Laboratory endurance capacity predicts variation in field locomotor behaviour among lizard species

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I measured locomotor endurance capacities of lizards on a motorized treadmill in the laboratory and compared average values for different species with quantitative measures of their movement in the field (percentage of time moving, $N=15$ species; moves/min, $N=13$; daily movement distance, $N=11$). I hypothesized that endurance would be positively related to all three movement indices. Relationships between log endurance and log movement were computed as conventional Pearson product–moment correlations and as the equivalent with phylogenetically independent contrasts. Endurance was significantly positively related to both the percentage of time moving and the daily movement distance. This is the first study to demonstrate such relationships with phylogenetically based statistical methods. These results suggest that endurance capacities of lizards are coadapted with their typical locomotor behaviour.

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Cross-species comparisons can provide important information about evolutionary patterns and processes (Harvey & Pagel 1991) and have a long history in animal behaviour (Hailman 1998). In particular, correlations between phenotypic traits and ecological or environmental variables provide evidence of adaptation; that is, that natural selection has played a role in causing the phenotypic differences among species (Garland & Adolph 1994; Doughty 1996). In addition to adaptation of single traits, different aspects of the phenotype are generally expected to show coadaptation. For example, species that show high movement rates should have high stamina, whereas those that sprint frequently should be able to attain high maximal speeds (Huey et al. 1984; Hertz et al. 1988; Irschick & Losos 1990; Losos 1990a, b; Pough & Taigen 1990; Pough et al. 1992; Garland 1993, 1994; Perry 1999).

Ecological and evolutionary physiologists and morphologists have provided many examples of cross-species correlations between morphology or physiology on the one hand and behaviour or ecology on the other (Feder et al. 1987; Pough et al. 1992; Wainwright & Reilly 1994), thus providing evidence of evolutionary adaptation. Traditionally, most studies have involved morphological or physiological traits at levels below the whole animal, such as limb proportions, bill dimensions, blood characteristics or enzyme activities. A weakness of these studies is that they neglect the crucial intermediate phenotype of

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maximal whole-animal performance abilities (Arnold 1983; Pough 1989). Hence, many recent studies have attempted to include direct measures of organismal performance (e.g. Jayne & Ellis 1998). Theoretically, measures of organismal performance should be more direct targets of natural selection and hence should correlate more strongly with behavioural ecology than would lower-level traits (Garland & Carter 1994; Garland & Losos 1994). Here, I tested the hypothesis that a laboratory measure of stamina can predict movement behaviour of lizards in the field. Following several previous studies (e.g. Huey et al. 1984; Pough et al. 1992; Garland 1993, 1994; references therein), I hypothesized that measures of field locomotor behaviour would correlate positively with endurance.

Lizards are diverse in form, behaviour and ecology (Greer 1989; Vitt & Pianka 1994) and have served as a particularly common model in comparative studies of locomotor performance (Garland & Losos 1994; Gans et al. 1997). Various aspects of locomotor ability have been measured in the laboratory, including clinging and jumping (Losos 1990a, b; Irschick et al. 1996). Sprinting ability has been especially commonly studied, usually by measurement on a photocell-timed racetrack (e.g. Huey et al. 1984; Losos 1990a, b; Miles 1994a; Bauwens et al. 1995; Zani 1996; Bonine & Garland, in press). Measures of locomotor endurance (stamina) have been less commonly compared among species of lizards (Bennett 1980; Garland 1993; see also Miles 1994b on population variation). Cullum (1997) compared sprint speed, maximal exertion (distance run to exhaustion

around a circular track; see also Bennett 1989; Garland 1993), and treadmill endurance of sexual and asexual whiptails (*Cnemidophorus*, Teiidae). Garland (1994) found that treadmill endurance at 1.0 km/h was positively correlated with both body mass and body temperature across 57 lizard species.

For any measure of locomotor performance ability in lizards, studies examining ecobehavioural correlates are scarce (Losos 1990a, b; Losos & Irschick 1996; Irschick & Losos 1998), and only two studies have examined endurance. Huey et al. (1984) presented treadmill endurance data for four species of lacertid lizards and found higher endurance in two of the three widely foraging species, as compared with the sit-and-wait species. Hertz et al. (1988) presented data on treadmill endurance and total daily movement distance (DMD) for nine species of lizards from six families. The correlation between log endurance and log DMD is positive (Pearson product–moment correlation: $r=0.402$) but not statistically significant (one-tailed $P=0.142$). Here, I updated and reanalysed their data, and also tested for associations between endurance (data from Garland 1994) and two other field measures, moves/min and percentage of time moving (data from Perry 1999). In all cases, I used both conventional statistical analyses and the method of phylogenetically independent contrasts.

METHODS

I measured endurance capacity with a standard protocol, described in detail elsewhere (Garland 1994). Briefly, I used a motorized treadmill with a belt speed of 1.0 km/h. This speed was chosen because it is representative of the speeds displayed by many species of lizards when moving at an undisturbed pace in the field (see Appendix I of Garland 1993). Moreover, previous studies have shown that endurance at 1.0 km/h is repeatable at the level of individual variation and that individual differences are highly correlated with morphological and physiological variation (e.g. Garland & Else 1987; Garland & Losos 1994 for review).

Lizards were placed on a rubberized-cloth belt and encouraged to walk by gentle tapping about the tail and hindlimbs. Temperature was regulated at or near the normal body temperature for each species when active in the field (see Table 11.1 in Garland 1994). Endurance was recorded as the time until an individual no longer kept pace with the moving belt. Each individual was tested twice and the higher value was used to compute a mean endurance time for each species. Average sample sizes (number of individuals per species) were 10.7, 10.2 and 15.2 for comparisons with percentage of time moving, moves/min, and daily movement distance, respectively.

Animals were measured within a few days of capture in the field. I measured all species included in this study except for *Dipsosaurus dorsalis*, which was taken from the literature (but measured with the same protocol: see Table 11.1 in Garland 1994).

Perry (1999) quantified movement patterns of lizards observed while active in the field as the number of moves made/minute (MPM) and the percentage of time spent moving (PTM). In combination with previously published information, his Table 1 provides data for a total of 83 species in 12 families of lizards. Data for MPM were available for 75 species; for PTM, 55 species were included.

Data on both endurance and PTM were available for 15 phylogenetically diverse species representing nine families (Table 1). For MPM, I included Perry's (1999) data for *Coleonyx variegatus* and *Holbrookia propinqua* in combination with endurance data for two closely related species, *Coleonyx brevis* and *Holbrookia maculata* (Garland 1994), thus allowing 13 species to be compared (Table 1). Both movement measures were strongly positively skewed (see Perry 1999) and hence were log-transformed to improve normality. Perry (1999) did not present information on body size, but neither MPM nor PTM (raw or log) was significantly correlated with the log-transformed maximum body masses shown in Table 1 (from Garland 1994).

To update the analysis of Hertz et al. (1988), I added three species (*Sceloporus jarrovi*, *Phrynosoma cornutum*, *Heloderma suspectum*) and deleted one. Following Garland (1994), I deleted *Cnemidophorus murinus* (55 g, 3.0 min, 768 m/day). This endurance value was one of the first reported for lizards (Bennett & Gleeson 1979) and now appears unacceptably low as compared with newer data reported for several other species of *Cnemidophorus*, all of which are smaller in body mass and hence would be expected to have lower endurance (Garland 1994; see also Cullum 1997). Omitting *C. murinus* left a total of 11 species (Table 1). The new DMD data were taken from Figure 1 in Garland (1993). All endurance data were taken from Table 11.1 in Garland (1994); for clarity, values shown here in Table 1 are antilogs of the values originally presented.

Because I had previously found that endurance was significantly related to both body mass and body temperature (Garland 1994), I also computed residuals from a multiple regression of endurance on both variables (body temperature data are in Table 11.1 in Garland 1994). As in that analysis, endurance and body mass were log-transformed, whereas body temperature (strongly negatively skewed on the arithmetic scale) was transformed by raising it to the 10th power.

Conventional statistical analyses are generally inappropriate when applied to interspecific comparative data because mean values for species cannot be assumed to represent independent and identically distributed data (reviews in Harvey & Pagel 1991; Martins 1996; Garland et al. 1999). Analyses were therefore redone with Felsenstein's (1985) method of phylogenetically independent contrasts. This is the best understood and most widely used of available phylogenetically based statistical methods (e.g. Losos 1990a, b; Harvey & Pagel 1991; Garland et al. 1992, 1999; Garland & Adolph 1994; Irschick et al. 1996; Losos & Irschick 1996; Martins 1996; Zani 1996; Díaz-Uriarte & Garland 1998) and was used in my previous analysis of endurance (Garland 1994). I used the PDTREE program (available for free from the author; latest version 5.0 described in Garland et al. 1999).

Table 1. Data for body mass, endurance and movement in nature for various species of lizards

| Species | Species code | Mass* (g) | Endurance† (min) | Movement index | | |
				MPM‡	PTM‡	DMD§ (m)
Anolis carolinensis	AC	5.94	1.59	0.86	7.04	—
Dipsosaurus dorsalis	dd	65.0	15	—	—	169
Ctenosaura similis	CS	760.1	15.10	0.53	7.73	—
Juvenile	CS	23.0	5.90	—	—	53
Gambelia wislizenii	gw	31.75	18.22	—	—	314
Crotaphytus collaris	cc	33.59	8.77	1.51	—	—
Uta stansburiana	us	4.84	2.14	—	—	200
Urosaurus ornatus	uo	4.40	1.67	1.33	3.41	—
Sceloporus undulatus	su	11.65	2.33	0.29	0.81	—
Sceloporus olivaceus	sl	30.56	1.58	0.62	1.98	—
Sceloporus jarrovii	sj	23.36	1.65	—	—	30
Uma inornata	ui	17.33	8.11	—	4.2	—
Callisaurus draconoides	cd	19.22	8.65	—	1.5	250
Cophosaurus texanus	cx	14.25	3.48	2.83	4.98	—
Holbrookia maculata/propinqua	hm	6.38	2.03	0.86	—	—
Phrynosoma cornutum	pc	49.92	3.94	—	—	47
Phrynosoma modestum	pm	16.57	2.32	0.12	—	—
Coleonyx brevis/variegatus	cb	1.81	1.10	0.57	—	—
Hemidactylus turcicus	ht	3.6	0.95	0.31	1.12	—
Hemidactylus frenatus	hf	4.33	1.44	0.75	2.66	—
Egernia cunninghami	ec	313.6	6.80	—	—	84
Tiliqua rugosa	tr	652.3	23.71	—	10.4	—
Cnemidophorus tigris tigris	ct	25.80	120	—	81.3	900
Cnemidophorus sexlineatus	cs	6.76	40.27	—	46.3	—
Pedioplanis lineoocellata	EL	4.34	4.59	1.54	14.3	171
Heloderma suspectum	hs	673.0	15.34	—	21.5	215

MPM: Movements/min; PTM: percentage of time moving; DMD: daily movement distance.
*Maximum in sample from Garland (1994).
†Laboratory running time (Garland 1994).
‡From Perry (1999).
§From Hertz et al. (1988) and Garland (1993).

The phylogenetic topology (branching order) used follows Figure 11.3 in Garland (1994). As in my analysis of the data for 57 species, branch lengths in units of estimated divergence times yielded negative relationships in diagnostic plots of the absolute values of the standardized contrasts versus their standard deviations (Garland et al. 1992). Such relationships can lead to inflated type I error rates (Díaz-Uriarte & Garland 1998). I therefore tried various transformations of branch lengths as well as arbitrary branch lengths. When all branch lengths were set equal, none of the diagnostic correlations was significantly different from zero (with the exception of log DMD: see Results); therefore, equal branch lengths were used for all characters. Figure 1 shows the phylogenies used for analyses. I computed residual log endurance as before except that body temperature was not transformed (because contrasts of raw temperature met the requirements for use, as indicated by the diagnostic), and I used multiple regression through the origin with standardized independent contrasts.

The phylogenies used for analyses (Fig. 1) contained some polytomies (unresolved nodes), indicating branches whose phylogenetic placement is uncertain (one for PTM, two for MPM, and one for DMD). Therefore, to be maximally conservative in the analyses with independent contrasts (see Purvis & Garland 1993; Garland & Díaz-Uriarte, in press), degrees of freedom for hypothesis testing were reduced by one, two and one, respectively, yielding 12, 9 and 8. All tests for associations between movement variables and endurance were one tailed, consistent with the directional hypothesis (see Introduction), and statistical significance was judged at $P<0.05$.

RESULTS

Figure 2 shows a positive relationship between the log of percentage of time moving and log treadmill endurance (conventional Pearson product–moment correlation: $r=0.802$, one-tailed $P=0.0004$) as well as residual log endurance ($r=0.783$, $P=0.0003$). Log MPM was not significantly correlated with either log endurance ($r=0.270$, one-tailed $P=0.1865$) or residual endurance ($r=0.320$, $P=0.1435$).

As might be expected, Fig. 2 suggests that values of both endurance and PTM are related to phylogenetic position (see also Garland 1994; Perry 1999). For example, the two *Cnemidophorus* (Teiidae) have by far the highest values for both traits. Also, the relationship appears very strongly positive across the seven species in half of the lizard phylogenetic tree (Scleroglossa: families
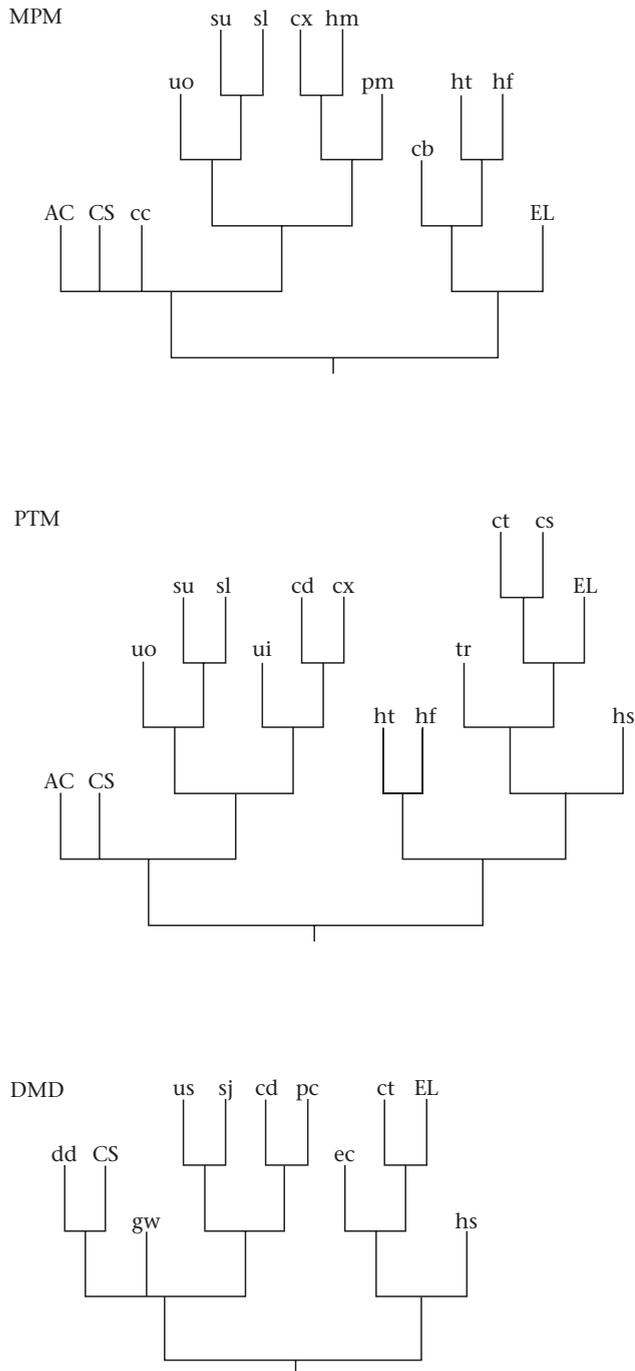
Figure 1. Phylogenetic trees (following Garland 1994) used for statistical analyses with Felsenstein's (1985) method of phylogenetically independent contrasts (PDTREE program). Multiway splits indicate uncertainty about branching order (soft polytomies; see text). Abbreviations for movement patterns and species as in Table 1. Extant 'lizards' are recognized as comprising two major clades that probably diverged in the mid-Triassic (references in Pough et al. 1998); 'snakes' are derived from within Scleroglossa. Species on the left side of the root of each tree are: Iguania, represented by families Polychridae (AC); Iguanidae (dd, CS); Crotaphytidae (gw, cc) and Phrynosomatidae (us, uo, su, sl, sj, ui, cd, cx, hm, pc, pm). Those on the right side of the root are Scleroglossa: geckos (cb, ht, hf); Scincidae (ec, tr); Teiidae (ct, cs); Lacertidae (EL) and Helodermatidae (hs). Note that all branch segments are arbitrarily set to be equal in length.
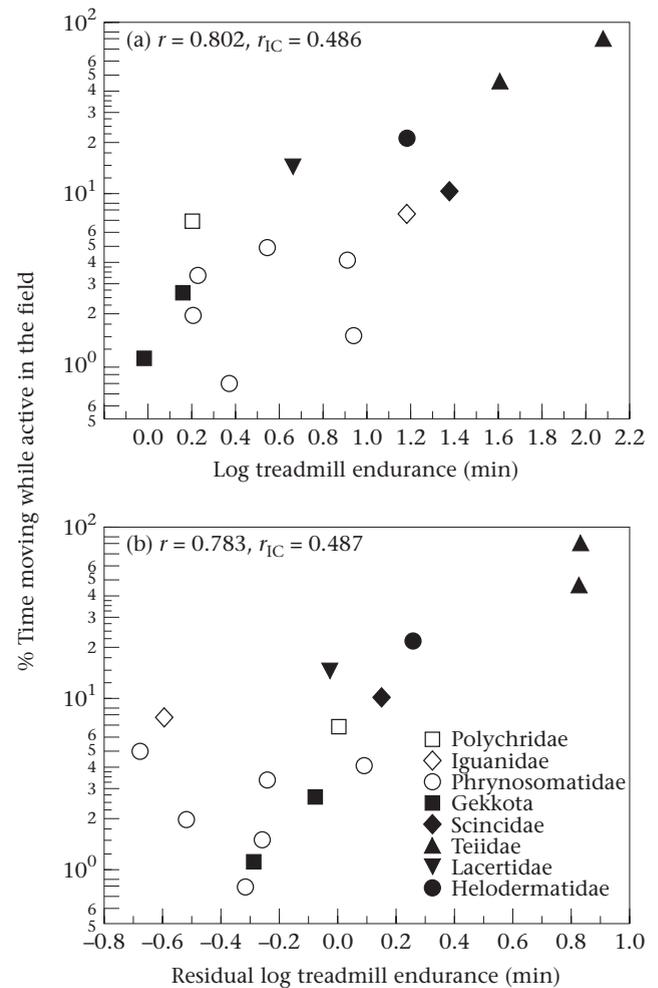
Figure 2. (a) Percentage of time moving while active in the field for 15 species of lizards (from Perry 1999) in relation to their treadmill endurance running performance at 1.0 km/h (from Garland 1994). (b) Residual endurance values, adjusted for correlations with body mass and body temperature. Both relationships were statistically significant (one-tailed $P<0.05$) by the method of phylogenetically independent contrasts (see text). Open symbols are families within Iguania, closed symbols are Scleroglossa.

in closed symbols in Fig. 2), but nonexistent among the eight species of Iguania (the other half of the lizard phylogenetic tree). Hence, a phylogenetically based statistical analysis might be expected to yield somewhat different results. With independent contrasts, however, log PTM was still significantly related to both log endurance (Pearson correlation computed through the origin: $r_{IC}=0.486$, one-tailed $P<0.05$) and residual log endurance ($r_{IC}=0.487$, $P<0.05$); as before, log MPM was not ($r_{IC}=0.169$, NS and $r_{IC}=0.286$, NS, respectively).

Log DMD was unrelated to log body mass ($r=-0.1$) but was strongly correlated with both log endurance (Fig. 3a: $r=0.789$, one-tailed $P=0.002$) and residual log endurance (Fig. 3b: $r=0.857$, $P=0.0008$). For the independent contrasts analysis, log DMD remained significantly related to both log endurance ($r_{IC}=0.767$, one-tailed $P<0.005$) and residual log endurance ($r_{IC}=0.858$, $P<0.001$).
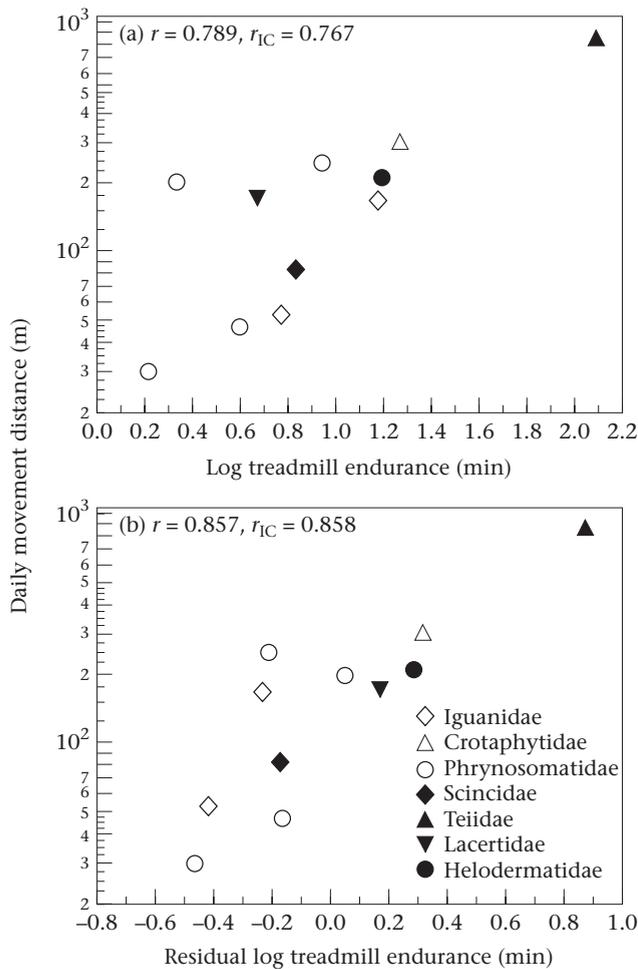
Figure 3. (a) Total daily movement distance for 11 species of lizards (from Garland 1993) in relation to treadmill endurance. (b) Residual endurance values. Both relationships were statistically significant (one-tailed $P<0.05$) by phylogenetically independent contrasts (see text). Open symbols are families within Iguania, closed symbols are Scleroglossa.

For log DMD, the plot of absolute values of standardized contrasts versus their standard deviations was significantly negative ($r=-0.792$), which suggested that branch lengths might not be adequately standardizing the contrasts (see Díaz-Uriarte & Garland 1998). Therefore, as a test for the robustness of the relationship with log endurance, I conducted a nonparametric sign test (see Felsenstein 1985). All 10 standardized contrasts were in the same direction for both log DMD and log endurance, thus indicating a highly significant positive relationship (one-tailed $P<0.01$).

DISCUSSION

This is the first study using a phylogenetically based statistical method to demonstrate a significant relationship between quantitative measures of field behaviour and a quantitative measure of endurance capacity. The strength of the relationships (Figs 2, 3) is impressive when one considers that the field behavioural and laboratory endurance data were gathered by different investigators using different populations. Thus, 'noise' in the data sets should be substantial.

My results suggest that the endurance capacities of lizards show evidence of evolutionary (genetic) adaptation to their behavioural ecology. In other words, physiology and behaviour are coadapted. However, endurance was measured on animals taken recently (within days) from the field. Hence, it is not possible to exclude the alternative (but not mutually exclusive) hypothesis that different species may have been 'self-trained' by their typical movement behaviour. In other words, individuals from highly mobile species (e.g. Teiidae) may have developed higher endurance capacities ontogenetically as they moved about more than did relatively sedentary species (e.g. some Phrynosomatidae). Arguing against this possibility is the fact that physical conditioning studies of lizards have been largely unsuccessful in altering endurance (Garland et al. 1987; and references therein). Also, training effects are unlikely to be near the magnitude of differences observed among species (i.e. less than 1 min to 120 min: Figs 2, 3; Garland 1994).

Rare as they are in lizards, quantitative studies of stamina in relation to field behaviour are even less common in other vertebrates. The only other study of which I am aware involved anuran amphibians: Pough & Taigen (1990) indicated a positive correlation between aerobic capacity and distance moved/h across four species of dendrobatid frogs. Aerobic capacity, measured as maximal rate of whole-animal oxygen consumption during forced locomotion, is not a measure of endurance per se, but it is an important determinant of locomotor endurance. For their data, the conventional Pearson correlation between residual (mass-corrected) log distance moved and residual log aerobic capacity is 0.912 (one-tailed $P<0.05$).

Published information on both field behaviour and laboratory measures of locomotor performance has expanded substantially in the last 5 years (cf. Garland & Losos 1994). Unfortunately, the two data sets still show little overlap. So long as standardized methods are employed to gather further data, however, comparative studies can be a cumulative enterprise (Garland et al. 1999). It is my hope that this report will encourage others to expand on the existing data and conduct further quantitative, phylogenetically based studies of relationships between performance abilities and field behaviour.

Most previous studies of lizard movement have emphasized the importance of foraging behaviour, including the continuum of sit-and-wait to widely foraging (Huey et al. 1984; Perry 1999). None the less, many lizards engage in other activities that may require high stamina, such as searching for mates, courtship, territorial defence, male–male combat, and escaping from pursuit predators (Hertz et al. 1988; Thompson et al. 1992; Garland 1993, 1994; Vitt & Pianka 1994; Christian et al. 1997). Thus, an important task for future studies will be separating overall measures of movement into their components and determining which are the most strongly correlated

with endurance (see also Pough 1989; Pough & Taigen 1990; Pough et al. 1992; Thompson & Withers 1997). When better documented, such relationships will play a crucial role in our understanding of how natural and sexual selection act to shape organismal form and function.

Acknowledgments

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