EFFECTS OF BODY SIZE AND SLOPE ON SPRINT SPEED OF A LIZARD (*STELLIO (AGAMA) STELLIO*)

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SUMMARY

1. The agamid lizard *Stellio stellio* L. accelerates quickly and reaches maximum speed over short distances.

2. Maximum speed on the level is proportional to body mass to the $\frac{1}{3}$ power. This relation differs from predictions based on an interspecific scaling model of "geometric" similarity (M^0) and is intermediate between predictions based on interspecific scaling models of "elastic" similarity ($M^{\frac{1}{4}}$) and of "static stress" similarity ($M^{\frac{2}{5}}$).

3. Maximum speed was also measured on slopes ranging from $-15°$ to $+60°$. The effect of slope on speed varies with body mass. The maximum speed of large lizards decreases on steep slopes, but that of small lizards is remarkably independent of slope.

INTRODUCTION

Many animal species have a remarkable ability to scamper quickly over nearly vertical surfaces on rocks or trees. Although the effect of body size and of slope on maximum sprint speed of terrestrial animals has been debated from a theoretical perspective (Hill, 1950; Henry & Trafton, 1951; Maynard Smith, 1968; Heglund, Taylor & McMahon, 1974; McMahon, 1975; Wilkie, 1977; Elliott, Cowan & Holling, 1977), empirical analyses bearing on this topic are rare (Hill, 1950). Indeed, the actual effect of slope on speed is apparently unstudied.

In this paper we examine how body mass and slope jointly affect maximum sprint speed of an agamid lizard [*Stellio (Agama) stellio* (Moody, 1980)]. These intraspecific results are compared with theoretical predictions based on interspecific scaling models.

Our investigation was prompted by the research of Taylor, Caldwell & Rowntree (1972) on the energetic cost of locomotion in mammals. Using steady-state aerobic metabolic rate as the metric of energetic cost, they found that cost increased with slope for large but not for small mammals. We wished to determine whether this result might pertain for lizards, a metabolically different group of terrestrial vertebrates. In contrast to mammals, most lizards are specialized for sprint (anaerobic) rather than endurance (aerobic) locomotion (Bennett, 1978). Consequently, maximum

sprint speed (or acceleration) is an ecologically more relevant metric (Huey &
Stevenson, 1979) for a parallel study of how size and slope affect locomotor performance.

We selected the lizard *Stellio stellio*, which is a moderate-sized (maximum mass
about 125 g, maximum snout-to-vent length about 150 mm) insectivorous lizard
that occupies diverse habitats in the Middle East. Because these lizards regularly
live in complex microhabitats (rocks, boulders, walls) and because a large size range
of individuals can be obtained, *Stellio* are ideally suited for a study of the effect of
slope and size on sprint speed.

MATERIALS AND METHODS

Lizards were collected at several localities in Israel in late June 1980, shipped to
Seattle, acclimated for 10 days at 12:12 L:D and 34:26 °C (centred at 12.00 h local
time), and used initially in a 3-week experiment on the thermal dependence of sprint
speed (P. E. Hertz, R. B. Huey & E. Nevo, in preparation). Thus all lizards were
well trained (see Bennett, 1980).

Subsequently, we selected 23 lizards for the present experiments. Beginning in
mid-August 1980, lizards were raced daily (1 slope/day, 6 trials/lizard/day, about
1 trial every 45 min) in a 2·4 m × 20 cm racetrack with a rough, rubberized substrate
that provided excellent traction. We induced a lizard to run by tapping its hindquarters
and then chased it the length of the track. Speeds measured under these artificial
conditions undoubtedly differ somewhat from those measured in nature: con-
sequently, our results are relative, rather than absolute.

To measure speeds of lizards along the racetrack, 12 stacks of 4, vertically aligned
photocells (height = 6 cm) were positioned at set intervals along the runway (total
interval = 2 m) and connected to an AIM 65 microprocessor that produced a printed
record of elapsed times, interval times, and interval speeds (Huey *et al.* 1981). Interval
speeds were calculated to 0·01 m s^{-1} over each 0·5 m section of the track, and we
report the maximum interval speed ever achieved by a given lizard for a given
slope. Because maximum speed was unrelated to trial number for all slopes, the
experimental regime of 6 trials per day did not fatigue lizards within days. Body
temperature was controlled at about 34 °C, which approximates the mean T_b of
active *Stellio stellio* in nature (P. E. Hertz & E. Nevo, in preparation) and is near
the apparent 'optimal' T_b for sprint speed on the level (P. E. Hertz, R. B. Huey
and E. Nevo, in preparation).

Lizards were raced at the following sequence of slopes: 0°, 15°, −15°, 30°, 45°
and 60°. Because this sequence was non-random, observed changes in speed during
the experiment could be due to factors other than slope. To guard against this
possibility, we re-ran all lizards at a slope of 0° on the day after the 60° run and
eliminated four lizards that failed to run at least 90% as fast as the maximum speed
in the initial series at 0° (an *a priori* criterion for elimination). Consequently, this
analysis is based only on lizards that maintained sprint capacity during the entire
experiment and for which the regime of daily trials did not induce cumulative fatigue.

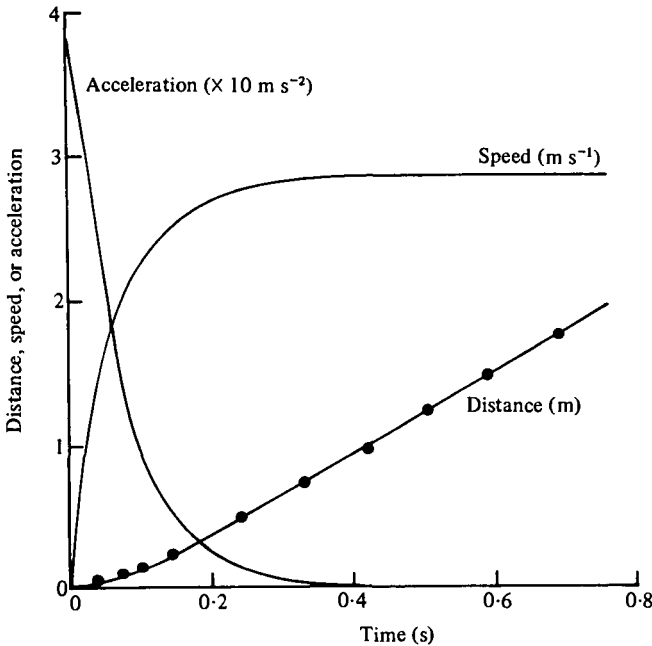The experimental lizards ranged from 10 to 99 g in mass and from 68 to 132 mm

Fig. 1. Distance, speed, and acceleration of a 65 g *Stellio stellio* running on a 60° slope. The scale of the ordinate is in metres for distance, m s⁻¹ for speed, and 10 m s⁻² for acceleration. The curves are derived from equation (2).

in snout-to-vent length. The relationship between mass (g) and length (cm) can be described by a power function:

$$\text{mass} = 0.04 \quad \text{length}^{3.0}, \tag{1}$$

and 96% of the variation in log mass is accounted for by log length.

To describe cumulative distance run as a function of time, we used the following formula (Henry & Trafton, 1951):

$$s = v_m\left(t + \frac{e^{-kt}}{k} - \frac{1}{k}\right), \tag{2}$$

where s = distance (metres), v_m = maximum speed (m s⁻¹), t = time (s), and k = a constant. This curve was fitted using Marquardt's algorithm (SPSS). Progressive differentiation permits specifications of speed and acceleration as functions of time.

RESULTS

Speed profile during a run

Lizards in nature appear to have high initial rates of acceleration and to reach maximum speed quickly. This subjective impression is supported in Fig. 1, which shows distance, speed, and acceleration as functions of time for a 65 g *S. stellio* running up a 60° slope. Even on this acute slope, the lizard achieved 95% of v_m (2.9 m s⁻¹) within the first 0.4 m (or in 0.2 s).
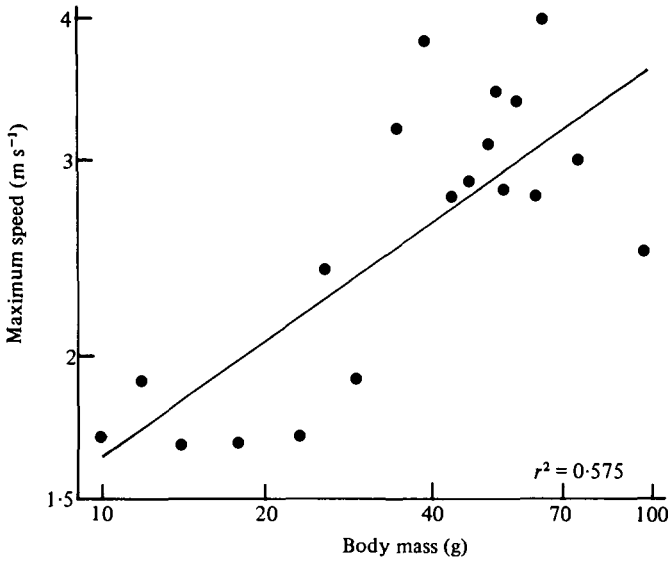
Fig. 2. Maximum speed v. body mass for *S. stellio* with the calculated allometric curve.

Maximum speed versus body mass on level slope

Maximum speed on a level slope varies considerably among individuals ($1\cdot7$–$4\cdot0$ m s^{-1}). However, most of the variation in log v_m is accounted for by log body mass ($r^2 = 0\cdot575$, $P < 0\cdot001$, Fig. 2); and v_m can be predicted from mass by the following relationship:

$$v_m = 0\cdot74\ M^{0\cdot34}. \tag{3}$$

Thus, maximum speed varies with mass approximately to the one-third power.

Maximum speed versus slope

To examine the effect of slope on sprint speed, slopes were first transformed to $\sin\theta$ to generate a linear measure of the vertical displacement of a lizard running a distance of 1 m on a slope of θ degrees; the linear regression of v_m versus $\sin\theta$ was then determined for each lizard (Fig. 3). The effect of slope on v_m is demonstrated by determining from these regressions the predicted difference in v_m of a lizard running on slopes of $0°$ and $+60°$.

The effect of slope on speed ($v_{0°}$–$v_{60°}$) is strongly and inversely related to body mass ($r = -0\cdot590$, $P < 0\cdot01$, Fig. 4). Large lizards run much slower up a $60°$ slope than on the level. Remarkably, however, some small and medium-sized lizards (Figs. 3 and 4) appear to run as fast up steep slopes as on the level.

Speed versus mass, slope variable

The patterns in Figs. 2–4 raise the question of whether large lizards can always outrun small lizards even on steep slopes. In other words, is there an uphill slope at which speed is independent of mass? To investigate this question we calculated the exponential relationship for v_m versus body mass [see equation (3)] at each
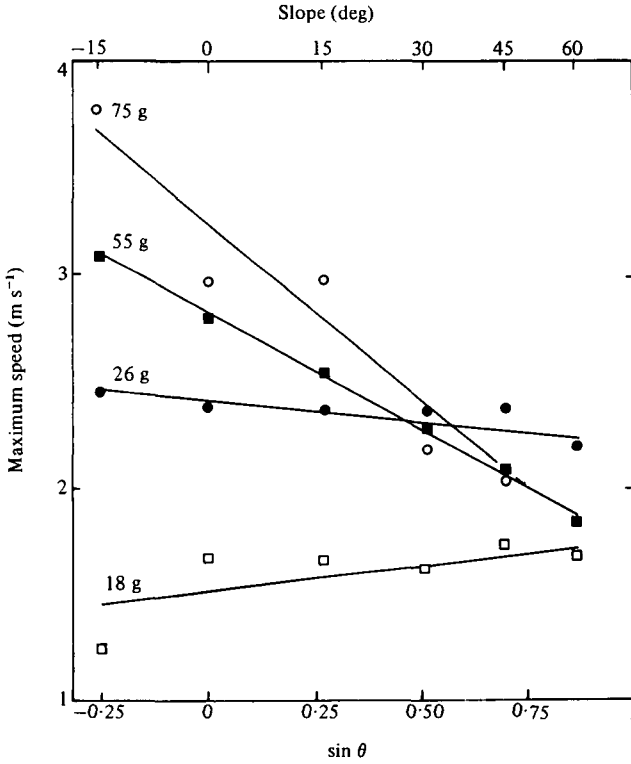
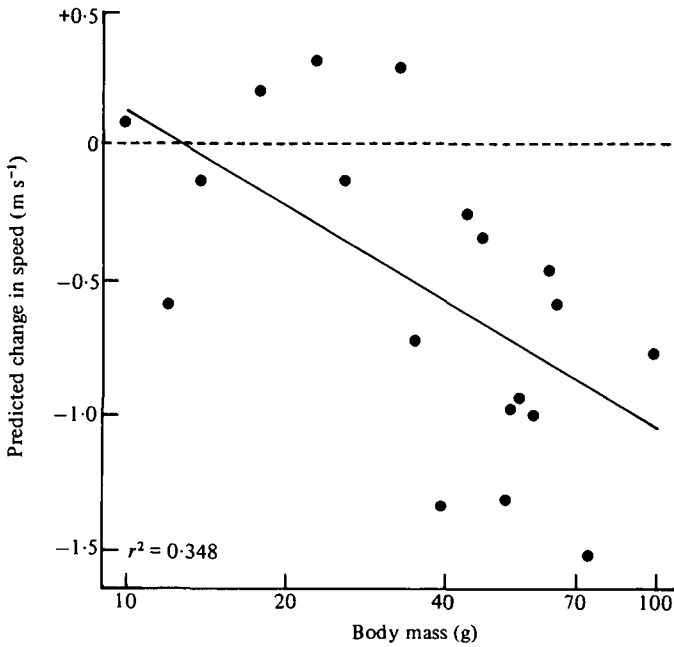Fig. 3. Maximum speed *v.* sin *θ* for four representative *Stellio* of different sizes.

Fig. 4. Predicted difference in speeds of a lizard running on slopes of 0° *v.* +60° as a function of mass. A value of 0 on the ordinate indicates that speed is independent of slope, and negative values indicate that speed is lower uphill.
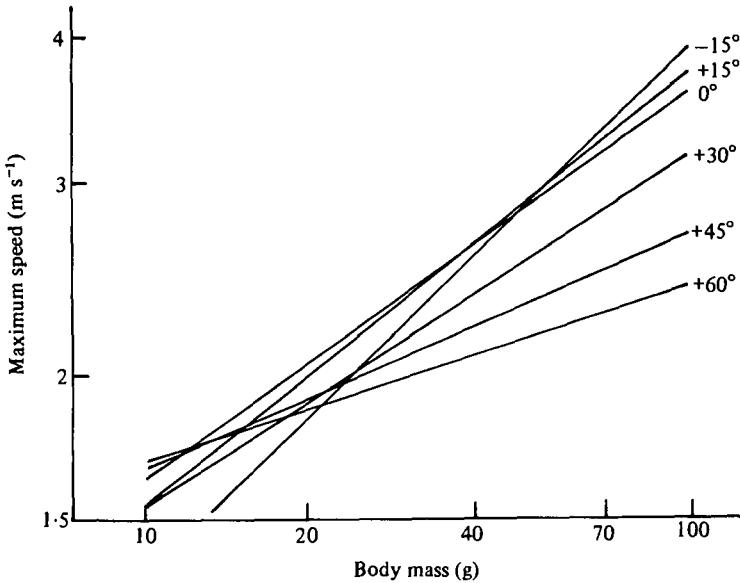
Fig. 5. Allometric relations of maximum speed v. mass for slopes from $-15°$ to $+60°$. The actual regressions (in order of increasing slope, with r^2 in parenthesis) are $0.45M^{0.47}$ (0.55), $0.75M^{0.34}$ (0.58), $0.63M^{0.39}$ (0.73), $0.74M^{0.31}$ (0.64), $1.02M^{0.21}$ (0.49) and $1.17M^{0.16}$ (0.34).

slope. The effect of mass on v_m (Fig. 5) is progressively reduced as slope increases (Spearman rank correlation of exponent of the above equation versus slope $= -0.943$, $P < 0.01$), but large lizards still run slightly faster on average than do small lizards even on slopes as steep as $60°$, where $v_m \propto M^{0.16}$. However, information on speeds at steeper slopes would be of interest.

DISCUSSION

In the following Discussion the results of our experiments on the effects of size and slope on sprint of *Stellio stellio* are first described with reference to theoretical models of sprint locomotion. Our comparisons of intraspecific trends with several theoretical scaling models do not, however, constitute an empirical test of those models, which are more appropriately tested by interspecific data from individuals at a particular growth stage (Gould, 1975; Sweet, 1980).

Scaling spring speed with body mass

The theoretical basis of scaling top speed with mass of quadrupedal animals has a controversial history. Hill's pioneering model (Furusawa, Hill & Parkinson, 1928; Hill, 1950; Wilkie, 1977) is based on the assumption that small and large animals are geometrically similar [i.e. the length (l) of every anatomical element is maintained proportional to diameter (d), thus $l \propto d$]. This static model predicts that speed is independent of size ($\propto M^0$). In other words, small and large animals should run equally fast. McMahon (1974, 1975) has proposed two dynamic scaling models which assume that animals maintain either 'elastic' similarity ($l \propto d^{\frac{2}{3}}$) or 'static stress' similarity ($l \propto d^{\frac{1}{2}}$). These models predict that maximum speed is proportion

lo $M^{\frac{1}{4}}$ and $M^{\frac{3}{8}}$, respectively. Thus, unlike Hill's static model, both of McMahon's dynamic models predict that speed increases with size.

Available data on the maximum speeds of mammals (Howell, 1944; Hill, 1950; Layne & Benton, 1954; Hildebrand, 1974) roughly support Hill's prediction (1950) only for mammals ranging in size from a whippet ($\sim$ 9 kg) to a horse. Unfortunately, a variety of different and often inaccurate methods were used to estimate speed (Hill, 1950). Heglund *et al.* (1974) found that running speeds of mammals (a 30 g mouse to a 680 kg horse) at the trot–gallop transition was proportional to $M^{0.24}$, supporting the model of elastic similarity (Heglund *et al.* 1974; McMahon, 1975). However, the phyletic diversity in the above experiments somewhat weakens the comparative strength of the conclusions: scaling models assume that the body form of species being compared are structurally similar.

Our data for a single species of lizard demonstrate that maximum speed on the level is proportional to $M^{\frac{1}{3}}$ (Fig. 2). Indeed, manipulation of equation (3) suggests that a 100 g *Stellio* should run about 2·2 × faster than a 10 g individual. This general result differs strikingly from that predicted for interspecific comparisons by a model of geometric similarity (M^0), but is roughly intermediate between those predicted for models of elastic ($M^{\frac{1}{4}}$) and static stress ($M^{\frac{3}{8}}$) similarity.

Size, slope, and maximum speed

The work against gravity in running uphill is proportional to slope (sin θ) and mass. Consequently, maximum speed should be inversely proportional to sin θ for a given sized animal. However, because the power output of muscles increases with $M^{\frac{3}{4}}$, whereas the work expended increases with M^1, steep slopes should slow large animals more severely than small animals (Hill, 1950; Maynard Smith, 1968).

Our results confirm the prediction that maximum speed of large lizards is negatively related to slope (Figs. 3 and 4). Indeed, a 100 g *Stellio* will run only about 30% as fast on a 60° slope as on a 0° slope.

Our results also confirm the prediction (Hill, 1950; Maynard Smith, 1968) that maximum speed of small lizards is less affected by slope than that of large lizards (Figs. 3 and 4). This pattern neatly complements the demonstration by Taylor *et al.* (1972) that the incremental metabolic cost of running uphill is significant for large but not for small mammals (Reichman & Aitchison, 1981; but see Cohen, Robbins & Davitt, 1978).

We were surprised, however, to find that maximum speed of small *Stellio* is essentially independent of slope. Indeed, some small lizards actually run as fast up 60° slopes as on the level (Figs. 3 and 4). Perhaps small lizards that have evolved to live in structurally complex microhabitats might have morphological specializations (e.g. body proportions, patterns of muscle recruitment) that can compensate for the effects of slope (Armstrong & Taylor, 1980). We leave this as an open problem.

Ecological implications of scaling speed with size and slope

Differences in maximum sprint speed influence an animal's ability to capture prey, to avoid becoming prey for another animal, and to interact socially (Howland 1974; Webb, 1976; Elliott *et al.* 1977). Consequently, our results on changes in speed with size and slope have significant implications for the behavioural ecology

of *S. stellio* and potentially other species that occupy habitats with high structural complexity.

The observed effects of size and slope on maximum speed (Fig. 4 and 5) suggest, for example, that the orientation of predatory lizards lying in ambush should vary with body size: large lizards should preferentially attack on level or downhill slopes, whereas small lizards might attack on any slope. (Similarly, the distance a lizard might venture from its retreat should vary with size and slope.) Data on attack angles of *Stellio* in nature are unavailable, but T. C. Moermond (personal communication) notes that the predicted patterns hold for some arboreal lizards of the genus *Anolis*.

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