EFFECTS OF BODY SIZE AND SLOPE ON ACCELERATION OF A LIZARD (*STELLIO STELLIO*)

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SUMMARY

1. The agamid lizard *Stellio* (= *Agama*) *stellio* L. accelerated quickly on a level track. Lizards reached 95 % of maximum speed in an average of only 0·31 m and 0·19 s.
2. Large lizards had higher initial accelerations ($\sim M^{1/3}$) and accelerated over longer distances and times than did small lizards. As a result, larger lizards achieved higher maximum speeds. Lizards of a given size that accelerated quickly also achieved high maximum speeds.
3. Acceleration was also measured on slopes ranging from $-15°$ to $+60°$. Steep inclines did not differentially reduce the initial acceleration of large *versus* small lizards, a result which contrasts with a previous demonstration that such inclines significantly reduce the maximum speed of only large lizards.
4. Simulations of simple predatory-prey chases suggest that large lizards will be more successful if they attack distant prey on level or downhill slopes and that small lizards will be more likely to escape larger quadrupedal predators by fleeing uphill, unless the predators are near.

INTRODUCTION

Sprint locomotion of vertebrates has recently been a focus of considerable attention from physiologists, morphologists and ecologists (Heglund, Taylor & McMahon, 1974; McMahon, 1975; Margaria, 1976; Alexander, 1977, 1982; Elliott, Cowan & Holling, 1977; Bennett, 1980; Hertz, Huey & Nevo, 1982; Taylor & Heglund, 1982; Huey, 1982; Garland, 1983). With the exception of studies dealing with aquatic organisms (Weihs, 1973; Webb, 1976, 1978a,b), studies have concentrated on maximum burst speed but have generally ignored the initial acceleration phase of locomotion, in part because acceleration is technically difficult to estimate. Nevertheless, acceleration is often more important than maximum speed in determining the outcome of predator-prey encounters (Webb, 1976; Elliott *et al.* 1977).

Here we present an empirical analysis of how acceleration of an agamid lizard (*Stellio stellio*) is influenced by body mass and by slope. We use new technological developments that facilitate the estimation of both acceleration and maximum speed

(Huey, Schneider, Erie & Stevenson, 1981). Our analysis complements a previo[ ]
study (Huey & Hertz, 1982) of size, slope and maximum speed in *Stellio stellio*. We
demonstrated that big lizards always run faster than small lizards on slopes ranging
from $-15°$ to $+60°$: we are now able to determine whether the greater speed of larger
lizards is a result of greater acceleration at the beginning of a run or of a prolonged
acceleration phase. We found also that steep inclines sharply reduce the speed advan-
tage of large lizards. These differential effects of slope on maximum speed of large
versus small lizards suggested that the predatory and anti-predator behaviour patterns
of lizards might change with age (Huey & Hertz, 1982). We are now able to test the
realism of these suggestions by using complete speed profiles in simulations of
predator-prey encounters (Webb, 1976; Elliott *et al*. 1977).

Our investigations (Huey & Hertz, 1982, herein) were stimulated by the research
of Taylor, Caldwell & Rowntree (1972), Webb (1976) and Elliott *et al*. (1977). Taylor
et al. (1972) demonstrated that the energetic cost of steady-state (not sprint)
locomotion increased with slope for large but not for small mammals. Our subsequent
findings for sprint speed of *Stellio* (Huey & Hertz, 1982) provided a direct parallel for
lizards, which are generally specialized for sprint (anaerobic) rather than for en-
durance (aerobic) locomotion (Bennett, 1983). Webb (1976) and Elliott *et al*. (1977)
effectively used locomotor data in simulations of predator-prey encounters and drew
attention to the importance of initial acceleration.

Stellio stellio, a moderate-sized (maximum mass about 125 g, maximum snout-to-
vent length about 150 mm) lizard from the Middle East, is ideally suited for an
analysis of the effect of size and slope on acceleration. A large size range of individuals
can be obtained, and these sit-and-wait lizards routinely ambush insect prey from
perches on rocks, boulders and walls. Consequently, acceleration should influence
their ability to capture prey and to evade predators.

MATERIALS AND METHODS

The animals used in these experiments, acclimation regimes, training programmes,
and running protocols are detailed in Huey & Hertz (1982). In summary, lizards
($N = 17$) were sprinted down a 2·4 m racetrack with 11 photocell stations positioned
along the track at fixed points (0·05, 0·10, 0·15, 0·25, 0·50, 0·75. . .2·00 m). An AIM-
65 microprocessor recorded the elapsed time to each photocell station (Huey *et al*.
1981).

To induce sprinting, we placed the lizard just behind the first set of photocells and
held it for a few seconds while lightly tapping its hind legs and tail. We then released
the lizard and chased it down the track. Each lizard was raced at each of the following
slopes (1 slope day^{-1}, six trials lizard^{-1} day^{-1}, about 1 trial every 45 min): 0°, 15°,
$-15°$, 30°, 45° and 60°. We report only the fastest acceleration from each set of six
runs and assume that this approximated the maximal possible acceleration for a given
lizard on a given slope. This assumption cannot presently be verified, but we note that
the maximum speeds of *Stellio* are high for lizards of this size (T. Garland, Jr.,
personal communication), which suggests that the lizards were often running at near
maximal effort. Nevertheless, some variability in our data is undoubtedly attributabl[ ]
to the difficulty of obtaining smooth and maximal accelerations from all lizards. Als[ ]

ards would sometimes hit a wall of the track, hesitate during a run, or be accident-ally touched by us during a chase: we subjectively excluded such cases prior to analysis of the data.

To describe the cumulative distance run as a function of time, we then fitted a modified exponential equation (Henry & Trafton, 1951) to the data on elapsed times and distances from the best run of each lizard at each slope using Marquardt's algorithm (SPSS):

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

where d = distance (m), v_m = maximum speed (m s^{-1}), t = time (s), and k = a con-stant. This equation is a better description of distance *versus* time than is a simple exponential, which incorrectly assumes that velocity never reaches a maximum value (Webb, 1976). Instantaneous speed (v) and acceleration (a) were then estimated (see Fig. 1) by progressive differentiation of equation (1). Note that we estimate accelera-tion only along the plane of the racetrack. We report the 'initial' acceleration of lizards at $t = 0.05$ s (rather than at $t = 0$ s) to reduce the impact of measurement error on estimates of initial acceleration (see Fig. 1).

Lizards were run at $T_b = 34$ °C. This temperature approximates the mean body tem-perature (T_b) of active *Stellio stellio* in nature (Hertz & Nevo, 1981) and is near the apparent 'optimal' temperature for sprint locomotion (Hertz, Huey & Nevo, 1983).

RESULTS

Acceleration on a level slope

Stellio stellio have high initial rates of acceleration and reach maximum speed quickly. To compute the length and duration of the acceleration phase, we estimated both the distance covered and the time elapsed before each lizard reached 95 % of its maximum speed: the average distance and the average time to reach 95 % of maximum speed was only 0.31 ± 0.05 m (range $= 0.08$–0.67) and only 0.19 ± 0.02 s (range $= 0.08$–0.35), respectively, for all lizards in our sample ($N = 17$). For example, a 35 g *S. stellio* running on the level (Fig. 1) achieved 95 % of maximum speed (3.00 m s^{-1}) within the first 0.51 m (or in 0.25 s).

Initial acceleration (acceleration at 0.05 s) on the level averaged 13.8 ± 1.13 m s^{-2} ($N = 17$, range $= 5.1$–23.6). Not surprisingly, initial acceleration is negatively cor-related with the elapsed time to run short distances (for 0.15 m, $r = -0.576$, $P < 0.05$; for 0.25 m, $r = -0.701$, $P < 0.01$).

Large lizards have higher initial accelerations than do small lizards. Log initial acceleration was positively correlated with log body mass (Fig. 2A, $a = 3.758M^{0.334}$, $r = 0.491$, $P = 0.045$). Thus, initial acceleration varies with mass to the 1/3 power, but the 95 % confidence limits are broad (± 0.326).

The average distance (but not the average time) of the acceleration phase was positively rank correlated with body mass ($r_s = 0.466$, $P = 0.05$ and $r_s = 0.273$, $P = 0.31$, respectively; Table 2). Thus, large *Stellio* not only have higher initial ac-celerations but also accelerate over longer distances than do small *Stellio*; this accounts the higher maximum speeds achieved by large *Stellio* (Huey & Hertz, 1982).
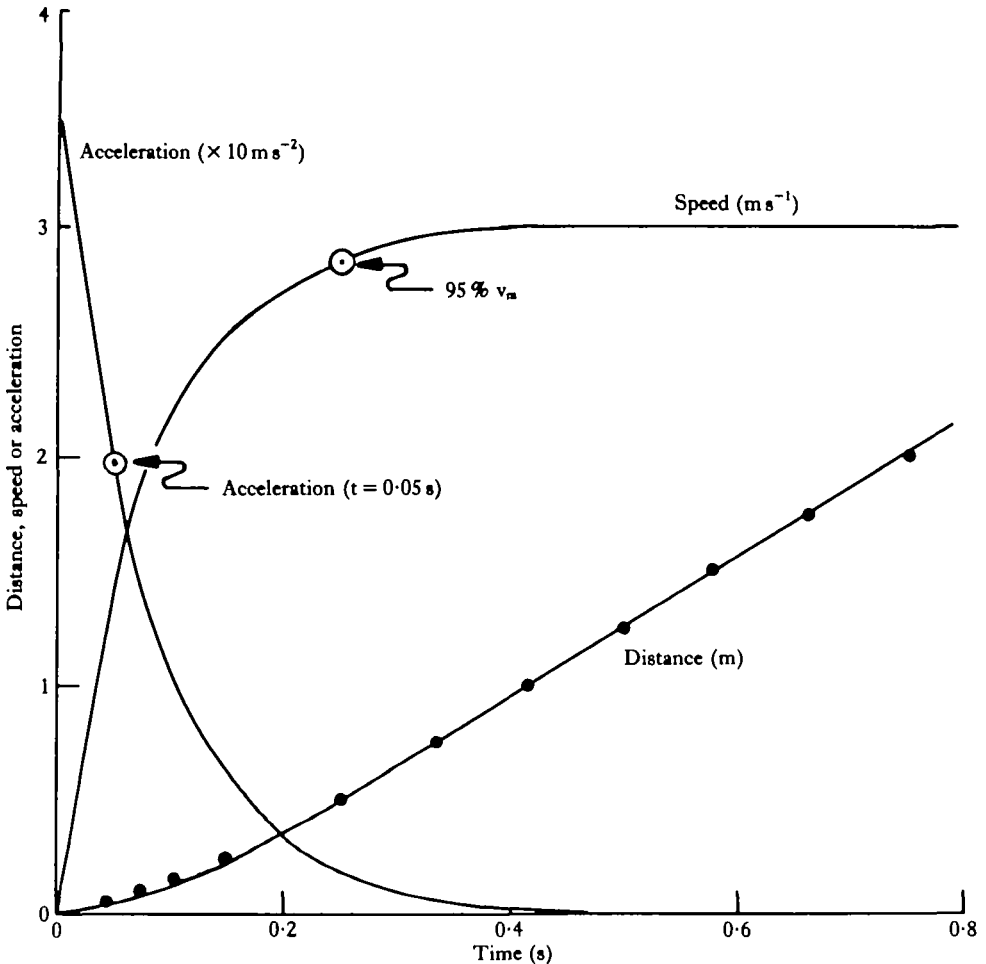
Fig. 1. Distance, speed and acceleration as functions of time for a 35 g *Stellio stellio* running on a 0° slope. The scale of the ordinate is in m for distance, m s^{-1} for speed, and 10 m s^{-2} for acceleration. The curves are derived from equation (1). Initial acceleration (at t = 0·05 s) and the duration and length of the acceleration phase (time, distance to 95 % v_m) are indicated.

Lizards of a given size that accelerate quickly also reach high maximum speeds. Log initial acceleration (above) and log maximum speed (Huey & Hertz, 1982) are each positively correlated with log body mass and with each other ($r = 0.891$, $P < 0.001$). Moreover, partial correlation analysis demonstrates a strong relationship between acceleration and speed even when log body mass is held constant (Fig. 2B, $r = 0.854$, $P < 0.001$).

Acceleration, mass and slope

Initial acceleration increases with body mass at most slopes from $-15°$ to $+60°$ (Table 1), although the relationship is often weak at a given slope. Nevertheless, the positive relationship between acceleration and mass is highly significant overall (Fisher combined probability test, $P < 0.001$).

The time and length of the acceleration phase (when speed = 95 % v_m) are positively related to body mass at many slopes (Table 2). Both relationships are significant overall.

To examine directly the effect of different slopes on acceleration of individuals, slopes were first transformed to sin θ to generate a linear measure of the vertical displacement of a lizard running a distance of 1 m on a slope of θ degrees (see Huey & Hertz, 1982); the linear regression of acceleration *versus* sin θ was then determined for each lizard. The effect of slope on acceleration can then be demonstrated by determining from these regressions the predicted difference in acceleration of a lizard running on slopes of 0° and +60°.

Slope appears to have a small and variable effect on acceleration of different sized lizards. The median percentage change in acceleration of individual lizards running on slopes of 0° *versus* 60° was only −0·7 %, but the variation among lizards was large (Fig. 3). Steep uphill slopes did not significantly reduce the acceleration of large lizards more than that of small lizards (Fig. 3, $r = -0·392$, $P = 0·12$).
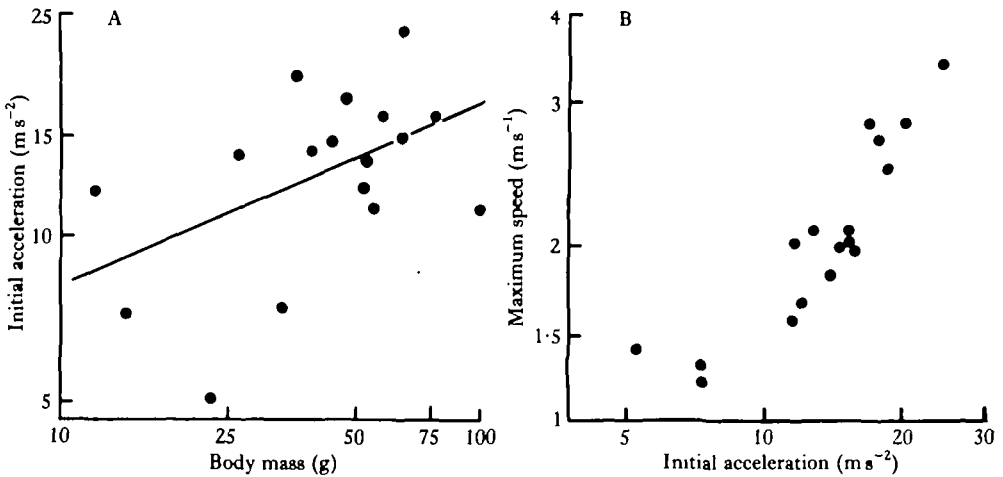

Fig. 2. (A) Initial acceleration *vs* mass for *Stellio stellio* running on the level. (B) Initial acceleration *vs* maximum speed for *Stellio stellio* running on the level.

Table 1. *Allometric equations of initial acceleration (m s^{-2}) versus mass (M, in g) for* Stellio stellio *on various slopes*

Slope	Equation	r	P
−15°	2·275 $M^{0·426}$	0·387	0·154
0°	3·758 $M^{0·334}$	0·491	0·045
+15°	3·690 $M^{0·339}$	0·330	0·196
+30°	2·270 $M^{0·469}$	0·640	0·004
+45°	1·233 $M^{0·579}$	0·517	0·028
+60°	4·592 $M^{0·221}$	0·229	0·393

Combined probability < 0·001

Table 2. *Spearman rank correlation coefficients at different slopes for the length (distance in m) and the duration (time in s) for lizards to reach 95 % of maximum speed as a function of body mass*

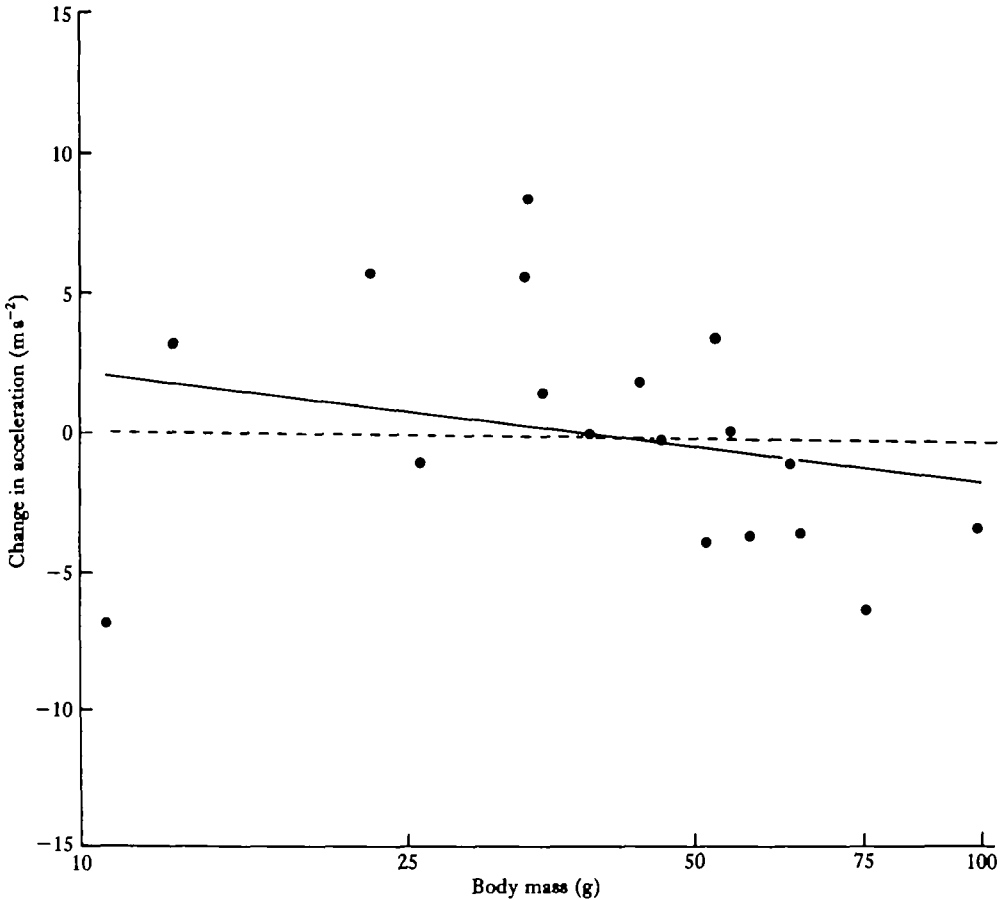|	Distance		Time	
Slope	r_s	P	r_s	P
−15°	0·101	0·710	0·081	0·765
0°	0·466	0·043	0·273	0·273
15°	0·556	0·019	0·515	0·033
30°	0·514	0·028	0·420	0·078
45°	0·479	0·042	0·353	0·148
60°	0·390	0·133	0·336	0·203
Combined probability		0·001		0·037

Fig. 3. Predicted difference in initial acceleration of lizards running on slopes of 0° *vs* +60° as a function of mass. A value of 0 on the ordinate indicates that initial acceleration is independent of slope, and negative values indicate that acceleration is reduced when sprinting uphill.

Ecological consequences of size, acceleration, speed and slope

The ability of an animal to accelerate and run quickly affects its ability to capture prey, to avoid becoming prey for another animal, and to interact socially. Consequently, our results on changes in acceleration and speed with size and slope should have significant implications for the behavioural ecology of this species and perhaps of other 'arboreal' animals that rely on speed to capture prey or to avoid predators.

We address indirectly the relationship between sprint ability and behavioural ecology by using sprint data in simulated predator-prey chases (Webb, 1976; Elliott *et al.* 1977) in which large *Stellio* attack smaller conspecifics in straight-line chases up or down hills of constant slope. (We emphasize that *Stellio* is not known to be cannibalistic. Thus our simulations are intended only to be heuristic.) Equation (1), which specifies distance run as a function of time, was fitted to sprint data (at each of six slopes) for two pairs of large and small lizards, which were arbitrarily selected on the basis of size and consistent running performance. Small lizards were given simulated headstarts ranging from 0·1 to 2·0 m. We then calculated the time (which was converted to distance run) before the small lizard would be overtaken by the large lizard for a given separation distance and slope. These simulations assume that reaction times are instantaneous, that both lizards sprint from a standing start, and that both run straight ahead in the same direction (but see Howland, 1974; Webb, 1976; Elliott *et al.* 1977; Alexander, 1982; and below).

We use distance run before capture as the dependent variable rather than time run before capture. Distance and time are obviously related (see equation 1).
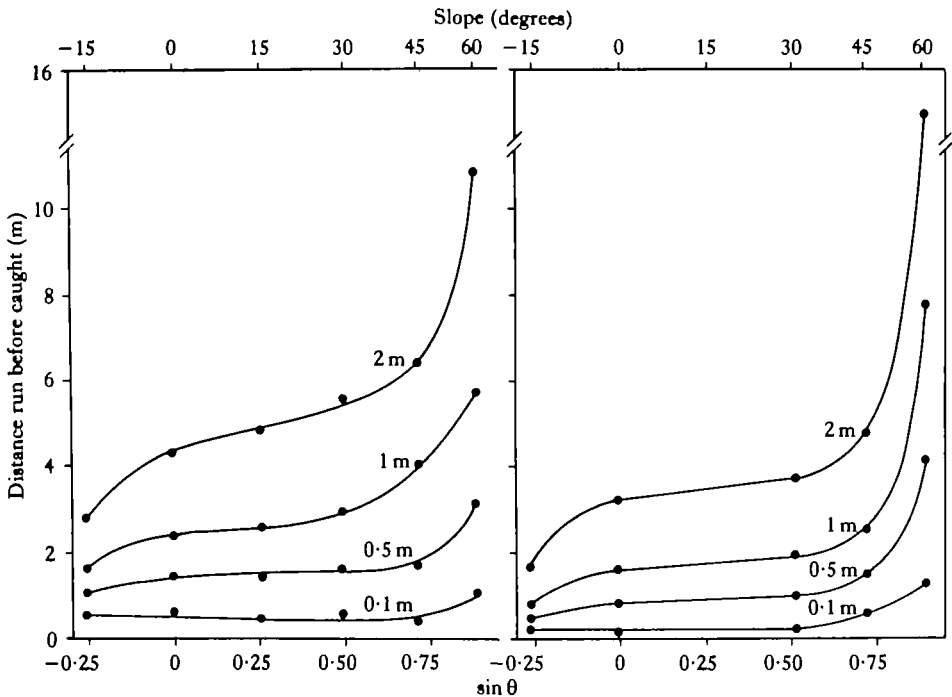

Fig. 4. The distance a small lizard can run before being overtaken by a large lizard as functions of the slope of the escape route and the initial separation distance (0·1–2 m). Two pairs of lizards are plotted.

Nevertheless, the critical ecological variable (*sensu* Huey & Stevenson, 1979) to▮ lizard being chased is its proximity to a refuge. In essence our simulations estimate the linear 'safety zone' for a small lizard.

Sample simulations are shown in Fig. 4. For initial separation distances of 1 or 2 m, slope profoundly affects safety zone: a small lizard that runs uphill will have a relatively large safety zone. However, for shorter separation distances, the safety zone is relatively independent of slope, except for $-15°$ and $+60°$ slopes. For short separation distances safety zones must be more sensitive to relative acceleration, which is independent of slope (Fig. 3), than to maximum speed, which is more sensitive to slope (Fig. 5 in Huey & Hertz, 1982).

These simulations are samples only, and safety zones will vary depending on individual abilities of predator and prey. For example, if the large lizard in Fig. 4B attacked the small lizard in Fig. 4A, the large lizard would capture the small lizard only at a slope of $-15°$. On level or uphill slopes, this small lizard would always outrun this large lizard.

DISCUSSION

In the following Discussion the results of our experiments on the effects of size and slope on initial acceleration of *Stellio stellio* are first compared with our previous results concerning maximum speed (Huey & Hertz, 1982). We then explore some ecological and practical consequences of our analysis.

Scaling acceleration with body mass, level slope

Initial acceleration on the level increases with body mass approximately to the 1/3 power in *Stellio stellio*. Interestingly, maximum speed also increases with $M^{1/3}$ (Huey & Hertz, 1982). Not surprisingly, initial acceleration and maximum speed are positively correlated, even when body mass is held constant.

The theoretical and empirical bases for the scaling of acceleration with mass of quadrupedal animals have not yet been developed. In contrast, the theoretical basis of the scaling of maximum speed has attracted considerable debate (Furusawa, Hill & Parkinson, 1928; Hill, 1950; Maynard Smith, 1968; McMahon, 1974, 1975). Recent empirical analyses for mammals document inconsistent scaling relationships of maximum speed (Garland, 1983) and of limb-bone proportions (Alexander, Jayes, Maloiy & Wathuta, 1979), suggesting that the theoretical basis of the scaling of locomotion may be more complex than generally believed (Garland, 1983).

Size, slope and acceleration

The work against gravity expended in sprinting uphill is proportional to slope ($\sin \theta$) and body mass. If an animal of a given size is sprinting at full capacity, speed should be inversely proportional to $\sin \theta$. Moreover, because the power output of muscles does not increase in direct proportion to body mass, steep slopes should slow large animals more severely than small animals (Hill, 1950; Maynard Smith, 1968; Taylor *et al.* 1972; Elliott *et al.* 1977).

The maximum speed of large lizards decreases dramatically on steep uphill slope▮

whereas the maximum speed of small lizards is remarkably independent of slope (Huey & Hertz, 1982). In contrast, acceleration was seemingly independent of slope in both small and large lizards (Fig. 3). Consequently, big lizards always accelerate faster than do small lizards (Table 1). The differential effects of slope on acceleration *versus* maximum speed are problematical, and we pose the mechanistic and morphological bases of this pattern as open topics for future research.

Ecological consequences of size, acceleration, speed and slope

Body size and slope influence the acceleration and maximum speed of lizards, but the effect of slope differs for acceleration and speed: initial acceleration is independent of slope for both large and small lizards (Fig. 3), whereas maximum speed on steep slopes is reduced only for large lizards (Huey & Hertz, 1982). These patterns suggest that the predatory and anti-predator behaviour patterns of lizards might change with age (Huey & Hertz, 1982). For example, large lizards might preferentially attack distant prey only on near level or downhill slopes, because of the relatively slow maximum speeds of such lizards up steep inclines. Nevertheless, large lizards might successfully attack very close prey on any slope, because acceleration of such lizards is independent of slope. Furthermore, a small lizard that is being chased by a large predatory lizard might have a better chance of reaching a safe retreat by fleeing uphill, at least if the initial distance separating predator and prey were large.

Our sample simulations (Fig. 4) support the prediction that size and slope should influence predatory and anti-predatory behaviour. For separation distances of 1 m or greater, the safety zone for a small lizard increases with slope, apparently because maximum speed dominates acceleration in determining safety zones. For shorter separation distances, however, the safety zone is always small, apparently because acceleration here dominates maximum speed in determining safety zones.

Our simulations and speculations are based on the simple assumption that both predator and prey start sprinting at the same instant. In fact, the prey's start will often be delayed because of a lag in reaction time (Webb, 1976), whereas the attack by the predator might sometimes be delayed by defensive displays (mimicry, bluffing) of the prey. Simulations can easily incorporate such reaction latencies, but actual lag times are unknown for lizards and would probably vary with circumstance and temperature (Webb, 1978b). The effect of a reaction lag by the prey should be the same as decreasing the initial separation distance, thereby significantly decreasing the safety zone, especially on steep slopes (see Fig. 4). In contrast, a delay in the attack by a predator will have the same effect as increasing the initial separation distance, thereby significantly increasing the safety zone of the prey (Webb, 1976; Fig. 4). Consequently, defensive measures that merely delay a predator's attack can provide significant protection to a potential prey, even if the defensive measures do not actually prevent the attack (C. Gans, personal communication).

Modification of these simulations could permit consideration of more complex predator-prey encounters (P. W. Webb, personal communication). For example, the predator could attack along a path that differs from that of the prey (Webb, 1976; Elliott *et al.* 1977). Similarly, predator and prey could run at an angle to the slope. Any deviation of the prey from a course straight up the slope should reduce its safety zone (P. W. Webb, personal communication), because such a course would reduce the

actual slope traversed by these animals (see Reichman & Aitchison, 1981, p. 417). Finally, predators and prey could run along curvilinear trajectories such that the slope they experience is constantly changing. Up to now, such curvilinear chases have been modelled only for horizontal planes (Howland, 1974; Webb, 1976; Alexander, 1982).

The simulations bear on the practical question of whether maximum speed alone provides an adequate estimate of locomotor performance (Huey & Stevenson, 1979) or whether complete speed profiles are required. Maximum speed alone will often suffice for many studies because (1) lizards reach maximum speed very quickly (Fig. 1, Tables 1, 2) and (2) initial acceleration and maximum speed are often correlated (Fig. 2B). Nevertheless, it is also crucial to know acceleration when animals sprint over very short distances (Webb, 1976) or over complex topography. Consider, for example, that a prediction based on maximum speed alone would seriously over-estimate the significance of slope to the safety zone for a small lizard whenever the initial separation distance is small. Thus whether maximum speed alone is an adequate description of performance depends on the length of sprint distances in nature. Quantitative data are unavailable for *Stellio*, but our own impression from extensive field experience with many species of lizards on five continents is that sprint distances can be extremely variable (a few cm to >10 m), both intra- and interspecific-ally, which suggests that any comprehensive ecological analyses will probably require complete speed profiles as well as reaction times.

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