

# Speed and Endurance Do Not Trade Off in Phrynosomatid Lizards

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## ABSTRACT

Trade-offs are a common focus of study in evolutionary biology and in studies of locomotor physiology and biomechanics. A previous comparative study of 12 species of European lacertid lizards found a statistically significant negative correlation between residual locomotor speed and stamina (controlling for variation in body size), consistent with ideas about trade-offs in performance based on variation in muscle fiber type composition and other subordinate traits. To begin examining the generality of this finding in other groups of squamates, we measured maximal sprint running speed on a high-speed treadmill and endurance at 1.0 km/h (0.28 m/s) in 14 species of North American phrynosomatid lizards, plus a sample of nine additional species to encompass some of the broadscale diversity of lizards. We used both conventional and phylogenetically informed regression analyses to control for some known causes of performance variation (body size, stockiness, body temperature) and then computed residual performance values. We found no evidence for a trade-off between speed and endurance among the 14 phrynosomatids or among the 23 species in the extended data set. Possible explanations for the apparent difference between lacertids and phrynosomatids are discussed.

**Keywords:** comparative methods, endurance, high-speed treadmill, locomotion, performance, Phrynosomatidae, phylogeny, sprint speed.

## Introduction

Most traits are involved in multiple functions, and specialization of a trait for one function may lead to decreased performance of that trait for another function. Conflicting func-

tional requirements are one cause of biological trade-offs, generally defined as situations in which one trait cannot be increased without another trait decreasing (Roff and Fairbairn 2007, 2012; Garland 2014). Although often mentioned in the context of both function and adaptation, the general importance of trade-offs in ecological and evolutionary physiology is controversial (e.g., see Townsend and Calow 1981; Garland 1988; Garland and Losos 1994; Fry 1996; Wang et al. 1997). The timescale over which selection has acted, the organisms involved, and the magnitude of conflicting selection all play a role in determining whether a trade-off will occur as species diverge. For example, the classic egg size versus number trade-off (Roff 1992; Stearns 1992) can, in principle, be overcome by increasing the volume of the body cavity. Moreover, many trade-offs that seem plausible based on first principles of morphology, physiology, or biochemistry have not been examined empirically (Sinervo 1994).

Here, we address a potential trade-off between locomotor speed and endurance. These two whole-animal performance measures are driven by a complex combination of morphology, physiology, biomechanics, and biochemistry, but many of the lower-level (subordinate) traits that would increase speed would also tend to decrease endurance (Alexander 1968; Bennett 1978; Garland and Losos 1994). For example, greater proportions of slow-twitch oxidative muscle fibers should enhance stamina, whereas more fast-twitch glycolytic fibers would facilitate sprinting abilities (see Garland 1988; Sorci et al. 1995; Dohm et al. 1996 and references therein; Tobalske 1996; Bonine et al. 2001, 2005; Pasi and Carrier 2003). Increased muscle mass in the limbs would help produce greater burst sprinting speeds (e.g., consider human Olympic sprinters), but the effect on stamina is less clear. With more muscle mass, the cost of limb cycling is increased, but more muscle is available to share the workload and to store high-energy compounds (glycogen, fat), and a positive correlation between thigh muscle mass and endurance has been reported at the level of individual variation in lizards (Garland 1984). Increased leg length should increase sprint speed, but the effect on stamina is again less clear. Overall, however, our understanding of locomotor function suggests that selection for increased speed or endurance would shift muscle properties one way or the other, leading to a trade-off between the two phenotypes.

Few multispecies studies addressing speed versus endurance trade-offs have been published for terrestrial vertebrates. Garland et al. (1988) found no correlation between sprint and maximal aerobic speed (one important predictor of endurance) among 18 mammal species. However, Huey et al. (1984) reported a trade-off between speed and endurance among four lacertid lizard species, and Vanhooydonck et al. (2001) verified this result among 12 lacertid species. A more recent study of 17 lacertid species failed to find a trade-off between sprint speed

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and sustained locomotion measured on a circular track with lizards “running at their ‘preferred’ speed” (e.g., Vanhooydonck et al. 2014, p. 5). It is not entirely clear how this type of measurement of stamina compares with endurance measured on a motorized treadmill at a single speed (Garland 1993), but it has been shown that the suborganismal predictors of treadmill endurance and circular-track stamina are completely different at the level of individual variation in one species (Garland 1984).

The purpose of this study was to examine the relation between maximal sprint speed and running endurance in a non-lacertid lineage of lizards, the North American Phrynosomatidae, which have served as models for numerous previous studies of locomotor biology (e.g., Bonine et al. 2001, 2005; Bergmann and Irschick 2010). This family is also of particular interest because it contains three ecologically and morphologically distinct lineages. The fence lizards (*Sceloporus*; ~97 species) and their relatives (see fig. 1) may be considered typical of many diurnal, heliothermic lizards in the Iguania clade of the squamate phylogenetic tree (Bonine and Garland 1999; Bonine et al. 2005; Pyron et al. 2013). The sister lineage of fence lizards and their allies includes two specialized clades. The ant-eating horned lizards (*Phrynosoma*; ~18 species) have wide bodies, short limbs, a low proportion of fast-glycolytic muscle fibers in the iliofibularis muscle, relatively low maximum sprint speeds, and heads protected by spines, and they generally rely on extreme crypsis for predator avoidance (Sherbrooke 1987; Bonine and Garland 1999; Bonine et al. 2001). In contrast, the sand lizards (~12 species) have long limbs, a high proportion of fast-glycolytic muscle fibers, and generally high maximal sprint speeds, and they typically flee from predators (Dial 1986; Bulova 1994; Bonine and Garland 1999). This diversity in locomotor morphology and sprint performance should enhance the ability to detect a trade-off with endurance, if such a trade-off exists.

In addition to 14 species of phrynosomatids, we also sampled an additional nine species of similar body size from disparate branches of the lizard phylogenetic tree. Analysis of this extended data set (23 species) allows us to begin exploring the speed-stamina relation more generally for lizards. Within the constraints of availability, we attempted to restrict these additional species to those that we believed would provide meaningfully comparable results. The included species (see fig. 1) represent much of the range of phylogenetic diversity of lizards yet are reasonably similar to the Phrynosomatidae in terms of body size and ecology (e.g., all are small terrestrial, primarily insectivorous lizards), thereby removing complications inherent in comparing fossorial or strictly arboreal species with terrestrial ones. The additional species also vary widely in relative limb length and muscle fiber type composition of the iliofibularis muscle, which is predicted to have an important role in locomotion and may be specialized for either short-burst, powerful contractions or longer-lasting, sustained contractions, depending on its fiber type composition (Bonine and Garland 1999; Bonine et al. 2005). For both sets of species, we hypothesized that speed and endurance would show a negative relationship.

## Material and Methods

### Animal Collection

We collected lizards in three different years. In 1996 and 1997, lizards were field collected in the southwestern United States, primarily in Arizona and New Mexico, within close proximity of the American Museum of Natural History’s Southwestern Research Station (SWRS; Portal, AZ). We caught lizards using slip noose, modified drift fence, and, occasionally, excavation. We measured locomotor abilities at SWRS in 1996 and 1997.

In 1999, free-living lizards were collected by colleagues (see “Acknowledgments”) at various localities in the United States

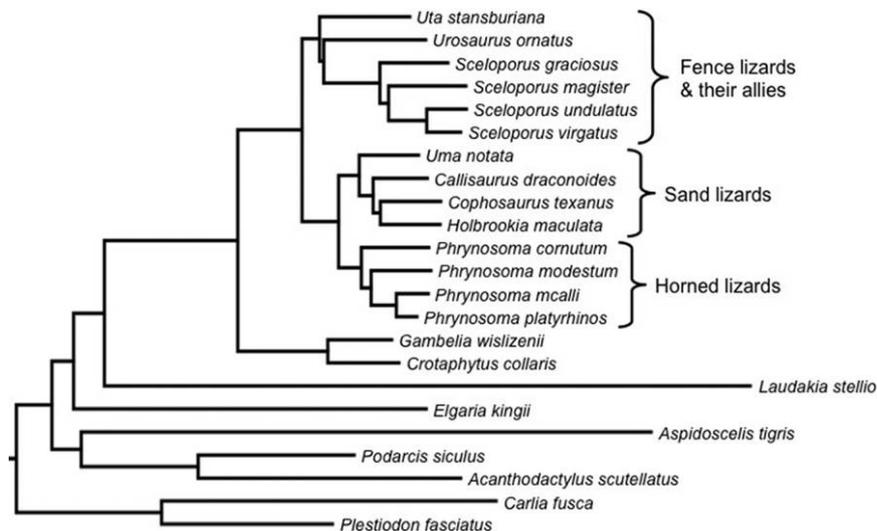


Figure 1. Hypothesized phylogenetic relationships for 23 species of lizards included in this study. Branch lengths are proportional to expected substitutions per site, as provided by Pyron et al. (2013), after pruning species not in our data set.

Table 1: Mean body mass, maximal sprint speed, and endurance for 23 species

Species (species code)	Maximal sprint speed						Endurance (at 1 km/h)				
	Body mass (g)	SVL (mm)	Speed (m/s)	Speed			Body mass (g)	SVL (mm)	Endurance (s)	$T_b$ (°C)	End. $N^b$
				$N^a$	$T_b$ (°C)	$T_b N$					
1 <i>Uta stansburiana</i> (us)	3.83 ± .504	54.1 ± 2.12	2.17 ± .268	8	34.8 ± .36	7	3.73 ± .557	53.0 ± 2.69	137.8 ± 46.12	34.6 ± .76	8
2 <i>Urosaurus ornatus</i> (uo)	3.47 ± .531	52.6 ± 2.39	2.29 ± .407	19	35.0 ± 1.06	16	3.28 ± .665	51.7 ± 3.03	99.4 ± 39.83	34.4 ± .75	18
3 <i>Sceloporus graciosus</i> (sg)	7.03 ± 1.913	65.1 ± 3.32	2.32 ± .331	10	33.7 ± .64	10	7.03 ± 1.913	65.1 ± 3.31	208.5 ± 100.83	34.0 ± 1.35	10
4 <i>Sceloporus magister</i> (sm)	31.01 ± 10.214	101.5 ± 10.14	3.11 ± .230	6	35.8 ± .75	6	30.05 ± 11.355	100.3 ± 11.24	288.6 ± 244.63	35.8 ± .52	6
5 <i>Sceloporus cowlesi</i> (su)	4.51 ± .452	58.1 ± 2.46	2.20 ± .232	5	35.0 ± .50	5	4.96 ± 1.492	59.5 ± 4.01	134.5 ± 36.81	34.2 ± .48	7
6 <i>Sceloporus virgatus</i> (sv)	5.23 ± .893	60.3 ± 2.25	1.76 ± .253	8	34.9 ± .47	7	4.64 ± .957	58.5 ± 3.37	114.2 ± 36.16	34.8 ± 1.11	11
7 <i>Uma rufopunctata</i> (un)	29.67 ± 3.993	108.3 ± 7.45	3.31 ± .620	5	39.7 ± .68	5	23.37 ± 12.643	95.3 ± 24.86	256.7 ± 119.95	38.2 ± 1.10	10
8 <i>Callisaurus draconoides</i> (cd)	11.93 ± 6.382	77.9 ± 13.02	4.81 ± .785	7	39.3 ± .46	5	9.23 ± 4.278	72.0 ± 12.12	174.2 ± 37.22	38.0 ± .51	3
9 <i>Cophosaurus texanus</i> (cx)	9.94 ± 2.707	72.5 ± 6.85	3.81 ± .598	12	39.2 ± .66	11	15.49	86.5	133.2	39.6	1
10 <i>Holbrookia elegans</i> (hm)	4.05 ± .905	51.3 ± 5.44	2.95 ± .545	7	36.8 ± 1.18	6	3.85 ± .833	49.9 ± 2.43	136.8 ± 31.71	35.9 ± .62	5
11 <i>Phrynosoma cornutum</i> (pc)	33.62 ± 6.847	90.8 ± 7.61	1.76 ± .325	13	35.2 ± .79	13	33.91 ± 7.646	90.8 ± 7.49	466.5 ± 488.49	34.9 ± 1.20	15

12	<i>Phrynosoma mcallii</i> (pM)	11.46 ± .667	71.0 ± 1.80	1.54 ± .67	3	35.1 ± .67	3	9.17 ± 4.172	63.3 ± 13.82	146.4 ± 30.36	33.2 ± 3.06	3
13	<i>Phrynosoma modestum</i> (pm)	5.95 ± 1.214	53.4 ± 5.26	1.25 ± .273	6	34.4 ± .77	6	5.95 ± 1.214	53.4 ± 5.26	46.3 ± 19.37	33.9 ± .95	6
14	<i>Phrynosoma platyrhinos</i> (pp)	16.26 ± 4.936	75.3 ± 6.71	1.55 ± .298	6	34.2 ± .57	6	16.73 ± 4.675	76.3 ± 6.62	173.7 ± 49.54	34.4 ± .66	7
15	<i>Gambelia wislizenii</i> (gw)	19.81 ± 6.152	94.6 ± 9.96	3.28 ± .555	6	39.3 ± 1.05	6	20.61 ± 5.392	96.1 ± 9.78	267.3 ± 121.81	37.4 ± .88	4
16	<i>Crotaphytus collaris</i> (cc)	40.15 ± 3.564	107.7 ± 2.98	3.36 ± .561	10	37.3 ± 1.45	10	40.25 ± 4.276	107.4 ± 3.31	521.3 ± 372.28	36.7 ± 1.22	7
17	<i>Laudakia stellio</i> (ls)	48.54 ± 13.239	111.3 ± 7.17	3.03 ± .472	6	36.0 ± 2.56	6	51.31 ± 12.707	113.0 ± 6.59	131.5 ± 31.96	35.4 ± .52	5
18	<i>Elgaria kingii</i> (gk)	9.73 ± 2.471	96.6 ± 6.20	1.17 ± .082	5	34.0 ± 1.56	5	8.86 ± 3.818	90.9 ± 13.13	112.9 ± 22.42	34.3 ± 1.43	9
19	<i>Aspidoscelis tigris</i> (ct)	11.42 ± 4.694	84.4 ± 10.89	4.27 ± .705	8	37.9 ± 1.04	6	11.81 ± 4.815	84.8 ± 11.03	1,238.0 ± 1,138.48	39.1 ± .95	6
20	<i>Podarcis sicula</i> (Ps)	5.39 ± 2.051	66.5 ± 6.83	2.40 ± .296	12	33.5 ± .87	12	4.69 ± 1.661	63.8 ± 7.10	164.8 ± 61.28	33.6 ± 1.41	13
21	<i>Acanthodactylus scutellatus</i> (As)	7.84 ± .867	73.2 ± 1.61	3.32 ± .300	3	37.2 ± .56	3	7.64 ± .819	73.0 ± 1.35	438.6 ± 197.78	38.8 ± 1.51	4
22	<i>Carlia fusca</i> (Cf)	3.35 ± .506	58.0 ± 2.03	1.73 ± .149	12	32.3 ± .83	10	3.33 ± .630	58.0 ± 1.98	86.9 ± 22.03	32.7 ± .59	10
23	<i>Eumece fasciatuss</i> (ef)	7.35 ± .869	74.2 ± 2.59	1.80 ± .108	5	32.6 ± .40	3	6.02 ± 2.407	69.3 ± 8.96	289.4 ± 73.47	35.0 ± .17	7

Note. Performance data were measured at the species' field-active body temperature ( $T_b$ ) and recorded at the end of each trial. Mean values ± standard deviations are reported, along with sample sizes. Two-letter species codes are used in the electronic versions of the database and phylogenetic tree (available from the authors on request). End. = endurance.

<sup>a</sup>For sprint speed data, body mass, snout-vent length (SVL), and speed have the same sample sizes, as reported in the first  $N$  column, except for body mass and SVL of *Callisaurus* ( $N = 6$ ).

<sup>b</sup>For endurance and related body mass, SVL, and  $T_b$ , sample size is as reported, except  $T_b$  for *Holbrookia* ( $N = 4$ ) and for *Aspidoscelis* ( $N = 5$ ).

and by G. Perry in Guam and Israel. Soon after capture, lizards were mailed overnight to the University of Wisconsin–Madison, where we measured locomotor performance.

For each species, we attempted to collect individuals from a restricted geographic area, because populations may differ in physiological characteristics (Garland and Adolph 1991). Because of potential seasonal differences in metabolism and performance (e.g., Garland and Else 1987), we restricted animal collections to late May–August (except for individuals from Guam). During captivity (locomotion was typically measured on days 1–6, <10 d until sacrifice or release for most individuals), we kept individual lizards isolated in cloth bags or plastic cups (depending on size), with periodic access to water but without food. We withheld food because recent feeding can affect locomotor performance (e.g., Garland and Arnold 1983; Huey et al. 1984; Martin 1996). The exception to the above regimen was that species captured in Israel (*Laudakia stellio*, *Acanthodactylus scutellatus*) and Guam (*Carlia fusca*) were fed insects before hand transfer by G. Perry to Madison, Wisconsin, and their time in captivity was approximately 21 d.

We studied only adult males to eliminate potential sex and ontogenetic effects. Animals were weighed (g) and measured (snout-vent length [SVL], mm) following both speed and endurance measurements. Some speed and morphometric data presented here were reported previously (Bonine and Garland 1999).

#### Locomotor Measurements

**Sprint Speed.** We measured sprint speed, usually within the first 4 d of capture, on a high-speed treadmill (Dohm et al. 1998; Bonine and Garland 1999) with a belt area of 155 cm long by 30 cm wide, with adjustable Plexiglas walls. For these relatively small lizards, we used an effective running area of about 140 cm in length by 15 cm (front) to 25 cm (rear) wide. The textured rubberized cloth belt (IAR-PT, American Star International, Brighton, MI) provided traction. A 3.0-hp motor could almost instantly accelerate to a maximum speed of 12.5 m/s.

As in previous comparative studies (Garland 1994a; Zani 1996; Bonine and Garland 1999; Vanhooydonck et al. 2001), we made sprint speed measurements near the lizard's field-active body temperature ( $T_b$ ; Avery 1982; Pianka 1986; Heatwole and Taylor 1987; Garland 1994a; R. E. Espinoza, personal communication, 1999; G. Perry, personal communication, 1999). We placed animals for at least 2 h before measurements in an environmental chamber warmed to between 33° and 40°C (except *Elgaria*, which prefers 30°C but was measured at 35°C for logistical reasons and because Bennett [1980] found the highest speed of a related species, *Elgaria multicarinata*, at 37.5°C). We removed lizards from the environmental chamber and placed them immediately on the rear of the horizontal treadmill. A light tap to the tail induced each animal to run, and we rapidly accelerated the treadmill to match the speed of the running lizard. Some lizards required additional taps to the tail to maintain sprinting, and we increased the belt speed until the animal reached an apparent maximum speed. We then held speed constant, and the lizard tired quickly, came off the back

of the moving belt, and was captured. We recorded  $T_b$  immediately after each trial with a quick-reading cloacal thermometer (Miller and Weber, Queens, NY). The treadmill apparatus was heated with overhead incandescent lamps before and during trials. A tachometer displayed the final speed. The total length of a trial averaged approximately 10–15 s. Each trial was subjectively scored for the perceived effort (i.e., trial quality) that the lizard was making to run as fast as possible: great, good, OK, fair, and poor (Bonine and Garland 1999). Only trials that were scored at least OK were used in subsequent analyses. Speed was measured once on each of two consecutive days for a given individual, and the higher of the two speeds was used in subsequent analyses. Within species, repeatability between days for a given individual was similar to that reported for animals on photocell-timed racetracks, as shown in table 1 of Bonine and Garland (1999), who studied most of the same species considered here and many of the same individuals.

We computed a mean maximal sprint speed for each species using the maximum value recorded for each individual (see Garland and Losos 1994; Bonine and Garland 1999). Species mean  $T_b$  was calculated using the body temperature of the fastest trial for each individual.

**Endurance.** Endurance running capacity was measured once on each of two consecutive trial days at 1.0 km/h on a motorized treadmill (Garland 1984, 1993, 1994a; Garland and Else 1987; Beck et al. 1995; Dohm et al. 1998) by individuals who had considerable previous experience with the technique and with most of these species. We used this treadmill speed because it was (1) the same as that used in a much larger comparative study (Garland 1994a) and (2) designed to give similar average endurance times for phrynosomatids as compared with the other comparable lizard data set for Lacertidae (Vanhooydonck et al. 2001). As noted in "Discussion," the latter goal was achieved. Endurance was measured on the same individuals, always after sprint speed measurements were completed, generally on days 5 and 6 of captivity. Occasionally, a third day of endurance was measured for uncooperative individuals (i.e., determined to be less than OK per the same ranking categories for sprint trials); we used the highest measure in subsequent analyses. Trials were stopped when lizards failed to maintain pace following 10 consecutive taps (at <1-s intervals) to the tail and hind limbs. As with sprint speed measurements, the treadmill apparatus was heated,  $T_b$  was measured at the end of the trial, and each trial was scored for the perceived effort each animal was making to maintain a steady pace. *Cophosaurus texanus* were often uncooperative, typically sprinting repeatedly to the front of the treadmill and refusing to run at the moderate pace needed to acquire valid endurance estimates. As a result, we used endurance data for only one of 12 individuals. This value (2.2 min) is slightly lower than the lowest value reported for eight cooperative individuals (2.8–4.7 min) in Garland (1994a). We decided to keep this species in the analysis for completeness and because we believed the datum to be reliable.

It is worth noting that measurement of endurance capacity necessarily involves a number of semiarbitrary decisions

concerning protocols. For example, rather than single-speed methods, studies of fishes (e.g., Oufiero et al. 2012 and references therein) and rodents (see Booth et al. 2010 and references therein) routinely use protocols in which speed is gradually increased over time. Another alternative is to test each individual at a series of fixed speeds, on different trial days, and attempt to determine the speed at which stamina declines precipitously, an approach that was not practical for this study (see discussion in Garland 1994a, p. 255).

### Phylogeny

A recent study provides a phylogenetic tree for all Squamata (Pyron et al. 2013) and includes all the species analyzed here or close relatives. We pruned their tree to include only the species analyzed here, as shown in figure 1. The taxonomy of all species sampled in North America is available in Crother (2000; Crother et al. 2003). The following three species are not available therein: *L. stellio* (Linnaeus, 1758), *A. scutellatus* (Audouin, 1809), and *C. fusca* (Duméril and Bibron, 1839).

### Statistical Analyses

Our general approach was to test for a correlation between residual speed and endurance (as in Vanhooydonck et al. 2001), statistically removing correlations with body size and with other traits known to affect speed or endurance in lizards. We  $\log_{10}$  transformed species' mean values (table 1) for SVL,  $T_b$ , speed, and endurance in order to achieve linearity of relations and normality of residuals from the multiple regression models. As a measure of body size, we used SVL (Vanhooydonck et al. 2001). We used  $T_b$  as a candidate independent variable because we have previously shown endurance to be correlated positively

with temperature across a sample of 57 species (or subspecies) of lizards (Garland 1994a). As an index of stockiness (e.g., see Bergmann et al. 2009; Bergmann and Irschick 2010), we computed (body mass in grams<sup>0.33</sup>)/(SVL in cm).

For analyses of the 14 species of phrynosomatids, we also computed residuals while adjusting for differences among the three clades because they are known to differ considerably in various aspects of morphology and behavior (see "Introduction"), as well as sprint speed (Bonine and Garland 1999). These differences in Bauplane (or grade shifts) may reset the rules for trade-offs (Garland 2014). We used 0–1 dummy variables to code for sand lizards and for *Phrynosoma*, relative to a baseline of *Sceloporus* and their allies (fig. 1). When entered together as independent variables, we refer to this as the clade variable for simplicity. We did not use the stockiness variable for the 14-species analysis because it was highly correlated with clade membership (*Phrynosoma* are very stocky, as shown in fig. 3C). For the 23-species analyses, we also used a dummy variable (OutEK) to code for the species *Elgaria kingii*, which was a statistical outlier (see below).

In summary, we considered residuals from the following four models for the 14-species data set: SVL +  $T_b$ , SVL +  $T_b$  + stockiness, SVL +  $T_b$  + clade, and SVL +  $T_b$  + stockiness + clade. For the 23-species data set, we considered residuals from the following four models: SVL +  $T_b$ , SVL +  $T_b$  + stockiness, SVL +  $T_b$  + OutEK, and SVL +  $T_b$  + stockiness + OutEK. Although we felt that the known biology of lizard locomotor performance strongly suggests use of these independent variables for computing residuals, we also report the correlation between speed and endurance without computing residuals.

In addition, because complex systems (such as locomotor performance) can sometimes elude our (simplistic) ideas about functional relations, we also computed multiple regressions with

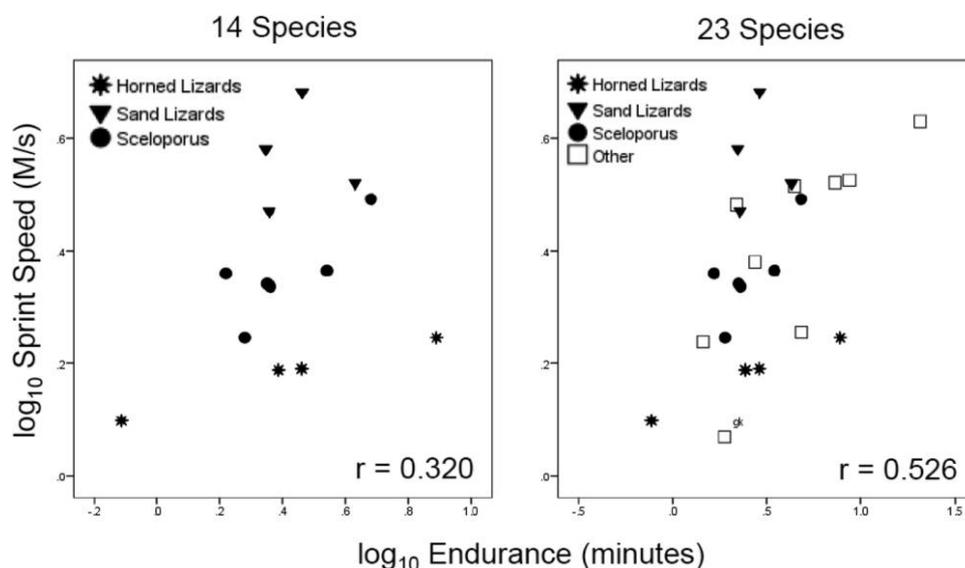


Figure 2. Bivariate scatterplots of  $\log_{10}$  maximal sprint speed (m/s) in relation to  $\log_{10}$  endurance (min). The Pearson correlations are conventional nonphylogenetic values (see also table 2).

all possible combinations of the independent variables. This agnostic approach potentially would allow us to discover a best-fitting model for speed and endurance that might differ from the ones we favored based on a priori expectations (see above). In practice, however, based on comparisons of the Akaike information criterion corrected for small sample sizes (AICc), we did not find any other models that fit the data well for both speed and endurance (results not shown).

In the multiple regressions to compute residuals, we tested for statistical outliers in a post hoc fashion following procedures in Cook and Weisberg (1999). Specifically, we computed a dummy variable to code for a particular datum that was a putative outlier, entered it into the multiple regression model in question, computed the  $P$  value, and then multiplied that  $P$  by the number of data points (14 or 23). If the resulting value was  $<0.05$ , then we concluded that the point was an outlier. In practice, this occurred only for *E. kingii* in analyses of sprint speed. Therefore, as noted above, we also computed multiple regressions including this dummy variable when analyzing the extended data set of 23 species. Doing so is equivalent to deleting the data point.

We computed residuals from multiple regressions estimated in two ways (reviews in Garland et al. 2005; Lavin et al. 2008;

Rezende and Diniz-Filho 2012): conventional, nonphylogenetic, ordinary least squares (OLS), and phylogenetic generalized least squares (PGLS), which uses a covariance matrix obtained from the phylogeny to account for similarities due to relatedness of the species. All regressions were computed using the Matlab Regressionv2.m program of Lavin et al. (2008). The OLS models were also checked against output from SPSS, version 11.5.

We did not attempt to use models that allow transformation of phylogenetic branch lengths (e.g., models using Pagel's lambda transformation; Freckleton et al. 2002; the RegOU model of Lavin et al. 2008) because the residuals from these models are not necessarily isomorphic across traits when different values of the transformation parameters are used. In addition, even the 23-species data set is near the minimum sample size required for reliable estimates (Freckleton et al. 2002; Blomberg et al. 2003).

## Results

Species' mean values and sample sizes are reported in table 1. When the entire set of 23 species was considered, sample sizes ranged from 3 to 19 (mean = 7.9) individuals per species for speed and from 1 to 18 (mean = 7.6) individuals per species

Table 2: Correlations between locomotor speed and endurance for unadjusted values and for residuals from multiple regression equations for both 14 and 23 species

Model	N species	Independent variables <sup>a</sup>	$r$	Two-tailed $P$ (df = $N - 2$ )	Two-tailed $P$ (df = $N - 4$ ) <sup>b</sup>
OLS	14	None	+ .320	.2643	
OLS	14	SVL + $T_b$	+ .467	.0919	.1259
OLS	14	SVL + $T_b$ + stockiness	+ .439	.1163	.1534
OLS	14	SVL + $T_b$ + clade	+ .298	.3007	.3468
OLS	14	SVL + $T_b$ + stockiness + clade	+ .285	.3238	.3697
PGLS	14	None	+ .390	.1680	
PGLS	14	SVL + $T_b$	+ .461	.0967	.1310
PGLS	14	SVL + $T_b$ + stockiness	+ .465	.0936	.1274
PGLS	14	SVL + $T_b$ + clade	+ .264	.3621	.4074
PGLS	14	SVL + $T_b$ + stockiness + clade	+ .233	.4229	.4663
OLS	23	None	+ .526	.0099*	
OLS	23	SVL + $T_b$	+ .366	.0859	.1027
OLS	23	SVL + $T_b$ + stockiness	+ .366	.0857	.1025
OLS	23	SVL + $T_b$ + OutEK	+ .267	.2188	.2427
OLS	23	SVL + $T_b$ + stockiness + OutEK	+ .114	.6044	.6226
PGLS	23	None	+ .454	.0295*	
PGLS	23	SVL + $T_b$	+ .391	.0647	.0793
PGLS	23	SVL + $T_b$ + stockiness	+ .413	.0504	.0630
PGLS	23	SVL + $T_b$ + OutEK	+ .307	.1549	.1766
PGLS	23	SVL + $T_b$ + stockiness + OutEK	+ .329	.1257	.1457

Note. All models included snout-vent length (SVL) and body temperature ( $T_b$ ; see "Material and Methods"). Figure 5 shows four of these models for the 14-species analysis, and figure 6 shows four for the 23-species analysis.

<sup>a</sup>Clade indicates two dummy variables comparing horned and sand lizards with *Sceloporus*. OutEK indicates a dummy variable coding for the outlier species *Elgaria* (formerly *Gerrhonotus*) *kingii*.

<sup>b</sup>The nominal degrees of freedom (df) are  $N - 2$  for a correlation, but because residuals are being correlated, it is appropriate to subtract two additional degrees of freedom.

\* $P < 0.05$ .

for endurance. Mean speeds varied from 1.17 m/s for *Elgaria* (an alligator lizard) to 4.81 m/s for *Callisaurus* (a sand lizard; see fig. 1). Mean endurance varied from less than 1 min for *Phrynosoma modestum* to over 20 min for *Aspidoscelis tigris*. Within the Phrynosomatidae ( $N = 14$  species), mean speeds ranged from 1.25 to 4.81 m/s, while endurance ranged from 0.8 to 7.8 min.

Log-transformed speed and endurance were positively correlated (fig. 2), and the correlation was statistically significant for the 23-species data set by both OLS and PGLS (table 2). Relationships of locomotor performance to body size, temperature, and stockiness are presented in figure 3 for the 14 species of Phrynosomatidae. The correlation between residual speed and endurance from both OLS and PGLS multiple regression models was positive (ranging from +0.23 to +0.47) but never statistically significant (table 2). Figure 5 shows some of the correlations for both OLS and PGLS models.

Relationships of locomotor performance to body size, temperature, and stockiness are presented in figure 4 for the extended data set with 23 species. Residual speed and endurance were positively correlated but again did not reach statistical significance (table 2; fig. 6).

## Discussion

Our major finding is that speed and endurance were not negatively related, whether we considered the 14 species of Phrynosomatidae or the expanded data set of 23 species, regardless of the independent variables or the type of regression (OLS and PGLS) used to generate residuals. In fact, all of the estimated correlations were positive, both for residuals and for unadjusted values of speed and endurance (table 2). This result differs from that of Vanhooydonck et al. (2001; but see also Vanhooydonck et al. 2014), who found a statistically significant negative rela-

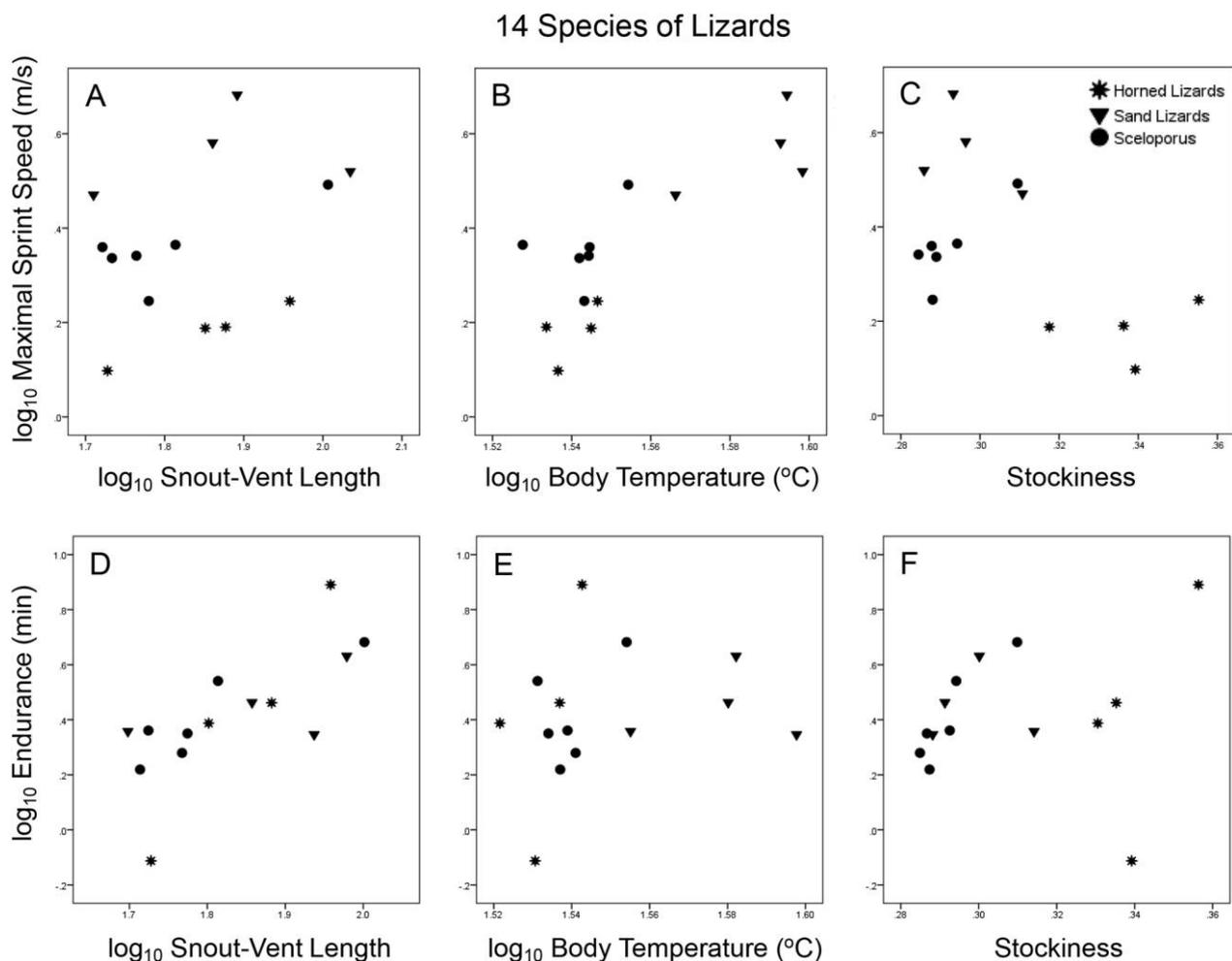


Figure 3. Top row shows bivariate scatterplots of log<sub>10</sub> maximal sprint speed (m/s) in relation to log<sub>10</sub> snout-vent length (A), log<sub>10</sub> body temperature (B), and stockiness (C) for 14 species of phrynosomatid lizards. Bottom row (D–F, respectively) shows the same but for log<sub>10</sub> endurance (min).

## 23 Species of Lizards

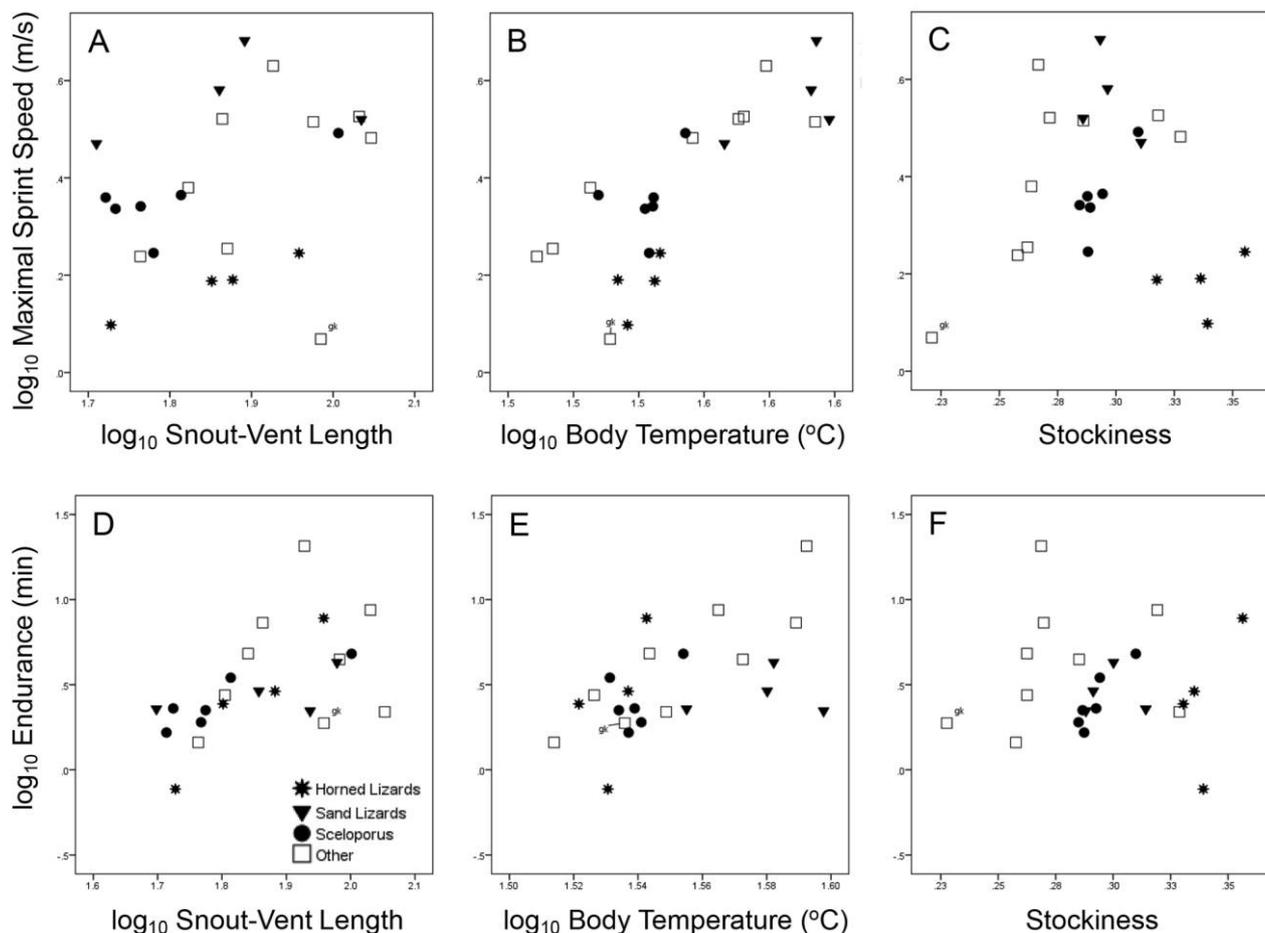


Figure 4. Top row shows bivariate scatterplots of  $\log_{10}$  maximal sprint speed (m/s) in relation to  $\log_{10}$  snout-vent length (A),  $\log_{10}$  body temperature (B), and stockiness (C) for 23 species of lizards (extended data set). Bottom row (D–F, respectively) shows the same but for  $\log_{10}$  endurance (min).

tion for 12 species of lacertid lizards. We consider three possible explanations for this difference.

First, some researchers have hypothesized that trade-offs might be evident only in species that are near the limits of one or both types of performance, such as species that are exceptionally fast runners and/or have high endurance (Garland 1994b; see also Van Damme et al. 2002). If the lacertids studied previously were closer to maximal performance limits, then they might be more likely to show trade-offs. However, when we compare the phrynosomatids studied here with the lacertids studied previously, this limit hypothesis does not appear to be supported. Available data indicate that lacertids are relatively slow (species' mean speeds range from 0.86 to 3.34 m/s; Vanhooydonck et al. 2001) as compared with phrynosomatids (1.25–4.81 m/s; see table 1). Direct comparisons of endurance values for the two species measured in both studies (*Acanthodactylus scutellatus* and *Podarcis sicula*) are not possible because Vanhooydonck et al. (2001) used a treadmill speed of

0.79 km/h, whereas we used 1.0 km/h. However, in spite of this difference, average endurance times are very similar between their lacertids (52–438 s) and our phrynosomatids (46–467 s), which was a methodological goal of this study (see “Material and Methods”). Thus, on average, the 12 lacertids from Vanhooydonck et al. (2001) and the 14 phrynosomatids studied here should have been operating under similar workloads relative to their maximal aerobic capacities and hence locomoting under similar physiological regimens when undergoing endurance tests (see discussion of the physiological bases of lizard endurance in Garland 1993). Furthermore, we studied one species that was both very fast and had high endurance (*Aspidoscelis tigris*; see also Garland 1993, 1994a; Bonine and Garland 1999).

Second, the amount of phenotypic diversity encompassed by the two studies might differ, either in absolute terms or relative to the total amount that exists within the two different lineages of lizards. Although lacertids are generally viewed as

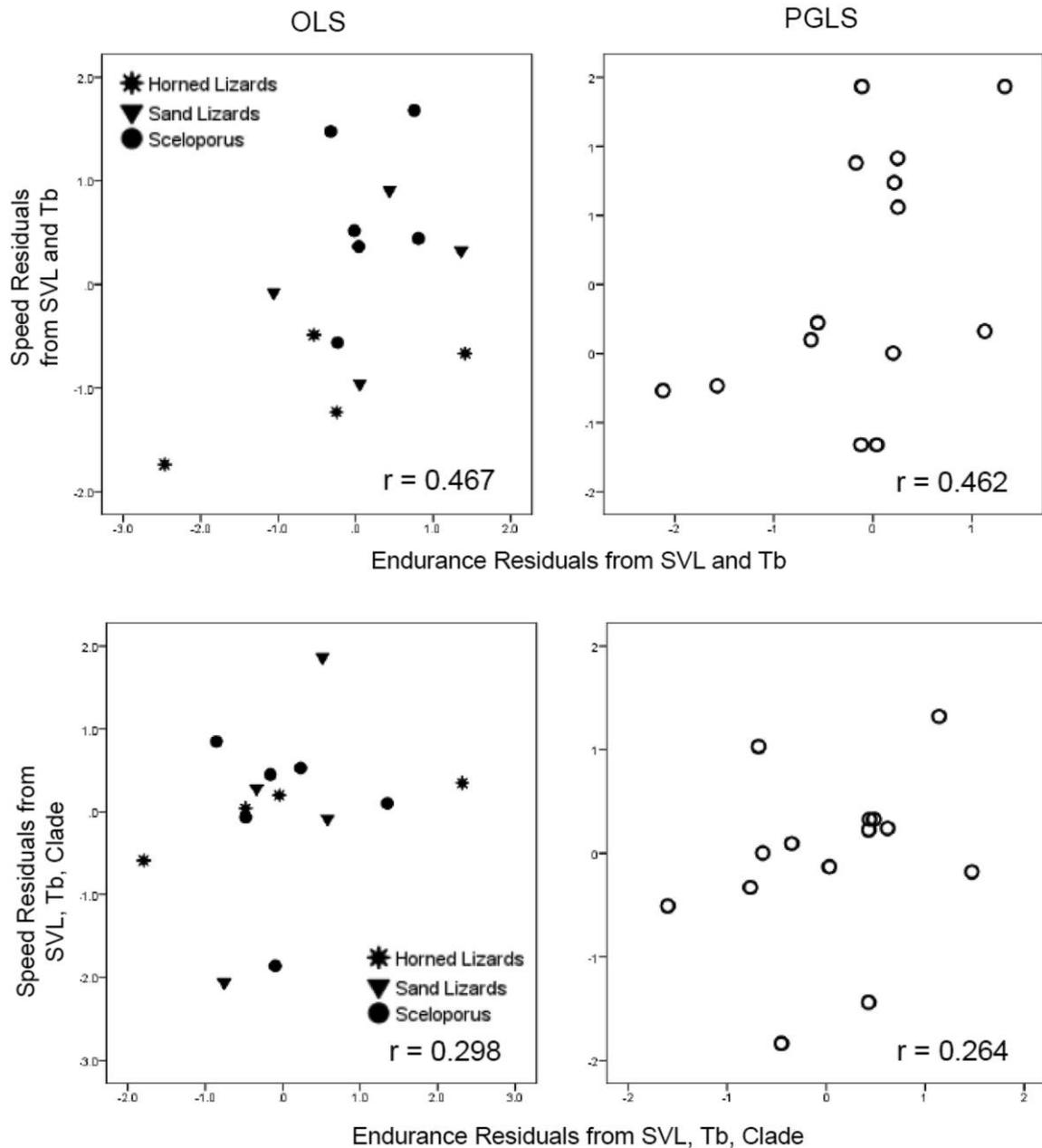


Figure 5. Scatterplots of residual  $\log_{10}$  sprint speed (m/s; X-axes) and residual  $\log_{10}$  endurance (min; Y-axes) for 14 species of phrynosomatid lizards using both ordinary least squares (OLS) and phylogenetic generalized least squares (PGLS) multiple regression models. Residuals were computed from regressions on  $\log_{10}$  snout-vent length (SVL) and  $\log_{10}$  body temperature ( $T_b$ ; top row) or those two variables plus dummy variables for the sand and horned lizard clades (bottom row). Correlations and significance levels are presented in table 2.

very similar in overall body form and appearance (e.g., Arnold 1989; Vanhooydonck et al. 2000), phrynosomatids exhibit remarkable differences in relative hind limb length (Bonine and Garland 1999), body plan (Irschick and Jayne 1999; see fig. 3C for variation in stockiness), and muscle fiber type composition (Bonine et al. 2001, 2005), as well as ecology and antipredator behavior (Norris 1958; Sherbrooke 1981; Dial 1986; Midden-dorf and Sherbrooke 1992; Bulova 1994). Vanhooydonck et al.

(2001) studied  $\sim 3.7\%$  of the extant lacertid species (12/321; Uetz 2015), whereas we studied  $\sim 9.5\%$  of extant phrynosomatids (14/148; Uetz 2015). These comparisons suggest that, if anything, the present study of phrynosomatids encompassed more phenotypic diversity, on both relative and absolute scales, than did the previous study of lacertids. Perhaps the apparently greater variation in many characteristics among phrynosomatids, as compared with lacertids, indicates an evo-

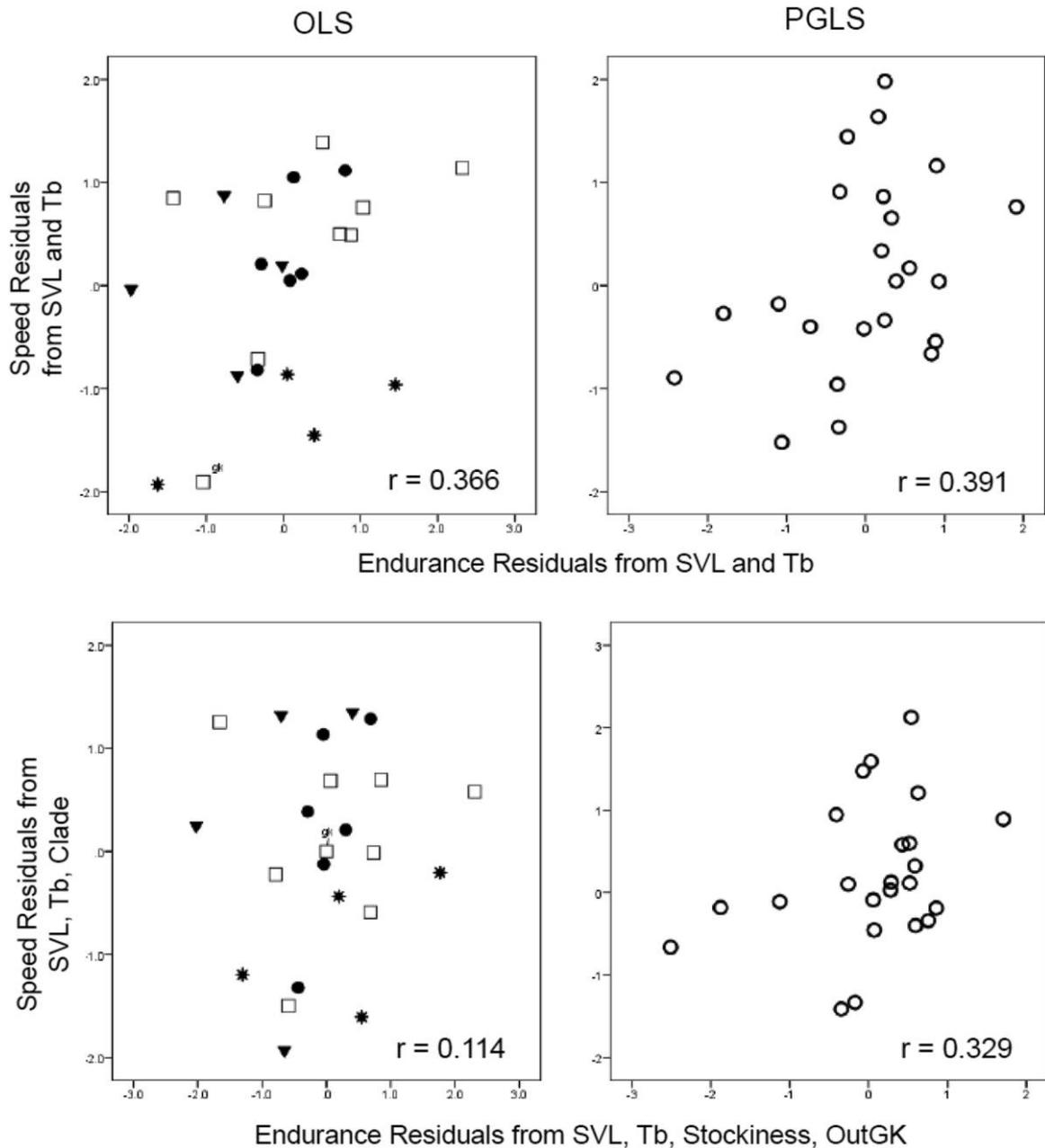


Figure 6. Scatterplots of residual  $\log_{10}$  sprint speed (m/s; X-axes) and residual  $\log_{10}$  endurance (min; Y-axes) for 23 species of lizards using both ordinary least squares (OLS) and phylogenetic generalized least squares (PGLS) multiple regression models. Residuals were computed from regressions on  $\log_{10}$  snout-vent length (SVL) and  $\log_{10}$  body temperature ( $T_b$ ); top row) or those two variables plus body stockiness and a dummy variable to code for *Elgaria kingii*, which was a statistical outlier in some analyses (see “Material and Methods”; bottom row). Correlations and significance levels are presented in table 2. Symbols are as in figure 4.

lutionary history in which the important subordinate traits have been more flexible, allowing the circumvention of hypothesized constraints between sprint speed and endurance.

By “subordinate traits” we mean lower-level phenotypes that affect speed, endurance, or both. This hypothesis could be tested with phylogenetically based statistical methods, once directly comparable data for such lower-level traits as relative limb length, muscle fiber types, maximal oxygen consump-

tion, and heart size become available for a substantial number of lacertids and phrynosomatids (e.g., Vanhooydonck et al. 2014). For example, it might be that variation in some of these subordinate traits is greater in phrynosomatids than in lacertids. Greater variation in the building blocks of locomotor performance could allow more degrees of freedom and hence more freedom from constraints on the joint evolution of speed and stamina. For example, if some species of phrynosomatids

were to evolve longer limbs, heavier muscles and hearts, and higher maximal oxygen consumption, then they might be able to achieve both higher sprint speed and endurance. Phylogenetic methods could also test whether any disparity in phenotypic diversity is greater than expected based on divergence times within the two lineages, thus indicating differences in rates of phenotypic evolution (e.g., Garland 1992; Hutcheon and Garland 2004; O'Meara et al. 2006).

Third, many functionally interrelated factors determine locomotor abilities—the system is highly complex (e.g., Emerson 1985; Emerson and Koehl 1990; Garland 1993; Foster and Higham 2014). Thus, simple trade-offs may be less likely to occur than for such traits as clutch size versus egg size in turtles (Congdon and Gibbons 1987), which are mainly a function of alternate ways to fill space or partition energy (Garland 2014). To understand locomotor trade-offs, or the lack thereof, we will need detailed studies of the morphological (Kohlsdorf et al. 2008; Barros et al. 2011), biomechanical (Higham 2007), physiological, and biochemical traits that underlie variation in speed and stamina (cf. Pease and Bull 1988). Although some such studies have been performed at the level of individual variation (e.g., Garland 1984; Garland and Else 1987; Gleeson and Harrison 1988), comparative studies of the correlates of speed or endurance are limited to relative limb length and fiber composition of a few muscles (e.g., Bauwens et al. 1995; Bonine and Garland 1999; Bonine et al. 2001, 2005; Vanhooydonck et al. 2014). In addition, if two characters do in fact trade off at a mechanistic level but both are positively or negatively correlated with some other factor(s), then a trade-off may not be apparent (see also Walker 2010).

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