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No trade-off between sprinting and climbing in two populations of the Lizard *Podarcis hispanica* (Reptilia: Lacertidae).

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Biomechanical reflections suggest that lizards that have specialized in running should differ in parts of their morphological design from lizards that have specialized in climbing. Moreover, adaptation in one direction may conflict with performance in the other. We tested this assumed trade-off by measuring climbing and running performance in two subspecies of the Mediterranean lizard *Podarcis hispanica.* One subspecies, *P. h. atrata*, inhabits a number of small islets near the Spanish coast. It is mainly ground dwelling. The other subspecies, *P. h. hispanica*, was sampled on the mainland of Spain. It frequently occupies vertical elements within its habitat. Our data do not support the notion of a trade-off between both types of locomotion. Individuals of *P. h. hispanica* both run and climb faster than those of *P. h. atrata.* There is no difference between subspecies in ability to cling onto tilted substrates. Predictions on the morphology of both subspecies, inspired by biomechanical arguments, are not supported by our measurements.

ADDITIONAL KEY WORDS:—clinging – evolutionary trade-off – intraspecific variation – locomotion – performance.

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INTRODUCTION

Closely related species or populations of lizards may differ substantially in running capacity, stamina, jumping power, climbing skills and other locomotor abilities (Bennett, 1980; Huey, 1982; Huey *et al.*, 1984, 1990; Losos & Sinervo, 1989; Losos 1990a,b; Sinervo & Losos, 1991; Losos, Walton & Bennett, 1993; Garland, 1994; Garland & Losos, 1994; Bauwens *et al.*, 1995). It has been argued that this variation may arise from evolutionary trade-offs. According to the 'habitat matrix' model (Moermond, 1979a,b; Pounds, 1988; Garland & Losos, 1994), excellence in one locomotor task may result from specialization to a particular habitat. Species will evolve behaviours and morphologies that are appropriate to the habitats occupied. If performance at several tasks is related to a single trait (or suite of traits), then trade-offs may exist such that performance at one task cannot be optimized without detrimentally affecting performance at the other (Lewontin, 1978; Rose, 1982; Losos, Papenfuss & Macey, 1989).

Lizards occupy a wide range of habitats and exhibit a great range of locomotor modes. Potentially conflicting pairs of locomotor modes include sprinting versus endurance (Alexander, 1968; Bennett, 1978; Bennett, Huey & John-Alder, 1984; Huey *et al.*, 1984; but see Bennett, 1980; Garland, 1984; Garland & Else, 1987; Tsuji *et al.*, 1989; Garland, Hankins & Huey, 1990); jumping versus running (Emerson, 1985; Pough *et al.*, 1992; but see Losos, Papenfuss & Macey, 1989; Losos, 1990a,b); and climbing versus horizontal locomotion (Peterson, 1984; Cartmill, 1985; Losos & Sinervo, 1989; Sinervo & Losos, 1991; Losos *et al.*, 1993). Although the notion of trade-off is central in our reasoning of the evolution of locomotion morphology and behaviour, it has seldom been tested.

In this paper, we investigate the trade-off between climbing and horizontal sprinting capacities in a lacertid lizard, *Podarcis hispanica*. From a biomechanical point of view, several considerations suggest that specialized runners and climbers should differ in parts of their morphological design, and, moreover, that adaptation in one direction may conflict with performance in the other (Kramer, 1951; Peterson, 1984; Cartmill, 1985; Losos *et al.*, 1993; Miles, 1994). For instance, having long, parasagittal limbs would be valuable for sprinting on horizontal surfaces, because it allows larger strides and reduces friction by elevating the body from ground surface. In contrast, short, transversal limbs would aid in climbing, because they bring the point of gravity closer to the substrate and broaden the plane of support. The distal limb segments should be long and light to reduce internal inertia in runners, but short and heavy to lower the point of gravity in climbers. Flattening of the body should be lateral in runners, because this facilitates the lateral flexibility needed to maximize stride length; it should be dorsoventral in climbers, again to lower the point of gravity. Trade-offs between sprint speed and stability or sure-footedness on arboreal surfaces have been reported for *Sceloporus occidentalis* (Sinervo & Losos, 1991), *Anolis* (Losos & Sinervo, 1989) and *Chamaeleo* (Losos *et al.*, 1993). However, a critical distinction needs to be made between moving on narrow surface such as branches and climbing on broad, flat surfaces such as rocks.

Lacertid lizards have radiated into most terrestrial habitats of Eurasia and Africa, occupying environments from tundra and high mountain habitats through heath, scrub and Mediterranean associations to tropical forest, semi-desert and desert (Arnold, 1989). In spite of the wide ecological radiation, the body shape of the

Lacertid family does not exhibit substantial morphological differentiation (Arnold, 1989). Populations of several lacertid species are known to thrive successfully in quite diverse types of habitats (see Böhme, 1986 for a review). Still, few studies have explicitly addressed the question of locomotory specialization in these lizards (but see Huey *et al.*, 1984; Bennett *et al.*, 1984). Trade-offs among locomotory functions and concordant morphological adaptation may therefore have gone unnoticed.

We present data on maximal sprinting, climbing and clinging capacities of *P. hispanica* lizards from two subspecies. *Podarcis hispanica hispanica* was sampled on the Spanish mainland, close to the town of Castellón (provincia Castellón). These lizards live on garden walls and other stone elevations and we seldom saw them moving on the ground surface. The other subpopulation, *P. hispanica atrata*, is endemic to the Columbretes archipelago (50 km out of the coast from Castellón). Adult lizards from the population on the main island of the archipelago (Isla Grossa) are on average bigger than their mainland conspecifics, and are seen more often running on ground surface. The aim of this paper is to inspect whether a trade-off exists between running, climbing and clinging performance.

MATERIAL AND METHODS

Animals and their maintainance

Podarcis hispanica is a small to medium sized lacertid lizard with a distribution ranging from SW-France throughout the Iberian peninsula and into NW-Africa. Like most lacertids, *P. hispanica* is a diurnal, heliothermic and actively foraging lizard that feeds mainly on small invertebrate prey. Although this species is catholic in its habitat choice, it is usually observed on or close to vertical elements within these habitats (e.g. walls, rocks, stony slopes, even trees). Some populations, like that of *P. h. atrata* sampled here, seem to have abandoned the saxicolous life style and occur on more horizontal terrain.

In September 1994, 15 adult *P. h. hispanica* (11 males and 4 females) and 15 adult *P. h. atrata* (8 males and 7 females) were caught by noose and transported from Spain to the laboratory in Antwerp, Belgium. These individuals were selected such that the snout-vent length (SVL) ranges of both subspecies overlapped (*P. h. hispanica*: 42.8–52.4 mm; *P. h. atrata*: 49.6–62.2 mm; males and females combined). One male *P. h. hispanica* was not used for the experiments. Lizards were housed in five large terraria with a sandy substrate, a few rocks and some vegetation. Two 150 W spots provided light and heat for 8 h day, enabling lizards to thermoregulate. Food (vitamin-dusted mealworms and crickets) and water were provided ad libitum.

Morphological measurements

To examine differentiation in general morphology between the subspecies, we measured the distance between front- and hindlegs, maximal body width and height, length and maximal diameter of femur, tibia, ulna and humerus, front- and hindfoot length, length of second toe of the left front- and hindfoot in 64 *P. h. atrata* and 35 *P. h. hispanica* specimens, using electronic callipers (precision 0.01 mm). We removed the influence of body size on these characters by regressing them against snout-vent length (SVL, all variables were log 10-transformed). The covariance matrix of size-free residuals was used as input for a principal component analysis (PCA). The mean factor scores of the sexes and subspecies were compared using two-way ANOVAs.

We tested the specific predictions that the 'climbing' subspecies (*P. h. hispanica*) should have shorter limbs (relative to SVL), shorter distal limb segments (relative to total leg length), and flatter trunks than the 'running' subspecies (*P. h. atrata*). 'Flatness' of the trunk was estimated by calculating the ratio of residuals of body width/body width.

Performance measurements

Before experimentation, lizards were put individually in plastic boxes that were placed in an incubator at 35°C. After at least 1 h, we removed a lizard from the chamber and measured its body temperature with a quick-reading electronic thermometer. We proceeded with the performance measurement only if the temperature was between 33 and 37°C. This range corresponds to the 80% thermal performance breadth for sprint speed in *P. hispanica* (Bauwens *et al.*, 1995) and falls within the range of body temperatures recorded in the field for active lizards (*P. h. hispanica*: 26.5–41.0°C (Pérez-Mellado, 1983); *P. h. atrata:* 26.6–39.3°C (Castilla & Bauwens, 1991)). Sprint speed, climbing speed and clinging performance were estimated on different days.

Sprint speed on a horizontal surface was measured by chasing lizards as fast as possible along a 2 m racetrack, on a substrate of cork tiles that provided excellent traction. Photocells, positioned at 25 cm intervals along the track, signalled passing lizards to a microcomputer that calculated sprint speed over each 50 cm section. We raced each individual three times on consecutive days. Each run was scored as 'poor' or 'good' (cf. van Berkum & Tsuji, 1987; Tsuji *et al.*, 1989). We took the fastest burst speed recorded over any 50 cm interval during all trials as an estimate of an individual lizard's maximum sprinting performance on a flat surface. None of the lizards were consistently scored as 'poor' runners.

Climbing capacity was estimated by chasing lizards up a similar race track, but only 100 cm long and tilted to an angle of 65 degrees. We repeated the experiment using two different types of substrate: (1) a copper mesh (mesh width 2 mm) and (2) smooth schists. Running procedures were the same as with the horizontal speed measurements. Some animals occasionally lost their grip while climbing on the schist slope. We counted the number of these 'errors' as an additional indicator of climbing ability.

For each individual lizard, we obtained two 'contrasts' by subtracting maximal climbing capacity (mesh, schists) from maximal sprinting capacity. We compared both contrasts between populations and sexes.

Clinging capacity was assessed by placing an individual lizard on a surface of schists and gently tilting the surface until the animal fell. The angle of inclination at which the lizard lost its grip was taken as an estimate of the clinging capability of the animal. Individuals were tested five times each. Performance measures were compared between subspecies and sexes using two-way analysis of variance.

RESULTS

Morphological measurements

PCA on the 16 size-free variables required four axes to explain 60% of the total variation. The first axis explained 35.3% of the variation and had high loadings for residual toe length (hind: 0.85, front: 0.68) and femur length (0.64). Mean factor scores on this axis did not differ between populations ($F_{1,80}=0.7$; $P=0.4$). The second axis (11.1%) was highly correlated with residual humerus diameter (0.74) and ulna diameter (0.61). Mean scores on this axis were higher for *P. h. hispanica* than for *P. h. atrata* (mean ± SD: 0.32 ± 0.91 vs -0.19 ± 1.00; $F_{1,80}=6.99$, $P=0.01$). The third axis (7.2%) had high loadings for residual body width (0.82), body height (0.77) and mass (0.72); scores on this axis did not differ between subspecies ($P=0.07$). The fourth axis was highly correlated with hindfoot length (0.74) and frontfoot length (0.68). Here, scores for *P. h. hispanica* were significantly higher than those for *P. h. atrata* (0.32 ± 1.03 vs -0.18 ± 0.93, $F_{1,80}=0.03$).

We found no effect of population ($P=0.6$) or population × sex ($P=0.8$) on lizard 'flatness'. Females had more deflated bodies than males ($F_{1,80}=9.03$, $P=0.004$). Total leg length did not differ significantly between subspecies or sexes (both $P>0.1$). Distal segments (midfoot and toe) were slightly longer (relative to total leg length) in *P. h. hispanica* than in *P. h. atrata* (two-way ANOVAs with total leg length entered as a covariate, midfoot: $F_{\text{pop }1,80}=5.34$, $P=0.02$; toe: $F_{\text{pop }1,80}=11.94$, $P=0.001$). No sex or population × sex effects were found significant for the latter two measures.

Sprint speed on a horizontal surface

Maximal sprint performance differed significantly between both populations (two-way ANOVA, $F_{1,25}=29.09$, $P<0.001$) but not between sexes ($F_{1,25}=1.71$, $P=0.2$, see also Van Damme *et al.* in prep.). *P. h. hispanica* specimens ran faster than *P. h. atrata* individuals.

Climbing on mesh

Maximal climbing speed was higher in *P. h. hispanica* than in *P. h. atrata* (two-way ANOVA, $F_{1,25}=7.24$, $P=0.013$), but did not differ between sexes ($F_{1,25}=0.31$, $P=0.3$). There was no significant sex-by-population interaction effect ($F_{1,25}=2.37$, $P=0.14$).

Climbing on schists

Whereas all 14 tested *P. h. hispanica* lizards succeeded in mounting the full 100 cm schist slope during at least one of the trials, 4 out of the 15 *P. h. atrata* never reached the top end of the track: they fell down half way or simply refused to climb. This interpopulational difference in climbing 'success' is significant (χ^2-test, $\chi^2=4.33$, $P=0.03$). The four individuals that did not succeed in covering the full length of the track were excluded from subsequent analyses of maximal speed. This procedure

TABLE. 1. Sprint speed and climbing speed (two substrates) of two subspecies of the lizard *Podarcis hispanica*. Shown are the mean, standard deviation (SD) and coefficient of variation (CV) of the maximal individual performances

		P. h. atrata ($n=15$)			*P. h. hispanica* ($n=14$)		
		mean	SD	CV (%)	mean	SD	CV (%)
sprint speed (horizontal)	cm/s	108.88	42.10	38.67	202.68	39.86	19.66
climbing speed* (schists)	cm/s	13.04	19.04	146.01	61.89	23.18	37.45
climbing speed (mesh)	cm/s	85.90	36.84	42.89	126.64	26.89	21.23

* $n=11$ for *P. h. atrata*

may lead to an underestimation of the difference in climbing capacities between both subspecies.

Mean climbing speed was higher in *P. h. hispanica* than in *P. h. atrata* (two-way ANOVA, $F_{1,21}=18.84$, $P<0.001$). There was no difference in climbing speed between sexes ($F_{1,21}=0.92$, $P=0.3$) and there was no sex-by-population interaction effect ($F_{1,21}=0.92$, $P=0.6$). The superior climbing skills of *P. h. hispanica* also follow from the lower number of 'errors' made while ascending the track. Lizards now and then lost their grip while climbing and fell over a short distance before they could restore their balance. *P. h. atrata* made more such mistakes than *P. h. hispanica* (mean number of drops over three trials: *P. h. atrata*: 4.44, SD = 2.4, $n=9$; *P. h. hispanica*: 1.36, SD = 2.4, $n=9$; Mann-Whitney *U*-test, $P=0.007$).

Contrasts between sprinting and climbing

The mean difference between sprint speed and climbing speed on mesh was smaller in *P. h. atrata* ($x=22.99\pm23.76$, $n=15$) than in *P. h. hispanica* ($x=76.04$, ±42.05, $n=14$, two-way ANOVA, $F_{1,25}=15.32$, $P=0.001$). The effects of sex ($F_{1,25}=0.24$, $P=0.6$) and the interaction between sex and population ($F_{1,25}=0.02$, $P=0.9$) on this contrast were non-significant. For the second contrast (sprint speed minus climbing speed on schists), we found a similar difference between subspecies (*P. h. atrata*: $x=97.43\pm48.21$, $\mathrm{n}=11$; *P. h. hispanica*: $x=140.79\pm42.76$, $\mathrm{n}=14$; $F_{1,21}=4.30$, $P=0.05$) and no sex or population × sex-effects (both $P>0.5$).

Clinging

We labelled lizards that loosened their grip during four or during all five trials as 'bad clingers'. All other lizards were considered 'good clingers'. Thus, nine out of 15 *P. h. atrata* performed 'bad', compared to 6 out of 14 *P. h. hispanica*. This difference is not significant ($\chi^2=0.86$, $P=0.64$).

Correlations among performances

There is no indication for a trade-off between climbing and horizontal running across subspecies. On the contrary, *P. h. hispanica* individuals were on average faster than *P. h. atrata* individuals, regardless of the inclination and the substrate of the race track used (Table 1). We also considered the possibility that the subspecies differ in *general* locomotory speed for some unknown reason, unrelated to the presumed trade-off. Such a difference may obscure the trade-off between climbing and sprinting. We can test this by considering the maximal speed obtained on the horizontal track as an indicator for 'general' swiftness and introducing it as a covariate in the model that describes differences between subspecies in climbing speed. In the case of a trade-off, we would expect animals that are slow on the horizontal track (*P. h. atrata*) to have high climbing speeds *relative to their running speeds*. Analysis of variance with sprinting speed entered as a covariate did not reveal an effect of population, sex or population × sex on climbing speed on mesh (all $P > 0.3$). A similar analysis of climbing speed on schists did reveal a difference between subspecies ($F_{1,20} = 8.12$, $P = 0.01$, no sex or population × sex-effects: both $P > 0.3$). *P. h. atrata* climbed worse on schists than *P. h. hispanica*, also when performance is expressed relative to performance on a horizontal track (mean residuals for *P. h. atrata* $x = -10.29$, $SD = 24.85$, $n = 11$; for *P. h. hispanica*: $x = 8.08$, $SD = 24.32$, $n = 11$).

DISCUSSION

Reflections on the conflicting morphological requirements of horizontal versus vertical locomotion (see Introduction) lead us to predict that specialization for climbing in *P. h. hispanica* would tend to compromise this subspecies' abilities as a sprinter. Our data do not support this hypothesis; there are no indications for a trade-off between running and rock climbing in this species.

First, we have found little evidence for morphological differentiation in *P. hispanica*. PCA did reveal some overall shape differences between two subspecies living in different habitats, but the low levels of significance and the small amount of variation explained by the PCA-axes make this result of questionable biological significance. The inconsistency between our predictions and results may imply that biomechanical models are inadequate or insufficient, or that the effect of external morphology is overruled by differences in physiology, biochemistry or behaviour that have not been assessed here.

Second, our performance measurements do not support the trade-off hypothesis. *P. h. hispanica* attains far higher speeds than *P. h. atrata*, irrespective of slope or substrate. Clinging ability does not differ between both subspecies. The interpopulational difference in performance therefore cannot be interpreted as the result of a trade-off between locomotion types. *P. h. hispanica* successfully combines features that allow it to run fast on horizontal surfaces with traits that enhance climbing capacity. This may not come as surprise from an ecological point of view, since the survival of *P. h. hispanica* probably depends on its locomotory skills on both horizontal and vertical substrates; although these lizards climb very frequently, they are also seen on ground level or moving on the tops of walls or horizontal rocks. From a biomechanical point of view however, the combination of sprinting and climbing skills is unexpected.

But why do individuals of *P. h. atrata* perform so poorly in the speed experiments? Interpopulational differences in locomotory capacity can be examined in mechanistic and in evolutionary terms (Huey *et al.*, 1990; Garland & Losos, 1994). With the present data, we cannot provide a definite answer on the proximate causes of the difference in locomotory speed between both subspecies. As the difference in speed remains regardless of slope and substrate, we are looking for design parameters that affect locomotion in all these conditions. These may include elements of morphology (e.g. dimensions, degree of axial flexion, orientation of level arms; Snyder, 1954; Sukhanov, 1968; Huey & Hertz, 1982; Garland, 1984), physiology (e.g. respiratory metabolism, heart function, muscle composition; Garland, 1984, 1985; Gleeson, 1980; Abu-Ghalyun *et al.*, 1988) and biochemistry (enzyme activity, histochemistry; Glesson, Mitchell & Bennett, 1980; Gleeson, 1982, 1985; Garland, 1984).

From an evolutionary point of view, the relatively poor performance of *P. h. atrata* could be interpreted in two ways. First, it may be the result of a trade-off other than the one considered. Huey & Hertz (1984) have raised the possibility of a trade-off between thermal tolerance and maximal locomotory performance. Assuming that 'a jack of all trades is master of none', lizards that perform well (compared to others) in their optimal temperature zone should perform relatively poorly at non-optimal temperatures. The few experiments that have been carried out to test this corollary of the Principle of Allocation (Levins, 1968) have failed to find support for it (Huey & Hertz, 1984). It is also unlikely that the principle could explain the differences in maximal performance in the species considered here, since the thermal performance breadth for sprinting is smaller for *P. h. atrata* than for *P. h. hispanica* (Bauwens *et al.*, 1995).

Other types of trade-offs may be expected among different ways of locomotion. We have investigated here one potentially conflicting pair (climbing versus sprinting), but sprint speed in *P. h. atrata* could be compromised by specialization for other functions (e.g. acceleration capacity, endurance, agility, Hertz, Huey & Garland, 1988) as well. We are unaware of studies that have explicitly tested the occurrence of these trade-offs in lizards, but data on fish (Webb, 1984) and birds (Norberg, 1985) have documented incompatibilities between these various components of locomotion. Checking the likeliness of this hypothesis, requires (1) gathering performance data for all these locomotory functions, and (2) assessing the relative importance of each of these functions for the fitness of lizards from both populations.

Along a second line of reasoning, the poor sprinting and climbing capacities of *P. h. atrata* compared to *P. h. hispanica* could reflect lower selection pressure on the former subspecies (Van Damme *et al.*, subm.). The ecological significance of maximal sprint performance remains largely untested (Hertz *et al.*, 1988, Pough, 1989, Garland & Losos 1994). Lizards rarely use maximal sprints during feeding and in social encounters, but possibly more frequently in predator avoidance (Hertz *et al.*, 1988 and references therein, but see Leal & Rodríguez-Robles 1995). Predation seems the most probable selective agent for sprinting capacity. Although we do not have quantitative data on predation pressure in both habitats, *P. h. atrata* seems to live in a relatively 'safe' environment. First, a number of typical lizard consumers (snakes, birds such as shrikes and corvids, feral cats and other mammals) are lacking on the Columbretes islands, leaving only two species of gulls (*Larus cachinnans michahellis* and *Larus audouinnii*, Castilla & Bauwens, 1991) as potential, but unspecialized, predators. Second, lizards on the island are most of the time in direct vicinity of vegetation cover, where they can hide from aerial pursuit. This situation is in sharp contrast with the mainland, where *P. h. hispanica* lives in a more open habitat, and with the full scale of potential predators present. Circumstantial evidence for a relaxed predatory situation on the island relative to the mainland comes from the difference in general behaviour between both subspecies: lizards from the continental population appear much more wary both in the field and in the lab than their island conspecifics.

Interestingly, the difference between climbing and sprinting proved larger in *P. h. hispanica* than in *P. h. atrata.* This might be the result of (1) higher selection on speed in *P. h. hispanica* and (2) different constraints on climbing and sprinting performance. In lizards that have not been selected for speed, climbing and sprinting performance may be correlated among individuals, because some (unknown) biochemical, physiological or morphological factors promote both types of performance. A higher selection regime may render lizards faster, but it is clear that this process can only continue upto a certain limit. This limit can be set by the biochemical, physiological or morphological particularities of the species. If the upper limit to climbing speed is lower than that of sprint speed, we may expect an uncoupling of the evolution of both performances and thus a larger discrepancy between both speeds (as found in *P. h. hispanica*). This scenario is not unlikely, because locomotion on vertical surfaces requires much more energy than sprinting on horizontal terrain. Therefore, constraints related to maximal power exertion are expected to be reached sooner for climbing than for running.

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REFERENCES

Abu-Ghalyun Y, Greenwald L, Hetherington JE, Grant AS. 1988. The physiological basis for slow locomotion in chameleons. *Journal of Experimental Zoology* **245:** 225–231.

Alexander RMcN. 1968. *Animal mechanics.* Seattle: University of Washington Press.

Arnold EN. 1973. Relationships of the palaearctic lizards assigned to the genera *Lacerta, Algyroides* and *Psammodromus* (Reptilia: Lacertidae). *Bulletin of the British Museum of Natural History (Zoology)* **25:** 291–366.

Arnold EN. 1989. Towards a phylogeny and biogeography of the Lacertidae: relationships within an Old-World family of lizards derived from morphology. *Bulletin of the British Museum of Natural History (Zoology)* **55:** 209–257.

Bauwens D, Garland TJr, Castilla AM, Van Damme R. 1995. Evolution of sprint speed in lacertid lizards: morphological, physiological and behavioral covariation. *Evolution* **49:** 848–863.

Bennett AF. 1978. Activity metabolism of the lower vertebrates. *Annual Review of Physiology* **400:** 447–469.

Bennett AF. 1980. The thermal dependence of lizard behaviour. *Animal Behaviour* **28:** 752–762.

Bennett AF, Huey RB, John-Alder H. 1984. Physiological correlates of natural activity and locomotor capacity in two species of lacertid lizards. *Journal of Comparative Physiology B* **154:** 113–118.

Böhme W. 1986. *Handbuch der Reptilien und Amphibien Europas. Wiesbaden:* AULA-Verlag.

Cartmill M. 1985. Climbing. In: Hildebrand M, Bramble DM, Liem KF, Wake DB, eds. *Functional vertebrate morphology.* Cambridge: The Belknap Press, 73–88.

Castilla AM, Bauwens D. 1991. Observations on the natural history, present status, and conservation of the insular lizard *Podarcis hispanica atrata* on the Columbretes archipelago, Spain. *Biological Conservation* **58:** 69–84.

Emerson SB. 1985. Jumping and leaping. In: Hildebrand M, Bramble DM, Liem KF, Wake DB, eds. *Functional vertebrate morphology.* Cambridge: The Belknap Press, 58–72.

Garland T Jr. 1984. Physiological correlates of locomotory performance in a lizard: an allometric approach. *American Journal of Physiology* **247:** R806–R815.

Garland T Jr. 1985. Ontogenetic and individual variation in size, shape and speed in the Australian agamid lizard *Amphibolurus nuchalis*. *Journal of Zoology (London)* **207:** 425–439.

Garland T Jr. 1994. Phylogenetic analyses of lizard endurance capacity in relation to body size and body temperature. In: Vitt LJ, Pianka ER, eds. *Lizard ecology—Historical and environmental perspectives*. Princeton: Princeton University Press, 237–260.

Garland T Jr, Else PE. 1987. Seasonal, sexual, and individual variation in endurance and activity metabolism in lizards. *American Journal of Physiology* **252:** R439–R449.

Garland T Jr, Hankins E, Huey RB. 1990. Locomotor capacity and social dominance in male lizards. *Functional Ecology* **4:** 243–250.

Garland T Jr, Losos JB. 1994. Ecological morphology of locomotor performance in squamate reptiles. In: Wainwright PC, Reilly SM, eds. *Ecological morphology—Integrative organismal biology.* Chicago: The University of Chicago Press, 240–302.

Gleeson TT. 1980. Metabolic recovery from exhaustive activity by a large lizard. *Journal of Applied Physiology* **48:** 689–694.

Gleeson TT. 1982. Lactate and glycogen metabolism during and after exercise in the lizard *Sceloporus occidentalis*. *Journal of Comparative Physiology* **147:** 79–84.

Gleeson TT. 1985. Glycogen synthesis from lactate in skeletal muscle of the lizard *Dipsosaurus dorsalis*. *Journal of Comparative Physiology* **156:** 277–283.

Gleeson TT, Mitchell GS, Bennett AF. 1980. Cardiovascular responses to graded activity in the lizards *Varanus* and *Iguana*. *American Journal of Physiology* **239:** R174–R179.

Hertz PE, Huey RB, Garland TJr. 1988. Time budgets, thermoregulation, and maximal locomotor performance: are reptiles olympians or boy scouts? *American Zoologist* **28:** 927–940.

Huey RB. 1982. Phylogenetic and ontogenetic determinants of sprint performance in some diurnal Kalahari lizards. *Koedoe* **25:** 43–48.

Huey RB, Bennett AF, John-Alder H, Nagy KA. 1984. Locomotor capacity and foraging behaviour in Kalahari lacertid lizards. *Animal Behaviour* **32:** 41–50.

Huey RB, Dunham AE, Overall KL, Newman RA. 1990. Variation in locomotor performance in demographically known populations of the lizard *Sceloporus merriami*. *Physiological Zoology* **63:** 845–872.

Huey RB, Hertz PE. 1982. Effects of body size and slope on sprint speed of a lizard (*Stellio (Agama) stellio*). *Journal of Experimental Biology* **97:** 401–409.

Huey RB, Hertz PE. 1984. Is a jack-of-all-temperatures a master of none? *Evolution* **38:** 441–444.

Kramer G. 1951. Body proportions of mainland and island lizards. *Evolution* **5:** 193–206.

Leal M., Rodríguez-Robles JA. 1995. Antipredator responses of *Anolis cristatellus* (Sauria: Polychrotidae). *Copeia* **1995:** 155–161.

Levins R. 1968. *Evolution in changing environments*. Princeton: Princeton University Press.

Lewontin RC. 1978. Adaptation. *Scientitic American* **239:** 156–169.

Losos JB. 1990a. Ecomorphology, performance capability, and scaling of West Indian *Anolis* lizards: an evolutionary analysis. *Ecological Monographs* **60:** 369–388.

Losos JB. 1990b. The evolution of form and function: morphology and locomotor performance in West Indian *Anolis* lizards. *Evolution* **44:** 1189–1203.

Losos JB, Papenfuss TJ, Macey JR. 1989. Correlates of sprinting, jumping and parachuting performance in the butterfly lizard, *Leiolepis belliani*. *Journal of Zoology (London)* **217:** 559–568.

Losos JB, Sinervo B. 1989. The effects of morphology and perch diameter on sprint performance of *Anolis* lizards. *Journal of Experimental Biology* **245:** 23–30.

Losos JB, Walton BM, Bennett AF. 1993. Trade-offs between sprinting and clinging ability in Kenyan chameleons. *Functional Ecology* **7:** 281–286.

Miles DB. 1994. Covariation between morphology and locomotory performance in sceloporine lizards. In: Vitt LJ, Pianka ER, eds. *Lizard Ecology—Historical and experimental perspectives*. Princeton: Princeton University Press, 207–236.

Moermond TC. 1979a. Habitat constraints on the behaviour, morphology, and community structure of *Anolis* lizards. *Ecology* **60:** 152–164.

Moermond TC. 1979b. The influence of habitat structure on *Anolis* foraging behavior. *Behaviour* **70:** 147–167.

Norberg U. 1985. Flying, gliding and soaring. In: Hildebrand M, Bramble DM, Liem KF, Wake DB, eds. *Functional vertebrate morphology*. Cambridge: The Belknap Press, 129–158.

Pérez-Mellado V. 1983. Activity and thermoregulation patterns in two species of Lacertidae: *Podarcis hispanica* (Steindachner, 1870) and *Podarcis bocagei* (Seoane, 1884). *Cienc. Biol. Ecol. Syst. (Portugal)* **5:** 5–12.

Peterson JA. 1984. The locomotion of *Chamaeleo* (Reptilia: Sauria) with particular reference to the forelimb. *Journal of Zoology* **202:** 1–42.

Pough FH. 1989. Organismal performance and Darwinian fitness: approaches and interpretations. *Physiol. Zool.* **62:** 199–236.

Pough FH, Magnusson WE, Ryan MJ, Wells KD, Taigen TL. 1992. Behavioral energetics. In: Feder ME, Burggren WW, eds. *Environmental physiology of the amphibians.* Chicago: Chicago University Press, 395–410.

Pounds JA. 1989. Ecomorphology, locomotion, and microhabitat structure: Patterns in a tropical mainland *Anolis* community. *Ecological Monographs* **58:** 299–320.

Rose MR. 1982. Antagonistic pleiotropy, dominance, and genetic variation. *Heredity* **48:** 63–78.

Sinervo B, Losos JB. 1991. Walking the tight rope: arboreal sprint performance among *Sceloporus occidentalis* lizard populations. *Ecology* **72:** 1225–1233.

Synder RC. 1954. The anatomy and function of the pelvic girdle and hindlimb in lizard locomotion. *American Journal of Anatomy* **95:** 1–36.

Sukhanov VB 1968. *General system of symmetrical locomotion of terrestrial vertebrates and some features of movement of lower tetrapods*. (translated into English by Amerind Publishing Co., New Delhi 1974), Nauka Pub., Leningrad.

Tsuji JS, Huey RB, Van Berkum FH, Garland T, Shaw RG. 1989. Locomotor performance of hatchling fence lizards (*Sceloporus occidentalis)*: quantitative genetics and morphometric correlates. *Evolutionary Ecology* **3:** 240–252.

van Berkum FH, Tsuji JS. 1987. Inter-familiar differences in sprint speed of hatchling *Sceloporus occidentalis* (Reptillia: Iguanidae). *Journal of Zoology (London)* **212:** 511–519.

Webb PW. 1984. Body form, locomotion and foraging in aquatic vertebrates. *American Zoologist* **24:** 107–120.