Several questions, however, remain open. It will be interesting to learn whether the magnetic compass of *C. hottentotus* is an inclination compass as reported for birds [18], and whether the mole-rats, which are virtually blind and have to orient in absolute darkness underground, can also use the magnetic field in total darkness. The latter will be very important for all considerations on magnetic perception [19–21].

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Heritability of locomotor performance and its correlates in a natural population

T. Garland Jr*, [a], A. F. Bennett [b] and C. B. Daniels [c]

[a] *Dept of Zoology, University of Wisconsin, Madison (Wisconsin 53706, USA),* [b] *Dept of Ecology and Evolutionary Biology, University of California, Irvine (California 92717, USA), and* [c] *Dept of Physiology, School of Medicine, Flinders University, Bedford Park, S.A. 5042 (Australia)*
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Summary. Locomotor capacities and their physiological bases are thought to be of considerable selective importance in natural populations. Within this functional complex, organismal performance traits (e.g., speed, stamina) are expected to be of more direct selective importance than their suborganismal determinants (e.g., heart size). Quantitative genetics theory predicts that traits of greater selective importance should generally have lower heritabilities at equilibrium. Contrary to these expectations, we report that organismal performance traits had the highest heritabilities in a natural population of garter snakes.
Key words. Evolution; genetics; heritability; locomotion; physiology.

Locomotor abilities set ultimate limits within which normal behavior must be accomplished; in turn, locomotor abilities depend on a large number of underlying physiological, morphological, and biochemical traits. The hierarchical nature of these relationships suggests that some components of activity metabolism will be of more direct selective importance than others. In particular, such whole-animal performance traits as maximal speed or stamina are presumed to be of greater selective importance than are lower-level traits [1–4].

Only traits with heritabilities greater than zero can evolve genetically in response to selection. Heritability (h^2 = ratio of additive genetic variance to total phenotypic variance [5]) is often seen as representing a balance between the rate of polygenic mutation, adding new genetic variance to a population each generation, and the strength of selection, tending to reduce genetic variance [6]. Theory indicates that, at equilibrium, traits that have been subject to strong selection will exhibit relatively little additive genetic variance and low heritabilities [7, 8]. Empirical evidence supports this prediction: major components of fitness (e.g., length of reproductive lifespan, fecundity) generally exhibit lower heritabilities than do morphological traits, with behavioral and physiological traits exhibiting intermediate values [5, 9, 10, 11].

Aside from major components of fitness versus other traits, it is not known whether the inverse correlation between strength of selection and heritability holds for traits within a functional complex. We therefore measured heritabilities of various components of activity metabolism, a functional complex of considerable behavioral and ecological relevance. Because locomotor performance capacities are expected to have more direct effects on fitness than do lower-level traits (e.g., tissue

oxidative or glycolytic capacities[1-4]), the former would be predicted to exhibit lower heritabilities.

Materials and methods

Gravid garter snakes (*Thamnophis sirtalis fitchi*) were captured near Eagle Lake, Lassen Co., CA, then returned to the laboratory for maintenance under standard conditions for approximately one month prior to parturition. Common family environments were disrupted within hours of birth by housing newborns individually in plastic cages placed randomly in an environmental chamber. We measured antipredator behavior[12,13], speed, endurance, maximal oxygen consumption, heart (ventricle) mass, liver mass, blood hemoglobin concentration, and maximal activities of citrate synthase (index of tissue oxidative capacity[14-16]) and pyruvate kinase (index of tissue anaerobic glycolytic capacity[14-16]) in liver, ventricle, and skeletal muscle in six or fewer presumed full-sibling offspring[12,13] from each of 45–46 dams, using standard techniques. Maximal burst crawling speed (fastest 0.5 m along a 2.0-m photocell-timed racetrack[12]) and endurance at a low speed (0.4 km/h on a motorized treadmill[12]) were chosen to bracket the range of locomotor activities engaged in by free-living garter snakes. Maximal oxygen consumption ($\dot{V}_{O_2max}$[15-18]) sets an upper limit to the intensity of locomotion that can be supported aerobically, and is expected to correlate with treadmill endurance (but not with burst speed). Suborganismal characters were chosen as likely determinants of locomotor performance or $\dot{V}_{O_2max}$, based on previous studies[14-17]. For example, hemoglobin concentration, as an indicator of blood oxygen carrying capacity, and ventricle mass, as a determinant of stroke volume, are likely functional correlates of $\dot{V}_{O_2max}$.

In an attempt to reduce non-genetic maternal effects[12,19], we used multiple regressions to remove variation related to body size, dam size, litter size, and age at time of testing, as well as assay batch for enzyme activities. Residuals from multiple regression equations were then used for genetic analyses[12,19]. Heritabilities were calculated as twice the among-family component of variance estimated from one-way analyses of variance[5]. (For comparison, we also calculated heritabilities based on the raw characters, i.e., before computing residuals. As expected, heritabilities estimated for raw characters were higher than those estimated for residuals [in every case], but the rank order of heritabilities was unchanged.)

One factor that may complicate comparisons of heritabilities is possible differences in the repeatabilities of traits. Repeatability sets an upper limit to heritability; if individual differences in a character cannot be measured reproducibly, then the trait (as measured) cannot be heritable[5]. Day-to-day repeatabilities for the four whole-animal measures were: antipredator display, 0.67; maximal crawling speed, 0.80; treadmill endurance, 0.69; $\dot{V}_{O_2max}$, 0.88. Strictly comparable repeatabilities for the other traits are not available. Some simply cannot be measured more than once; for example, the heart and liver can be dissected free and weighed but a single time from a given individual. For hemoglobin concentration and enzyme activities, values analyzed were means of duplicate assays within 10%. In any case, we believe our comparisons of heritabilities are both appropriate and relevant for consideration of how different types of traits – as defined and measured routinely by workers in different fields – may evolve.

Results and discussion

Estimated heritabilities for the residual characters ranged from 0.82 for $\dot{V}_{O_2max}$ and 0.70 for treadmill endurance to 0.08 and 0.01 for citrate synthase activity in skeletal muscle and heart, respectively (table 1). In general, organismal performance characters (speed, endurance, $\dot{V}_{O_2max}$) exhibited the highest heritabilities. Antipredator behavior showed an intermediate heritability of 0.42. One-way ANOVA comparing heritabilities for organismal performance (N = 3), morphology (N = 3), and biochemistry (N = 6) indicates significant heterogeneity among mean heritabilities for these groupings ($F = 9.28$, $p = 0.0065$). Because our heritability estimates are based on families of full-siblings, they may be inflated by dominance, common family environment, and maternal effects, and should be considered as upper limits to narrow-sense heritabilities[5,12,13]. However, we see no obvious reason that such factors should be more important for organismal performances than for suborganismal correlates, so our comparisons of relative heritabilities should be sound. Moreover, we probably reduced non-genetic maternal effects greatly by analyzing residuals from multiple regressions (e.g., among-family variation due to differences in dam size was removed statistically[12]).

Phenotypic correlations among residual characters were generally low (table 2). Speed, endurance, and antipredator behavior were significantly positively intercorrelated, as discussed previously[12]. As predicted, maximal oxygen consumption was positively correlated with treadmill endurance, but not with burst speed. Some lower-level traits were significant predictors of organismal performance. Using the residual characters in multiple regression analyses indicated that: 1) liver mass and (per gram) liver citrate synthase activity together explained small but significant amounts of the variation in burst speed (multiple $r^2 = 4.2\%$, $p = 0.0069$); and 2) heart size and skeletal muscle pyruvate kinase activity together explained 10.8% of the variation in $\dot{V}_{O_2max}$ ($p < 0.0001$). Individual variation in antipredator behavior was uncorrelated with $\dot{V}_{O_2max}$ or with any suborganismal character. Genetic correlations, as estimated by correlations among weighted litter means[12], also tended to be low (table 2). Only those between speed and endurance, and between $\dot{V}_{O_2max}$ and heart size, were statistically significant ($p < 0.05$ by restricted maximum likelihood tests[12]). The significantly positive genetic correlation between speed

Table 1. Estimated broad-sense heritabilities of various traits in a population of garter snakes

Character (# families, # individuals)	h^2 and 95% confidence interval	P
Behavior		
Antipredator display (46,249)	0.19 < 0.41 < 0.71	< 0.0001
Organismal performance		
Maximal crawling speed (46,249)	0.33 < 0.58 < 0.88	< 0.0001
Treadmill endurance (46,249)	0.44 < 0.70 < 1.00	< 0.0001
$\dot{V}_{O_2max}$ (45,245)	0.57 < 0.84 < 1.14	< 0.0001
Mean = 0.71		
Morphology		
Hemoglobin (45,244)	0.38 < 0.63 < 0.94	< 0.0001
Ventricle mass (45,244)	0.19 < 0.41 < 0.70	< 0.0001
Liver mass (45,245)	0.36 < 0.61 < 0.91	< 0.0001
Mean = 0.55		
Biochemistry		
Liver citrate synthase (45,242)	0.02 < 0.21 < 0.50	0.013
Liver pyruvate kinase (45,242)	0.32 < 0.58 < 0.90	< 0.0001
Ventricle citrate synthase (45,241)	− 0.14 < 0.01 < 0.26	0.437
Ventricle pyruvate kinase (45,242)	0.05 < 0.26 < 0.56	0.005
Muscle citrate synthase (45,244)	− 0.08 < 0.09 < 0.34	0.169
Muscle pyruvate kinase (45,242)	0.01 < 0.19 < 0.46	0.016
Mean = 0.22		

95% confidence intervals are from Bulmer's (1980, p. 84) algorithm[31].

Table 2. Phenotypic correlations (upper) and correlations among weighted litter means

	Speed	Endur	$\dot{V}_{O_2max}$	Hb	Heart	Liver	Liver CS	Liver PK	Ventricle CS	Ventricle PK	Muscle CS	Muscle PK
Behavior	**0.19**	**0.20**	0.07	− 0.07	0.06	0.05	− 0.02	0.11	− 0.09	− 0.10	− 0.09	0.03
	0.31	0.23	0.01	− 0.16	0.05	0.10	0.27	0.17	− 0.22	− 0.13	− 0.14	− 0.06
Speed		**0.36**	0.02	0.06	− 0.12	− 0.15	0.13	0.03	0.04	− 0.02	0.03	0.10
		0.49	− 0.09	− 0.09	− 0.24	− 0.19	0.14	0.24	− 0.14	− 0.25	− 0.02	0.10
Endurance			**0.18**	− 0.03	− 0.02	− 0.04	0.12	− 0.09	− 0.01	− 0.08	0.11	0.13
			0.13	− 0.20	− 0.09	− 0.08	− 0.02	− 0.00	− 0.16	− 0.23	0.26	0.06
$\dot{V}_{O_2max}$				− 0.01	**0.27**	0.14	0.08	− 0.10	0.00	0.04	0.12	**0.22**
				− 0.05	**0.47**	0.28	0.07	− 0.17	− 0.00	0.03	0.05	0.27
Hb					0.01	**0.24**	0.15	0.03	0.04	− 0.02	0.15	**0.28**
					− 0.17	0.34	0.15	0.08	0.13	− 0.20	0.21	0.29
Ventricle						**0.20**	0.02	− 0.10	**− 0.33**	**− 0.19**	0.06	0.13
						0.26	0.08	− 0.18	0.01	0.05	− 0.03	− 0.01
Liver							0.09	− 0.14	0.02	− 0.12	− 0.08	0.15
							0.09	− 0.07	0.05	− 0.26	− 0.10	0.11
Liver CS								**− 0.31**	0.10	0.06	0.13	0.10
								− 0.19	0.05	0.04	− 0.01	− 0.07
Liver PK									− 0.09	− 0.11	− 0.03	− 0.02
									− 0.03	− 0.31	0.03	0.02
Heart CS										**0.56**	− 0.05	− 0.02
										0.35	0.04	− 0.10
Heart PK											− 0.11	− 0.05
											− 0.06	− 0.10
Muscle CS												**0.46**
												0.34

Significant correlations are in boldface.

and endurance implies no necessary evolutionary trade-off, and is somewhat surprising[12,20]. As compared with published heritability estimates for other vertebrates, our values do not appear unusual. A heritability of 0.59 for sprint speeds of hatchling lizards[21] is virtually identical to our value (0.58). Estimates of heritabilities for racing performance in horses and greyhounds also are in this range[12,22,23]. The heritability of antipredator behavior is very similar in *Thamnophis sirtalis* (0.42; table 1) and *Thamnophis radix* (0.41[13]). Human heritability estimates vary widely for $\dot{V}_{O_2max}$, range from 0.3 to 0.7 for left ventricular volume, and are low and often non-significant for muscle enzyme activities[19,24]. Heritabilities for aerobic and anaerobic enzyme activities in liver, heart, and skeletal muscle range from 0.00 to 0.50 for mice[25]. Relatively high heritabilities for organismal performance traits, as compared with suborganismal traits, suggest that the former have not been under relatively stronger selection. This seems contrary to expectations that whole-animal performance traits generally will be more important determinants of Darwinian fitness than are lower-level traits. What may account for the apparent discrepancy between theory and observation? We suggest several possibilities.

First, perhaps behavior often acts as a 'filter', shielding locomotor capacities from the direct effects of selection. For example, snakes confronted with a particular predator might remain motionless, rather than crawling away at top speed. Such behavior could obviate the selective importance of variation in burst speed. Consistent with this view, antipredator behavior was less heritable than the three organismal performance traits (table 1; see also reference 10).

Second, some theoretical [26] and empirical [10, 27, 28] studies demonstrate that high heritabilities can be maintained in natural populations, even for characters thought to be under relatively strong selection. Moreover, the particular form of selection acting on a trait may have important consequences for the maintenance of genetic variation. Selection on organismal performance traits is probably directional – for higher performance – in most cases. In fact, separate studies indicate that individual differences in locomotor performance are significantly positively correlated with survival in this population of snakes [29], suggesting that locomotor performance is subject to directional natural selection at present. No information is presently available concerning selection acting on suborganismal traits in this population, but it is often presumed that such traits as enzyme activities are more likely to be routinely under stabilizing rather than directional selection.

Finally, it is important to be mindful that natural populations are not always at genetic equilibrium [30]. The general environment of this garter snake population has been altered by logging, cattle ranging, and fire management during the past hundred years of settlement. Only 20–25 generations of snakes have been produced in that time.

It also is of interest to ask why enzyme activities exhibit such low heritabilities. Perhaps such traits as tissue oxidative capacities (as indexed by citrate synthase activity), although only weakly correlated with any one organismal trait, nevertheless correlate with many organismal functions (e.g., development, growth, metabolic rate and energy requirements). Thus, the sum total of selection impinging on suborganismal traits through multiple pathways might be strong, leading to low heritabilities. Presumably, selection pressures on such fundamental organismic traits as development are less likely to change in relation to short-term fluctuations in ecological conditions.

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* To whom all correspondence should be addressed.

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