endurance is negatively genetically correlated with one or more life-history traits, such as growth rate. In this case, if both traits are under strong directional selection, then at equilibrium they may be maintained in a polymorphic compromise, because selection favoring the increase of one trait will cause a decrease in the correlated character (see, e.g., Stearns 1992). However, the only data available on this topic seem to show positive or no correlation between locomotor performances and survivorship in the field, which is one component of fitness (Jayne and Bennett 1990*b;* Brodie 1992).

Finally, we note that as our study was based on full-sib data, we were unable to estimate either a true narrow-sense or a "broad-sense" heritability (see Brodie and Garland 1993; Garland 1994*b*). As noted before, narrow-sense heritability is the ratio of the additive genetic variance to the phenotypic variance. Full-sib analysis allows the estimate of the among-family component of variance, and twice this value (because of the paternal contribution to the offspring gene pool) estimates not only the additive genetic variance but also half of the dominance variance plus half of the epistatic variance plus twice the common family environmental effects (Falconer 1989). Measuring the characters soon after birth (2–4 d of age) and statistically factoring out some indicators of maternal condition and environment should have reduced the contribution of common family effects to our estimates of quantitative genetic parameters. Indeed, the among-family components of variance were lower for the residual values than they were for the raw values, and this was true for all the traits (see also Garland 1988; Tsuji et al. 1989). However, we have no information on the possible magnitude of dominance or epistatic genetic effects.

Trade-off between Speed and Endurance

The phenotypic correlation between residual stimuli-corrected speed and endurance was 0.014; thus, individual lizards showed no tendency either to be fast or to have high endurance. The genetic correlation between residual stimuli-corrected speed and endurance was negative. The REML estimate ($r_G = -0.872$) was high and quite different from the least-squares estimate ($r_G = -0.208$). Neither of these correlations was statistically significant. Thus, speed and endurance do not tend to run together in families. However, note that statistical significance of genetic correlations is difficult to demonstrate (low statistical power), and could require very large sample sizes.

Irrespective of the issue of possibly low statistical power, our results are consistent with all those previously reported, as they also failed to find a trade-off between locomotor performances. Specifically, Garland (1988) found a significant positive genetic correlation between speed and endurance in a population of *Thamnophis sirtalis* ($r_G = 0.588$); Tsuji et al. (1989) found no genetic correlation between the two traits in a *Sceloporus occidentalis* population ($r_G = -0.039$); Brodie (1993) reported positive genetic correlations between speed and distance crawling capacity (treadmill endurance was not measured) in two populations of *Thamnophis ordinoides;* and Jayne and Bennett (1990*a*) reported a positive phenotypic correlation between speed and endurance in the same population of *T. sirtalis* studied by Garland (1988, 1994*b*).

We found no significant phenotypic, genetic, or environmental correlations between locomotor performance and tail length. These results are generally consistent with those of Tsuji et al. (1989), although that study did find a significant positive phenotypic correlation ($r = 0.218$) between endurance and tail length in a population of *S. occidentalis.*

Why have all existing quantitative genetic studies of reptiles failed to find evidence for a trade-off between speed and endurance? Several explanations are possible. First, dams coming from "good" environments (e.g., experiencing good nutritional conditions), could have produced offspring with both high speed and high endurance, leading to an overriding positive correlation between the two characters. The possible mechanistic bases for such a hypothetical connection are unknown, but cannot be related to body size alone, because residuals from regressions on body size have been analyzed in all studies to date. In any case, similar arguments have been suggested to explain positive correlations between life-history traits, such as current versus future fecundity (Reznick 1985; Rose 1991; Stearns 1992). However, by attempting to statistically remove the effects of maternal condition and one aspect of the environment (feeding treatment), we should have restricted the possibility that environmental effects could bias the quantitative genetic analyses. A second possible explanation is that muscle mass, which has not been measured in any study, might positively affect both speed and endurance, thus masking any effect of relative proportions of fiber types.

Garland (1988) presented another argument suggesting that a trade-off between speed and endurance should exist: the case of human athletes. World-class sprinters and marathoners have both different fiber types and locomotor performance abilities. These world-class athletes, however, may not be a representative subsample of the human population. Thus, Garland (1994*b*) suggested that if for the whole human population speed and endurance are positively correlated, and we consider only the individuals with the highest values for one character or the other (e.g., Olympic sprinters and marathoners), then we can, indeed, find that the two traits are negatively correlated in the highly selected subset of individuals.

Is Lack of Trade-off a General Feature of Squamates?

Before answering the question of generality, we must consider how natural selection can promote the appearance of negative genetic correlations. Antagonistic pleiotropy is generally assumed to be the most common mechanism leading to negative genetic correlations. Antagonistic pleiotropy refers to genes that have positive effects on one component of fitness but negative effects on another (Williams 1957; Rose 1991). If we imagine a distribution of allelic effects on two major components of fitness, then we should expect that all the alleles having positive effects on both components of fitness will tend to be fixed by natural selection. In contrast, those alleles with deleterious effects on both should be counterselected and disappear from the population, except for recurrent mutation. This process should, therefore, maintain genetic variation for alleles with an antagonistic effect on the two components of fitness (Rose 1991; Roff 1992). The net result is a negative genetic correlation between the two traits.

One implicit assumption in the antagonistic pleiotropy model is that the trade-off involves traits under strong directional selection. Therefore, we should expect that when strong directional selection has generally favored the highest values of both speed and endurance, these characters will come to be negatively correlated.

With respect to the foregoing arguments, we note that *L. vivipara, S. occidentalis,* and *T. sirtalis*—the three species showing no trade-off between speed and endurance (Garland 1988; Tsuji et al. 1989; this study)—all have relatively low endurance, as compared with many other species of squamates (Garland [1994*a*]; references on snakes in Garland and Losos [1994]). As well, none of these species is an unusually fast sprinter (Garland and Losos 1994; T. Garland, unpublished data). Therefore, we need to investigate the relationship between speed and endurance in species that have been pushed by natural selection to some extreme of locomotor abilities, for they should be more likely to show a trade-off. Good candidates would be some species of the lizard genus *Cnemidophorus,* which have both high speed and high endurance (Garland 1994*a*).

Finally, it could be possible that trade-offs are more evident at the interspecific level, which could be studied by comparing closely related taxa. Indeed, Huey et al. (1984) found that, within lacertid lizards, species with high endurance have low sprint speed, whereas those with high sprint speed have limited endurance. To fully explore this issue, however, we need more comparisons at the within-family level of other squamate groups.

Acknowledgments

We are grateful to the Parc National des Cévennes and the Office National des Forêts for providing facilities during our fieldwork. This research was supported by a grant from the Centre National de la Recherche Scientifique (CNRS—PIREN), and by the Ministère de l'Environnement (SRETIE) to J.C. and G.S., by a grant from the Conservation Biology and Sustainable Development Program at University of Wisconsin—Madison to J.G.S., and by a grant from the National Science Foundation (IBN-9157268; Presidential Young Investigator Award) to T.G.

Literature Cited

ARNOLD, S. J. 1981. Behavioral variation in natural populations. I. Phenotypic, genetic and environmental correlations between chemoreceptive responses to prey in the garter snake, *Thamnophis elegans.* Evolution 35:489–509.

———. 1987. Genetic correlation and the evolution of physiology. Pages 189–215 in M. E. FEDER, A. F. BENNETT, W. W. BURGGREN, and R. B. HUEY, eds. New directions in ecological physiology. Cambridge University Press, Cambridge.

———. 1992. Constraints on phenotypic evolution. Am. Nat. 140:S85–S107.

BAUWENS, D., T. GARLAND, JR., A. CASTILLA, and R. VAN DAMME. In press. Evolution of sprint speed in lacertid lizards: morphological, physiological, and behavioral covariation. Evolution.

BAUWENS, D., R. VAN DAMME, D. VANDERSTIGHELEN, C. THOEN, D. SANDERS, H. VAN WEZEL, and R. F. VERHEYEN. 1987. Individuality in common lizard (*Lacerta vivipara*): a provisional review. Pages 55–58 in J. J. VAN GELDER, H. STRIJBOSCH, and P. J. M. BERGERS, eds. Proceedings of the 4th ordinary general meeting of the Societas Europea Herpetologica. Faculty of Sciences, Nijmegen, The Netherlands.

BOAKE, C. R. B., ed. 1994. Quantitative genetic studies of behavioral evolution. University of Chicago Press, Chicago. 390 pp.

BOUCHARD, C., and G. LORTIE. 1984. Heredity and endurance performance. Sports Med. 1:38–64.

BOUCHARD, C., and R. M. MALINA. 1983*a*. Genetics for the sport scientist: selected methodological considerations. Exerc. Sport Sci. Rev. 11:274–305.

———. 1983*b*. Genetics of physiological fitness and motor performance. Exerc. Sport Sci. Rev. 11:306–339.

BRODIE, E. D., III. 1989. Genetic correlations between morphology and antipredator behaviour in natural populations of the garter snake *Thamnophis ordinoides.* Nature 342:542–543.

———. 1992. Correlational selection for color pattern and antipredator behavior in the garter snake *Thamnophis ordinoides*. Evolution 46:1284–1298.

———. 1993. Homogeneity of the genetic variance-covariance matrix for antipredator traits in two natural populations of the garter snake *Thamnophis ordinoides*. Evolution 47:844–854.

BRODIE, E. D., III., and T. GARLAND, JR. 1993. Quantitative genetics of snake populations. Pages 315–362 in R. A. SEIGEL and J. T. COLLINS, eds. Snakes: ecology and behavior. McGraw-Hill, New York.

CALOW, P. 1987. Evolutionary physiological ecology. Cambridge University Press, Cambridge. 239 pp.

CLOBERT, J., M. MASSOT, J. LECOMTE, G. SORCI, M. DE FRAIPONT, and R. BARBAULT. 1994. Determinants of dispersal behavior: the common lizard as a case study. Pages 183–206 in L. J. VITT and E. R. PIANKA, eds. Lizard ecology: historical and experimental perspectives. Princeton University Press, Princeton, N.J.

ESBJÖRNSSON, M., C. SYLVEN, I. HOLM, and E. JANSSON. 1993. Fast twitch fibres may predict anaerobic performance in both females and males. Int. J. Sports Med. 14: 257–263.

FALCONER, D. S. 1989. Introduction to quantitative genetics. 3d ed. Longman, London. 438 pp.

FISHER, R. A. 1930. The genetical theory of natural selection. Clarendon, Oxford.

FRIEDMAN, W. A., T. GARLAND, JR., and M. R. DOHM. 1992. Individual variation in locomotor behavior and maximal oxygen consumption in mice. Physiol. Behav. 52:97–104.

GARLAND, T., JR. 1984. Physiological correlates of locomotory performances in a lizard: an allometric approach. Am. J. Physiol. (Reg. Integr. Comp. Physiol. 16) 247:R806–R815.

———. 1985. Ontogenetic and individual variation in size, shape, and speed in the Australian agamid lizard *Amphibolurus nuchalis*. J. Zool. Lond. 207A:425–439.

———. 1988. Genetic basis of activity metabolism. I. Inheritance of speed, stamina, and antipredator displays in the garter snake *Thamnophis sirtalis*. Evolution 42: 335–350.

———. 1994*a*. Phylogenetic analyses of lizard endurance capacity in relation to body size and body temperature. Pages 237–259 in L. J. VITT and E. R. PIANKA, eds. Lizard ecology: historical and experimental perspectives. Princeton University Press, Princeton, N.J.

———. 1994*b*. Quantitative genetics of locomotor behavior and physiology in a garter snake. Pages 251–277 in C. R. B. BOAKE, ed. Quantitative genetic studies of behavioral evolution. University of Chicago Press, Chicago.

GARLAND, T., JR., and S. C. ADOLPH. 1994. Why not to do two-species comparative studies: limitations on inferring adaptation. Physiol. Zool. 67:797–828.

GARLAND, T., JR., and P. A. CARTER. 1994. Evolutionary physiology. Annu. Rev. Physiol. 56:579–621.

GARLAND, T., JR., F. GEISER, and R. V. BAUDINETTE. 1988. Comparative locomotor performance of marsupial and placental mammals. J. Zool. Lond. 215:505–522.

GARLAND, T., JR., and J. B. LOSOS. 1994. Ecological morphology of locomotor performance in squamate reptiles. Pages 240–302 in P. C. WAINWRIGHT and S. M. REILLY, eds. Ecological morphology: integrative organismal biology. University of Chicago Press, Chicago.

Gleeson, T. T., and J. M. Harrison. 1986. Reptilian skeletal muscle: fiber-type composition and enzymatic profile in the lizard, *Iguana iguana.* Copeia 1986:761–764.

Gustaffson, L. 1986. Lifetime reproductive success and heritabilities: empirical support for Fisher's fundamental theorem. Am. Nat. 128:761–764.

Harvey, P. H., and M. D. Pagel. 1991. The comparative method in evolutionary biology. Oxford University Press, Oxford. 239 pp.

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., A. E. Dunham, K. L. Overall, and R. A. Newman. 1990. Variation in locomotor performance in demographically known populations of the lizard *Sceloporus merriami.* Physiol. Zool. 63:845–872.

Jayne, B. C., and A. F. Bennett. 1990*a.* Scaling of speed and endurance in garter snakes: a comparison of cross-sectional and longitudinal allometries. J. Zool. Lond. 220:257–277.

———. 1990*b.* Selection on locomotor performance capacity in a natural population of garter snakes. Evolution 44:1204–1229.

Lande, R. 1975. The maintenance of genetic variation by mutation in a polygenic character with linked loci. Genet. Res. 26:221–235.

———. 1979. Quantitative genetic analysis of multivariate evolution, applied to brain: body size allometry. Evolution 33:402–416.

Lande, R., and S. J. Arnold. 1983. The measurement of selection on correlated characters. Evolution 37:1210–1226.

Lecomte, J., J. Clobert, and M. Massot. 1992. Sex identification in juveniles *Lacerta vivipara.* Amphibia-Reptilia 13:21–25.

Leroi, A. M., M. R. Rose, and G. V. Lauder. 1994. What does the comparative method reveal about adaptation? Am. Nat. 143:381–402.

Lynch, M. J. 1985. Spontaneous mutation for life-history characters in an obligate parthenogen. Evolution 39:804–818.

Mitchell-Olds, T., and J. J. Rutledge. 1986. Quantitative genetics in natural plant populations: a review of the theory. Am. Nat. 127:379–402.

Moore, A. J., and R. B. Boake. 1994. Optimality and evolutionary genetics: complementary procedures for evolutionary analysis in behavioural ecology. Trends Ecol. Evol. 9:69–72.

Mousseau, T. A., and D. A. Roff. 1987. Natural selection and the heritability of fitness components. Heredity 59:181–197.

Nakamura, T., S. Masui, M. Wada, H. Katoh, H. Mikami, and S. Katsuta. 1993. Heredity of muscle fibre composition estimated from selection experiment in rats. Eur. J. Appl. Physiol. Occup. Physiol. 66:85–89.

Norusis, M. J. 1988. SPSS/PC+ version 2.0 for the IBM PC/XT/AT. SPSS, Chicago.

Orzack, S. H., and E. Sober. 1994. Optimality models and the test of adaptationism. Am. Nat. 143:361–380.

Price, T. D., and D. Schluter. 1991. On the low heritability of the life-history traits. Evolution 45:853–861.

Reznick, D. N. 1985. Costs of reproduction: an evaluation of the empirical evidence. Oikos 44:257–267.