Correlates of sprinting, jumping and parachuting performance in the butterfly lizard, *Leiolepis belliani*

J. B. Losos[1,2], T. J. Papenfuss[1] and J. R. Macey[1,3]

[1] *Museum of Vertebrate Zoology, University of California, Berkeley, CA 94720*
[2] *Department of Zoology, University of California, Berkeley, CA 94720*
[3] *College VIII, Box 268, University of California, Santa Cruz, CA 95064*

(With 1 plate and 4 figures in the text)

Leiolepis belliani, a cursorial, beach-dwelling lizard, moves by running and jumping. The lizards' ability to flatten dorsoventrally, thereby increasing surface area and decreasing wing loading, may also confer parachuting ability. We measured locomotor performance of three ecologically relevant tasks: running, jumping and parachuting. In addition, we investigated whether, with the effect of size removed, locomotor performance capabilities are correlated, and whether they correlate with morphological features. Larger lizards fell and ran faster and jumped further. Lizards that were experimentally prevented from flattening fell faster than control lizards. When the effects of size were removed, limb length was uncorrelated with jumping and running performance; performance measures also were not correlated amongst themselves. The scant natural historical data available for this species suggests that lizards do not use their parachuting capability, and that dorsoventral flattening may have evolved for some other purpose. *Leiolepis* might serve as a useful model in understanding the evolution of gliding lizards (e.g. *Draco*).

Contents

Introduction

Study of adaptation has often been based on an assumed relationship between form and function (e.g. Bock & von Wahlert, 1965). At the populational level, slight differences in morphology could result in differences in fitness and serve as the basis for evolutionary change. Interspecifically, morphological differences may reflect adaptation to different biological roles; morphotypic series may parallel the evolution of an adaptive feature.

559

Recent interest in the performance capability of organisms at ecologically relevant tasks (e.g. Bennett, 1980; Hertz, Huey & Nevo, 1983; van Berkum & Tsuji, 1987) allows these hypotheses to be examined more carefully. For a trait to be an adaptation (*sensu* Gould & Vrba, 1982) to some environmental feature, a relationship must exist between that trait and performance capability; differences in performance capability, in turn, must lead to differences in fitness (Arnold, 1983, 1986). This implies, further, that if performance at several different tasks is related to a single trait, 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). By establishing the relationship between morphology and performance capability among extant taxa, it is possible to make deductions about whether a trait may have arisen historically as an adaptation to particular environmental circumstances (Greene, 1986).

Here we illustrate these approaches by examining correlates of locomotor performance in an Asian agamid, *Leiolepis belliani*, the butterfly lizard. Study of this species is particularly appropriate because it moves in several ways, by running, jumping and—it is claimed—by jumping from the ground and gliding on outstretched lateral folds (see below).

Our expectations are based on simple biomechanical models. At a given body size, relatively longer-legged lizards should have longer strides and run faster (Hildebrand, 1974). Jump distance should be proportional to the time through which the propulsive force acts, which should be a function of hind leg length (Hill, 1950; Emerson, 1985). Time of descent should be inversely proportional to the square root of wing loading (which refers herein to total ventral surface area, i.e. mass/ventral surface area [Rayner, 1981]).

Consequently, we predict that, when the effect of differences in body size are removed, long-legged lizards will perform better at both running and jumping, but should be no different at parachuting (differences in leg length do not substantially affect total surface area of a lizard). We further predict that lateral flattening will confer parachuting ability and may serve as a model for visualizing the early stages of evolution of gliding flight, as exemplified by the related agamid lizard genus *Draco*.

Materials and methods

Leiolepis belliani, a relatively large lizard (max. snout-vent length [svl] 175 mm), lives near beaches and sandy areas in tropical South-East Asia. It is terrestrial and uses its well-developed claws to dig burrows (Smith, 1935; Taylor, 1963). Little is known about the ecology or behaviour of this species, which can be abundant locally (Swinhoe, 1870; Smith, 1935). Forty specimens were captured by local residents between 24–27 September 1987 from beaches on Phuket Island, Phuket Province, Thailand, and transported to the Museum of Vertebrate Zoology, University of California, Berkeley. They were housed in seven 2 m × 3 m × 3 m wooden cages, subjected to natural California light-cycles, maintained at 20–28 °C (with diel fluctuations), and fed (waxworms, crickets and lettuce) and watered daily. All performance measurements were made within 3 weeks of capture at lizard body temperatures of 34–36 °C, which is within the optimal temperature range for sprint performance in other agamids (Hertz *et al.*, 1983).

Running

Lizards were placed at the lower end of a 2-m trackway with photocell stations at 0·25 m intervals and allowed to run into a dark cloth bag at the other end (protocol following Huey & Hertz, 1982). Most lizards ran as soon as they were released; those that did not were encouraged by repeated taps on the tail. The track was placed at a 35 ° incline from the horizontal because large lizards running bipedally on a horizontal track

sometimes stepped over and failed to trip the light beams. Lizards were trained to run in 2–3 trials on the track. Two days later, they were run 4 times at hourly intervals. The fastest 0·25 m interval was considered the maximum speed for a lizard. Only trials in which the lizard ran bipedally at a sustained and rapid pace were considered acceptable. Data are included only for lizards for which 3 of the 4 runs were acceptable.

Jumping

Lizards were placed with the tip of the snout on the edge of a foam mat on a table 0·75 m above the floor. Lizards were restrained by the base of the tail (most agamids do not have autotomy planes in their caudal vertebrae); when released, they immediately jumped on to a foam mat on the floor. The horizontal distance from the edge of the table to the tip of the snout upon landing was measured. Lizards were jumped 3 times in rapid succession. The longest jump was considered the maximum distance for that lizard. Lizards that only made poor jumps (those that headed downward and not outward) were excluded from the analysis.

Parachuting

These experiments tested whether lateral flattening, which occurs by extension of the ribs while falling (see Plate I), slows the descent of falling lizards. In the first experiment, time of descent was measured for 18 lizards that were dropped 8·5 m on to several large foam cushions. Lizards were unhurt, and rapidly ran away upon landing. The lizards were then killed by interperitoneal injection of Nembutal (the rationale for originally collecting the lizards was to preserve them as museum specimens), and dropped again in the same manner (prior to dropping, lizards were held horizontally by the trunk and released). In contrast to live lizards, which fell with legs outstretched, dead lizards tumbled by pitching forward and rolling. To assess the role of lateral flattening independent of posture, 22 lizards were dropped once unrestrained and once with their folds taped to their sides. Eleven lizards were dropped first unrestrained, and then 30 min later restrained. The other 11 were dropped in the reverse order.

Morphological measurements

Freshly dead specimens were weighed, measured and x-rayed. Humerus length, radius length, hand length (from proximal end of ulnare to distal end of the ungual phalanx of manal digit 3), femur length, tibia (including astragalocalcaneum) length, foot length (from proximal end of the fourth distal tarsal to distal end of the ungual phalanx of pedal digit 4), maximum forearm and foreleg width (body outlines were apparent on x-rays), and trunk width (the mean of the minimum and maximum trunk width), were measured from radiographs. Measurements were taken on the right side of the body except when appendages on that side did not lie flat on the x-ray plate. Tail length and width (at the base) and svl were measured on specimens. Maximum dorsoventral expansion was measured by manually flattening the lizard and measuring across the widest part. Minimum surface area was measured by treating a lizard as a combination of rectangles. The following products were summed: svl × trunk width, 2 × (humerus + radius) × maximal forearm width, 2 × (femur + tibia) × maximal foreleg width, tail length × tail width. Maximum (i.e. flattened) lizard surface area was measured similarly with the exception that trunk width was calculated as the mean of the minimum trunk width from the x-rays and the maximum width calculated by manual flattening. Specimens were sexed by internal inspection. Maximum rib length, measured as the chord from the head to the distal end of the longest rib, of *L. belliani*, *Uromastix geyrii*, *Agama stoliczkana* and *Draco maculatus* were measured from x-rays of specimens in the collections of the California Academy of Sciences and Museum of Vertebrate Zoology, University of California, Berkeley. All morphological and performance measurements were natural log transformed for statistical analysis, with the exception of wing loading, which was arcsine transformed.
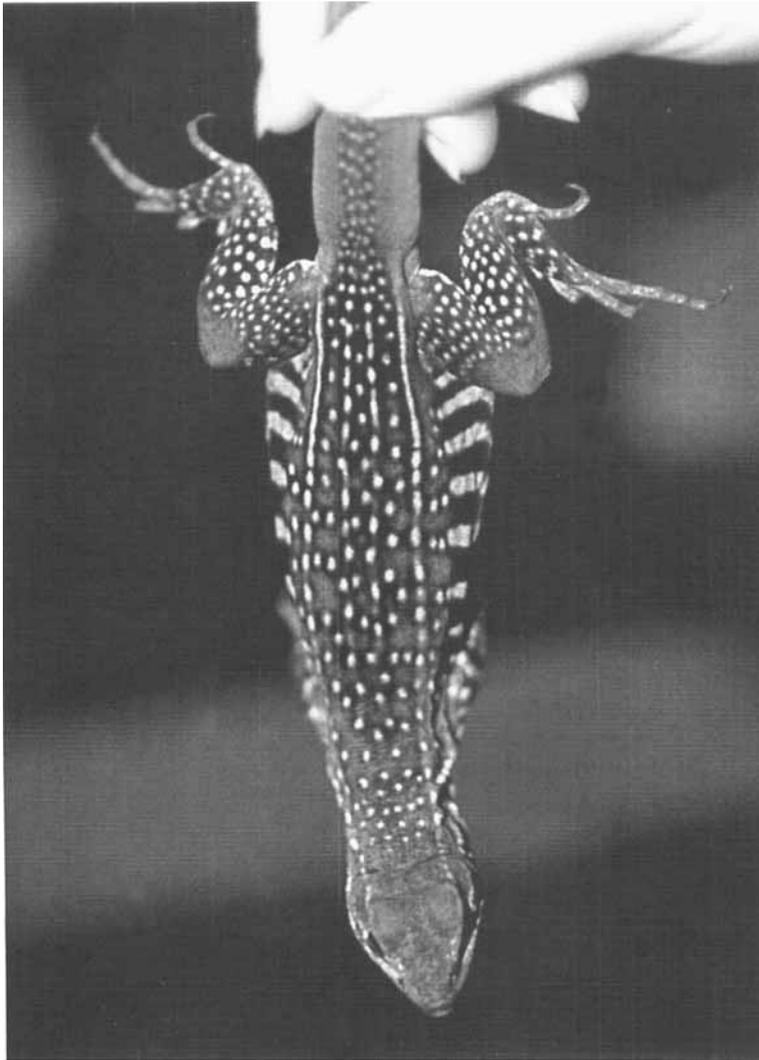
PLATE I. *Leiolepis belliani* demonstrating dorsoventral flattening. When the lizard is not flattened, the orange and black bars on the flank are barely visible from above.

Results

Morphology

Sexes did not differ in humerus length, radius length, femur length, tibia length, hind leg length, hind limb length, weight and surface area with and without dorsoventral flattening (analysis of covariance, test for heterogeneity of slopes, $P > 0.2$ in all cases, test for difference in intercepts, $P > 0.1$ in all cases). Discriminant function analysis could not distinguish between the sexes based

TABLE I
Principal components analysis of morphological and performance residuals

	PC axis					
	1	2	3	4	5	6
humerus	0·912	−0·207	0·156	−0·210	0·089	−0·131
radius	0·768	0·060	−0·104	−0·265	−0·397	0·008
hand	0·697	−0·283	−0·135	0·403	0·214	0·180
femur	0·913	0·026	0·015	−0·116	−0·027	−0·054
tibia	0·929	−0·182	0·076	0·129	−0·021	0·010
foot	0·889	−0·283	−0·018	0·165	−0·067	0·220
tail	0·297	0·460	−0·715	−0·166	0·056	0·317
maximum surface area	0·421	0·831	−0·143	−0·175	0·006	0·205
forearm width	0·513	0·238	0·065	0·585	−0·164	−0·480
foreleg width	0·098	0·870	0·188	0·032	0·056	−0·144
weight	0·248	0·673	0·560	−0·254	0·006	−0·115
jump	0·281	−0·030	0·024	−0·141	0·930	−0·126
run	−0·196	0·591	−0·212	0·634	0·113	0·111
descent time	−0·004	0·034	0·765	0·192	0·012	0·595
percentage variance	36·5	19·7	11·2	9·0	6·4	2·9

on these measurements (Wilks'-Lambda = 0·876, F = 0·504, $d.f.$ = 9, 32, $P < 0.9$) or their residuals (calculated as below; Wilks'-Lambda = 0·859, F = 0·583, $d.f.$ = 9, 32, $P < 0.9$).

Hind leg length (log hind leg [mm] = 2·790 + 0·282 * log mass [g], $r^2 = 0.977$), hind limb length (log hind limb = 3·472 + 0·265 * log mass, $r^2 = 0.967$), and maximum surface area (log maximum area [cm^2] = 6·594 + 0·652 *log mass, $r^2 = 0.983$) increase with negative allometry relative to mass. The slopes for all three equations differ from 0 ($P < 0.001$). The slopes of the limb element equations differ from the slope for isometric growth (b = 0·333, $P < 0.001$); the slope for maximum surface area does not differ from the slope for isometric growth (b = 0·667, $P < 0.4$). Size-related differences were removed by calculating residuals, with svl as the independent variable; residual values were then used in a principal components analysis. All components of the appendicular skeleton load strongly and postively on the first axis, i.e. the relative size of a lizard's leg elements are strongly correlated (Table I). The second axis indicates that relatively heavy lizards have a large surface area and wide hind legs, which is indicative of relatively great thigh muscle cross-sectional area.

The ribs of *Leiolepis* curve posteroventrally much more than the ribs of the other species, leading to a relatively large underestimate of their length. Despite this conservative bias, we found that *Leiolepis* has longer ribs than *Uromastix* and *Agama*, but considerably shorter than those of *Draco maculatus* (analysis of covariance, heterogeneity of slopes $P < 0.01$ in all cases; Fig. 1).

Performance

Sprint speed and jumping distance increase allometrically (Figs 2 and 3); size accounts for 21% of the variation in sprint speed ($F_{1,22}$ = 5·702, $P < 0.03$) and 52% of the variation in jump distance ($F_{1,29}$ = 31·32, $P < 0.001$). The allometric relationships do not differ between the sexes (analysis of covariance, test for heterogeneity of slopes, $P < 0.45$, test for difference in intercepts, $P < 0.6$).

With the effect of size removed, no relationship exists between either leg or limb length (= leg + foot length; we present here calculations using limb length) and sprint speed ($r^2 = 0.013$,
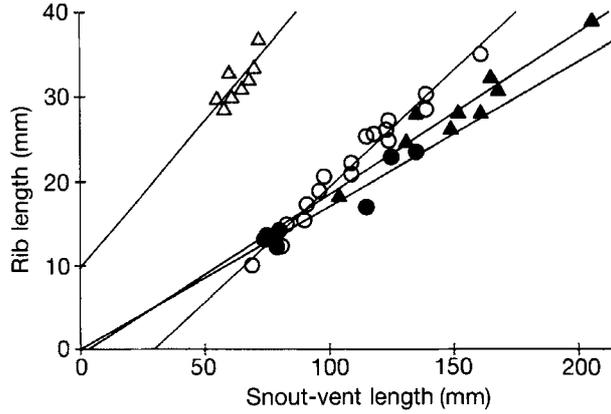
FIG. 1. Chord length of the longest rib vs. svl. Open triangles (△) = *Draco maculatus*; open circles (○) = *Leiolepis belliani*; closed triangles (▲) = *Uromastix geyrii*; closed circles (●) = *Agama stoliczkana*.
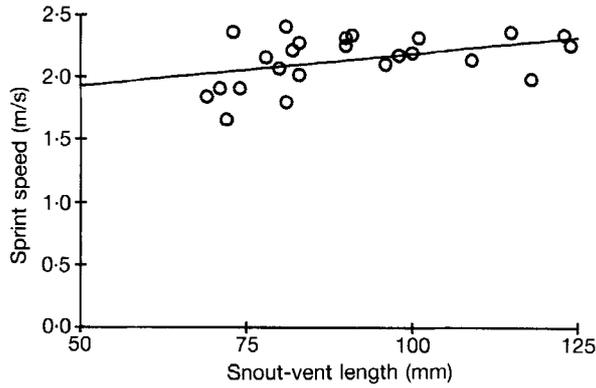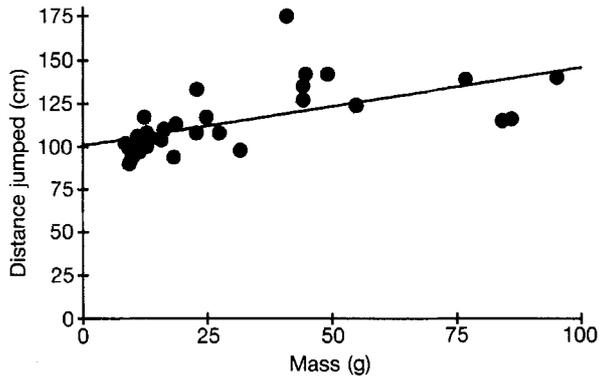
FIG. 2. Sprint speed vs. svl.
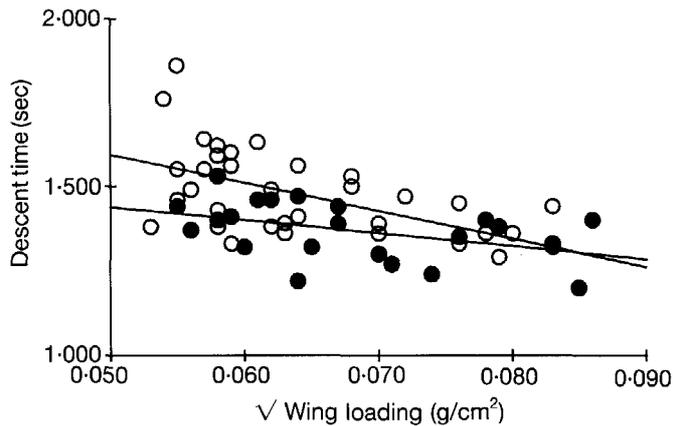
FIG. 3. Distance jumped vs. mass.

FIG. 4. Descent time vs. wing loading for restrained (●) and unrestrained (○) *Leiolepis belliani.*

$F_{1,22} = 0.289$, $P < 0.6$) or jumping distance ($r^2 = 0.051$, $F_{1,29} = 1.561$, $P < 0.25$). In bivariate comparisons between morphological and performance residuals, the only significant relationship is between tail length and descent time. This may result from the lesser surface area of lizards with shorter tails; alternatively, one would expect 1.65 significant correlations by chance alone in 33 comparisons. No relationship exists between sprint speed, jump distance, and descent rate (jump residual vs. descent residual, $r^2 = 0.017$, $F_{1,23} = 0.396$, $P < 0.6$; jump residual vs. sprint residual, $r^2 = 0.058$, $F_{1,16} = 0.993$, $P < 0.4$; descent residual vs. sprint residual, $r^2 = 0.003$, $F_{1,17} = 0.045$, $P < 0.9$). Table I summarizes these relationships among and between morphological and performance residuals.

Unrestrained lizards fell more slowly than both restrained (paired-samples $t = 2.653$, 20 *d.f.*, $P < 0.02$) and dead lizards (paired-samples $t = 5.600$, 12 *d.f.*, $P < 0.001$). Within each group, heavier lizards fell faster (Fig. 4). For both restrained and unrestrained lizards, time of descent was inversely correlated with wing loading (unrestrained lizards $r^2 = 0.331$, $F_{1,33} = 16.342$, $P < 0.001$; restrained lizards $r^2 = 0.193$, $F_{1,20} = 4.786$, $P < 0.05$). At all wing loadings, unrestrained lizards fell more slowly (analysis of covariance, difference of intercepts, $P < 0.001$).

Discussion

Large lizards have proportionately shorter fore- and hind legs. None the less, sprint speed and jumping distance increase allometrically, a trend seen in a number of other species of lizards and frogs (e.g. Zug, 1972, 1978; Emerson, 1978; Huey, 1982; Garland, 1985). Larger lizards have relatively greater wing loadings and, in accordance with predictions, fall more rapidly (a similar relationship occurs in the gecko *Ptychozoon lionatum* [Marcellini & Keefer, 1976]). At any given wing loading, unrestrained lizards fall more slowly than restrained lizards. This may result because the abdomen of a falling lizard is not planar, but is instead concave, creating a parachute effect; unrestrained lizards can flatten and produce a more effective parachute (cf. Shelford, 1906). An inverse relationship between rate of descent and both absolute running speed and absolute jumping ability suggests a size-related performance trade-off; larger lizards have greater running and jumping capability, but are poorer at parachuting.

Size-independent morphological variation is strongly correlated, e.g. a lizard with a relatively long humerus also has a relatively long radius, femur, tibia, hand and foot. Garland (1985) found a similar relationship between fore- and hind leg span in the Australian agamid *Ctenophorus nuchalis*. However, contrary to predictions, these differences in shape did not affect running or jumping performance. Similar findings have been reported for lizards (Garland, 1984, 1985) and frogs (Emerson, 1978). These findings suggest that either the assumptions of the biomechanical models are not met or that the models are inadequate. The models assume that leg length is the single most important parameter determining speed. This, however, may not be true. For example, relatively long-legged lizards would not run faster if stride length remained unchanged, perhaps as a result of changes in limb extension or pelvic rotation (Garland, 1985), or if stride frequency decreased. These models focus on only one aspect of locomotion, limb length. Other factors (e.g. stride frequency, limb muscle mass and orientation) may be more important determinants of performance. Alternatively, size accounts for almost all of the variation in limb length; any correlation that does exist may have been obscured by the greater degree of experimental error inherent in measurements of performance capability.

Size-independent performance measures were unrelated. Given that we could not find a relationship between any morphological feature and performance, we have no basis for expecting such a correlation. Consequently, selection theoretically could act to enhance performance capability at one task by selecting upon its underlying basis (be it physiological, morphological or behavioural), without affecting, either negatively or positively, performance capacity at the other tasks measured here. More detailed discussion of performance evolution and coevolution awaits an identification of the factors responsible for performance capability and an understanding of their genetic basis.

Dorsoventral flattening, on average, increases surface area 9·0% and slows rate of descent by 5·0%. Comparison of *Leiolepis* to closely related (*Uromastyx*) and ecologically similar (*Agama*) agamid lizards indicates that this capability results from the greatly elongated ribs of this species. It is not clear that enhanced parachuting ability has any ecological relevance to a beach-dwelling, cursorial lizard, such as *Leiolepis belliani*. This study was prompted by reports that *Leiolepis* 'glides' from trees (Cantor, 1847) and 'sails' from banks (Taylor, 1963). Swinhoe (1870: 240) stated that 'if surprised far from their holes, they spring into the air while running, and, expanding the loose red skin of their sides, skim along the surface of the sand for a considerable distance (say, often 20 yards at a time) and thus reach their retreats at greater speed.' We have shown that dorsoventral flattening only slightly increases descent rate and that maximum distance jumped (admittedly from a standstill) is closer to two yards than to 20. Thus, Swinhoe's observations appear greatly exaggerated. Further, a number of noted naturalists have failed to observe any behaviour of this sort, and report running as the sole locomotor mode (Theobald in Boulenger, 1890; Annandale in Boulenger, 1903; Pope in Schmidt, 1927; Smith, 1935; E. Zhao, pers. comm.). We conclude that it is unlikely that lateral flattening has evolved as an adaptation for parachuting.

The ability to extend these folds is potentially aptive for several other tasks:
1. Thermoregulation—many lizard species flatten themselves to absorb heat while basking. Casual observations on captive *Leiolepis* suggest a similar function, which was originally proposed by Boulenger (1890).
2. Intraspecific communication—male butterfly lizards have brightly marked flanks (Plate I). Fold extension could be used to display more prominently these markings in male-male or courtship behaviours in a fashion similar to displays of other lizards (e.g. *Anolis*, *Sceloporus*, *Sitana*). Lateral flattening has been observed during male combat in *L. belliani* (Annandale in Boulenger, 1903; Smith, 1935).

3. Escape from predation—*Leiolepis* flatten and extend their folds when frightened or handled (Cantor, 1847; Swinhoe, 1870; Boulenger, 1912, pers. obs.). Many reptile species alter their geometry to scare off predators or make ingestion by predators difficult (Greene, 1988).

We propose that the parachuting ability of *Leiolepis* is exaptive, i.e. fold extension ability has evolved as an adaptation to some other task, and has conferred parachuting capability as an incidental by-product. Russell (1979) has considered the factors responsible for the evolution of parachuting ability in certain gekkonid lizards. He argues that the folds seen in *Ptychozoon* evolved from structures originally used for fat storage or to enhance crypsis. Many geckos and other lizards extend their limbs and tail when jumping or falling (Oliver, 1951; Russell, 1979). In itself, these postural adjustments slow the rate of descent, as our results with live and dead *Leiolepis* confirm. Russell suggests that the independent evolution of this posture, and of lateral folds, were exapted (protoadaptations in the terminology of Gans, 1974 and Russell, 1979) and then facilitated the evolution of enhanced parachuting capability.

In a scenario similar to that of Russell's, we suggest that *L. belliani* has the prerequisites necessary for the evolution of true gliding (for a discussion of aerodynamical terms see Rayner, 1981). The morphological structures and behaviour patterns are present; all that is needed is a shift from terrestrial to arboreal habitats.

In this context, *Leiolepis* may shed light on the evolution of the only truly gliding living lizards, the agamid genus *Draco*. *Draco* glides on a large patagium formed from a membrane stretched over 5–7 elongated anterior ribs. One can envision selection for increased rib length in *Leiolepis* producing a similar structure. Interestingly, all ribs posterior to the patagium in *Draco* are quite short. By contrast, only the last four free ribs in *Leiolepis* are relatively short. Whether *Draco* evolved from a terrestrial or an arboreal ancestor is not clear. The precise phylogenetic position of *Draco* is uncertain, but both rupicolous and arboreal forms are among its near relatives (Moody, 1980). Consequently, the primitive condition for *Draco* is uncertain. In either case, the ancestors of *Draco* first may have evolved elongated ribs and increased surface area as an adaptation for something other than gliding, as *Leiolepis* apparently has, and then co-opted these structures for aerial locomotion.

REFERENCES

Arnold, S. J. (1983). Morphology, performance and fitness. *Am. Zool.* **23**: 347–361.
Arnold, S. J. (1986). Laboratory and field approaches to the study of adaptation. In *Predator-prey relationships: perspectives and approaches from the study of lower vertebrates*: 157–179. Feder, M. E. & Lauder, G. V. (Eds). Chicago: University of Chicago Press.
Bennett, A. F. (1980). The thermal dependence of lizard behaviour. *Anim. Behav.* **28**: 752–762.
Bock, W. J. & von Wahlert, G. (1965). Adaptation and the form-function complex. *Evolution, Lancaster, Pa* **19**: 269–299.
Boulenger, G. A. (1890). *The fauna of British India, including Ceylon and Burma. Reptilia and Batrachia.* London: Taylor & Francis.
Boulenger, G. A. (1903). Report on the batrachians and reptiles. In *Fasciculi Malayenses*: 131–176. Annandale, N. (Ed.). Liverpool: University of Edinburgh.
Boulenger, G. A. (1912). *A vertebrate fauna of the Malay Peninsula from the Isthmus of Kra to Singapore including the adjacent islands.* London: Taylor & Francis.

Cantor, T. (1847). Catalogue of reptiles inhabiting the Malayan peninsula and islands, collected or observed by Theodore Cantor, Esq., M.D. *J. Asiatic Soc. Bengal* **16**: 607–656, 896–951, 1026–1078.

Emerson, S. B. (1978). Allometry and jumping in frogs: helping the twain to meet. *Evolution, Lawrence, Kans*. **32**: 551–564.

Emerson, S. B. (1985). Jumping and leaping. In *Functional vertebrate morphology*: 58–72. Hildebrand, M., Bramble, D. M., Liem, K. F. & Wake, D. B. (Eds). Cambridge, Mass.: Belknap Press.

Gans, C. (1974). *Biomechanics: an approach to vertebrate biology.* Philadelphia: Lippincott.

Garland, T., Jr (1984). Physiological correlates of locomotory performance in a lizard: an allometric approach. *Am. J. Physiol.* **247** (*Regulatory Integrative Comp. Physiol.* **16**): R806–R815.

Garland, T., Jr (1985). Ontogenetic and individual variation in size, shape and speed in the Australian agamid lizard *Amphibolurus nuchalis*. *J. Zool., Lond. (A)* **207**: 425–439.

Gould, S. J. & Vrba, E. S. (1982). Exaptation—a missing term in the science of form. *Paleobiology* **8**: 4–15.

Greene, H. W. (1986). Diet and arboreality in the emerald monitor, *Varanus prasinus*, with comments on the study of adaptation. *Fieldiana (Zool.)* (NS) No. 31: 1–12.

Greene, H. W. (1988). Antipredator mechanisms in reptiles. In *Biology of the Reptilia* **16**: 1–152. Gans, C. & Huey, R. B. (Eds). New York: Alan R. Liss.

Hertz, P. E., Huey, R. B. & Nevo, E. (1983). Homage to Santa Anita: thermal sensitivity of spring speed in agamid lizards. *Evolution, Lawrence, Kans.* **37**: 1075–1084.

Hildebrand, M. (1974). *Analysis of vertebrate structure.* New York: John Wiley & Sons.

Hill, A. V. (1950). The dimensions of animals and their muscular dynamics. *Sci. Progr.* **38**: 209–230.

Huey, R. B. (1982). Phylogenetic and ontogenetic determinants of sprint performance in some diurnal Kalahari lizards. *Koedoe* **25**: 43–48.

Huey, R. B. & Hertz, P. E. (1982). Effects of body size and slope on sprint speed of a lizard (*Stellio (Agama) stellio*). *J. exp. Biol.* **97**: 401–409.

Lewontin, R. C. (1978). Adaptation. *Scient. Am.* **239**: 156–169.

Marcellini, D. L. & Keefer, T. E. (1976). Analysis of the gliding behavior of *Ptychozoon lionatum* (Reptilia: Gekkonidae). *Herpetologica* **32**: 362–366.

Moody, S. M. (1980). *Phylogenetic and historical biogeographical relationships of the genera in the family Agamidae (Reptilia: Lacertilia).* PhD dissertation, University of Michigan.

Oliver, J. A. (1951). "Gliding" in amphibians and reptiles, with a remark on an arboreal adaptation in the lizard, *Anolis carolinensis carolinensis* Voigt. *Am. Nat.* **85**: 171–176.

Rayner, J. M. V. (1981). Flight adaptations in vertebrates. *Symp. zool. Soc. Lond.* No. 48: 137–172.

Rose, M. R. (1982). Antagonistic pleiotropy, dominance, and genetic variation. *Heredity* **48**: 63–78.

Russell, A. P. (1979). The origin of parachuting locomotion in gekkonid lizards (Reptilia: Gekkonidae). *Zool. J. Linn. Soc.* **65**: 233–249.

Schmidt, K. P. (1927). The reptiles of Hainan. *Bull. Am. Mus. nat. Hist.* **54**: 395–465.

Shelford, R. (1906). A note on "flying" snakes. *Proc. zool. Soc. Lond.* **1906**: 227–230.

Smith, M. A. (1935). *The fauna of British India, including Ceylon and Burma. Reptilia and Amphibia* **II**—*Sauria.* London: Taylor & Francis.

Swinhoe, R. (1870). List of reptiles and batrachians collected in the island of Hainan (China), with notes. *Proc. zool. Soc. Lond.* **1870**: 239–241.

Taylor, E. (1963). The lizards of Thailand. *Univ. Kans. Sci. Bull.* **44**: 687–1077.

van Berkum, F. H. & Tsuji, J. S. (1987). Inter-familiar differences in spring speed of hatchling *Sceloporus occidentalis* (Reptilia: Iguanidae). *J. Zool., Lond.* **212**: 511–519.

Zug, G. R. (1972). Anuran locomotion: structure and function. 1. Preliminary observations on relation between jumping and osteometrics of appendicular and postaxial skeleton. *Copeia* **1972**: 613–624.

Zug, G. R. (1978). Anuran locomotion: structure and function. 2. Jumping performance of semiaquatic, terrestrial, and arboreal frogs. *Smithson. Contr. Zool.* **276**: 1–31.