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Master of them all: performance specialization does not result in trade-offs in tropical lizards

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ABSTRACT

Question: Does performance specialization lead to trade-offs among contrasting performance types?

Predictions: Evolutionary specialization for good performance at one task should result in relatively poor performance at contrasting tasks. We predicted that species with good sprinting ability would be relatively poor at the contrasting performance tasks of climbing, clinging, and jumping.

Organisms: Eighteen species of Lygosomine skinks from a diverse range of habitats in tropical Australia.

Methods: We measured four ecologically relevant modes of performance (sprinting, climbing, clinging, and jumping) and relevant morphological traits (e.g. body size, fore- and hind-limb length, body flatness).

Results: Contrary to predictions, phylogenetic analyses revealed a tight positive correlation between sprinting and climbing ability, climbing and clinging ability, and climbing and jumping. Sprinting, climbing, clinging, and jumping are presumably sufficiently similar tasks for scincid lizards for no trade-offs to be observed. There was no evidence that a flat body enhanced climbing in our study, but it may be related to energy efficiency in species from habitats that climb frequently on vertical surfaces.

Conclusions: The absence of trade-offs among performance traits, the converse to what has been observed for arboreal lizards (e.g. *Anolis*), suggests that such trade-offs are not general for lizards from all habitats or groups.

Keywords: ecomorphology, habitat specialization, performance, skinks, trade-offs.

INTRODUCTION

Natural selection acts on morphological traits, in theory shaping them to optimize habitat use (Futuyma, 1998; Schluter, 2000). Thus, based on the premise that form follows function, studying performance in the context of habitat variability provides a powerful test of adaptive traits (Arnold, 1983; Ricklefs and Miles, 1994; Lauder, 1996). It seems intuitive that some

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adaptations promoting excellent performance in a single habitat might reduce performance in other habitats, so that the 'jack-of-all-trades is master of none' (Huey and Hertz, 1984a; Futuyma and Moreno, 1988). Limb length of arboreal lizards provides a clear example of an adaptation that causes a trade-off between performance ability in one habitat compared with others: *Anolis* with long limbs that occupy wide perches are quick and agile (Losos, 1990a, 1990b; Losos *et al.*, 1994; Irschick and Losos, 1998; Irschick, 2000), but have reduced speed and agility on narrow perches (Losos and Sinervo, 1989; Macrini and Irschick, 1998). Similarly, chameleons trade-off sprint speed against clinging ability as leg length increases (Losos *et al.*, 1993). However, in lacertid lizards, a group that uses wide, flat substrates such as rock, there appears to be no trade-off between sprinting and climbing ability for species with longer limbs (Vanhooydonck and Van Damme, 2001). Thus, whereas the link between limb length and performance has been well explored (Garland, 1985; Losos 1990a; Garland and Losos, 1994), the extent to which morphology may constrain performance, causing trade-offs in performance in different habitats, remains a relatively open question (Losos and Sinervo, 1989; Sinervo and Losos, 1991; Vanhooydonck and Van Damme, 2001). Many trade-offs appear to depend on the substrate used. Examining the evolution of morphology (body shape and limb length) and performance in a group that uses a variety of substrates might clarify whether trade-offs are substrate-dependent.

Skinks occupy a wide array of habitats and exhibit a diverse range of morphologies, with different body shapes and limb lengths (Cogger and Heatwole, 1984; Greer, 1989; Melville and Swain, 2000; Pianka and Vitt, 2003). Long limbs and dorsoventral flattening associated with rock-using have evolved independently several times in Australian skinks (Ingram and Rawlinson, 1981; Covacevich, 1984; Greer, 1989; B.A. Goodman, unpublished data). Biomechanical theory predicts that long hind-limbs are beneficial for locomotion of ground-dwelling species in open habitats, where they enable longer strides and faster locomotion (Cartmill, 1985; Pounds, 1988; Vanhooydonck and Van Damme, 2001). Climbing species should have equal-length fore- and hind-limbs in order to grip securely (Cartmill, 1985; Losos *et al.*, 1993) and to stride similar distances with both limbs (Arnold, 1998; Vanhooydonck and Van Damme, 2001). Some climbing species have dorsoventrally flattened bodies, possibly to lower the centre of gravity and prevent toppling, and rigid bodies with reduced lateral bending perhaps to increase stability (Van Damme *et al.*, 1997). Despite the putative benefits of a flattened morphology for climbing, there has been no test of the influence of flattening on performance (Herrel *et al.*, 2002). Moreover, lacertid lizards show little evidence of body flattening or morphological differentiation among habitats (Vanhooydonck and Van Damme, 1999). Thus, an investigation of performance trade-offs using a group of morphologically divergent species should help to determine whether performance trade-offs due to limb length are generally present.

We measured four performance traits (sprinting, climbing, clinging, and jumping) in related scincid lizards that use a range of different habitats (trees, rocks, ground, and leaf litter), to examine how morphology and performance are related in lizards that use a variety of substrates, have different morphologies, and are not specialized solely for arboreal climbing. Specifically, we examined: (i) the relationship between key morphological traits and performance, and (ii) whether there was evidence for trade-offs among sprinting, climbing, clinging, and jumping of lizards with different morphological traits.

METHODS

Skinks in the sub-family Lygosominae occupy a range of microhabitat types [e.g. boulder-dominated mountains, rocky coastal inter-tidal zones, leaf litter, open ground, and trees

(Greer, 1989; Cogger, 2000)] and exhibit a broad array of morphological variation in body shape and limb length (Greer, 1989; Cogger, 2000). To explore the effect of evolutionary changes in morphology on locomotion in skinks, species from five genera (*Cryptoblepharus*, *Carlia*, *Eulamprus*, *Lampropholis*, *Techmarscincus*) and a diverse range of microhabitat types were examined (Ingram and Covacevich, 1980, 1989; Ingram and Rawlinson, 1981; Cogger, 2000; Goodman, in press).

Lizard sampling and captive husbandry

All species used in this study occur in tropical north-east Australia, and were collected by hand with the aid of baited sticky traps or with pit-fall traps modified for rocky habitats (Goodman and Peterson, 2005). In the laboratory, all individuals were maintained separately in a plastic container of one of three sizes for small (snout-to-vent length [SVL] < 45 mm, 350 mm long × 130 mm wide × 100 mm high), medium (SVL = 45–75 mm, 350 × 230 × 100 mm) or large individuals (SVL > 75 mm, 550 × 360 × 305 mm). Each container consisted of a substrate of moist potting mix (to a depth of 8–10 mm), a bark refuge, and water bowl, and was placed on a rack with a heating element positioned at one end that produced a thermal gradient within each box (range 23–45°C) that spanned the preferred body temperature range of the genera examined (Greer, 1980, 1989; B.A. Goodman, unpublished data). Containers were heated from 08.00 to 18.00 h and the temperature dropped to 23 ± 2°C when the heating was switched off. The photoperiod matched local tropical conditions and was produced by standard overhead fluorescent lighting that was on from 07.00 to 19.00 h. All captive lizards were fed a combination of live *Tenebrio* larvae and crickets dusted with mineral supplement (Repti-cal®) *ad libitum*.

Morphological measurements

All measurements were taken from live animals by first cooling each individual to 18 ± 1°C for a minimum of an hour. To avoid potential confounding effects of pregnancy on performance, only male lizards were used in the experiments. The following morphological traits were measured directly using digital callipers (± 0.01 mm): snout-to-vent length, body mass, inter-limb length, head width, head length, head height, tail length (if regenerated, both the original and regenerated tail portions), pectoral height, pectoral width, pelvis height, and pelvis width. In addition, each individual was radiographed to provide precise measurements of all skeletal elements. Radiograph measures were taken by first cooling each individual (as above) before securing it to a plexiglass plate (450 × 340 × 3 mm) using 3M™ Micropore Surgical tape (Hoefer *et al.*, 2003). Metal staples (12.9 mm wide × 6.2 mm high) fixed to the surface of each plate provided a size reference. Lizards were radiographed at two power intensities depending on the lizard's size: small-to-medium species (SVL = 30–75 mm) were radiographed at an exposure of 22 kV and 18 mA. Species with a snout-to-vent length > 75 mm were radiographed at an exposure of 24 kV and 20 mA. All skeletal measurements were taken directly from radiographs using digital callipers (± 0.01 mm) viewed on a light table at 20 × magnification. Repeated measures of radiographed staples and actual staple dimensions were used to scale a correction factor for all the skeletal measurements. All direct and radiograph measurements were taken three times and the mean used in the analyses.

Performance measures

Before conducting the performance trials, each individual was transferred in its container to a constant-temperature heating chamber set to 32°C (30°C for *Eulamprus*), where individuals were allowed to acclimate for at least an hour before each performance trial. This temperature range is within the field active body temperature range of members of these genera (Greer, 1989; B.A. Goodman, unpublished data). Only one performance trait was recorded per day, with at least one day between consecutive performance trials. Sprint speed was determined using a 2-m horizontal racetrack with a series of infra-red sensors positioned at 100-mm intervals along the entire length of the track. To ensure lizards were detected during normal locomotion (see below), two infra-red sensors were positioned one on top the other 5 mm apart at each interval along the length of the racetrack. The surface of the racetrack was course particle size sandpaper that provided excellent traction. Speed was the time elapsed between successive breaks of a series of beams positioned at 100-mm intervals along the length of racetrack. A trial began when a single lizard was removed from the incubator and placed at the start of the racetrack and encouraged to sprint using an artist's paintbrush. Each lizard was raced with at least an hour between successive trials and each trial was rated as either 'good' or 'poor'. A trial was rated as 'poor' if an individual jumped along or out of the raceway, turned 180° and ran in the opposite direction along the raceway, or simply stopped and refused to run the full length of the raceway. Trials were rated 'good' if individuals ran relatively constantly (i.e. only paused momentarily) while running along the entire length of the raceway.

Climbing ability was measured as for sprint speed except with the racetrack placed on a 70° angle; only individuals that produced two or more 'good' climbing trials were used in analyses. Both sprinting and climbing used the maximum 0.5-m interval as the measure of speed.

Cling performance was measured using a 5-g (for small *Carlia* and *Lampropholis*), 60-g (large *Carlia*, *Cryptoblepharus*, *Lampropholis*, *Techmarscincus*) or 300-g (the two *Eulamprus* species) Pesola™ spring-balance connected to a 25-cm long fine-gauge nylon fishing line (5 kg) with a slipknot noose tied to one end (Losos, 1990a; Zani, 2000). Trials were conducted by placing each individual on a flat, horizontal board covered with medium-course grain sandpaper. Each lizard was attached to the spring-balance by placing the noose around the mid-body just anterior to the pelvis, such that the line connecting the spring-balance was parallel to the lizards' body axis (Zani, 2000). Each trial consisted of placing a single lizard on the test surface and applying force at a constant horizontal speed ($0.3\ \mathrm{m \cdot s^{-1}}$) in a posterior direction until the lizard became dislodged (Losos, 1990a; Zani, 2000). Trials were conducted on each individual and graded as 'good' or 'poor' depending on whether an individual maintained a posture with outstretched limbs with the ventral surface in contact with the test surface; a minimum of two 'good' trials were obtained for each individual.

Jump distance was measured by placing each individual onto a circular podium (25 cm high × 13 cm wide at the top) positioned in the centre of a circular arena (130 cm diameter and 35 cm high) lined with sand to a depth of 5 cm. Individuals were encouraged to jump by lightly tapping the base of the tail using an artist's paintbrush. Jump distance was recorded as the maximal radial distance between the landing point of a lizard and the base of the podium. Individuals that did not jump within 15 s were returned to their box and placed back in the constant-temperature chamber to acclimate for another hour before being re-tested. Three jumps were recorded for each individual.

Statistical analyses

Mean values for each morphological measure for each species was $\log_{10}$-transformed before analyses to improve normality (Sokal and Rohlf, 1995). Each trait was regressed against $\log_{10}$-transformed snout-to-vent length and the residuals calculated and used in subsequent analyses as size-corrected performance and morphological measures. Body height was calculated as the mean of mid-body, pectoral, and pelvis height. Biomechanical predictions posit that terrestrial lizards should have shorter fore-limbs than hind-limbs. We calculated the limb ratio using a regression of log hind-limb length regressed against log fore-limb length (Vanhooydonck and Van Damme, 2001; Zaaf and Van Damme, 2001). Furthermore, the tibia should be long relative to the femur in the hind-limb of ground dwelling species to assist rapid running on broad, level surfaces. However, in climbers, both limbs should have a low intra-limb ratio, which should increase the ability to grip perches (Vanhooydonck and Van Damme, 2001). We calculated tibia–femur length from the regression of tibia length against femur length (Vanhooydonck and Van Damme, 2001). Species with a large tibia–femur length have a long tibia relative to their femur.

Related species share, to varying extents, part of their evolutionary history and for this reason do not constitute independent data (Felsenstein, 1985; Harvey and Pagel, 1991). Consequently, conventional statistical tests are invalid if used directly for interspecifc comparisons. The use of phylogenetic comparative methods that account for phylogenetic relationships provides a solution to this impasse. Phylogenetic comparative methods that incorporate Felsenstein's (1985) method of independent contrasts require information on the relationships between species, including correct information on the phylogenetic topology, branch lengths proportional to known variance in character evolution, character evolution that occurs by a process of Brownian motion, and little within-species variation within traits of interest (Felsenstein, 1985; Harvey and Pagel, 1991). However, although it is necessary to conduct analyses within a phylogenetic framework, whether hypotheses based on phylogenetic or conventional statistics should be considered more informative depends on whether the data show evidence of significant phylogenetic signal (Freckleton *et al.*, 2002; Blomberg *et al.*, 2003; Garland *et al.*, 2005). The descriptive statistic K provides one index of the amount of phylogenetic signal within a trait, based on the Brownian motion model of evolution of a given phylogenetic tree with known topology and branch lengths (Blomberg *et al.*, 2003). K-values equal to 1 indicate that a trait shows an expected amount of phylogenetic signal, whereas K-values less than 1 indicate a trait has less signal than expected and values of K greater than 1 suggest there is more phylogenetic signal than expected. To test for phylogenetic signal and calculate a K statistic and P-value for tests of significance for each trait, we used the program PHYSIG.M (Blomberg *et al.*, 2003), as implemented in the program MatLab. We performed 1000 randomizations on the current 'best-estimate' phylogeny and report K-values for all morphological traits examined in this study (Blomberg *et al.*, 2003) (Table 1). However, while K-values are likely to be more than 80% reliable for phylogenies consisting of 20 or more species, they are considerably less so for phylogenies with fewer than 20 species. As this study consisted of 18 species, we also report P-values for significance testing of all traits as produced in PHYSIG.M to provide an additional diagnostic of whether traits display phylogenetic signal (Blomberg *et al.*, 2003).

The phylogenetic hypothesis used in this study (Fig. 1) was based on current 'best-estimate' phylogenetic relationships of the molecular (Stuart-Fox *et al.*, 2002), immunological (Hutchinson *et al.*, 1990), and morphological relationships for members of the scincid sub-family

Table 1. *K*- and *P*-values of morphological traits of male lizards examined in this study

Trait	Number of MSE values ≤ original MSE	*K*	*P*
Snout-to-vent length	6	0.6771	0.006
Inter-limb length	5	0.7408	0.005
Head width	0	0.7462	<0.001
Head height	0	0.7538	<0.001
Body width	0	0.7092	<0.001
Body height	0	0.6637	<0.001
Radius–ulna length	4	0.5782	0.004
Humerus length	3	0.5949	0.003
Tibia–fibula length	11	0.5131	0.011
Femur length	13	0.5852	0.013
Fore-limb length	7	0.5780	0.007
Hind-limb length	6	0.5470	0.006
Tail length	32	0.4562	0.032

Note: All values calculated with branch lengths set to unity. Number of mean square error values (MSE) less than the original value is provided for reference. All values calculated using PHYSIG.M [see Blomberg *et al.* (2003) for details on methodology].

Lygosominae (Ingram and Covacevich, 1989). Supra-generic positions of genera were based on the phylogenetic relationships reported in Reeder (2003), with additional information taken from Hutchinson *et al.* (1990) and Greer (1989) for *Lampropholis* and *T. jigurru* (as *Leiolopisma jigurru*). While the position of *E. quoyii* was provided within Reeder (2003), the position of *E. brachysoma* was inferred from the close relationships and inclusion within the *E. murrayi* species group (Greer, 1989). The position of *Cryptoblepharus* was based on the inter-generic basis that the most primitive members of this genus are closely related to *Emoia* (Greer, 1974).

A recent molecular phylogeny of the genus *Carlia* (the rainbow skinks) failed to resolve fully many of the relationships within this genus and proposed *Lygisaurus* should be synonymized with *Carlia* where they form a small clade nested within the overall *Carlia* phylogeny (Stuart-Fox *et al.*, 2002). Additional sequence data from several new *Carlia* species failed to enhance the phylogenetic relationships (Couper *et al.*, 2005), and the presence of unresolved polytomies within the genus *Carlia* likely reflects a rapid (explosive) speciation event that probably occurred from the mid-Miocene onwards (Stuart-Fox *et al.*, 2002). The position of *C. rubrigularis* and *C. rhomboidalis* was based on mitochondrial DNA (mtDNA) evidence (Dolman and Moritz, 2006). Species in this study formerly within *Lygisaurus* (i.e. *Carlia rococo* and *C. laevis*) were placed in this sub-clade with several other arrangements also used in analyses. The position of *C. scirtetis* was based on evidence from morphological traits shared with the species *C. coensis* and *C. mundivensis*, with additional analyses performed with this species placed in other phylogenetic arrangements. As branch length information was not available for most species used in this study, branch lengths were set to unity. Several studies have shown that setting branch lengths to unity produces results that are robust and reliable (Diaz-Uriarte and Garland, 1996, 1998). As analyses involving all other phylogenetic arrangements, with and without polytomies treated as 'hard' (Purvis and Garland 1993; Garland and Diaz-Uriarte 1999), did not qualitatively change the analyses, we report only results for analyses using the 'best-estimate' phylogeny with potential polytomies treated as hard in this paper.

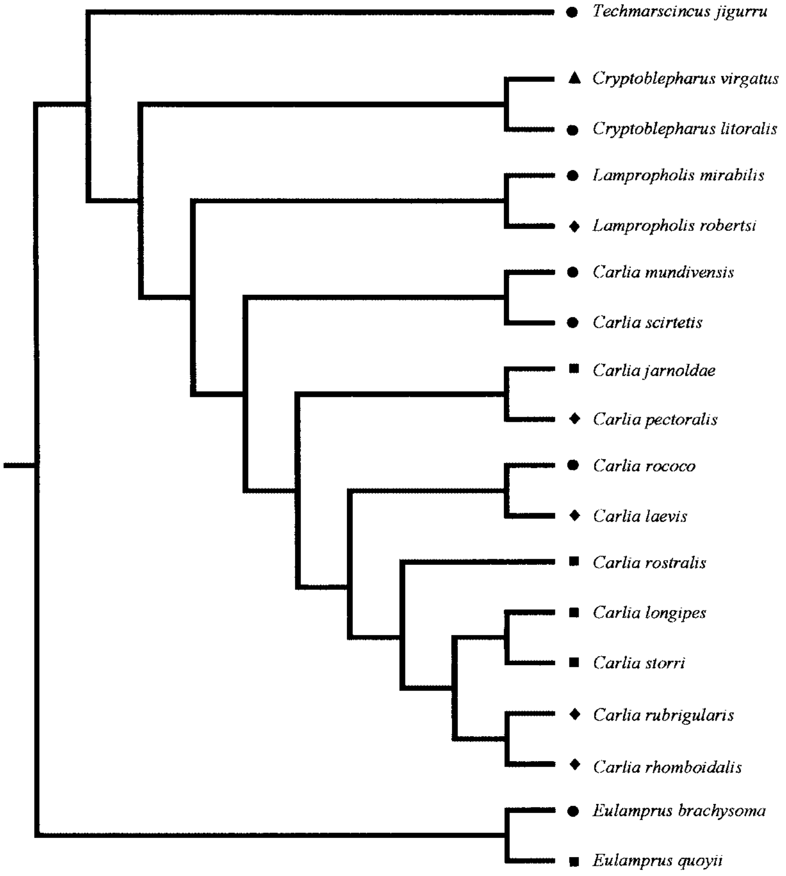


Fig. 1. Phylogenetic relationships of the 18 scincid lizard species examined in this study. The tree represents the current 'best-estimate' working hypothesis and is based on genetic (mitochondrial DNA, ND4), immunological, and morphological evidence (Greer, 1974, 1989; Covacevich, 1984; Stuart-Fox *et al.*, 2002; Reeder, 2003; Dolman and Moritz, 2006). Symbols indicate the four habitat types occupied by each species: ▲, arboreal; ■, generalist; ◆, leaf-litter dwelling; ●, rock-using.

Independent contrasts were calculated for all morphological and performance data sets using PDTREE. Because significant linear and non-linear trends indicate inadequate standardization of branch lengths, both statistical correlations and visual inspection of all diagnostic plots were performed. Contrasts of trait values were checked for adequacy of standardization by dividing the independent contrast of each trait by the standard deviation of the branch length (square root of the corrected branch lengths) for that trait (Garland *et al.*, 1992). However, as there was no evidence of any trends within the data ($r < 0.4$; all P-values > 0.12), branch lengths were considered adequately standardized under the Brownian motion model of evolution. The independent contrasts of the morphological data were size-corrected by regressing (through the origin) the standardized independent contrast of the trait of interest against the standardized independent contrast of snout-to-vent length (Garland *et al.*, 1992).

Limb ratio was calculated using an ordinary least-squares regression of the contrasts of hind-limb length against the contrasts of fore-limb length (Vanhooydonck and Van Damme, 2001; Zaaf and Van Damme, 2001). Tibia–femur length was calculated from the regression of the contrasts of tibia length against the contrasts of femur length (Vanhooydonck and Van Damme, 2001).

To determine those morphological traits (body height, fore-limb length, hind-limb length, and tibia–femur ratio) – both phylogenetic and non-phylogenetic – that accounted for most of the variation in performance, we used backwards stepwise, multiple regression [phylogenetic data through the origin (see Garland *et al.*, 1992)]. This technique provides a partial regression coefficient (β) between the response variable (performance trait) and significant morphological traits with each of the other variables statistically held constant. As correlated predictors may introduce problems of (multi)collinearity in multiple regression analyses, we tested that tolerance among correlated variables was above 0.1 (Quinn and Keough, 2002). Initial data inspection revealed fore-limb and hind-limb length were highly correlated, with low tolerance (both < 0.09). Consequently, we used the measure of limb-length with the highest significant correlation with each performance measure. In the absence of a significant correlation, we used hind-limb length, due to its importance in most aspects of lizard locomotion (Garland, 1985; Garland and Losos, 1994; Bonine and Garland, 1999). The use of a single measure of limb-length in the analyses considerably increased tolerance (all > 0.2). We report partial regression coefficients (β) ± standard errors and model r^2 values for both non-phylogenetic and phylogenetic analyses.

RESULTS

Non-phylogenetic analyses

Considerable interspecific differences in size and morphology were observed (Table 2), with a similar degree of interspecific variation in performance among the species examined (Table 3). There was a significant positive correlation between sprinting and climbing speed ($r = 0.55$, $P = 0.01$) and between climbing speed and cling force ($r = 0.76$, $P < 0.001$; Fig. 2, Table 3). All other performance measures were not significantly correlated (Table 4).

A backwards, stepwise multiple-regression model with residual sprint speed as the dependent variable and residual body height, hind-limb length, and the ratio of tibia–femur length as independent variables resulted in a significant model ($r^2 = 0.54$, $F_{1,17} = 5.44$, $P = 0.011$), with body height as the only contributing independent variable, indicating that lizards with flatter bodies sprint faster (partial regression coefficient $\beta \pm$ standard error $= -0.748 \pm 0.199$). The same model using climbing speed as the dependent variable identified fore-limb length as the only contributing variable ($r^2 = 0.72$, $F_{1,17} = 11.98$, $P < 0.001$): species with longer fore-limbs climb faster ($\beta = 0.780 \pm 0.297$). Cling force was determined by fore-limb length ($r^2 = 0.50$, $F_{1,17} = 4.73$, $P = 0.018$), so that species with longer fore-limbs cling more strongly ($\beta = 0.991 \pm 0.395$). There was no relationship between jump distance and any of the morphological variables measured ($r^2 = 0.26$, $F_{1,17} = 1.63$, $P = 0.228$). Interestingly, sprint speed was negatively correlated with the degree of body flattening (Fig. 3); however, this relationship did not hold for the phylogenetic comparison (Table 4).

Table 2. Species' names (*n*, sample sizes) and mean morphological traits (all in millimetres, except body mass in grams) for each of the 18 scincid lizards examined in this study (mean ± standard error)

Species	*n*	Snout-to-vent length (mm)	Body mass (g)	Inter-limb length (mm)	Body height (mm)	Fore-limb length (mm)	Hind-limb length (mm)	Tibia length (mm)	Femur length (mm)
Carlia jarnoldae	12	41.16 ± 0.71	1.59 ± 0.09	19.97 ± 0.40	4.37 ± 0.15	14.75 ± 0.28	19.90 ± 0.30	4.88 ± 0.08	6.58 ± 0.12
Carlia laevis	5	35.21 ± 0.28	0.73 ± 0.05	18.14 ± 0.36	3.10 ± 0.12	9.31 ± 0.27	13.37 ± 0.34	3.17 ± 0.06	4.87 ± 0.08
Carlia longipes	14	61.57 ± 1.21	5.66 ± 0.47	29.95 ± 0.78	7.58 ± 0.23	23.08 ± 0.36	33.47 ± 0.50	7.94 ± 0.15	10.45 ± 0.21
Carlia mundivensis	8	55.53 ± 1.82	4.29 ± 0.46	26.86 ± 1.01	6.27 ± 0.25	21.26 ± 0.69	28.24 ± 0.84	7.32 ± 0.27	9.75 ± 0.29
Carlia pectoralis	10	44.45 ± 1.02	1.87 ± 0.14	21.81 ± 0.59	5.18 ± 0.14	15.85 ± 0.34	22.64 ± 0.36	5.30 ± 0.11	7.19 ± 0.16
Carlia rhomboidalis	15	47.20 ± 0.93	2.54 ± 0.25	23.09 ± 0.53	5.50 ± 0.17	16.73 ± 0.26	22.58 ± 0.34	5.48 ± 0.09	7.36 ± 0.10
Carlia rococo	9	39.77 ± 1.13	1.06 ± 0.08	19.72 ± 0.72	3.64 ± 0.13	12.63 ± 0.34	17.16 ± 0.39	4.15 ± 0.08	5.96 ± 0.10
Carlia rostralis	8	59.89 ± 2.01	5.48 ± 0.45	29.68 ± 1.05	7.62 ± 0.30	22.09 ± 0.19	30.69 ± 0.37	7.32 ± 0.14	9.70 ± 0.17
Carlia rubrigularis	13	51.79 ± 1.20	3.53 ± 0.14	25.96 ± 0.59	6.21 ± 0.16	19.18 ± 0.42	25.76 ± 0.50	6.12 ± 0.14	8.42 ± 0.16
Carlia scirtetis	16	65.08 ± 1.71	5.32 ± 0.37	30.47 ± 0.88	6.55 ± 0.17	29.19 ± 0.59	39.76 ± 0.88	10.88 ± 0.29	13.19 ± 0.30
Carlia storri	5	40.72 ± 0.95	1.59 ± 0.17	19.67 ± 0.31	5.02 ± 0.11	15.59 ± 0.51	21.64 ± 0.44	5.07 ± 0.16	6.82 ± 0.21
Cryptoblepharus litoralis	14	42.48 ± 0.74	1.14 ± 0.08	21.89 ± 0.52	3.27 ± 0.08	16.08 ± 0.33	20.10 ± 0.28	4.81 ± 0.09	6.69 ± 0.13
Cryptoblepharus virgatus	14	36.06 ± 0.63	0.55 ± 0.04	18.40 ± 0.34	2.40 ± 0.06	13.44 ± 0.27	15.94 ± 0.28	3.84 ± 0.06	5.21 ± 0.08
Eulamprus brachysoma	12	68.43 ± 1.59	6.79 ± 0.39	35.45 ± 0.99	7.35 ± 0.24	22.85 ± 0.39	31.94 ± 0.58	7.23 ± 0.14	10.60 ± 0.19
Eulamprus quoyii	5	103.39 ± 2.58	30.03 ± 2.80	52.88 ± 1.75	12.71 ± 0.51	31.16 ± 0.64	45.57 ± 0.51	10.02 ± 0.21	14.46 ± 0.51
Lampropholis mirabilis	13	47.24 ± 0.89	1.89 ± 0.12	23.00 ± 0.43	4.55 ± 0.10	16.66 ± 0.29	23.19 ± 0.43	5.75 ± 0.13	7.64 ± 0.15
Lampropholis robertsi	12	46.97 ± 0.75	2.06 ± 0.12	25.13 ± 0.38	5.16 ± 0.14	14.28 ± 0.15	18.60 ± 0.29	4.33 ± 0.06	6.44 ± 0.09
Techmarscincus jigurru	10	70.43 ± 1.34	5.51 ± 0.31	37.71 ± 0.81	6.26 ± 0.11	24.28 ± 0.44	33.36 ± 0.57	7.69 ± 0.16	10.74 ± 0.24

Table 3. Species' names (*n*, sample sizes) and mean performance traits [in $m \cdot s^{-1}$, except cling force (see footnote) and jump distance in millimetres] for each of the 18 scincid lizards examined in this study (mean ± standard error)

Species	Label	*n*	Climbing speed ($m \cdot s^{-1}$)	Sprint speed ($m \cdot s^{-1}$)	Cling force (mN)*	Jump distance (mm)
Carlia jarnoldae	Cj	12	0.73 ± 0.05	0.52 ± 0.05	157.72 ± 12.41	268.50 ± 27.70
Carlia laevis	Cle	5	0.39 ± 0.03	0.57 ± 0.02	11.34 ± 03.36	237.60 ± 12.06
Carlia longipes	Cln	14	1.24 ± 0.05	1.20 ± 0.10	373.47 ± 20.43	351.25 ± 17.51
Carlia mundivensis	Cm	8	0.83 ± 0.07	0.83 ± 0.06	358.56 ± 26.48	257.88 ± 48.58
Carlia pectoralis	Cp	10	0.80 ± 0.06	0.86 ± 0.05	135.33 ± 08.75	316.60 ± 21.28
Carlia rhomboidalis	Crh	15	0.93 ± 0.04	0.77 ± 0.06	202.02 ± 10.34	323.07 ± 9.98
Carlia rococo	Crc	9	0.63 ± 0.03	0.90 ± 0.05	77.47 ± 20.82	194.11 ± 19.66
Carlia rostralis	Cro	8	1.07 ± 0.08	0.99 ± 0.11	343.23 ± 34.77	408.88 ± 31.64
Carlia rubrigularis	Crb	13	0.89 ± 0.04	1.02 ± 0.08	185.57 ± 19.93	304.85 ± 17.07
Carlia scirtetis	Csc	16	1.49 ± 0.08	2.06 ± 0.08	470.07 ± 25.22	330.20 ± 19.98
Carlia storri	Cst	5	0.82 ± 0.08	0.80 ± 0.09	125.53 ± 15.63	264.00 ± 46.24
Cryptoblepharus litoralis	Cyl	14	0.90 ± 0.08	1.48 ± 0.06	203.14 ± 08.20	229.00 ± 12.25
Cryptoblepharus virgatus	Cyv	14	0.86 ± 0.06	0.90 ± 0.06	119.43 ± 07.62	222.43 ± 9.92
Eulamprus brachysoma	Eb	12	1.28 ± 0.03	1.67 ± 0.07	809.05 ± 42.17	342.67 ± 13.24
Eulamprus quoyii	Eq	5	1.37 ± 0.09	2.33 ± 0.25	1398.43 ± 69.18	364.20 ± 30.50
Lampropholis mirabilis	Lm	13	0.92 ± 0.06	1.27 ± 0.07	196.51 ± 07.40	274.54 ± 24.11
Lampropholis robertsi	Lro	12	0.63 ± 0.05	0.58 ± 0.04	140.56 ± 13.19	242.67 ± 16.83
Techmarscincus jigurru	Tj	10	1.10 ± 0.05	1.22 ± 0.06	392.27 ± 17.30	280.00 ± 14.67

* Cling forces used in the analyses were raw gram pull-force values. The values presented have been converted to Newtons [1 g pull-force = 9.80665 mN (Losos, 1990a)].

Phylogenetic analyses

Overall, the results from the phylogenetically corrected data were broadly congruent with those of the uncorrected data. The four measures of performance were all positively correlated with each other (Table 4), with sprinting speed significantly positively correlated with climbing speed ($r = 0.71$, $P < 0.001$; Fig. 2). Climbing speed was significantly correlated with the ability to cling to a rock-like substrate ($r = 0.67$, $P < 0.001$; Fig. 2), and climbing ability was significantly positively correlated with jump distance ($r = 0.59$, $P < 0.05$; Fig. 2). There was a positive non-significant relationship between cling force and sprint speed.

In a backwards, stepwise multiple regression (through the origin) with sprint speed as the dependent variable and the residual contrasts of body height, hind-limb length, and the ratio of tibia–femur length as independent variables, only hind-limb length contributed significantly ($r^2 = 0.75$, $F_{1,16} = 40.56$, $P < 0.001$), indicating that the evolution of longer hind-limbs has coincided with faster sprint speeds (partial regression coefficient $\beta = 0.856 \pm 0.135$). A similar model, using jump distance as the dependent variable, was not significant ($r^2 = 0.20$, $F_{1,16} = 1.14$, $P > 0.36$). The same model with climbing speed as the dependent variable indicated that residual contrasts of fore-limb length contributed significantly to variation in climbing speed ($r^2 = 0.87$, $F_{1,16} = 62.51$, $P < 0.001$). This suggests that increased fore-limb length has evolved in concert with an increase in climbing speed

Table 4. Pearson correlation coefficients of performance and morphological traits for 18 scincid species of the sub-family Lygosominae

	Climbing speed	Cling force	Jump distance	Body height	Fore-limb length	Hind-limb length	Tibia–femur ratio	Fore-limb–hind-limb ratio
Sprint speed	0.55* **0.71****	0.24 **0.21**	−0.09 **0.44**	−0.55* **−0.20**	0.35 **0.78****	0.27 **0.85****	0.24 **0.08**	−0.13 **0.41**
Climbing speed		0.76** **0.67****	0.32 **0.59***	−0.13 **−0.39**	0.83** **0.88****	0.74** **0.82****	0.73** **0.48***	−0.07 **0.05**
Cling force			0.10 **0.19**	−0.04 **−0.10**	0.69** **0.56***	0.50* **0.42**	0.52* **0.37**	−0.33 **−0.25**
Jump distance				0.46 **−0.20**	0.17 **0.50***	0.33 **0.53***	0.27 **0.20**	0.45 **0.21**
Body height					0.05 **0.89****	0.29 **0.90****	0.12 **−0.46**	0.64** **0.19**
Fore-limb length						0.92** **0.94****	0.88** **0.21**	0.00 **0.07**
Hind-limb length							0.87** **0.14**	0.39 **0.41**
Tibia–femur ratio								0.17 **−0.14**

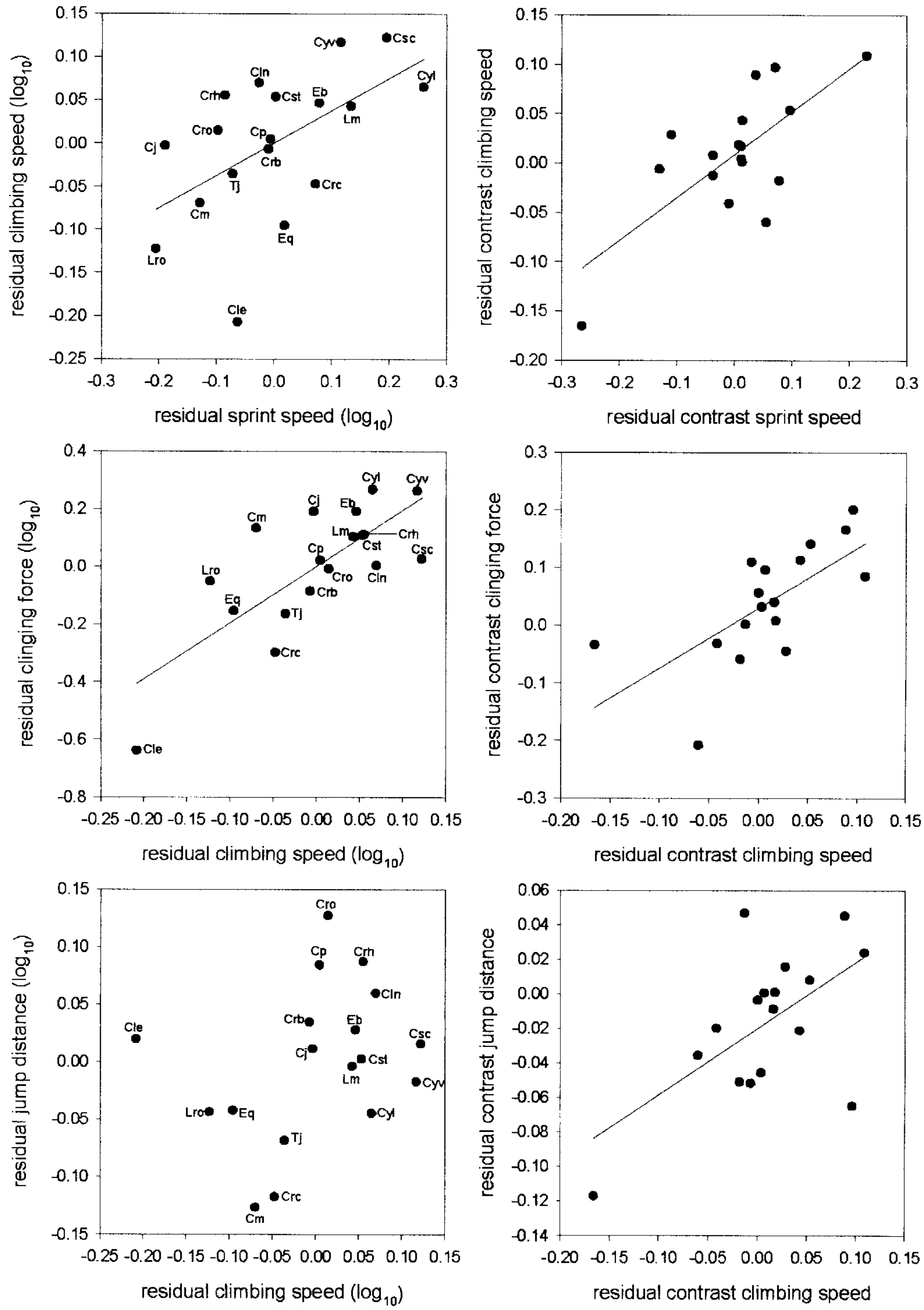
Note: Non-phylogenetic correlations ($n = 18$, above) are for residual (size-corrected against SVL) values. Phylogenetic correlations ($n = 17$, in bold below) are for (size-corrected against SVL contrasts) standardized independent contrasts.

* $-0.05 > P > 0.01$; **$0.01 > P > 0.001$.

($\beta = 0.795 \pm 0.101$). A similar model with cling force as the dependent variable retained residual contrasts of fore-limb length as the only variable contributing significantly to the model ($r^2 = 0.43$, $F_{1,16} = 6.11$, $P < 0.05$), indicating that an increase in fore-limb length evolved in concert with clinging ability ($\beta = 0.515 \pm 0.209$).

DISCUSSION

Specialization for a given task is thought to preclude simultaneous specialization for others, thus preventing specialized species from performing well at multiple tasks [e.g. 'jack-of-all-trades is master of none' (Huey and Hertz, 1984a; Stearns, 1992)]. However, in cases where selection for performance at one task enhances performance in other areas (e.g. sprinting, climbing, and clinging), there might be no trade-off in ability. We found no evidence of trade-offs in performance at sprinting, climbing, and clinging in this group of skinks; instead, good performance in one of these tasks was positively correlated with good performance in the others. Differences in limb length explained much of the variation in performance among species, with sprint speed correlated with hind-limb length, whereas climbing speed and clinging ability were correlated with fore-limb length. Hind- and fore-limb lengths were


residual climbing speed (log10)
residual sprint speed (log10)
Cyv
Csc
Cln
Crh
Cst
Eb
Cyl
Lm
Cro
Cp
Cj
Crb
Tj
Crc
Cm
Eq
Lro
Cle
0.15
0.10
0.05
0.00
-0.05
-0.10
-0.15
-0.20
-0.25
-0.3
-0.2
-0.1
0.0
0.1
0.2
0.3
residual contrast climbing speed
residual contrast sprint speed
-0.20
residual clinging force (log10)
residual climbing speed (log10)
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
-0.25
-0.20
-0.15
-0.10
-0.05
0.00
0.05
0.10
0.15
residual contrast clinging force
residual contrast climbing speed
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
residual jump distance (log10)
residual climbing speed (log10)
residual contrast jump distance
residual contrast climbing speed
0.06
0.04
0.02
0.00
-0.02
-0.04
-0.06
-0.08
-0.10
-0.12
-0.14

correlated as well. However, despite theoretical predictions, phylogenetic analyses revealed no evidence that the evolution of a flatter body *per se* has led to a direct performance benefit.

Absence of performance trade-offs

Biomechanical predictions suggest performance trade-offs should occur when morphological traits that enhance performance at one task negatively affect another. Based on this reasoning, some studies have predicted a trade-off between sprinting and climbing, as morphological traits optimal for horizontal locomotion apparently oppose those required for optimal vertical locomotion (Cartmill, 1985; Zaaf *et al.*, 1999; Zaaf and Van Damme, 2001). However, we found no support for this, as all performance measures (including both horizontal and vertical locomotion) were positively associated. Recent work suggests that trade-offs among performance abilities must be considered within the ecological context of the group examined (Vanhooydonck and Van Damme, 2001). No trade-offs were observed among sprinting, clambering, and climbing in lacertid lizards (Vanhooydonck and Van Damme, 2001). Thus, the relationships between sprinting, climbing, and clinging for scincids resemble those of lacertids. The strong positive correlation between sprinting and climbing in both these groups, and between clinging and climbing in scincids, implies that these traits require similar morphological features.

Positive correlations between sprinting and climbing are directly opposite to the findings for *Anoles* and chameleons, where trade-offs occur between sprinting speed and climbing speed. Characters enhancing sprinting and climbing apparently vary with substrate use. *Anoles* and chameleons use twigs and branches as perches (Schoener, 1968; Losos, 1990a; Irschick *et al.*, 1997), whereas skinks and lacertids typically use broad (relative to the lizard's body width), flat substrates such as rocks, bare earth, and leaf litter (Pianka, 1969; Vanhooydonck and Van Damme, 1999; B.A. Goodman, unpublished data). Surprisingly, the morphological features that enhance sprinting and climbing speed on broad surfaces do not enhance the same performance traits on narrow perches.

The apparent absence of trade-offs among performance traits in skinks and lacertids does not mean that they do not occur in other areas. For example, body shape has a strong influence on reproductive output in lizards (Vitt and Congdon, 1978; Vitt, 1981; Vitt and Price, 1982), and the flat body of many fast, rock-using skinks may reduce fecundity. Alternatively, a trade-off may occur in other performance measures, such as endurance (Vanhooydonck *et al.*, 2001). However, the clear message from this study is that morphologically more derived species are simply better at a greater range of tasks that are sufficiently similar that no trade-offs among them occur.

Fig. 2. Relationships between four performance measures (sprinting, climbing, clinging ability, and jumping distance). Left panels show non-phylogenetic residuals of performance means per species. Right panels show residual phylogenetic independent contrasts of performance means per species. Cj = *Carlia jarnoldae*, Cle = *Carlia laevis*, Cln = *Carlia longipes*, Cm = *Carlia mundivensis*, Cp = *Carlia pectoralis*, Crh = *Carlia rhomboidalis*, Crc = *Carlia rococo*, Cro = *Carlia rostralis*, Crb = *Carlia rubrigularis*, Csc = *Carlia scirtetis*, Cst = *Carlia storri*, Cyl = *Cryptoblepharus litoralis*, Cyv = *Cryptoblepharus virgatus*, Eb = *Eulamprus brachysoma*, Eq = *Eulamprus quoyii*, Lm = *Lampropholis mirabilis*, Lro = *Lampropholis robertsi*, Tj = *Techmarscincus jigurru*.

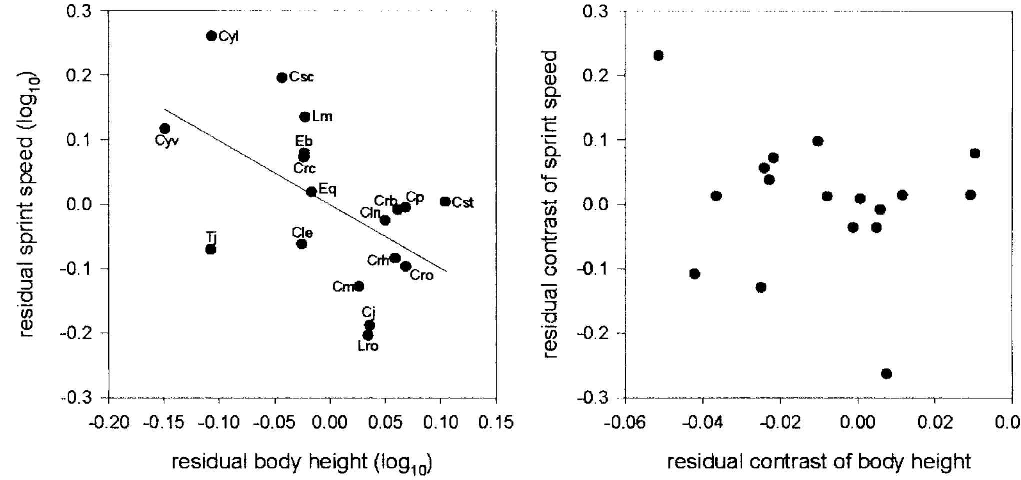


Fig. 3. Relationship between body height and sprint speed. Left panel shows non-phylogenetic residuals of species means for sprint speed. Right panels show residual phylogenetic independent contrasts of species mean body height against species mean sprint speed. Cj = *Carlia jarnoldae*, Cle = *Carlia laevis*, Cln = *Carlia longipes*, Cm = *Carlia mundivensis*, Cp = *Carlia pectoralis*, Crh = *Carlia rhomboidalis*, Crc = *Carlia rococo*, Cro = *Carlia rostralis*, Crb = *Carlia rubrigularis*, Csc = *Carlia scirtetis*, Cst = *Carlia storri*, Cyl = *Cryptoblepharus litoralis*, Cyv = *Cryptoblepharus virgatus*, Eb = *Eulamprus brachysoma*, Eq = *Eulamprus quoyii*, Lm = *Lampropholis mirabilis*, Lro = *Lampropholis robertsi*, Tj = *Techmarscincus jigurru*.

Limb length and performance

In this study, lizards with longer hind-limbs sprinted faster. This relationship has been noted for lizards and in other vertebrate groups (e.g. Losos, 1990a; Garland and Janis, 1993; Garland and Losos, 1994), and is caused by the increased stride length achieved with longer hind-limbs (Hildebrand, 1974; Cartmill, 1985; Losos, 1990a). Losos (1990b) observed an inverse relationship between fore-limb length and sprint speed in 14 species of *Anolis*. But for the group of scincids in our study, there was no indication that running was impeded by long fore-limbs; longer fore-limbs were either unrelated to running speed (uncorrected data) or were strongly positively correlated with running speed (phylogenetically corrected data). Climbing speed was also enhanced by long fore-limbs, and by long fore-limbs and hind-limbs. Increased fore-limb length, or fore-limbs and hind-limbs of equal length, are beneficial for climbing species, as it allows them to stride similar distances with each limb (Arnold, 1998; Vanhooydonck and Van Damme, 2001). Individuals climbing angled substrates should also benefit from increased tension provided by longer fore-limbs, which would prevent tumbling backwards (Cartmill, 1985; Alexander, 1992; Aerts *et al.*, 2003). Relative to the width of their body, the species in this study generally occupy broad substrates, such as rocks (B.A. Goodman, unpublished data). Thus, longer hind- and fore-limbs appear to combine to allow increased stride length, equal stride length, and increased pulling forces to enhance locomotion when climbing.

A direct consequence of increased running speed in lizards is the tendency for the body to lift, leading to bipedal locomotion (Aerts *et al.*, 2003). While increased stride length increases speed, the increased propensity for the fore-body to lift in a way that leads to bipedalism presents an obvious problem of flipping backwards on inclined surfaces (Aerts *et al.*, 2003). In climbing lizards, morphological traits that lower the centre of mass and bring it forward should reduce the possibility of fore-body lifting. In addition to body flattening (Van Damme *et al.*, 1997), these traits include increased fore-limb length to widen the base of support, and a more sprawled form of locomotion (Aerts *et al.*, 2003). Our study found support for increased fore-limb length to increase performance in climbing and clinging, and while non-phylogenetic analyses revealed that body flattening aided sprint performance, the phylogenetic analyses did not support this finding (see 'Alternative hypotheses for the role of body flattening' below).

Lizards with longer fore-limbs had greater clinging ability. The basis of this increased clinging ability is unclear, but may be related to an increased base of support (Aerts *et al.*, 2003), or an increased number of sub-digital lamellae, which may increase frictional forces and improve contact on irregular surfaces (Cartmill, 1985; Losos, 1990a). Increased clinging ability in species with longer fore-limbs should also assist climbing by improving traction on an inclined slope. In a comparative examination of lizard clinging ability, Zani (2000) found that an evolutionary increase in claw height and a reduction in toe length were correlated with an increased ability to cling to course substrates, but provided no information on how limb-length was related to cling ability or toe length. In another study (Goodman, in press), I found that limb-length and digit-length were strongly correlated in this group of scincids, suggesting that increased limb-length and toe-length may act in concert to increase clinging ability in this group. For example, species with longer limbs may be able to produce greater tension, or may possess greater amounts of muscle mass or different muscle fibre types that are better suited for clinging. Increased amounts of muscle mass in long-limbed species is unlikely in this group, with most high-performance species having thin, gracile limbs; however, muscle fibre types have not been examined.

Jumping ability was correlated with both fore-limb and hind-limb length in this study. There should be a tight correlation between relative hind-limb length and jump performance (Emerson, 1985; Losos *et al.*, 1989; Losos, 1990a, 1990b; Harris and Steudel, 2002), as a greater hind-limb length provides a greater distance over which it can extend and accelerate the body (Cartmill, 1985; Alexander, 1992). The correlation between fore-limb length and jump distance is presumably due to the tight correlation between fore-limb and hind-limb lengths (Table 4). That is, species with long hind-limbs jump the greatest distances, but also have long fore-limbs; it is unlikely that long fore-limbs are directly related to increased jump distance (Emerson, 1985; Losos, 1990a).

The absence of performance trade-off may be the result of reduced selection on performance in some situations, such as species that occupy closed habitats, or which use crypsis as a predator avoidance strategy. For example, selection on performance ability may be maximal in high-performance species, and considerably lower for low-performance species. Under this scenario, interspecific comparisons of performance would still be positive with no evidence of a trade-off, even if high-performance taxa do experience performance trade-offs.

An important consideration for comparative studies is the presumption that all species will undergo evolutionary changes in morphology that lead to greater performance. Even in the absence of constraints, natural selection may only shape individuals to be 'just good enough' to perform those tasks relevant to the habitats they occupy. Thus, while species that inhabit more specialized habitats will display associated performance traits, the prediction that they will perform the best at these performance tasks might not always be upheld.

Alternative hypotheses for the role of body flattening

While the non-phylogenetic analyses suggest there is a benefit of body flattening on sprint speed in scincid lizards, this relationship disappeared in the phylogenetic analyses, which suggests this relationship is relatively weak. Counter to predictions, there was no evidence that dorsoventral flattening aided climbing, despite a relatively strong (phylogenetic) correlation between body flattening and climbing speed. In this case, a comparison involving a larger number of species might prove worthwhile. However, dorsoventral flattening may have a more indirect benefit on climbing not identified in this study. One aspect of vertical locomotion that would likely benefit from a flatter body is energy efficiency. Efficiency of locomotion at low temperatures might have been an important factor in the evolution and ecology of arboreal lizards, such as geckos (Autumn *et al.*, 1999; Zaaf and Van Damme, 2001). For example, a ground-dwelling skink used almost 200% more energy to perform one unit of vertical work than a climbing gecko (Farley and Emshwiller, 1996). Within a taxonomic group, more dorsoventrally flattened species should expend less energy on postural adjustments and overcoming the forces of gravity due to their lowered centre of mass and reduced propensity to topple backwards on inclined surfaces [e.g. *Plica plica* (Vitt, 1991; Aerts *et al.*, 2003)]. In this scenario, body flattening may be unrelated to climbing speed, but would allow species to perform such tasks more efficiently. The majority of species in this study, other than *E. quoyii*, are relatively light (< 6 g) and weigh considerably less than the threshold mass (40 g) at which climbing performance is notably reduced by a heavy body in agamids (Huey and Hertz, 1982, 1984b). However, it is unknown whether climbing species in this study had lowered energetic costs, relative to non-climbing congeners. Field observations of flattened, rock-using species (e.g. *Carlia scirtetis*) indicate that they are extremely swift-moving (Goodman, in press), relative to less flattened congeners. To test this idea, future research should include measurements of field metabolic rates, energetic costs of climbing, and food acquisition and assimilation efficiency.

A further, alternative hypothesis for the function of a flat body is that it may increase the ease with which individuals can take refuge in crevices, as do iguanids (Vitt, 1981; Vitt *et al.*, 1997; Pianka and Vitt, 2003). While plausible, field observations of many of the flattest rock-using species in this study suggest that the evolution of flatness as an adaptation for crevice use is relatively minor for this group of skinks (personal observation). When approached, most species tend to use large gaps (relative to the height of the lizard) between rocks or rock overhangs as refuges (Goodman, in press). In addition, when observed inside rock crevices, these species do not wedge themselves into the narrowest part of the crevices and lack the sharply keeled scales that aid this behaviour in other taxa [e.g. *Egernia cunninghami* group (Cogger, 2000; Chapple, 2003)]. An additional alternative hypothesis is that a flattened body may assist a species to remain undetected against the substrate. A flat body, dorsal colouration that matches the background, and remaining motionless at the approach of a predator have co-evolved in numerous iguanian lizard clades (Schulte *et al.*, 2004). Indeed, most of the flattened, rock-using species examined in this study exhibit dorsal colouration that matches the rocks they typically occupy (Ingram and Rawlinson, 1981; Ingram and Covacevich, 1989), suggesting this could be a strategy used by this group of lizards.

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