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LOCOMOTOR CAPACITY AND FORAGING BEHAVIOUR OF KALAHARI LACERTID LIZARDS

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Abstract. Closely related lacertid lizards (*Eremias*, *Nucras*) in the Kalahari desert differ in patterns of foraging behaviour. Some species are relatively sedentary ('sit-and-wait'), whereas others are more active ('widely-foraging') predators. We determined whether whole-animal locomotor capacities (cruising endurance on a treadmill, initial speed and maximum burst speed in a racetrack, and sprint endurance in a torus-shaped track) correlated with interspecific differences in foraging behaviour. Two of three widely-foraging species had greater cruising endurance, greater sprint endurance, but lower burst speed than did a sit-and-wait species. However, the two species that sprinted quickly also had limited endurance, and vice versa. Pre-feeding negatively influenced endurance but not sprint capacity. Theoretical models of foraging behaviour should recognize that ectotherms have limited endurance, that there can be a trade-off between speed and endurance, and that pre-feeding can reduce some aspects of locomotor capacity.

Some species are ambush predators that typically 'sit and wait' for prey, whereas other species are active searchers that 'forage widely'. These extremes along a possible continuum of foraging modes are conspicuous in many taxa of animals (Pianka 1966; Schoener 1971; Regal 1978; Moermond 1979; Janetos 1982) and have recently prompted considerable interest in the ecological and behavioural correlates (Stamps 1977; Regal 1978, 1983; Eckardt 1979; Toft 1980, 1981; Anderson & Karasov 1981; Huey & Pianka 1981; Taigen & Pough 1982; Dunham 1983; Pough 1983; Andrews, in press), physiological bases (Bennett & Licht 1973; Ruben 1976a, b; Taigen et al. 1982), and theoretical implications (MacArthur & Pianka 1966; Schoener 1971; Ware 1975; Weihs 1975; Norberg 1977; Andersson 1981; Janetos 1982; Vitt & Price 1982) of foraging mode.

Closely related lacertid lizards in the southern Kalahari desert of Africa exemplify this divergence in foraging mode. Adults of all species travel at about 0.5 km/h while actually moving, but do so for very different proportions of time (Huey & Pianka 1981). Several species (*Eremias lineoocellata*, *Meroles suborbitalis*) are relatively sedentary, moving only 10–15% of the time when abroad, and appear to be sit-and-wait predators. In contrast, other species (*E. lugubris*, *E. namaquensis*, *Nucras tessellata*, and *N. intertexta;* possibly *Ichnotropis squamulosa*, see Broadley 1979) are relatively active, moving 50–70% of the time when abroad, and appear to be widely-foraging predators. Thus, whereas *E. lineoocellata* may traverse only 0.07 km in an hour, *E. lugubris* may cover 0.31 km, and *Nucras tessellata* may even cover 0.46 km (Pianka et al. 1979). The ecological correlates of differences in foraging behaviour among these lacertids are considerable and have been detailed elsewhere (Huey & Pianka 1981).

Here we address two new and general questions concerning the relationship between foraging behaviour and locomotor capacities:

(i) Is endurance capacity correlated with foraging behaviour? Specifically, is greater endurance a characteristic of widely-foraging lacertids? Alternatively, perhaps locomotor capacities are broad and similar among all lacertids, and widely-foraging and sit-and-wait species emphasize in their behaviour different parts of a similar range of potential activity levels.

(ii) Is there a trade-off between sprint and endurance capacity? Specifically, do fast sprinters have limited endurance, and vice versa?

We addressed these questions by studying the locomotor performance (endurance on a treadmill and on a circular track, and sprint ability in a racetrack) of Kalahari lizards in the laboratory. Sprint and endurance capacities can profoundly influence the ability of organisms to capture prey, to evade predators, and to interact socially. Measurements of these locomotor capacities provide a crucial, but unstudied, link between the ecology (Huey & Pianka 1981) and physiology (Bennett et al., in press) of foraging behaviour.

Kalahari lacertids are ideal for examining the relationship between foraging behaviour and locomotor capacity. Background ecological data are extensive (Huey et al. 1977; Broadley 1979; Pianka et al. 1979; Huey & Pianka 1981; Nagy et al., in press), thus permitting the design and interpretation of ecologically relevant experiments (Huey & Stevenson 1979). We concentrated on two ecologically well known, abundant, syntopic and similarly sized species, *E. lineoocellata* and *E. lugubris*, but gathered supplementary data on two lesser known and relatively rare species, *E. namaquensis* and *N. tessellata*.

The close evolutionary relationships among most of these lacertids provide the phylogenetic control necessary for meaningful comparative studies. Biologists attempting to answer related questions are often forced to compare distantly related species (Bennett & Licht 1973; Ruben 1976a, b; but see Taigen et al. 1982; Taigen & Pough 1982): any resulting correlations between foraging behaviour and locomotor capacity are potentially confounded by major anatomical physiological and behavioural differences that are unrelated to foraging behaviour.

Methods

Field Sites and Dates

These studies were conducted in late October through early December (late spring in the southern hemisphere) 1981. Adult lizards had recently emerged from hibernation and were reproductively quiescent. Consequently, differences in movement patterns in nature should be related to foraging rather than to reproductive or other concerns, at least at this time of year. We collected experimental animals near Leeudril, Botswana (14 km NE of Twee Rivieren, Kalahari Gemsbok National Park, Republic of South Africa). (Voucher specimens are deposited in the Los Angeles County Museum of Natural History.) This site, a small section of the study area 'L' of Pianka (1971), lies within the sand-ridge region of the southern Kalahari (Leistner 1967). The vegetation and climate are detailed in Pianka & Huey (1971).

All laboratory experiments were conducted at Twee Rivieren, where electricity was available. We used only freshly captured lizards to eliminate potential deconditioning effects associated with captivity, and only lizards with complete (or rarely with substantially regenerated) tails. Individual lizards were tested only once in a given experiment and normally in only one type of experiment. However, the four *Nucras tessellata* (a rare species) were used in two different experiments (sprint speed, cruising endurance but with a rest of at least 1 day between experiments. Locomotor performance can change during ontogeny (Huey & Hertz 1982; Huey 1982), so we therefore report data only on adult lizards (sprint data for juveniles and adults, and for other Kalahari lizards are reported in Huey 1982). Both sexes were sampled.

Apparatus

Temperature control. Body temperature is known to influence locomotor capacity in lizards (Moberly 1968; Tracy 1978; Bennett 1980; John-Alder & Bennett 1981; Hertz et al., 1983). Consequently, meaningful comparisons of locomotor capacity must be conducted at ecologically appropriate body temperatures. We therefore controlled body temperatures of lizards between 35 and 37°C, which is within the range of body temperatures of active lacertids in spring (about 35–39°C; Huey et al. 1977).

To control temperature, we placed lizards in individual cloth sacks which were hung inside a portable environmental chamber (based on a design by G. A. Bartholomew). The chamber (0.4 × 0.4 × 0.6 m) was illuminated and was constructed from an insulated wood–cardboard box. A hair-dryer provided convective heat, and chamber temperature was regulated by a Versatemp electronic temperature controller.

To prevent body temperature of lizards from dropping below 35°C during the treadmill and distance-run experiments, we regulated the temperature of the experimental room at 35–37°C. Various heat sources (stove, hair-dryer and solar heat) were used, and a fan minimized thermal gradients in the room. The humidity was not controlled but was often high.

Cruising endurance of lizards walking on a treadmill. Lizards (*E. lugubris*, $N = 8$; *E. lineoocellata*, $N = 8$; *E. namaquensis*, $N = 8$; *Nucras tessellata*, $N = 4$) were captured in the morning and their endurance on a treadmill was determined on the same or the following afternoon. Animals were thermally equilibrated in the environmental chamber for at least 3 h before testing. Lizards were then removed individually and placed on the rubberized belt of a motor-driven treadmill. The belt was moving at 0.5 km/h, the normal foraging speed of *Eremias* (Huey & Pianka 1981). The speed of the belt was regulated by a variable transformer and monitored frequently. Lizards were confined within a restricted area (about 15 × 75 cm) of the belt which was bounded on the front and sides by a three-sided cardboard enclosure (35 cm high). The front was marked with a darkened area to simulate a retreat. An experimenter regulated the movement of the lizards by tapping the animals lightly on the tail and hind limbs. The behaviour of the lizards was noted frequently. Lizards were walked on the treadmill surface for a maximum of 30 min or until they no longer could maintain station. A run was terminated when a lizard fell off the treadmill a second time. At the end of a run, animals were checked for loss of the righting response, and body (cloacal) temperatures were monitored with a thermocouple connected to a Wescor TH-65 thermocouple thermometer.

In a related series of experiments, the endurance of *E. lugubris* ($N = 34$) and *E. lineoocellata* ($N = 43$) was measured at several speeds ranging between 0.3 and 1.0 km/h. Ability to maintain activity on the treadmill for 15 min at each speed was measured as above.

Sprint capacity. To measure initial speed, maximum speed, stride length and stride frequency, we chased lizards (*E. lugubris*, $N = 23$; *E. lineoocellata*, $N = 13$; *E. namaquensis*, $N = 9$; *Nucras tessellata*, $N = 4$) down a 2.45 × 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 interrupted photocell beams, and the microprocessor produced a printed record of elapsed times to each photocell station, interval times, and interval velocities (see Hertz et al., 1983).

Except for *Nucras tessellata* (above), all lizards were 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 continued until each lizard had been raced eight times.

To index the relative ability of lizards to accelerate quickly, we computed from the eight trials the fastest initial speed (m s^{-1}) for each lizard over the first 0.15 m of the track from a standing start. To determine maximum sprint speeds (m s^{-1}), we calculated the fastest speed of each lizard over all 0.5-m sections of the track (see Hertz et al., 1983).

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

Distance running capacity. Distance running capacity at high speed (Bennett 1980) was assessed on a torus-shaped track, composed of an inner wall of galvanized sheet metal 45 cm high, an outer wall of cardboard 30 cm high, and a running space 15 cm wide filled with 1 cm of Kalahari sand. Two experimenters in the centre of the torus vigorously chased a lizard until the lizard was exhausted and unable to right itself or for a maximum of 15 min. Two additional experimenters recorded the cumulative distance run (outside circumference of the track (by the lizard at 15-s intervals for the first 2 min and at 1-min intervals thereafter. After 15 min or fatigue, body temperature was measured as above. Lizards typically ran rapidly along the outside wall (circumference = 4.5 m) for about 1 min and then ran markedly slower thereafter.

Effects of pre-feeding on performance. To determine the effects of prior feeding on the locomotor capacity of *E. lugubris*, we force-fed termites (mainly worker castes of *Trinervitermes*) to these lizards. Termites are the predominant prey of this lacertid (Pianka et al. 1979). The termites were stuffed into tuberculin syringes, and the slurry was gently and slowly forced into the lizard's mouth. We gave each lizard an amount of termites such that the total food in its stomach increased its body mass by 23% on average (range = 14–32%). (We have collected *E. lugubris* in the field that had even greater amounts of food—one lizard contained food that increased its body mass by 33%.) After allowing for thermal equilibration for 3 h, we measured endurance at 0.5 km/h ($N = 7$), distance running capacity ($N= 4$), and sprint ability ($N = 7$) of force-fed lizards following the procedures described above for comparison with data on control (not force-fed) lizards. To ensure that force-feeding did not induce injury, we autopsied all individuals after the experiments, carefully examining the mouth, lungs and stomach of each lizard for haemorrhage or other damage. We also determined the mass of the carcass and of the stomach and its contents.

Results

Locomotor Endurance on a Treadmill

To determine whether the capacity for 'cruising' endurance in the laboratory reflects patterns of foraging behaviour in nature, we measured the time lizards could sustain walking on a treadmill that was moving at 0.5 km/h, their normal foraging speed. When placed on the treadmill surface, lizards of both species typically sprinted and jumped for short periods before settling down and walking at the speed of the treadmill. Some lizards walked for the entire 30-min trial, whereas others fatigued more rapidly, as evidenced by their noticeably laboured locomotion. Often these lizards fell off the treadmill twice within 30 min, and many of these had lost the ability to right themselves.

The widely-foraging *E. lugubris* had significantly greater endurance at 0.5 km/h than did *E. lineoocellata* (Fig. 1; Fisher exact test, $P < 0.025$). Five of eight *E. lugubris* completed the 30-min trial, but none of nine *E. lineoocellata* did so. Fall-off times for animals that failed to complete the trial were also significantly greater (Fig. 1; Mann–Whitney *U*-test, $P < 0.01$) for *E. lugubris* ($\bar{X} \pm \text{SE} = 25.0 \pm 2.70$ min) than for *E. lineoocellata* ($\bar{X} \pm \text{SE} = 7.4 \pm 1.14$ min).

We gathered limited data on two other widely-foraging lacertids. Four *Nucras tessellata* successfully completed the 30-min trial, and the fifth was exhausted after 29.5 min. None of the eight *E. namaquensis*, nominally a widely-foraging lacertid (Huey & Pianka 1981), completed the trial. Fall-off times of *E. namaquensis* ($\bar{X} \pm \text{SE} = 7.3 \pm 1.52$ min) were similar to those of *E. lineoocellata* above.

We also examined the relative ability of *E. lugubris* and of *E. lineoocellata* to sustain locomotion for 15 min at several belt speeds (Fig. 2). At low belt speeds, both species successfully completed these trials. At higher speeds, lizards had difficulty maintaining position and were often exhausted before 15 min. This experiment further emphasized that *E. lugubris* has markedly greater endurance than does *E. lineoocellata*. Specifically, *Eremias lugubris* had significantly greater endurance than did *E. lineoocellata* at 0.5, 0.6 and 0.7 km/h (Mann–Whitney *U*-tests, all $P < 0.05$). At a high belt speed (1 km/h), performances declined rapidly (Fig. 2), and both species quickly became exhausted.

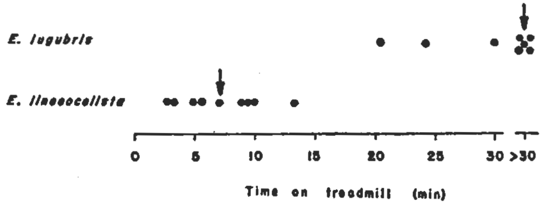

Fig. 1. Length of time (30 min maximum) that individual *E. lugubris* (widely-foraging) and individual *E. lineoocellata* (sit-and-wait) ran on a treadmill moving at 0.5 km/h before exhausting. Arrows indicate median time until exhaustion. Endurance is significantly greater in *E. lugubris.*

Sprint Capacity

When pursued by humans in the field, *E. lineoocellata* sometimes sprinted away at high speeds for 15 m or more, but generally they sprinted for shorter distances. In contrast, *E. lugubris* rarely sprinted even short distances. Instead, this species typically walked briskly or made short, controlled runs to the edge of a nearby thorn shrub.

The seemingly greater sprint capacity of *E. lineoocellata* in nature was paralleled by its behaviour and sprint characteristics in a labora-

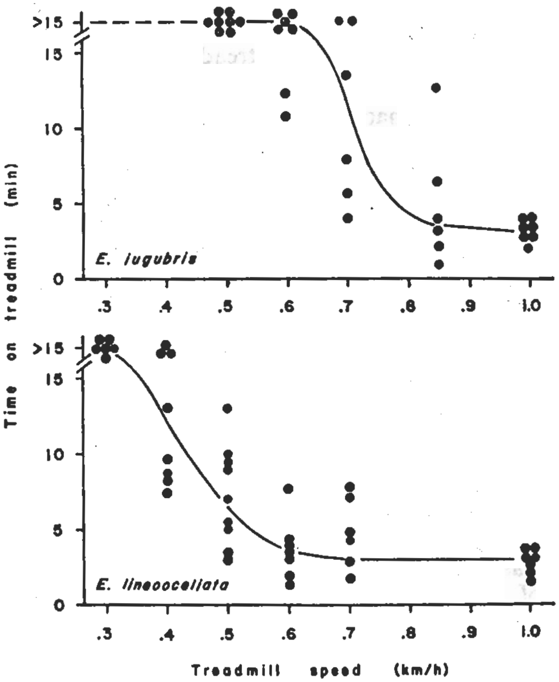

Fig. 2. Length of time (15 min maximum) that *E. lugubris* (widely-foraging) and *E. lineoocellata* (sit-and-wait) ran on a treadmill before exhausting as a function of belt speed. Curves drawn by eye. *Eremias lugubris* can sustain locomotion at much higher speeds than can *E. lineoocellata.*

tory racetrack (Table I). This species often accelerated quickly and smoothly, sprinted the length of the track, reached high maximum speeds, and had fast stride frequencies. In contrast, *E. lugubris* rarely accelerated quickly or smoothly, and invariably ran slowly and intermittently down the track.

Escape behaviour and sprint capacity were also examined in two other widely-foraging lacertids. The few *Nucras* we observed in the field fled slowly and for short distances. In contrast, *E. namaquensis* sprinted away at high speeds. In the laboratory, *Nucras* was relatively slow, whereas *E. namaquensis* was very fast (Table I).

Overall, the three widely-foraging lizards had significantly slower initial burst speeds than did the sit-and-wait species (Table I, a priori ANOVA, $P < 0.001$). Widely-foraging lizards also had significantly slower maximum burst speeds (Table I, $P < 0.001$).

Distance-running Capacity

When chased in the torus, lizards of both species typically sprinted for about 1 min. During the first 15 s of burst activity, *E. lugubris* and *E. lineoocellata* averaged 0.75 and 0.89 m s^{-1}, respectively. (These average speeds from a standing start on a circular track are substantially less than the maximum speeds observed over 0.5-m sections of the straight racetrack; see Table I.) Thereafter, they appeared to tire, and their speeds became progressively reduced. Some lizards, primarily *E. lineoocellata*, became exhausted well before the 15-min time limit.

Distance-running capacities (Table II) paralleled the patterns described above for sprint and endurance capacity. *Eremias lineoocellata* ran consistently (but not significantly, all $P > 0.05$) farther than did *E. lugubris* for the first 2 min. Soon thereafter *E. lineoocellata* began to tire, and only one individual could sustain activity for more than 5 min. In contrast, *E. lugubris* continued moving long after most *E. lineoocellata* were exhausted (Table II), and seven of eight *E. lugubris* were still moving (average speed = 0.2 km/h between the tenth and fifteenth minutes) at the termination of the experiments. Consequently, *E. lugubris* ran more than twice as far as did *E. lineoocellata* during the 15-min test. No data on distance-running capacity were gathered for the other species of lacertids.

Effects of Pre-feeding on Locomotor Capacity

Individuals of *E. lugubris* stuffed with termites are frequently found in nature (Huey & Pianka 1981). The additional mass (up to 33% of body mass) and bulk might impede locomotion (Shine 1980; Vitt & Price 1982) and potentially alter behaviour as well.

Cruising endurance at 0.5 km/h was markedly limited in pre-fed *E. lugubris* (Mann–Whitney *U*-test, $P < 0.01$). Although five of eight control (i.e. not pre-fed) animals successfully completed the 30-min trial, only one of seven fed lizards were able to do so; and fall-off times for animals that failed to complete the trial were much lower for fed ($\bar{X} \pm \text{SE} = 11.6 \pm 2.54$, $N = 6$) than for control ($\bar{X} \pm \text{SE} = 25.0 \pm 2.70$ min, $N = 3$) *E. lugubris*.

Sprint ability was slightly but not significantly reduced in pre-fed *E. lugubris* ($0.1 > P > 0.05$, one-tailed test). Fed lizards averaged 1.2 ± 0.24 m s^{-1}, whereas control *E. lugubris* averaged 1.6 ± 0.10 m s^{-1}.

Pre-feeding also reduced distance-running capacity in the torus. Pre-fed ($N = 4$) and control (Table II) *E. lugubris* ran similar distances at time intervals of 2 min or less (all $P > 0.10$). Thereafter, pre-fed animals had relatively limited endurance. Pre-fed animals became exhausted after 2.8 min on average (range 1.1–5.1 min), whereas seven of eight control lizards were still running after 15 min ($P < 0.001$). Not surprisingly, pre-fed *E. lugubris* covered much shorter distances ($\bar{X} \pm \text{SE} = 25.4 \pm 6.80$ m) than did control lizards ($\bar{X} \pm \text{SE} = 70.8 \pm 10.55$ m) during the 15 min ($P < 0.001$).

Discussion

We have demonstrated striking interspecific differences in several measures of locomotor capacity (initial speed, maximum speed, distance run, endurance) among closely related lacertid lizards. Our findings have significant implications for studies of the relationships between foraging behaviour and locomotor capacity and between sprint and endurance abilities. We initially outline these relationships, consider alternative explanations, and speculate on the direction of evolutionary change that led to current patterns. We also evaluate the primary implications of our results for theoretical models of foraging behaviour.

Locomotor Capacity and Foraging Behaviour

Differences in foraging behaviour could reflect (in a proximate sense) either underlying

Table I. Sprint Capacities and Body Sizes of Kalahari Lacertid Lizards

Species	Foraging mode	Body size		Sprint capacities			
		Mass (g)	SVL (mm)	Initial speed ($m\ s^{-1}$)	Max. speed ($m\ s^{-1}$)	Stride length (m)	Stride frequency (Hz)
E. lineoocellata	SW	4.20 ± 0.191	58.3 ± 1.00	1.33 ± 0.061 (13)	2.63 ± 0.092 (13)	0.151 ± 0.005 (5)	16.8 ± 0.87 (5)
E. lugubris	WF	3.97 ± 0.135	54.4 ± 0.68	0.70 ± 0.086 (23)	1.58 ± 0.103 (23)	0.136 ± 0.005 (12)	12.3 ± 0.89 (10)
E. namaquensis	WF	2.51 ± 0.209	51.3 ± 1.41	1.36 ± 0.062 (8)	2.68 ± 0.078 (9)	0.130 ± 0.005 (4)	19.6 ± 0.81 (4)
N. tessellata	WF	4.70 ± 0.769	67.8 ± 3.86	0.81 ± 0.192 (4)	2.05 ± 0.094 (4)	0.130 ± 0.010 (3)	16.3 ± 1.98 (3)

Mean values ± SE and sample size (in parentheses) are reported for adult lizards. SVL is snout-to-vent length.
SW = sit-and-wait; WF = widely foraging.

Table II. Cumulative Distance Travelled by Various Times in the Distance-run Experiment

Species	Foraging mode	Distance travelled after:					Total distance run
		30 s	1 min	2 min	5 min	15 min	
E. lineoocellata	SW	20.2 ± 1.99 (8)	24.2 ± 2.64 (7)	30.7 ± 2.37 (6)	31.1 (1)	0 (0)	29.9 ± 2.79 (8)
E. lugubris	WF	16.4 ± 0.92 (8)	20.4 ± 1.09 (8)	25.6 ± 1.70 (8)	41.5 ± 4.45 (7)	77.6 ± 9.30 (7)	70.8 ± 10.55(8)

Means ± SE are reported for each time interval. Adjacent numbers (in parentheses) indicate number of animals that were still moving at particular times.
SW = sit-and-wait; WF = widely foraging.

differences in locomotor capacity or merely that widely foraging and sit-and-wait lizards behaviourally select different regions of a continuum of potential activity levels. Our results suggest that these alternatives are not mutually exclusive. Overall, the widely-foraging species have greater endurance (Figs 1 and 2, Table II), whereas the sit-and-wait species has a greater sprint capacity (Table I). These results support the proposition that differences in locomotor capacity coevolve with foraging behaviour. The widely-foraging *E. namaquensis*, which seems to have limited endurance but high sprint capacity, does not fit this general pattern. This exception supports the alternative proposition that differences in behavioural emphasis as well as in locomotor capacity can sometimes underlie foraging mode.

Sprint Versus Endurance Capacity

Locomotor abilities of animals are influenced by physiology and by morphology. Both physiological (Bennett 1978) and anatomical considerations (Alexander 1968) associated with high endurance and with high sprint capacity are fundamentally different, suggesting that good sprinters are unlikely to have good endurance, and vice versa. Empirical evidence presented here supports this expectation. Species that sprinted quickly (*E. namaquensis*, *E. lineoocellata;* Table I) had very limited endurance, whereas species that sprinted slowly (*E. lugubris*, *Nucras*) had considerable endurance. These differences probably do not reflect intrinsic differences in the contractile or biochemical properties of the muscles themselves (Bennett et al., in press), but perhaps rather reflect differences in the patterns of muscular–skeletal architecture, of muscle fibre recruitment, or of neuro–muscular coordination.

The close phylogenetic relationships of species in the genus *Eremias* suggests an evolutionary scenario involving trade-offs for sprint versus endurance abilities. This trade-off must significantly influence foraging and defensive behaviours. This genus offers an important opportunity for further studies examining the physiological and morphological trade-offs involved in this pattern as well as the ecological bases for the change.

Alternative Hypotheses

The observed patterns of locomotor capacity could be an artifact of motivation: perhaps *E. lineoocellata* and *E. namaquensis* do have endurance comparable to that of *E. lugubris* and *Nucras* but were somehow not motivated, or were incapacitated, by the experiments. We reject this hypothesis, at least for *E. lineoocellata*. The ability of *E. lineoocellata* to maintain position on the treadmill at low tread speeds (Fig. 2) suggests that endurance, not behaviour, sets limits on performance at higher tread speeds. The poor sprint ability of *E. lugubris* is partially due to behaviour (see Results). Nevertheless, the fastest speed ever recorded for this species (2.3 m s^{-1}) is less than the average speed for *E. lineoocellata* (Table I), and our subjective impression is that *E. lugubris* is relatively slow even when chased in nature. Consequently, behavioural artifacts may affect the absolute performance levels obtained in these experiments, but should not alter the qualitative patterns in the results.

The observed pattern of locomotor capacity could also be a result of differential conditioning: perhaps the greater endurance of *E. lugubris* merely reflects its better physical condition resulting from its greater (self-induced) activity in nature. Locomotor capacity is influenced by training in mammals (Edington & Edgerton 1976), fish (Hammond & Hickman 1966) and frogs (Cummings 1979). Additional studies exposing these lacertids to equivalent training regimes before testing would be necessary to evaluate this hypothesis directly. Nevertheless, we anticipate that the observed differences reflect primarily genetic rather than training effects: (i) The only study on a lizard to date (Gleeson 1979) did not show a training effect on sprint or distance-run capacity or on several underlying physiological measures. (ii) The enzymatic and contractile properties of the skeletal muscles of *E. lugubris* and *E. lineoocellata* are identical (Bennett et al., in press), suggesting the absence of a training effect.

Evolutionary Considerations

Foraging behaviour appears to be a conservative trait within families of lizards (Stamps 1977; Vitt & Price 1982). For example, iguanid lizards are almost invariably sit-and-wait foragers, whereas sympatric teiid lizards are typically widely-foraging. The Kalahari lacertids demonstrate that movement rates (and thus presumably foraging mode) can sometimes diverge, even among congeneric species. Consequently, foraging mode—and by extension, physiological capacity (Bennett et al., in press)

— is not always evolutionarily conservative. The extent to which lacertids are unusual among lizards in this regard will require intensive, parallel studies of lizards in other families.

Most lacertid lizards are believed to be widely-foraging predators (Stamps 1977; Pianka et al. 1979). If this generalization is valid, and if the generalization holds in particular for lizards within the genus *Eremias*, then the sit-and-wait behaviour, limited endurance and high sprint capacity of *E. lineoocellata* represent evolutionarily derived conditions.

Implications for Theoretical Models

Theoretical models of foraging behaviour have been intensively and successfully developed in recent years (Schoener 1971; Gerritsen & Strickler 1977; Pyke et al. 1977; Vitt & Price 1982). Locomotor speed or intensity is an independent variable in some models (Gerritsen & Strickler 1977; Norberg 1977; Andersson 1981; Janetos 1982), under the implicit assumption that a given individual can sustain locomotion over broad ranges of speeds.

Our results demonstrate that limited stamina constrains the range of speeds in these lizards. In particular, the sit-and-wait *E. lineoocellata* simply does not have the stamina to be a wide-foraging lizard for more than a few minutes (Fig. 1). Moreover, even the widely-foraging *E. lugubris* exhausts quickly at speeds above normal (Fig. 2).

Sustainable speeds are thus limited in lizards, reflecting their relatively limited aerobic capacities in comparison with birds and mammals (Bennett 1978, 1983; Regal 1978, 1983; Bennett & Ruben 1979). Sustainable speeds are almost certainly less constrained in birds and mammals, and thus current theoretical models of foraging behaviour may be more directly appropriate for these species.

The trade-off between sprint and endurance capacity suggests that widely-foraging lacertids may be too slow to be effective sit-and-wait predators. Indeed, widely-foraging lacertids eat relatively sluggish (termites) or inactive (scorpions in burrows) prey; whereas the faster sit-and-wait species is able to capture more mobile prey (Huey & Pianka 1981).

The negative-feedback effects of feeding on locomotor capacity suggest further complications for current theoretical models. As a lizard acquires food during its foraging bouts, its cost of transport necessarily increases (from having to move a larger total body mass; Armstrong & Taylor 1982) and, as we demonstrate here, its endurance decreases. Moreover, its risk of predation might also increase because of a somewhat diminished ability to sprint. Thus, optimal foraging speed may vary during a given foraging period in response to these factors.

Our results therefore suggest that future theoretical models of foraging behaviour might profitably incorporate and explore the consequences of limitations on the locomotor capacities of animals, of the trade-off between sprint and endurance ability, and of the negative feedback between feeding and foraging behaviour. Sit-and-wait lizards may be constrained to ambush foraging because of their limited stamina, whereas widely-foraging lizards may be ineffective ambush predators because of their limited speed. These considerations are most appropriate for models relating to ectotherms —organisms with limited endurance capacities (Regal 1978; Bennett & Ruben 1979; Pough 1980).

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REFERENCES

Alexander, R. McN. 1968. *Animal Mechanics* Seattle: University of Washington Press.

Anderson, R. A. & Karasov, W. H. 1981. Contrasts in energy intake and expenditure in sit-and-wait and widely foraging lizards. *Oecologia*, (*Berl.*), **49,** 67–72.

Andersson, M. 1981. On optimal predator search. *Theor. Pop. Biol.*, **19,** 58–86.

Andrews, R. M. In press. Energetics of sit-and-wait and widely-searching lizard predators. In: *Vertebrate Ecology and Systematics: A Tribute to Henry S. Fitch* (Ed. by R. A. Seigel). Special publication no. 10 of the Museum of Natural History, University of Kansas.

Armstrong, R. B. & Taylor, C. R. 1982. Relationship between muscle force and muscle area showing glycogen loss during locomotion. *J. exp. Biol.*, **97,** 411–420.

Bennett, A. F. 1978. Activity metabolism of the lower vertebrates. *Ann. Rev. Physiol.*, **400,** 447–469.

Bennett, A. F. 1930. Thermal dependence of lizard behaviour. *Anim. Behav.*, **28,** 752–762.

Bennett, A. F. 1983. Ecological consequences of activity metabolism. In: *Lizard Ecology: Studies of a Model Organism* (Ed. by R. B. Huey, E. R. Pianka & T. W. Schoener), pp. 11–23. Cambridge, Mass.: Harvard University Press.

Bennett, A. F., Huey, R. B. & John-Aler, H. In press. Physiological correlates of natural activity and locomotor capacity in two species of lacertid lizards. *J. comp. Physiol.*

Bennett, A. F. & Licht, P. 1973. Relative contributions of anaerobic and aerobic energy production during activity in amphibia. *J. comp. Physiol.*, **87,** 351–360.

Bennett, A. F. & Ruben, J. A. 1979. Endothermy and activity in vertebrates. *Science, Wash., D.C.*, **206,** 649–654.

Broadley, D. G. 1979. A field study of two sympatric 'annual' lizards (genus *Ichnotropis*) in Rhodesia. *S. Afr. J. Zool.*, **14,** 133–138.

Cummings, J. W. 1979. Physiological and biochemical adaptations to training in *Rana pipiens*. *J. comp. Physiol.*, **134,** 345–350.

Dunham, A. E. 1983. Realized niche overlap, resource abundance, and intensity of interspecific competition. In: *Lizard Ecology: Studies of a Model Organism* (Ed. by R. B. Huey, E. R. Pianka & T. W. Schoener), pp. 261–280. Cambridge, Mass.: Harvard University Press.

Eckhardt, R. C. 1979. The adaptive syndromes of two guilds of insectivorous birds in the Colorado Rocky Mountains. *Ecol. Monogr.*, **49,** 129–149.

Edington, D. W. & Edgerton, V. R. 1976. *The Biology of Physical Activity*. Boston: Houghton-Mifflin.

Gerritsen, J. & Strickler, J. R. 1977. Encounter probabilities and community structure in zooplankton: a mathematical model. *J. Fish. Res. Bd Can.*, **34,** 73–82.

Gleeson, T. T. 1979. The effects of training and captivity on the metabolic capacity of the lizard *Sceloporus occidentalis*. *J. comp. Physiol.*, **129,** 123–128.

Hammond, B. R. & Hickman, C., Jr. 1966. The effect of physical conditioning on the metabolism of lactate, phosphate and glucose in rainbow trout, *Salmo gairdneri*. *J. Fish. Res. Bd Can.*, **23,** 65–83.

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

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 of slope on sprint speed of a lizard *Stellio* (*Agama*) *stellio*. *J. exp. Biol.*, **97,** 401–409.

Huey, R. B. & Pianka, E. R. 1981. Ecological consequences of foraging mode. *Ecology*, **62,** 991–999.

Huey, R. B., Pianka, E. R. & Hoffman, J. A. 1977. Seasonal patterns of thermoregulatory behavior and body temperature of diurnal Kalahari lizards. *Ecology*, **58,** 1066–1075.

Huey, R. B., Schneider, W., Erie, G. L. & Stevenson, R. D. 1981. A field-portable racetrack for measuring acceleration and velocity of small cursorial animals. *Experientia*, **37,** 1356–1357.

Huey, R. B. & Stevenson, R. D. 1979. Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. *Am. Zool.*, **19,** 357–366.

Janetos, A. C. 1982. Active foragers vs. sit-and-wait predators: a simple model. *J. theor. Biol.*, **95,** 381–385.

John-Alder, H. B. & Bennett, A. F. 1981. Thermal dependence of endurance and locomotor energetics in a lizard. *Am. J. Physiol.*, **241,** R342–R349.

Leistner, O. A. 1967. The plant ecology of the southern Kalahari. *Bot. Surv. S. Afr. Mem.*, **38,** 1–172.

MacArthur, R. H. & Pianka, E. R. 1966. On optimal use of a patchy environment. *Am. Nat.*, **100,** 603–609.

Moberly, W. R. 1968. The metabolic response of the common iguana, *Iguana iguana*, to activity under restraint. *Comp. Biochem. Physiol.*, **27,** 1–20.

Moermond, T. C. 1979. The influence of habitat structure on *Anolis* foraging behavior. *Behaviour*, **70,** 147–167.

Nagy, K. A., Huey, R. B. & Bennett, A. F. In press. Field energetics and foraging mode of Kalahari lacertid lizards. *Ecology*.

Norberg, R. A. 1977. An ecological theory on foraging time and energetics and choice of optimal food-searching method. *J. Anim. Ecol.*, **46,** 511–529.

Pianka, E. R. 1966. Convexity, desert lizards, and spatial heterogeneity. *Ecology*, **47,** 1055–1059.

Pianka, E. R. 1971. Lizard species density in the Kalahari desert. *Ecology*, **52,** 1024–1029.

Pianka, E. R. & Huey, R. B. 1971. Bird species density in the Kalahari and the Australian deserts. *Koedoe*, **14,** 123–129.

Pianka, E. R., Huey, R. B. & Lawlor, L. R. 1979. Niche segregation in desert lizards. In: *Analysis of Ecological Systems* (Ed. by D. J. Horn, G. R. Stairs & R. D. Mitchell), pp. 67–115. Columbus, Ohio: Ohio State University Press.

Pough, F. H. 1980. The advantages of ectothermy for tetrapods. *Am. Nat.*, **115,** 113–120.

Pough, F. H. 1983. Amphibians and reptiles as low-energy systems. In: *Behavioral Energetics* (Ed. by W. P. Aspey & S. I. Lustick), pp. 141–188. Columbus, Ohio: Ohio State University Press.

Pyke, G. H., Pulliam, H. R. & Charnov, E. L. 1977. Optimal foraging: a selective review of theory and tests. *Q. Rev. Biol.*, **52,** 137–154.

Regal, P. J. 1978. Behavioral differences between reptiles and mammals: an analysis of activity and mental capabilities. In: *Behavior and Neurology of Lizards* (Ed. by N. Greenberg & P. D. Maclean), pp. 67–115. Washington, D.C.: Publication (ADM) 77–491, Department of Health, Education and Welfare.

Regal, P. J. 1983. The adaptive zone and behavior of lizards. In: *Lizard Ecology: Studies of a Model Organism* (Ed. by R. B. Huey, E. R. Pianka & T. W. Schoener), pp. 105–118. Cambridge, Mass.: Harvard University Press.

Ruben, J. A. 1976a. Aerobic and anaerobic metabolism during activity in snakes. *J. comp. Physiol.*, **109**, 147–157.

Ruben, J. A. 1976b. Correlation of enzymatic activity, muscle myoglobin concentration and lung morphology with activity metabolism in snakes. *J. exp. Zool.*, **197**, 313–319.

Schoener, T. W. 1971. Theory of feeding strategies. *Ann. Rev. Ecol. Syst.*, **2**, 369–404.

Shine, R. 1980. "Costs" of reproduction in reptiles. *Oecologia*, (*Berl.*), **46**, 92–100.

Stamps, J. A. 1977. Social behavior and spacing patterns in lizards. In: *Biology of Reptilia Volume* 7 (*Ecology and Behaviour A*) (Ed. by C. Gans & D. W. Tinkle), pp. 265–334. New York: Academic Press.

Taigen, T. L., Emerson, S. B. & Pough, F. H. 1982. Ecological correlates of anuran exercise physiology. *Oecologia*, (*Berl.*), **52**, 49–56.

Taigen, T. L. & Pough, F. H. 1982. Foraging behavior and metabolic characteristics of poison-dartfrogs. *Am. Zool.*, **22**, 980. (Abstr.)

Toft, C. A. 1980. Feeding ecology of thirteen syntopic species of anurans in a seasonal tropical environment. *Oecologia*, (*Berl.*), **45**, 131–141.

Toft, C. A. 1981. Feeding ecology of Panamanian litter anurans: patterns in diet and foraging mode. *J. Herpetol.*, **15**, 139–144.

Tracy, C. R. 1978. Further thoughts on anuran thermoregulation. In: *The Behavioral Significance of Color* (Ed. by E. H. Burtt), pp. 63–68. New York: Garland.

Vitt, L. J. & Price, H. J. 1982. Ecological and evolutionary determinants of relative clutch mass in lizards. *Herpetologica*, **38**, 237–255.

Ware, D. M. 1975. Growth, metabolism and optimal swimming speed in a pelagic fish. *J. Fish. Res. Bd Can.*, **32**, 33–41.

Weihs, D. 1975. An optimum swimming speed of fish based on feeding efficiency. *Isr. J. Technol.*, **13**, 163–167.

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