

## PHYLOGENETIC AND ONTOGENETIC DETERMINANTS OF SPRINT PERFORMANCE IN SOME DIURNAL KALAHARI LIZARDS

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*Abstract* — Sprint capacities (maximum speed, acceleration, stride length, stride frequency) of diurnal lizards from the Kalahari were measured on sandy substrates in the laboratory. Despite major interfamilial differences in body sizes and in body proportions, measures of sprint capacity were remarkably similar among families: some heavy bodied skinks ran as fast as did some sleek lacertids. Sprint capacities change during ontogeny in lizards. Maximum speed, stride length, and possibly acceleration all increase with size and presumably with age.

### *Introduction*

The ability of an animal to accelerate and to sprint quickly influences its ability to capture food, to avoid becoming food, and to interact socially. Consequently, information on ontogenetic and interspecific variation in sprint performance is relevant to diverse issues in ecology and in behavior. Moreover, because of pronounced phylogenetic variation in morphological traits that should influence sprint capacity, sprint data are also useful for exploring evolutionary trends in functional morphology. Nevertheless, because of technical difficulties involved in estimating key aspects of sprint performance (e. g. acceleration), little information is currently available on most aspects of sprint capacities of lizards.

New technological developments (Huey, Schneider, Erie & Stevenson 1981) greatly facilitate the acquisition of sprint data for small cursorial animals. Using and extending these techniques, quantitative information on the maximum speed, acceleration, stride length, and stride frequency for some diurnal Kalahari lizards running on natural substrates in the laboratory were gathered. These data were used to determine whether several families of lizards, which differ strikingly in body proportions, also differ in locomotor patterns. Moreover, it was examined whether locomotor capacity changes during ontogeny.

### *Material and Methods*

These studies were conducted in late October through early December (late spring in the southern Hemisphere) in 1981. Animals from several localities were collected in the Kalahari Gemsbok National Park near the border of the Republic of South Africa and the Republic of Botswana (voucher specimens on deposit at the Los

Angeles County Museum of Natural History, U.S.A.). All laboratory experiments were conducted at Twee Rivieren, where electricity was available. Freshly captured lizards only were used to eliminate potential deconditioning effects associated with captivity (but see Gleeson 1979).

Body temperature influences the locomotor capacities of lizards (Bennett 1980). Consequently, meaningful comparisons of locomotor capacities of lizards must be conducted at ecologically appropriate body temperatures. I therefore controlled body temperatures of these diurnal lizards between 35°C to 37°C, which is within the range of body temperatures of active lizards in spring (about 34°C to 39°C, Huey, Pianka & Hoffman 1977).

To achieve control over temperature, lizards were placed individually in cloth sacks that were hung inside a portable environmental chamber (based on a design of G. A. Bartholomew). The chamber was constructed from an insulated wood-cardboard box (0.4 x 0.4 x 0.6 m). A hair dryer provided convective heat, and chamber temperature was regulated by a Versa-temp Electronic Temperature Controller. The inside of the chamber was illuminated.

To measure acceleration ability, maximum speed, stride length and stride frequency of lizards, I chased lizards down a 2.45 x 0.17 m racetrack. Photocell stations were spaced at 0.25 m (or less) intervals along 2 m of the track and were connected to an AIM microprocessor (Huey *et al.* 1981). Sprinting lizards would interrupt the photocell beams, and the microprocessor produced a printed record of elapsed times (nearest 0.001 s) to each photocell station, interval times, and interval velocities (see Hertz, Huey & Nevo 1982). Active lizards with complete (or occasionally with substantially regenerated) tails were usually tested on the day of capture. After thermal equilibration for at least 1 h, a lizard was raced twice in quick succession. After a rest of 1 h, the lizard was then raced twice more. This sequence was repeated until each lizard had been raced 8 times.

To estimate the relative ability of lizards to accelerate quickly, the fastest time ( $=t_{0.15}$ ) from the 8 trails were determined for each lizard to sprint 0.15 m from a standing start. (Note that acceleration is inversely related to  $t_{0.15}$ ). To determine maximum sprint speed ( $=V_{max}$ ), the fastest speed of each lizard over all 0.5 m sections of the track was calculated (see Hertz *et al.* 1982).

Kalahari sand served as the substrate in the racetrack. This substrate not only is ecologically appropriate but also permitted me to measure stride lengths (m, from spoor) and stride frequency (Hz, from spoor and interval speeds) of lizards running at their maximum speed along the racetrack.

### *Results and Discussion*

#### Interfamily comparisons

Representatives of three families of Kalahari lizards (Lacertidae, Agamidae, Scincidae) differ strikingly in external morphology. Kalahari lacertids are typically small and light (Table 1) and have relatively long limbs (Ricklefs, Cochran & Pianka 1981). *Agama aculeata* is the largest and heaviest of the lizards sampled (Table 1), and agamids typically have moderately long limbs (Ricklefs *et al.* 1981). Most of the skinks are intermediate in size, heavy bodied (Table 1), and have moderately short limbs (Ricklefs *et al.* 1981).

Table 1  
Body size and sprint parameters for Kalahari lizards

Species	Mass (g)		$V_{\max}$ (m s <sup>-1</sup> )		$t_{0.15}$ (s)	Stride length (m)		Stride frequency (Hz)		
	$\bar{X} \pm \text{s.e.}$	N	$\bar{X} \pm \text{s.e.}$	N		$\bar{X} \pm \text{s.e.}$	N	$\bar{X} \pm \text{s.e.}$	N	
Family Lacertidae <i>Eremias lineocellata</i>	3.41±0.28	20	2.46±0.09	20	0.12±0.01	20	0.14±0.01	7	16.99±0.88	7
<i>E. lugubris</i>	3.92±0.16	21	1.72±0.08	21	0.29±0.04*	21	0.13±0.01	11	12.85±0.73	11
<i>E. namaquensis</i>	2.51±0.21	9	2.68±0.08	9	0.11±0.01	8	0.13±0.01	5	19.31±0.68	5
<i>Nucras tessellata</i>	4.70±0.77	4	2.05±0.09	4	0.23±0.07*	4	0.13±0.01	3	16.27±1.98	3
average	3.64±0.46	4	2.23±0.21	4	0.19±0.04	4	0.13±0.01	4	16.36±1.34	4
Family Agamidae <i>Agama (hispidata)</i> <i>aculeata</i>	16.79±3.90	13	2.38±0.10	13	0.14±0.01	13	0.19±0.01	7	12.53±0.64	7
Family Scincidae <i>Mabuya striata</i>	15.82±2.84	5	2.10±0.18	5	0.15±0.01	5	0.13±0.01	4	16.45±1.28	4
<i>M. spilogaster</i>	9.50	1	2.37	1	0.15	1	—	—	—	—
<i>M. occidentalis</i>	13.67±0.56	6	1.73±0.11	6	0.18±0.03	6	0.13±0.01	3	14.23±0.93	3
<i>M. variegata</i>	1.30	1	1.36	1	0.12	1	0.05	1	24.7	1
average	10.07±3.20	4	1.89±0.22	4	0.15±0.01	4	0.10±0.03	3	18.46±3.19	3

\**Eremias lugubris* and *Nucras tessellata* did not accelerate smoothly in the racetrack. Thus, measurements of  $t_{0.15}$  for these two species are unreliable.

These patterns of morphological differences among families might lead one to expect, for example, that the lacertids, which are sleek, should run much faster than do the skinks, which are generally heavy bodied. Such expectations are not, however, supported by actual data (Table 1). In fact, sprint speeds vary considerably within families and overlap broadly among families. Some lacertids (e.g. *Eremias namaquensis*) are very fast, but others (e.g. *E. lugubris*) are slow. The heavy bodied and short legged skink *Mabuya striata*, is surprisingly fast, whereas the tiny *M. variegata* is slow.

Other sprint parameters (acceleration, stride length, and stride frequency) also show little variation among families (Table 1). Stride length is longest in *Agama aculeata*, but this undoubtedly reflects the large body size of this species (Table 1, see below).

The apparent lack of correspondence between phylogeny and sprint ability in these interfamilial comparisons should not be taken as evidence that morphology is an unimportant determinant of sprint ability. Detailed comparisons within families of species that differ in body proportions are a more appropriate way of approaching this issue.

#### Ontogeny of sprint capacity

To determine whether measures of sprint capacity change during ontogeny, estimates of sprint parameters (maximum speed, acceleration, stride length, and stride frequency) were regressed against body mass using power functions for four species of Kalahari lizards in which individuals with diverse body sizes were studied. Because data on stride lengths and on stride frequencies were gathered only near the end of the study, analyses of ontogenetic changes in these parameters are hindered by small sample sizes.

Maximum speed is positively and significantly correlated with body size in three species (Table 2), and this relationship is highly significant among all species ( $P < 0.001$ , Fisher combined probability test, Sokal & Rohlf 1969). Thus speed increases with size and presumably with age in Kalahari lizards. Speed also increases with size in the Middle Eastern agamids, *Stellio stellio* and *Agama savignyi* (Huey & Hertz, 1982; Hertz, Huey, & Nevo, *in preparation*).

Acceleration is positively but not significantly correlated with body size (Table 2, recall that acceleration is inversely related to  $t_{0.15}$ , see *Material and Methods*), and this relationship is likewise not significant among all species ( $P > 0.1$ ). Few data are available on the size-dependence of acceleration in other lizards: acceleration is positively correlated with size in *Stellio stellio* (Huey & Hertz 1982). Thus there is a consistent, but weak, trend for acceleration to increase during ontogeny in lizards. Nevertheless, whether the weakness of this trend reflects biological reality or merely the large error inherent in estimating acceleration (Huey & Hertz, *in preparation*) is unknown.

Stride length is positively and significantly correlated with size in two species (Table 2) and among all four species overall ( $P < 0.001$ ). Stride frequency is positively and significantly correlated with size in only one species, and considerable variation in

Table 2

Ontogeny of sprint capacity for some Kalahari lizards, where  $M$  = mass (g),  $V$  = maximum speed (m s<sup>-1</sup>),  $t_{0.15}^*$  = time (s) to run 0,15 m,  $S.L.$  = stride length (m), and  $S.F.$  = stride frequency (Hz). \* = significant frequency (Hz). \* = significant correlation at  $P < 0,05$ , \*\* at  $P < 0,01$ , and \*\*\* at  $P < 0,001$

Species	Maximum Speed		$t_{0.15}^*$		Stride Length		Stride Frequency	
	equation	r	equation	r	equation	r	equation	r
<i>Eremias lineocellata</i>	$V=1,85M^{0,24}$	0,61**	$t^{0.15}=0,15M^{-0,18}$	-0,40	$S.L.=0,10M^{0,24}$	0,89**	$S.F.=16,53M^{0,02}$	0,07
<i>E. lugubris</i>	$V=0,81M^{0,54}$	0,44*	—	—	$S.L.=0,09M^{0,27}$	0,44	$S.F.=5,36M^{0,64}$	0,66*
<i>E. namaquensis</i>	$V=2,02M^{0,31}$	0,91***	$t^{0.15}=0,12M^{-0,08}$	-0,15	$S.L.=0,13M^{0,01}$	0,02	$S.F.=17,76M^{0,11}$	0,23
<i>Agama (hispidia) aculeata</i>	$V=2,29M^{0,01}$	0,06	$t_{0.15}^*=0,15M^{-0,03}$	-0,27	$S.L.=0,12M^{0,17}$	0,82*	$S.F.=16,24M^{0,10}$	-0,56

the qualitative relationship between this parameter and body size is evident among species (Table 2).

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