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How inclines affect the escape behaviour of a dune-dwelling lizard, *Uma scoparia*

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Abstract. Although previous laboratory studies have commonly determined sprinting speeds of lizards on horizontal surfaces, the speeds and slopes used during the escapes of lizards in natural habitats with variable inclines are virtually unstudied. To quantify performance and the use of inclined surfaces during escape, we took advantage of the footprints left in soft substrate and the simple surface topography of the natural dune habitat of the Mojave fringe-toed lizard, *U. scoparia*. The lengths of 52 escape paths ranged from 1.7–34 m, and the inclines of 1-m portions of escape paths ranged from −25° to 28°, which effectively encompassed the entire range of inclines in the habitat. The cumulative frequencies ($N=550$) of inclines along 1-m intervals of the escape paths were not a simple random sample of the habitat. Less than 10% of the cumulative distance travelled during escape was bipedal, and the escape paths were relatively straight. Trajectories of the first metre of escapes were oriented significantly away from the presumed threat (observer) but were random with respect to the orientation of both the nearest cover and steepest incline. Eleven per cent of the cumulative number ($N=1382$) of strides measured were within 90% of the maximum stride length within each path. Multiple regressions revealed that stride lengths (and hence speed) during escapes in the field were maximized on level surfaces with no turning. For lizards tested on a level racetrack in the laboratory, maximum speeds averaged 2.8 m/s (range=2.1–3.9) and approximated 75% of the maximum performance attained in the field.

Arnold (1983) and others have provided compelling arguments that the performance (effectiveness) of a complex system is the intermediary through which natural selection may act on a variety of traits. Although the individual components of complex systems such as muscle physiology can be tested for performance in isolation, the complicated interactions between behaviour, physiology and morphology often limit the usefulness of such reductionist approaches for predicting what intact animals do in a natural setting. Hence, tests of organismal performance have played a prominent role in recent attempts to understand the adaptive value of traits.

Few tests of organismal performance have been conducted as commonly as tests of speed and endurance of locomotion of lizards (reviewed in Garland & Losos 1994). Laboratory tests of locomotor performance commonly involve chasing lizards along flat racetracks that are approximately 2 m long, and maximal sprinting speeds obtained by such methods show significant inter-individual differences that are heritable and repeatable for as long as 1 year (Huey & Dunham 1987; van Berkum et al. 1989). The lack of studies accurately determining locomotor performance of lizards in both the field and laboratory, however, leaves unknown the extent to which laboratory measures of performance, although repeatable, may be sub-maximal compared to what animals do in their natural environment (Hertz et al. 1988).

Lizards have also served as model organisms for ecological studies (Milstead 1967; Huey et al. 1983; Vitt & Pianka 1994), and some studies have integrated measures of locomotor performance with structural features of habitat such as substrate type (e.g. Carothers 1986; Miles 1994) and perch diameter (e.g. Losos & Sinervo 1989; Losos & Irschick 1996) and several other aspects of

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vegetation (e.g. Moermond 1979; Pounds 1988; Bulova 1994). However, the inclination of surfaces in the environment has received scant attention, although incline is an attribute of the environment with predictable mechanical consequences for the locomotion of all animals. Furthermore, movement up and down inclined surfaces is a very general feature of the biology of lizards, in part because their size is often small compared to obstacles in the environment. Few studies of lizard locomotion, however, have tested the effects of varying incline (Huey & Hertz 1982, 1984; Carothers 1986; Farley & Emshwiller 1996).

Moving up inclines increases the energetic cost of locomotion (Farley & Emshwiller 1996) and may decrease maximum speed depending on the substrate and size of the lizard (Huey & Hertz 1984; Carothers 1986). Despite significant decreases in the maximal speed of large lizards on inclines, the initial accelerations of both large and small lizards are remarkably unaffected by incline (Huey & Hertz 1984). As a result of the differential effects of incline on speed, Huey & Hertz (1984) suggested that small (<30 g) lizards could enhance their ability to escape larger lizards by running uphill. Equally plausible alternative hypotheses might negate the prediction that small lizards will run uphill during escapes. For example, lizards may travel a path directly away from a potential predator regardless of the incline encountered. Similarly, lizards might run towards the nearest available refuge regardless of its orientation with respect to either incline or the location of the predator. We attempted to differentiate among these possibilities by studying the escape locomotor behaviour of fringe-toed lizards, *U. scoparia*, because the simplicity of their dune habitat allows one to quantify the occurrence and utilization of inclined surfaces. Furthermore, the soft surface of the sand dunes readily preserves footprints which can be used to (1) reconstruct the escape path, (2) estimate locomotor performance and (3) test alternative hypotheses of escape tactics.

The overall purpose of our study was to determine the escape tactics and performance of an animal in its natural habitat and integrate this information with laboratory measures of performance. We addressed the following four issues. (1) Are the escapes of lizards random with respect to inclines in the habitat? (2) To what extent do lizards perform maximally during the entire duration of an escape? (3) Do lizards orient their escapes randomly with respect to the location of the threat or cover? (4) To what extent do laboratory measures of performance estimate performance in natural habitat?

METHODS

Study Animals

To estimate the size of lizards in the study area, we captured a total of 30 adult *U. scoparia* for which snout–vent length ranged from 5.6 to 10.1 cm. Three lizards with snout–vent length from 9.4 to 10.1 and masses from 28 to 32 g were much larger than the next largest individual measured (snout–vent length = 8.6 cm, mass = 21 g). For the six *Uma* captured after directly observing an escape, snout–vent length ranged from 6.3 to 7.5 cm. The size of the other lizards that we observed escaping subjectively appeared to be within the range of sizes measured after excluding the three largest individuals, and the mean values of snout–vent length and mass for this subset of 27 individuals were 7.2 cm and 12.4 g, respectively. We never observed *Uma* climbing in the vegetation; therefore, tracks on the sand provided a convenient, indirect means of recording nearly all of the surface locomotion of this species.

Study Site

All field observations and animal collections occurred in the Kelso dune system of the Mojave desert approximately 13 km southwest of Kelso in San Bernadino County, California. The primary study site (1 km × 50 m between 34°53.684′N, 115°42.211′W and 34°54.031′N, 115°42.762′W) had an altitudinal gain of approximately 100 m and was approximately 2 km from the highest point of the dune (780 m). We also recorded field active body temperatures and collected some of the *Uma* for laboratory observations at a second location approximately 4 km west of the primary site. No creosote bushes, *Larrea divaricata*, were in the primary study area, although the downhill end of the site was located within 10 m of the transition between areas with and without creosote. The study area was sparsely vegetated, and most cover was from two species of plants, *Croton californicus* and *Petalonyx thurberi*, which were often on top of distinct mounds of sand. Most permanent burrows were at the base of such clumps of vegetation, since the sand in areas lacking vegetation generally could not support openings large enough to accommodate the locally occurring species of lizards. Within the primary study site, *U. scoparia* were abundant and were sighted on more than 200 occasions (including neonates); the total sightings of other species of lizards included only three *Cnemidophorus tigris*; one *Callisaurus draconoides*, one *Phrynosoma platyrhinos* and one *Gambelia wislizenii*. The sightings of lizard species other than *U. scoparia* were all confined to the lower 300 m of the site, and their tracks could be readily distinguished from those left by *Uma*. The combination of the wind-blown sand and relatively open habitat were ideally suited both for locating the tracks of *Uma* and quantifying the slope of the surfaces upon which they ran.

At locations 10 m apart along the entire length of each 1-km edge of the rectangular study area, we used a digital level on a 1-m rod to measure the maximum incline of the ground. For each of these measurements, the orientation of the rod was in the direction of the steepest incline rather than necessarily being parallel to the edge of the study area. The orientations of these steepest inclines were highly variable and showed no conspicuous pattern with respect to the orientation of the study area, in part because the distance for the incline measurement (1 m) and the size of the localized inclined surfaces were small compared to the distance from the base to the overall peak of the dune (>2 km). The 200 resulting angles of maximal inclination were transformed into the rise per metre (Rise) by multiplying the sine of the angle by 1 m. For any inclined plane, an infinite number of lines (and slopes) pass through a single location; however, the inclines of all these lines are between ± the maximum slope of the inclined plane. Consequently, for each of the 200 intervals of ± maximal Rise, we used a spreadsheet function to generate four random samples. The resulting frequency distribution reflects the probability of a particular slope for a random 1-m trajectory of an animal traversing the dune within the study area, and can therefore be used to generate the expected frequencies of incline for a random path in this environment.

Field Measurements of Escape Behaviour

Fieldwork was from 10 to 13 June and from 28 August to 3 September 1996, and on each of these days we searched for lizards and footprints during approximately 0730–1130 hours and 1630–1930 hours. Between the June and August samples, the young of the year hatched; however, we excluded the neonatal individuals from the later sample to minimize variation in size. Over the entire study, we quantified 52 complete footprint paths made by 51 lizards. Forty-four of the 52 paths were made by individuals that we observed directly as they attempted to escape from us, and we included eight additional paths that had a fundamentally similar pattern of footprints but were lacking direct observations of the lizard's escape. We searched for lizards by walking haphazardly within the study area, and roughly equal amounts of our searching time were spent walking in the general direction from the base to the higher portions of the dune and returning in the reverse direction. Consequently, we had no systematic bias in whether we were either uphill or downhill of an escaping lizard.

After marking 1-m straight-line distances along an entire escape path with surveyor's flags, for each 1-m interval we then used a digital level (± 0.1°) to measure the angle of the incline rounded to the nearest 0.5°. We transformed each angle into values of Rise as was done for the sample of habitat. We then calculated the total amounts of uphill (Up) and downhill (Down) change in vertical position along the entire path, and Up–Down yielded the Net vertical gain from the beginning to the end of the entire path. Vertical gains are useful quantities, because they are proportional to the change in potential energy and the additional mechanical work required to traverse an incline compared to an identical distance on a level surface. Because the steepness of inclines on a path may vary in a complex fashion, however, vertical gains convey almost no information about the distances that are travelled on inclines. Thus, we also calculated the percentage of the 1-m intervals that had positive (%Up) and negative (%Down) vertical gains, and because some intervals were horizontal (± 0.5°), %Up + %Down did not always equal 100%. We also measured maximum incline of the substrate (in any direction) at the mid-point of each 1-m interval along the escape path.

We recorded whether the end of each path was (1) an exposed location (neither under vegetative cover nor within a burrow), (2) under vegetative cover or (3) a permanent burrow. To be considered cover, the minimum diameter of a clump of vegetation had to exceed the average total length of the lizards (15 cm). *Uma* can burrow rapidly (‘sand swim’) into loose sand which collapses onto the animal rather than leaving a distinct opening (Stebbins 1944). Hence, we also noted whether tracks terminated with sand swimming and whether this occurred in an area lacking cover, beneath cover or near the entrance of a permanent burrow.

For each 1-m interval, we recorded tracks as one of four qualitative categories that other studies and our preliminary observations of *Uma* footprints in the study area suggested corresponded from fastest (1) to slowest (4) speeds. Category 1 lacked visible prints of the forefeet, all visible footprints were large circular impressions in the sand, and tail drag marks could be either present or absent (Stebbins 1944, figure 16). Category 2 had fairly circular footprints of all four feet but no tail drag marks (Mosauer 1935, figure 5). Category 3 had intermittent drag marks of the tail and less circular footprints that more closely resembled the shape of each foot. Category 4 had distinct impressions of individual hind toes and tail drag marks were usually continuous (Mosauer 1935, figure 4). We calculated the occurrence of the different tracks as the percentage of 1-m intervals that had a particular category, and because a 1-m interval could have more than one category of track, these percentages did not necessarily sum to 100% for each path.

For the June sample, we photographed at least the first 1 m of each path. All photographs were direct overhead views to avoid problems of parallax, and we included a 1-m reference rod within the field of view. From projections of the resulting 35-mm slides of footprints, we measured stride lengths of the hind limbs to the nearest mm. For the August–September sample, we used a ruler to measure the length of each stride of one hind limb directly from the footprints in the sand for the entire path.

For the 28 paths in the August–September sample for which we directly observed the lizard running away, we made several additional measurements. To clarify the direction of each escape path and its relation to the stimulus (observer), we used compass bearings (±2°) to determine the orientation of several different line segments, including: (1) each 1-m interval of the path; (2) the start to the end points of the entire path; (3) the point at which an observer noticed the fleeing lizard to the starting point of the path; (4) the starting point of the path to the nearest available cover; and (5) 1 m parallel to the steepest incline along the first metre of the path.

We subtracted pairs of angles indicating orientation to calculate five variables that quantified the trajectories of the escapes, and each trajectory variable was standardized to allow values to be pooled meaningfully and analysed with circular statistics (Zar 1996). The five variables were as follows. All–M1 is the difference between the trajectory from the beginning to end points of the entire path and that of the first metre. All–Obs and M1–Obs indicate the trajectories of the entire path and first metre, respectively, relative to the observer so that 0° indicates movement directly away from the observer. M1–Cov indicates the trajectory of the first metre of the path relative to the nearest available cover so that 0° indicates movement directly towards the nearest cover. M1–Up indicates the trajectory of the first metre of the path relative to the steepest uphill incline along the first metre of the path so that 0° indicates running directly uphill.

We also quantified approach distance (Approach) as the straight-line distance between the observer and the start of the path. To clarify how convoluted the escape path was, we also measured the straight-line distance between the start and end points of the entire path (Straight).

During the August–September fieldwork, we used a thermocouple and a Tegam 871A digital thermometer to obtain temperatures of the air (at chest height in the shade) and ground surface at the starting point of 25 escape paths and the cloacal temperatures of four lizards that were captured immediately after they attempted to escape. While collecting additional *Uma* for use in laboratory experiments, we measured the cloacal temperature of 22 active individuals both from within the study site and a nearby (4 km) location in the same dune system. For all adult lizards that were captured, we measured snout–vent length to the nearest mm and mass to the nearest 0.1 g.

Laboratory Measurements of Performance

We collected animals for laboratory performance trials during the August–September field work (California Department Fish and Game permit no. 4746). For both the level and inclined trials, we chased each lizard two or three times in rapid succession on each of two successive days, and the horizontal and 30° uphill trials began 2 and 6 days, respectively, after the end of the fieldwork. Time is a potentially confounding factor in our experimental design, but at least the time between level and uphill trials was minimal (4 days). Randomizing trials with respect to time would have prolonged the number of days required to complete the tests because of the logistics of, for example, realigning the racetrack and cameras and warming the lizards. We were most concerned about minimizing the total time between capture of the lizard and the last test.

We discarded trials where the lizards abruptly turned to the side, because this posed complications for determining displacement (and hence velocity and acceleration) from the lateral-view videotapes. Furthermore, if the feet of the lizard contacted the sides rather than the sand bottom of the track, then we could not determine stride length from the overhead photographs of the footprints. Thus, we restricted our quantitative analyses to the eight individuals with suitable uphill and level trials that lacked either of these complications and hence created a balanced experimental design. Mean (range) values of snout–vent length and mass of the eight lizards were 7.2 (7.2–8.6) cm and 12.7 (8.4–21.1) g, respectively, and except for the largest lizard, masses were less than 15.6 g. During trials we maintained body temperatures of the lizards at 38–42°C, which was within the range of values that we observed for field active body temperatures.

The racetrack (3 m × 25 cm × 25 cm) for testing lizards had a 2-cm deep layer of fine sand (passed through a 0.5-mm sieve), which was similar to that in the natural habitat. The side of the track facing the video-cameras was clear Plexiglas, and the back wall of the track was painted with a 10-cm reference grid. Four 500-W lights approximately 1 m above the track provided illumination. At the end of the track opposite the release location, we placed a shelter made of black construction paper with an opening resembling that observed for many of the burrows encountered in the field. We videotaped a lateral view of running *Uma* using a two-camera NAC HSV-500 high-speed video system operating at 250 images/s. The width of the view of each camera was 80 cm with a 10-cm region of overlap between the two images, for a resulting total length of 150 cm in the middle of the track that was videotaped. We used a 35-mm still camera mounted 1.5 m directly above the middle of the track to obtain slides of the footprints in the sand, which were analysed similarly to field photographs to quantify the stride lengths of the right hind limb.

We quantitatively analysed only the results of performance tests of the single trial per individual with the longest stride for both the horizontal and 30° uphill tests. We used single-field playback of the videotapes to determine the elapsed time of each footfall to the nearest 4 ms, and we calculated the average forward velocity per stride by dividing stride length by stride duration (time between successive footfalls of the right hind foot). We used custom software to digitize the forward displacement of the snout of each lizard during each trial. Beginning one video image (4 ms) before the first perceptible forward movement, we digitized images at 8-ms intervals for the first 80 ms, and then used 16-ms intervals for the remainder of the images in each trial. We standardized forward displacements and times so that initial values were zero, and the resulting values were fitted to the model of Huey & Hertz (1984),

$$s = V_m \times (t - 1/k + (1/k) \times e^{-kt}) \qquad (1)$$

where s equals forward displacement (m), V_m equals maximum forward velocity (m/s), t equals time (s) and k is a constant. The first and second derivatives of this function provided functions for forward velocity and acceleration, respectively.

RESULTS

Temperature and Habitat

For 22 *Uma*, active field body temperatures ranged from 34.3 to 45.1°C, with 12 values exceeding 40°C, and a mean ± SD value of 39.7 ± 2.8°C. These temperatures are noteworthy because studies have suggested that 40°C is the maximum voluntary temperature and 45°C is the critical thermal maximum for this species (Stebbins 1944;

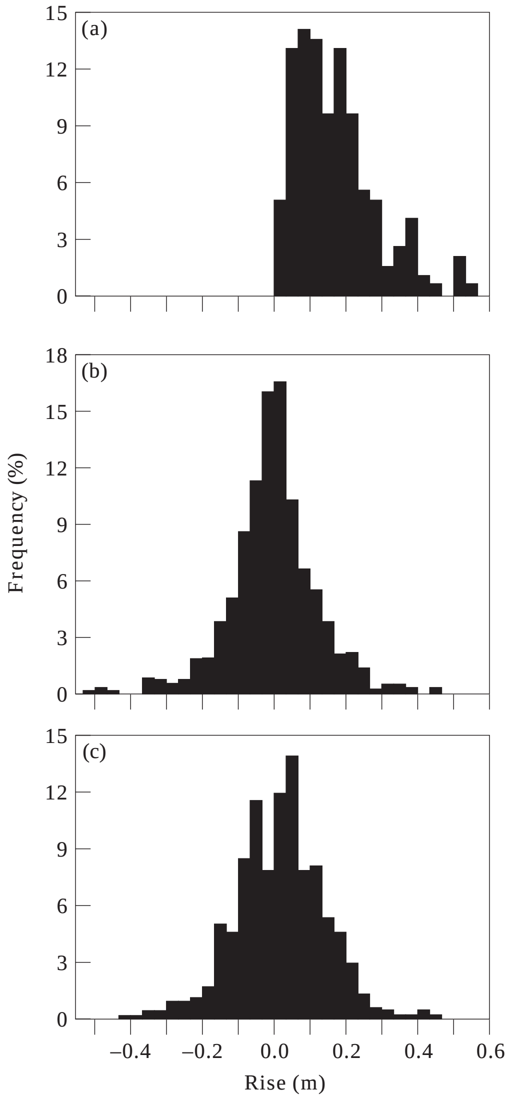

Figure 1. Frequency distributions for values of Rise per metre. (a) Maximal values measured at 10-m intervals along two 1-km transects; $N=200$. (b) A random sample of 800 values derived from the distribution shown in (a). (c) All values for each metre of 52 escape paths; $N=550$.

Brattstrom 1965; Pianka 1986). Ground temperatures at the starting point of 25 escape paths in the August–September sample ranged from 30.3 to 56.3°C, and the surface temperatures of the racetrack in the laboratory were 35–45°C.

Figure 1a shows the frequency distribution of the maximal values of Rise measured along each of the 1-km sides of the rectangular study area. Rise per metre of the steepest dune surface was 0.545 m (33° incline), which approximates the angle of repose for this particular sand. The mean and median values of maximal Rise per metre were 0.169 and 0.156 m, respectively.

For the random sample of 800 slopes (Fig. 1b) derived from the initial distribution of maximal slopes (Fig. 1a), neither the mean of −0.003 m (two-tailed $t=-0.75$, $P>0.4$) nor the skewness of −0.161 ($t=-1.85$, $P>0.05$) differed significantly from zero. In contrast, the kurtosis (2.181) of the random sample (Fig. 1b) did differ significantly from the value (0) of a normal distribution ($t=12.8$, $P<0.001$).

Escape Paths: Field Study

Figure 1c shows the frequency distribution of all values ($N=550$) of Rise per metre that were measured for the 52 escape paths. The mean ± SE value of Rise of escape paths was 0.016 ± 0.005 m. The values of Rise for the escape paths were not significantly skewed ($g_1=-0.161$, $t=0.47$, $P>0.5$), and they were leptokurtotic ($g_2=0.802$, $t=3.84$, $P<0.001$) but to a lesser extent than those for the random sample of the habitat (Fig. 1b, c). Because of the significant leptokurtosis, parametric tests such as a *t*-test comparing means with the random sample of habitat could be misleading. Consequently, we performed a Kolmogorov–Smirnov goodness-of-fit test for continuous grouped data (Zar 1996, page 478), and detected an overall significant difference between Rise for the random sample and the escape paths ($d_{\mathrm{max},\,30,550}=136$; $P<0.001$; Fig. 1b, c). The greatest deviations of the path inclines from those in the habitat were the less than expected occurrence of values of Rise from 0 to 0.067 m and greater than expected occurrence of values from 0.067 to 0.233 m. Hence, during escapes, the paths travelled by *Uma* were not entirely random with respect to the slopes occurring in the habitat.

Figure 2 summarizes major attributes of the entire escape paths. The lengths of the 52 escape paths ranged from 1.7 to 34 m with a mean ± SD value of 10.6 ± 6.8 m. The mean ± SD (range) amounts of uphill (Up) and downhill (Down) change in vertical position per escape path were 0.61 ± 0.67 (0–2.85) m and 0.39 ± 0.41 (0–1.50) m, respectively. A two-tailed *t*-test pairing values of Up and Down within each escape ($t_{51}=2.00$, $P=0.051$) indicated a non-significant tendency for

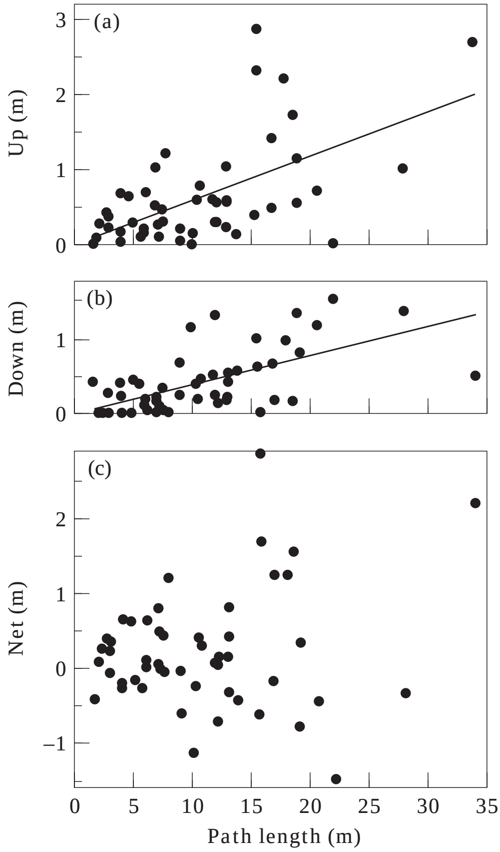

Figure 2. Amounts of change in vertical position versus length of each escape path ($N=52$). Regressions are shown only for significant relationships. (a) Total uphill, Up = 0.008 + 0.056 × Length ($r^2=0.34$, $P<0.001$). (b) Total downhill, Down = 0.001 + 0.037 × Length ($r^2=0.38$, $P<0.001$). (c) Net change ($r^2=0.098$, $P>0.2$).

more uphill than downhill running within each escape. The mean ± SD (range) amount of total change (Up + Down) in the vertical position per escape was 1.00 ± 0.79 (0.09–3.15) m; the mean value of Net change was 0.22 ± 0.78 (1.50–2.85) m. Values of both Up and Down increased significantly with path length, whereas values of Net were not correlated with path length (Fig. 2). The mean percentages of the metres per escape path that were uphill (%Up) and downhill (%Down) were 57.8% (29.8; 0–100%) and 37.6% (29.5, 0–100%), respectively, and the mean remaining fraction (4.6%) of each path occurred on level ground. Within each path, %Up was significantly greater than %Down (two-tailed paired $t_{51}=2.42$, $P=0.019$). Nine of the 52 escape paths consisted entirely of uphill locomotion, but only three escapes were entirely downhill. Hence, regardless of whether the amounts of uphill and downhill running were expressed in absolute or relative terms, the normal escape behaviour of *Uma* at this site included substantial movements up and down inclines.

For the entire sample of 52 paths, 29 ended in a permanent burrow, and 17 ended beneath vegetative cover. Only six escapes ended at exposed locations, and one of these included an individual that used sand-swimming to bury itself.

For the 28 escapes observed in the August–September sample, values of Approach distances (between location of observer and the beginning of the path) ranged from 0.3 to 20.5 m. The mean value of Approach was 4.2 m, and 16 of the escapes had values of Approach between 1 and 3 m. For all 28 escapes, Approach had a significant positive correlation with path length ($r=0.46$, $P=0.014$), but if the longest path was excluded from the sample, the correlation was not significant ($r=0.13$, $P>0.5$).

Figure 3 summarizes values of five trajectory variables for the 28 escapes observed during August–September. The trajectory of the entire path (All–M1) did not differ significantly from that of the first metre of the path (mean ± 95%CL difference in angles = − 5 ± 14°; Fig. 3a). The trajectories of the entire path (All–Obs) were not random (Raleigh's test for circular uniformity $Z=3.7$, $P<0.05$) with respect to the location of the observer (Fig. 3b). Instead the mean ± 95%CL value of All–Obs, − 14 ± 45°, did not differ significantly from 0°, which indicates running directly away from the observer (Fig. 3b). Similarly, the values indicating the trajectory of the first metre of the path relative to the observer (M1–Obs) did not have a uniform circular distribution ($Z=6.8$, $P<0.001$), and the mean ± 95%CL angular value of − 15 ± 30° did not differ significantly from 0° (Fig. 3c). The smaller dispersion for the values of M1–Obs compared to that of All–Obs indicates that the initial trajectory of the escape was more predictably away from the observer than the overall trajectory of the entire path (Fig. 3b, c). The trajectory of the first metre relative to the nearest vegetative cover (Fig. 3d) was random, as indicated by a uniform circular distribution ($Z=2.3$, $P=0.1$). The trajectory of the first metre of the escape was also random with

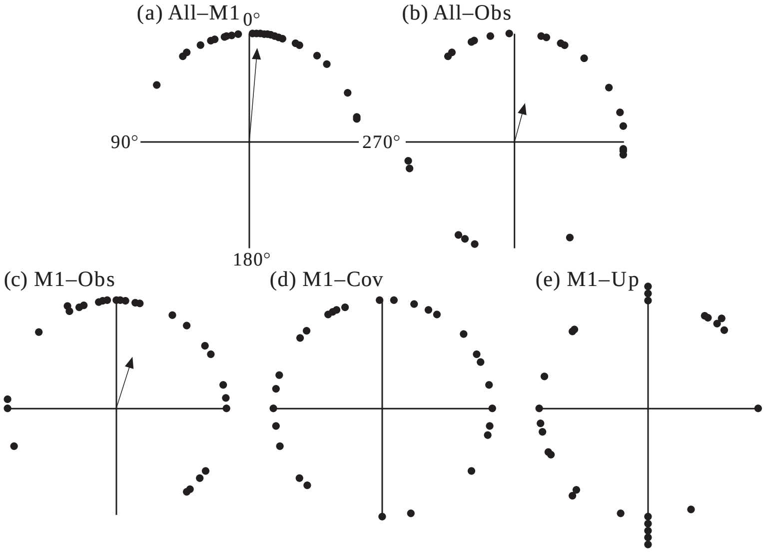

Figure 3. Angular frequency distributions for the trajectories of the 28 lizard escapes observed during August–September. For distributions that were not uniform, the direction of the arrows indicate the angular means, and the length of the arrows is inversely proportional to the dispersion of the data. (a) The difference in trajectories between the endpoints of the entire path (All) and the first metre of the path (M1) such that 0° indicates identical trajectories. (b) and (c) show the trajectories of the entire path and first metre of the path, respectively, relative to the location of the observer (Obs), such that 0° indicates running directly away from the observer. (d) Trajectories of the first metre of the path relative to the location of the nearest vegetative cover (Cov), such that 0° indicates running directly towards the nearest cover. (e) Trajectories of the first metre of the path relative to the steepest uphill path (Up), such that 0° indicates running directly uphill.

respect to the orientation of the steepest uphill grade (unimodal $Z=0.5$, $P>0.5$; bimodal $Z=2.3$, $P=0.1$; Fig. 3e).

Length of escape paths deviated minimally from the shortest distance (Straight) from the beginning to the end of the escape; the mean value of Length divided by Straight was only 109% (Fig. 4). Of 260 turns that were measured between successive 1-m intervals along 28 escape paths, only 17 values of turning exceeded 45° and the modal value was 7.5° (Fig. 5a). We found no significant trends comparing the amount of turning per 2 m for the beginning versus the final 2 m of the path or for the middle portions of the path versus the beginning and end. Near the end of the escape paths, however, *Uma* commonly turned when they were behind small (<2-m high) mounds of sand or vegetation (Fig. 4b, last 3 m).

Footprints and Stride Length: Field Study

For the 550 intervals for the 52 escape paths for which categories of track were scored, 10.0% had category-1 tracks. For 30 of the 52 escape paths, category-1 tracks were limited to the first metre. Fourteen escapes lacked category-1 tracks. The greatest absolute amount of category-1 tracks observed for any of the escapes was 5 m for a path 22 m long. Thus, the absolute amounts of category-1 tracks (and bipedal running) per escape were often similar, but because of the highly variable lengths of the escape paths, the percentages of the total distance covered per escape by category-1 locomotion varied from 0 to 65%. Only 0.9% of the 1-m intervals along the escape paths had category-4 tracks, and the percentage of occurrences of categories 2 and 3 were 85.1 and 12.5%, respectively.

In the August–September sample, we measured 1382 strides for 28 escape paths; Length ranged from 2 to 28 m ($\bar{X}=9.9$ m). The corresponding number of strides per path ranged from 10 to 112 ($\bar{X}=48$). The mean value of absolute stride length was 21.9 cm; range of individual strides was 4.7–39.8 cm. For the frequency distribution of relative (% of maximum within a path) stride

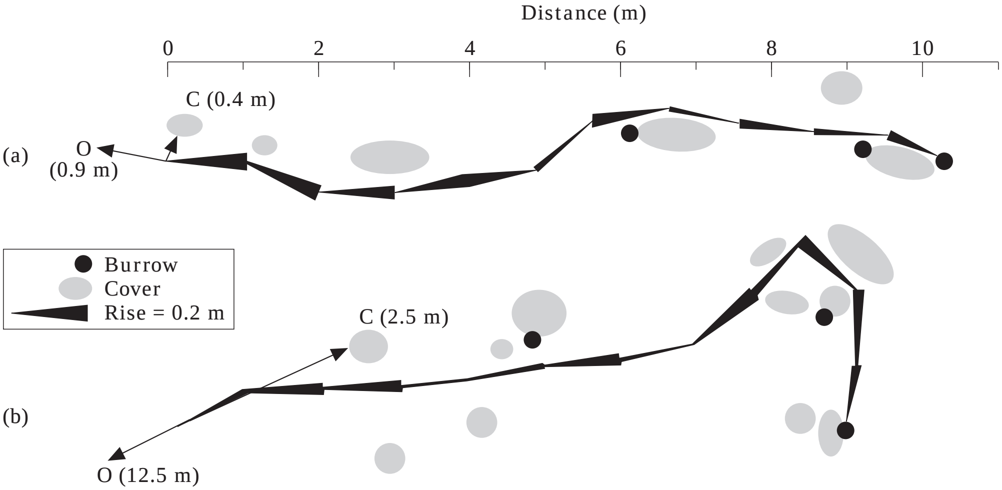

Figure 4. Schematic illustrations of two representative escape paths. Both paths are aligned so that the starting point is opposite 0 on the distance scale, and the overall trajectory from beginning to end is parallel to the distance scale. Triangles indicate 1-m intervals along the escape path, and their width at the base is proportional to the change in vertical position per metre. Triangles with their bases oriented away from and towards the start of the path indicate uphill and downhill, respectively. At the beginning of each path, arrows indicate the location of the observer (O) and nearest vegetative cover (C). (b) The arrow indicating observer location is not drawn to scale. The lizards did not end their escapes at either the nearest available cover or burrow.

length, the bin from 65 to 70% was the model (Fig. 5b). Only 17.6% of the strides were less than 50% of the maximum length. Furthermore, 34.9 and 10.9% of the strides had values of relative length exceeding 75 and 90%, respectively.

Stride length always changed conspicuously within the first metre of each path as a result of the rapid initial acceleration (Fig. 6). The mean ± SE value of the first stride of the 28 escapes of the August–September sample was 30 ± 1.6% of the maximum attained within each escape. Each successive value of mean relative stride length increased up to the tenth stride (72 ± 2.8%), which corresponded to an average cumulative path distance of 1.65 m. Near the fifteenth stride (mean cumulative path distance = 2.78 m), mean relative stride length approximated 74% and no further conspicuous increases were apparent. Several individuals did not attain maximal stride length until well beyond the first 3 m of the escape, and maximal stride length was attained within the first metre of a path in only one instance (Fig. 7).

For the 28 escape paths in the August–September sample, we used a combination of simple correlations and multiple regression analyses to clarify the factors that affected mean relative stride length per metre after excluding values from the first metre of each path (resulting $N = 231$). Contrary to our expectation that longest strides would be downhill and shortest strides would be uphill, the mean relative stride length per metre lacked a significant linear decrease (intercept = 85.3, slope = 0.915, $r^2 = 0.0008$, $P =$ 0.89) with Rise per metre of the path. Mean relative stride length per metre did decrease significantly both with values of Rise^2 (intercept = 76.7, slope = -124, $r^2 = 0.056$, $P < 0.001$) and values of Turn (intercept = 77.9, slope = -0.209, $r^2 = 0.062$, $P < 0.001$). Furthermore, when Turn and Rise^2 were entered simultaneously into a multiple regression predicting mean relative stride length per metre, both variables were individually significant and the multiple r^2 was 0.14 (Fig. 8). Hence, stride length was maximized by running horizontally with no turning (Fig. 8).

Footprints, Stride Length and Speed: Laboratory Study

Laboratory observations revealed that category-1 tracks could be made by either bipedal running or rapid accelerations during which the

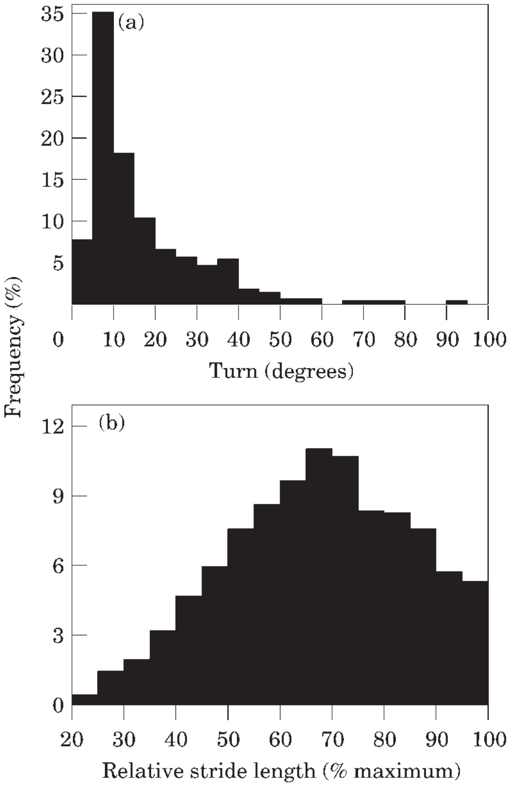

Figure 5. Frequency distributions for (a) the amount of turning between each successive complete 1-m interval for each path ($N=260$) and (b) the relative stride lengths for all paths for the 28 escapes ($N=1382$) observed in the August–September sample.

hind footfalls obliterated the track of the forelimb. After allowing for the sub-maximal speeds during the initial acceleration, the combination of videotapes and photographs of footprints in the laboratory verified that our four categories of tracks had a rank order that was generally consistent with speed.

Both level and uphill trials had large increases in the lengths of successive strides, with a third stride approximately twice as long as the first stride (Table I). The cumulative times and distance travelled for the first six strides were approximately 0.5 s and slightly less than 1 m, respectively (Table I). Despite the small number of strides per escape in the laboratory trials, the location of the longest stride varied considerably, ranging from the third to ninth (and last) stride that was visible in the videotapes. In contrast to the length of strides, stride duration varied minimally when the animals accelerated (Table I). Although mean values of stride length and velocity were almost always greater for the level compared to the uphill trials, most pairs of mean values for each stride number had overlapping 95% confidence limits.

For the level trials, values of maximal velocity per stride and stride length ranged from 2.11 to 3.87 m/s and from 17.9 to 28.3 cm, respectively (Table II). Four individuals had maximal stride lengths in the level laboratory trials of 18.6, 28.3, 17.9 and 22.1 cm, which corresponded, respectively, to 60%, 87%, 62% and 119% of the maximal stride length observed in the field for each individual. Accelerations at 0.05 s approximated 16 m/s^2 on the horizontal surface, then diminished rapidly, as indicated by mean values of 3.92 and 1.25 m/s^2 at 0.2 and 0.4 s, respectively (Table II).

For the level trials, velocity had a significant linear relationship with stride length ($N=54$, $r^2=0.74$, $P<0.001$; Fig. 9a). A quadratic term of stride length was not included in the regression model because its coefficient was not significant. Changes in stride length (which could not be calculated for the first stride) were also significantly related to change in velocity between successive strides ($N=46$, $r^2=0.37$, $P<0.001$). The negative values of change in velocity and stride length indicate that not all running was maximal, even though only 1.5 m were used for the laboratory observations (Fig. 9b). For different combinations of stride number (1 = first), stride length, and change in stride length as independent variables, the regression accounting for the greatest amount of variance in velocity and for which each independent variable was statistically significant was velocity (m/s) = 0.20 + 10.9 × Stride length + 3.24 × Change in stride length ($N=46$, $r^2=0.67$, $P<0.001$).

The mean values of the uphill laboratory tests were consistent with the expectations of decreased speed and acceleration; but only a few of these differences between uphill and level trials were statistically significant (Table II). The mean value for the parameter V_m of equation (1) was significantly greater for the level trial (2.83 m/s) than for uphill (2.31 m/s), and the velocity calculated from equation 1 at 0.4 s for the level trials was significantly greater than that of the uphill trial.

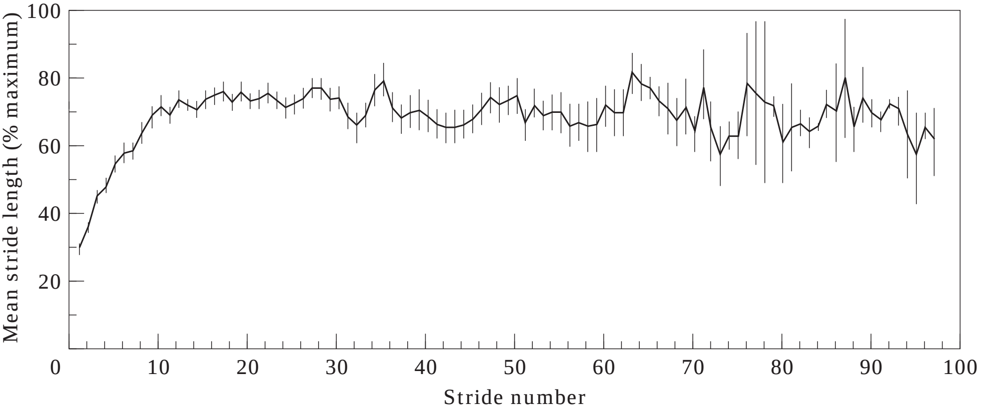

Figure 6. Mean ± SE values of relative stride length versus the number of the stride within each of the 28 paths of the August–September sample (mean maximum value of absolute stride length = 29.8 cm). Because of the variation in path length, $N=28$ for strides 1–10; for greater values of stride numbers N progressively declined. For strides 20, 30, 40, 50 and 60–97 sample sizes were 23, 19, 15, 12 and 8–2, respectively.

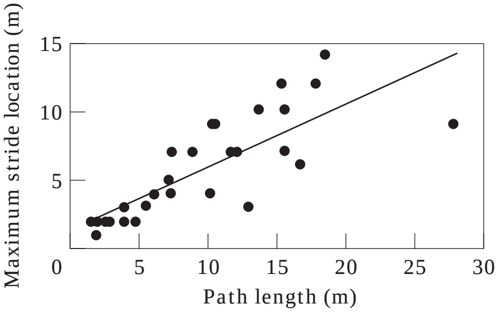

Figure 7. Location of the longest stride within a path versus length of the path for the August–September sample. The slope and intercept of the regression ($r^2=0.63$, $N=28$, $P<0.001$) are 0.46 and 1.37, respectively.

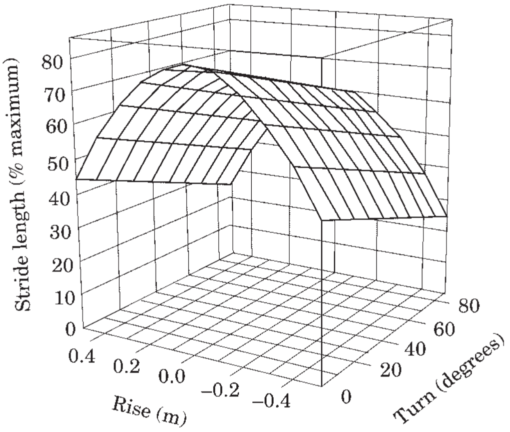

Figure 8. Predicted values of mean relative stride length per metre from a multiple regression using all except the first 1-m intervals of the 28 paths of the August–September sample. Multiple regression for mean relative stride length per metre = 80.0 − 0.22 × Turn − 142 × Rise^2 ($r^2=0.14$, $N=231$, $P<0.001$). Standard errors of the coefficients for Turn and Rise^2 were 0.052 and 31.5, respectively.

DISCUSSION

This was the first study of lizard locomotion to quantify the occurrence and use of inclines in a natural setting, and we found considerable amounts of movement up and down inclines even though we were studying a terrestrial rather than arboreal species of lizard. We also detected significant decreases in locomotor performance during escapes with increased amounts of turning and steep paths.

For escapes in the field, *Uma* had unexpectedly little amount of horizontal movement (Fig. 1c). Decreased performance could result from travelling a horizontal path on an inclined surface because the heights of the left and right feet differ proportionally to the difference between the Rise of the path and that of the maximal slope at that location. This difference, however, was not significantly correlated with relative stride length in either a simple regression ($r=0.044$, $N=231$, $P=0.51$) or any multiple regressions. If the axial structures of a lizard are parallel to a tilted surface, then movements of the left and right

Table I. Mean ± SE values of stride length, duration and velocity for the first six strides of *Uma* escapes

Stride number	Stride length (cm)			Stride duration (ms)		Velocity (m/s)	
	Field	Level	Uphill	Level	Uphill	Level	Uphill
1	9.2 ± 0.5	6.7 ± 0.7	7.1 ± 1.4	71 ± 9.8	87 ± 8.0	0.97 ± 0.04	0.80 ± 0.13
2	11.2 ± 0.5	13.0 ± 0.7	12.9 ± 1.3	78 ± 7.6	81 ± 6.2	1.74 ± 0.16	1.58 ± 0.13
3	13.9 ± 0.5	15.5 ± 0.9	15.1 ± 1.4	72 ± 4.9	80 ± 4.8	2.20 ± 0.12	1.87 ± 0.15
4	14.9 ± 0.7	19.3 ± 0.6	17.4 ± 1.6	82 ± 5.3	85 ± 4.6	2.44 ± 0.20	2.06 ± 0.18
5	16.8 ± 0.7	21.4 ± 1.4	18.7 ± 2.4	86 ± 5.7	86 ± 5.7	2.60 ± 0.29	2.14 ± 0.22
6	17.8 ± 0.8	20.9 ± 2.8	18.5 ± 1.9	95 ± 6.1	82 ± 5.6	2.27 ± 0.40	2.28 ± 0.23
Total	83.8	96.9	89.6	484	503		

Level and uphill refer to laboratory observations ($N=8$ for level strides 1–4 and uphill strides 1–5, and $N=5$–7 for the remaining laboratory observations). $N=28$ for field observations. Cumulative totals of distance and time are given below the columns with values of stride length and duration.

Table II. Summary of laboratory tests ($N=8$) of locomotor performance for a horizontal surface and 30° uphill incline

Variable	Level		Uphill		t
	$\bar{X}$ ± SE	Range	$\bar{X}$ ± SE	Range	
Maximum stride (cm)	22.8 ± 1.5	17.9–28.3	22.2 ± 1.3	15.9–27.6	0.48
Mean duration (ms)	82 ± 3	70–93	83 ± 4	69–101	−0.35
Maximum velocity (m/s)	2.79 ± 0.20	2.11–3.87	2.58 ± 0.16	1.63–3.11	1.15
V_m parameter (m/s)	2.83 ± 0.40	1.10–4.35	2.31 ± 0.20	1.65–3.24	3.38*
k parameter	16.14 ± 4.49	3.81–42.97	13.02 ± 3.36	6.20–34.53	−0.40
V at 0.05 s (m/s)	1.14 ± 0.19	0.54–2.16	0.96 ± 0.10	0.57–1.45	0.94
V at 0.2 s (m/s)	2.37 ± 0.27	1.72–4.07	1.95 ± 0.15	1.53–2.65	2.08
V at 0.4 s (m/s)	2.82 ± 0.27	1.86–4.33	2.24 ± 0.19	1.65–3.13	3.22*
a at 0.05 s (m/s^2)	16.32 ± 2.28	9.97–30.09	13.28 ± 1.12	9.78–18.38	1.49
a at 0.2 s (m/s^2)	3.92 ± 0.88	0.41–7.71	2.99 ± 0.61	0.06–5.03	0.85
a at 0.4 s (m/s^2)	1.25 ± 0.52	0.00–3.32	0.55 ± 0.14	0.00–1.12	1.21

Mean durations of strides were calculated for all visible strides during the escape of each individual; maximum velocities and stride length used only a single stride per individual. k and V_m were calculated separately for each individual and then used in equation (1) to predict forward velocity (V) and acceleration (a) at 0.05, 0.2 and 0.4 s after the beginning of forward movement. Paired t-tests compared level versus uphill measures of performance for each individual.
*Two-tailed $P<0.05$.

limbs could be symmetrical relative to the body and perhaps facilitate performance. The adhesive toe structures in specialized arboreal lizards might alleviate some of the functional problems associated with left–right tilt, and additional insights might be gained by comparing arboreal taxa with a terrestrial species such as *Uma* that regularly moves on tilted surfaces.

Despite the unexpectedly low amounts of horizontal locomotion, field performance (stride length) was maximal for horizontal paths (Fig. 8). We had expected maximal performance down hills because of the accelerating effect of gravity. Perhaps steep inclines adversely affect locomotor performance of *Uma* regardless of the orientation of the path (uphill, downhill or horizontal), and comparing the predictive value of maximum Rise of the substrate versus Rise of the path helps to resolve this issue. Maximal Rise of the substrate, however, was not significant when included with values of turning angle and path Rise^2 as independent variables in a multiple regression predicting

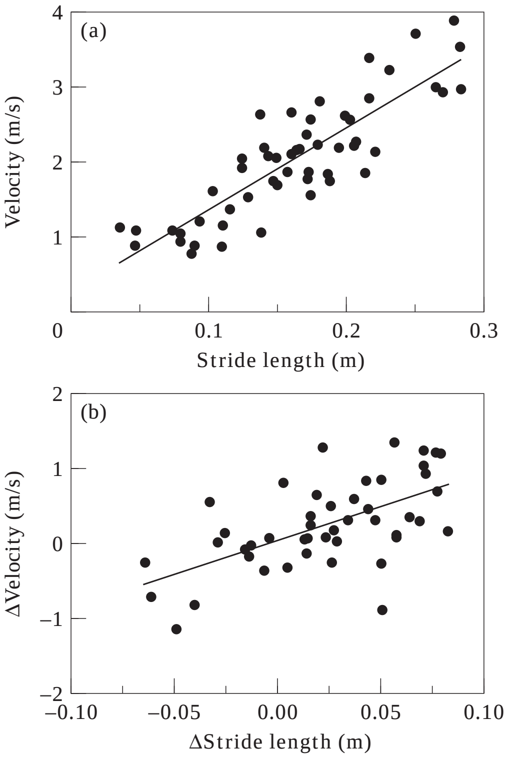

Figure 9. Regressions for laboratory observations of speed and stride length for lizards running on a level surface. (a) Relationship between average forward velocity per stride and stride length ($N=54$, slope=10.9, intercept=0.27, $r^2=0.74$, $P<0.001$). (b) Relationship between change in average forward velocity per stride and stride length ($N=46$, slope=8.98, intercept=0.04, $r^2=0.37$, $P<0.001$).

mean relative stride length per metre. Thus, we were unable to detect a decrease in performance that was attributable to steep surfaces and not accounted for by steep inclines of the path travelled by the lizard.

The effects of incline on locomotor performance may also depend on both the size of the lizard (Huey & Hertz 1982, 1984) and the mechanical properties of the inclined surface (Carothers 1986). For our laboratory study of running performance on sand, we minimized variation in the size of lizards for a representative sample of animals observed in the field. Huey & Hertz (1982, 1984) used a racetrack with a hard rubberized surface to test performance of a *Stellio* (or *Laudakia* or *Agama*) *stellio* with masses ranging from 10 to 100 g. Initial accelerations of all sizes of *Stellio* were unaffected by running up steep inclines with rises of 0.5 and 0.75 (Huey & Hertz 1982, 1984), whereas maximal speeds declined significantly for large but not small (<30 g) individuals. Our laboratory observations of the maximum velocity uphill averaged 92% of the values for the level trials, and two performance variables declined significantly on the incline (Table II). Furthermore, the multiple regression for our field observations (Fig. 8) predicts that stride lengths on a rise of 0.5 will be 56% of those attained by *Uma* running a level path. Carothers (1986) also tested *U. scoparia* running on sand with a rise of 0.5, and uphill maximal velocities averaged 84% of the level values (2.38 m/s). Thus, biologically meaningful inclines can have a negative effect on the speed of *Uma*, and the lack of an effect on the similar sized *Stellio* could result from using a substrate that maximized traction of this rock-dwelling species.

Two general behavioural mechanisms of increasing locomotor speed are increasing the amplitude and frequency (inverse of cycle duration) of movements. The limited kinematic data available indicate that lizards (Urban 1965; Sukhanov 1968; Jayne et al. 1990), resemble many diverse taxa of limbed animals (Gray 1968) that increase speeds of steady locomotion by simultaneously increasing stride length and frequency. In contrast to the positive correlation between stride frequency and different speeds of steady locomotion, stride frequency (and thus stride duration) was nearly constant and approximated 12.9 Hz as *Uma* accelerated (mean value of the first five strides for level trials are summarized in Table I). Consequently, compared to our laboratory observations of stride length, the values of stride frequency may be closer to the value that is physiologically attainable. The physiological constraints on limb cycling frequencies of lizards at high temperatures are still not well understood (Marsh & Bennett 1986), but the decoupling of stride length and frequency that occurs during accelerating locomotion may facilitate designing experiments to resolve this issue.

We used stride length in the field as a surrogate measure of speed, but we can also use field measurements of stride length with laboratory observations to estimate the maximal speeds obtained by animals in the field. Multiplying mean stride frequency observed in the laboratory

(12.9 Hz) by the maximal stride length of each path in the field ($N=28$) estimates maximal field velocities ranging from 2.38 to 5.11 m/s with a mean ± SE value of 3.96 ± 0.15 m/s. Maximal field velocities predicted from the regression of stride length observed in the laboratory (Fig. 9a) ranged from 2.29 to 4.61 m/s with a mean ± SE value of 3.62 ± 0.14 m/s. Thus, the average maximal velocity (2.79 m/s) observed for the level laboratory trials was either 77 or 71% of estimated field values, depending on the method used. Our laboratory measurements of speed agree with those of Carothers (1986), but field values of 6.7 m/s given by Norris (1951) are probably the result of using inaccurate methods. For the escapes of *Uma* observed directly in both the field and the laboratory ($N=4$), maximal values of laboratory stride lengths averaged 81% of the field values, and the mean value of all maximal stride lengths observed in the laboratory (22.8 cm, $N=8$) was 74% of the mean values of the field observations. Hence, for the four different comparisons of performance, the laboratory values averaged 75% of the field values or estimates. Although not all of the escape running in the field was maximal (Fig. 6a), 34.9% of the strides measured in the field exceeded the value of 75% maximal field performance, which approximated maximal laboratory performance.

Workers that have tested locomotor performance have forthrightly acknowledged that laboratory values may be below maximal performance in the field (Hertz et al. 1988; Garland & Losos 1994). Our study did not address whether individuals that are faster in the laboratory are also faster in the field, but we now have insights into the potential magnitude of the disparity between laboratory and field observations. Submaximal performance in the laboratory also emphasizes the primacy of behaviour in determining the extent to which physiological capacities are used, and species probably vary in this regard. For example, laboratory and field escape speeds of the lizard *Anolis gundlachi* are statistically indistinguishable (D. J. Irschick & S. Koruba, unpublished data). *Uma* that we observed in the field were always capable of running immediately after all escapes, but one *Callisaurus draconoides* that we observed became immobile after four successive field escapes. Thus, species of lizards other than *Uma* may very well run closer to a physiological maximum in the laboratory and/or field. Another potential implication of submaximal performance for level laboratory trials is that if lizards used a greater proportion of their physiological capacity when running uphill, then this could diminish the ability to detect experimentally a decrement in performance associated with uphill running.

Speed is only one of many potential measures of locomotor performance. We also quantified acceleration of *Uma* and the values calculated for 0.05 s (10–30 m/s^2) overlapped with those (5–12 m/s^2) reported for *Stellio* with similar mass (Huey & Hertz 1984). The length of the initial strides of *Uma* observed in the laboratory trials were similar or even slightly greater than those observed in the field (Table I), suggesting that average initial acceleration in the laboratory may have exceeded average field performance. The model used to calculate acceleration for the laboratory observations fit the first 0.5 s quite well, with an initial exponential increase in speed followed by a continued running at a high and constant speed. Near the end of runs in the laboratory, however, additional accelerations were often apparent. Furthermore, field observations of individual escape paths often lacked a simple pattern of continuously increasing stride length up to the maximum. Thus, in both the laboratory and field, *Uma* appear to obtain the fastest running speeds by an initial acceleration and then additional bouts of acceleration once the animal is already running rapidly. Consequently, relatively long distances are often required before *Uma* attain maximal speeds, and this seems the most likely cause of maximal laboratory speeds (over 1.5 m) that were less than estimated field speeds.

Huey & Hertz (1984) simulated the potential advantages of small lizards running uphill to escape larger lizards. Although we found a slight overall tendency for running uphill (Fig. 1c), the first metres of *Uma* escapes were random with respect to the orientations of maximal incline. The majority of *Uma* accelerations occur within the first metre, and early events are likely to be most important for determining the outcome of an escape. Consequently, the slope of the first metre or so of the escape path should be most relevant for determining whether lizards use uphill locomotion to facilitate escape. In light of large ontogenetic variation in mass and some of the ontogenetic differences in escape behaviour of *Anolis* lizards (D. J. Irschick & S. Koruba, unpublished data), one might obtain different conclusions regarding inclines for neonatal and adult *Uma*.

The seeming irrelevance of inclines for determining the initial orientation of *Uma* escape paths may be the result of *Uma* escaping to familiar retreats. Familiarity with habitat may facilitate escape (Stamps 1995), and three lines of evidence suggest that *Uma* may escape to familiar retreats. First, the final destinations commonly had a proliferation of *Uma* tracks suggesting an area of heavy use. Second, many seemingly suitable burrows and refuges were bypassed (Fig. 4). Third, escape paths to final destinations were quite direct rather than being convoluted. In the early morning we commonly found *Uma* emerging from permanent burrows and then basking in the sun at the burrow entrances. As temperature increased, we often found *Uma* on the surface at a considerable distance from any burrow. Thus, foraging and other activities of the lizards determine their location relative to their retreat prior to the time when we discovered them and elicited an escape. Consequently, any bias in the location of these burrows (such as being in a localized high region) or in the use of inclines when moving away from these sites can also bias the inclines that are traversed during escapes back to starting locations. This provides a cautionary note for interpreting the departure from random use of incline in the habitat during escapes (Fig. 1).

Bipedal running is relatively common in lizards, including many species that apparently lack morphological specializations, and bipedal running is presumed to be associated with maximal locomotor speeds (Snyder 1952, 1962; Urban 1965). Field and laboratory observations suggest that the bipedal locomotion of *Uma* correlates better with large accelerations than with maximal speed. Furthermore, based on the cumulative field occurrence of category-1 tracks, we estimate that less than 10% of the cumulative escape distance of *Uma* involves bipedal (striding) locomotion. Rather than being a means of increasing speed, bipedal (saltatory) locomotion of the heteromyid rodents may more important for enhancing manoeuvrability (Djawdan & Garland 1988). Because *Uma* turned minimally during the escapes, however, the use of bipedality to enhance manoeuvrability seems unlikely.

So far, we have quantified only the escape performance of *Uma*, and an unanswered question for effectively all species of lizards, is the extent to which they exert themselves for the sum of all locomotor activity in a natural setting (Hertz et al. 1988). We still lack a frequency distribution such as that in Fig. 5b for the entire locomotor activity of a lizard. Animals such as *Uma* that move on soft substrates lend themselves to the sort of focal-animal observations that will be required to obtain such information. For example, just as Secor (1994) used tracks of sidewinder rattlesnakes to document movement distances, one could use the tracks of *Uma* not only to document the distance travelled, but also to estimate the speed of travel (Fig. 9a) for all surface locomotor activity.

When accounting for the entire locomotor activity of *Uma*, additional attributes of locomotor performance such as energetic cost are likely to assume greater importance. Small lizards (5 g) moving up a 50° incline may expend nearly twice the energy used for level locomotion (Farley & Emshwiller 1996). Consequently, for *Uma* a detectable energetic cost is expected for moving up biologically meaningful inclines, and the slippage of sand and left–right tilting could affect energetic economy without noticeably affecting escape performance. Thus, when travelling through the dune environment for distances longer than those observed in escapes, *Uma* may face trade-offs between energetics, path steepness, time and total distance travelled to reach a destination.

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REFERENCES

Arnold, S. J. 1983. Morphology, performance and fitness. *Am. Zool.*, **23,** 347–361.

van Berkum, F. H., Huey, R. B., Tsuji, J. S. & Garland, T. 1989. Repeatability of individual differences in locomotor performance and body size during early ontogeny of the lizard *Sceloporus occidentalis* (Baird & Girard). *Func. Ecol.*, **3,** 97–105.

Brattstrom, B. H. 1965. Body temperatures of reptiles. *Am. Midl. Nat.*, **73,** 376–422.

Bulova, S. J. 1994. Correlates of population and individual variation in antipredator behavior in two species of desert lizards. *Copeia*, **1994,** 980–992.

Carothers, J. H. 1986. An experimental confirmation of morphological adaptation: toe fringes in the sand-dwelling lizard *Uma scoparia*. *Evolution*, **40,** 871–874.

Djawdan, M. & Garland, T. J. 1988. Maximal running speeds of bipedal and quadrupedal rodents. *J. Mammal.*, **69,** 765–772.

Farley, C. T. & Emshwiller, M. 1996. Efficiency of uphill locomotion in nocturnal and diurnal lizards. *J. exp. Biol.*, **199,** 587–592.

Garland, T., Jr & Losos, J. B. 1994. Ecological morphology of locomotor performance in squamate reptiles. In: *Ecological Morphology Integrative Organismal Biology* (Ed. by P. C. Wainwright & S. M. Reilly), pp. 240–302. Chicago: University of Chicago Press.

Gray, J. 1968. *Animal Locomotion*. London: Weidenfield & Nicolson.

Hertz, P. F., Huey, R. B. & Garland, T. 1988. Time budgets, thermoregulation, and maximal locomotor performance: are reptiles Olympians or Boy Scouts? *Am. Zool.*, **28,** 927–938.

Huey, R. B. & Dunham, A. E. 1987. Repeatability of locomotor performance in natural populations of the lizard *Sceloporus merriami*. *Evolution*, **41,** 1116–1120.

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.

Huey, R. B. & Hertz, P. E. 1984. Effects of body size and slope on acceleration of a lizard (*Stellio stellio*). *J. exp. Biol.*, **110,** 113–123.

Huey, R. B., Pianka, E. R. & Schoener, T. W. 1983. *Lizard Ecology: Studies of a Model Organism*. Cambridge, Massachusetts: Harvard University Press.

Jayne, B. C., Bennett, A. F. & Lauder, G. V. 1990. Muscle recruitment during terrestrial locomotion: how speed and temperature affect fibre type use in a lizard. *J. exp. Biol.*, **152,** 101–128.

Losos, J. B. & Irschick, D. J. 1996. The effect of perch diameter on escape behaviour of *Anolis* lizards: laboratory predictions and field tests. *Anim. Behav.*, **51,** 593–602.

Losos, J. B. & Sinervo, B. 1989. The effect of morphology and perch diameter on sprint performance of *Anolis* lizards. *J. exp. Biol.*, **145,** 23–30.

Marsh, R. L. & Bennett, A. F. 1986. Thermal dependence of sprint performance of the lizard *Sceloporus occidentalis*. *J. exp. Biol.*, **126,** 79–87.

Miles, D. B. 1994. Covariation between morphology and locomotory performance in sceloporine lizards. In: *Lizard Ecology: Historical and Experimental Perspectives* (Ed. by L. J. Vitt & E. R. Pianka), pp. 207–235. Princeton, New Jersey: Princeton University Press.

Milstead, W. W. 1967. *Lizard Ecology: A Symposium*. Columbia, Missouri: University of Missouri Press.

Moermond, T. 1979. Habitat constraints on the behavior, morphology, and community structure of *Anolis* lizards. *Ecology*, **60,** 152–164.

Mosauer, W. 1935. The reptiles of a sand dune area and its surroundings in the Colorado desert, California: a study in habitat preference. *Ecology*, **16,** 13–27.

Norris, K. S. 1951. The lizard that swims in the sand. *Nat. Hist.*, **60,** 404–407.

Pianka, E. R. 1986. *Ecology and Natural History of Desert Lizards*. Princeton, New Jersey: Princeton University Press.

Pounds, J. A. 1988. Ecomorphology, locomotion, and microhabitat structure in a tropical mainland *Anolis* community. *Ecology*, **58,** 299–320.

Secor, S. M. 1994. Ecological significance of movements and activity range for the sidewinder, *Crotalus cerastes*. *Copeia*, **1994,** 631–645.

Snyder, R. C. 1952. Quadrupedal and bipedal locomotion of lizards. *Copeia*, **2,** 64–70.

Snyder, R. C. 1962. Adaptations for bipedal locomotion of lizards. *Am. Zool.*, **2,** 191–203.

Stamps, J. A. 1995. Motor learning and the value of familiar space. *Am. Nat.*, **146,** 41–58.

Stebbins, R. C. 1944. Some aspects of the ecology of the iguana genus *Uma*. *Ecol. Monogr.*, **14,** 313–332.

Sukhanov, V. B. 1968. *General System of Symmetrical Locomotion of Terrestrial Vertebrates and Some Features of Movement of Lower Tetrapods*. Washington, D.C.: Smithsonian Institution.

Urban, E. K. 1965. Quantitative study of locomotion in teiid lizards. *Anim. Behav.*, **13,** 513–529.

Vitt, L. J. & Pianka, E. R. 1994. *Lizard Ecology: Historical and Experimental Perspectives*. Princeton, New Jersey: Princeton University Press.

Zar, J. H. 1996. *Biostatistical Analysis*. 3rd edn. Upper Saddle River, New Jersey: Prentice Hall.