A FIELD STUDY OF INCLINE USE AND PREFERRED SPEEDS FOR THE LOCOMOTION OF LIZARDS

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Abstract. The maximal running speeds of lizards have commonly been measured using level racetracks in a laboratory, but the normal speeds of locomotion of lizards and most animals in their natural habitats are not well documented. Thus we quantified the locomotor activity of the lizard *Uma scoparia* in its natural sand-dune habitat to determine how commonly animals run near their maximal speed and how inclines in the environment might affect habitat use and the speed of locomotion. We used leaf blowers to erase footprints in the sand in three 40 m × 100 m plots differing in surface topography and vegetation and then measured attributes of the paths and tracks left by *U. scoparia* that were not disturbed (by observers) during their period of peak activity. Laboratory observations allowed us to estimate speed for each field measurement of stride length ($n = 5993$). The frequency distribution of stride speed had two distinct modes (mean values 0.25 and 2.00 m/s), for which only the lower one is likely to be aerobically sustainable. Bipedal locomotion was extremely rare (<0.5% of all strides), but much undisturbed locomotion was unexpectedly fast. The inclines of the surfaces upon which locomotion occurred conformed to random habitat use. In contrast, the inclines of paths made by lizards had lower than expected amounts of nearly horizontal locomotion and a propensity for traveling almost directly uphill, especially when surfaces were steep. Habitat structure varied significantly among plots and affected several aspects of locomotion. For example, path length, average speed per path, and average magnitudes of path and surface inclines per path varied significantly among the three plots. Multiple regression analysis also revealed that the average speed per 1-m interval was maximized for paths with relatively shallow downhill slopes (−6% grade) and decreased significantly both with increased amounts of vegetative cover and increased turning between successive intervals. Unexpectedly, during undisturbed and escape locomotion, lizards used inclines similarly.

Key words: desert; lizard; locomotion, preferred speed; Mojave Desert, USA; sand dune; slope; Uma scoparia.

INTRODUCTION

A central issue in ecology is how organisms are distributed in space and time, and because the location of many organisms changes with time, accounting for movement is essential for understanding such fundamental phenomena as dispersal and use of resources (reviewed in Turchin 1998). Most animals have well-developed capacities for moving actively, and bouts of movement within individuals and among different species often have considerable variation in distance, duration, speed, steadiness, and directness. Some of this variation in the patterns of animal movement is commonly used by behavioral ecologists as the basis for fundamental distinctions such as those between sit-and-wait vs. actively foraging predators (Cooper 1994). In addition to behavioral and environmental influences, the physiological capacities of animals impose constraints on locomotion. Thus, a powerful integrative approach for studying patterns of animal movement is to first determine the physiological constraints on lo-

comotor capacity and then determine how the animals actually behave in the field and the extent to which environmental factors correlate with variation in locomotor behavior.

For well over a decade physiological ecologists have commonly tested organismal performance to determine maximal functional capacities and to gain insights into the adaptive significance of variation in physiological and morphological traits (Huey and Stevenson 1979, Arnold 1983). The locomotion of lizards and other squamate reptiles has been a model system for testing organismal performance, and the vast majority of data for reptiles are maximal speeds of locomotion obtained by testing animals on flat race tracks 2–3 m long in a laboratory (Garland and Losos 1994). These laboratory measurements of locomotor performance usually have significant heritability and are repeatable over long periods of time (Huey and Dunham 1987, Tsuji et al. 1989, van Berkum et al. 1989). Additional studies have examined the correlation between locomotor performance and survivorship of reptiles in natural populations (Bennett and Huey 1990, Jayne and Bennett 1990), but they have also relied on laboratory methods to document locomotor performance. Only a few very

recent studies have examined whether or not lizards use maximal speeds in the field either by eliciting escapes (Irschick and Losos 1998, Jayne and Ellis 1998, Irschick and Jayne 1999*a*) or observing feeding behavior (Irschick and Losos 1998). Thus, for well-studied squamate reptiles as well as other taxonomic groups, important but largely unresolved issues include how fast animals move in nature and how frequently animals move near maximal speeds when not disturbed by humans.

Several aspects of natural conditions differ from those of laboratory performance tests and are likely to affect the locomotion of lizards and other animals. First, rather than being flat, natural habitats often have a complex topography that requires animals to go up and down inclines of varying steepness. Many lizards run up and down steep inclines with apparent ease, but depending on the size and species, moving up inclines can decrease maximal speed or acceleration and increase the energetic cost of locomotion (Huey and Hertz 1982, 1984, Carothers 1986, Farley and Emshwiller 1996, Irschick and Jayne 1998). Second, the relatively small size of most laboratory racetracks may contribute to some lizards running slower than they do in the field (Jayne and Ellis 1998, Irschick and Jayne 1999*a*). Third, the amount and location of vegetation and other objects in natural habitats can affect the distance or straightness of movements. For instance, decreased amounts of vegetative cover increase the distances run by some species of lizards during escapes (Snell et al. 1988, Bulova 1994). Fourth, familiarity with the environment may affect the speeds of movement, especially during the rapid locomotion that typifies escapes (Stamps 1995). Finally, in a natural setting, in addition to escaping threats, animals have diverse behaviors such as feeding, courtship, territorial defense, exploration, and thermoregulation that are likely to increase the variance in the voluntary speeds of locomotion compared to those measured in laboratory tests (Irschick and Losos 1998).

For the voluntary locomotion of animals, the existence of preferred speeds has been discussed widely, but supporting empirical evidence is limited. Two of the most thorough studies of preferred speeds of vertebrates in their natural habitat are for mammals, and both Pennycuick (1975) and Kenagy and Hoyt (1989) found two distinct preferred speeds within each of the species that they studied. The existence of preferred speeds in mammals may be related to gait selection (Hoyt and Taylor 1981) and the biomechanics of limb function (Perry et al. 1988). The distinct gait transitions of most mammalian species are absent in lizards for which the limbs differ from mammals in morphology and posture (Hildebrand 1976); therefore, mammalian data may have limited predictive value regarding the preferred speeds of lizards. Van Damme et al. (1998) documented the voluntary speeds of locomotion of lizards in relatively small cages, but comprehensive data

quantifying the voluntary speeds of movement of lizards in the field are lacking.

For quantifying the speeds of movement of animals in their natural habitat, sand dunes have several advantages that were exploited in two recent studies (Jayne and Ellis 1998, Irschick and Jayne 1999*a*) of the escape locomotion of lizards in the Kelso dunes of southern California, USA. The soft surface of the sand preserves footprints and facilitates measuring stride length, which increases with increased speed for most limbed animals. Hence, field measurements of stride length can estimate speed by using laboratory data that relate these two quantities (Jayne and Ellis 1998). Another advantage of the Kelso sand dune system is that it provides a natural source of inclined surfaces (up to 33°), and quantifying this resource is technically feasible. The Mojave fringe-toed lizard, *Uma scoparia,* is a terrestrial species that does not climb vegetation; hence, its footprints in the sand provide a complete record of all of its surface locomotor activity. *U. scoparia* occurs throughout the Kelso dune system which also has considerable variation in the amounts and types of vegetation. Thus, *U. scoparia* in the Kelso dunes is unusually well suited for quantifying the speeds of voluntary locomotion and how they are affected by habitat structure.

In the present study, we used the tracks of *U. scoparia* in the Kelso dunes to quantify the entire locomotor effort of undisturbed animals in nature and test the following four specific null hypotheses. (1) The speed of most undisturbed locomotion of *U. scoparia* in the field is slower than that quantified previously for animals escaping a threat (Jayne and Ellis 1998). We expected *U. scoparia* to use rapid locomotion sparingly because most species of lizards exhaust quickly at rapid speeds and during the recovery period after rapid locomotion the ability to escape rapidly might be reduced. (2) The choice of habitat surface inclines and the orientation of the paths traveled by *U. scoparia* relative to the steepest possible trajectory are random. (3) Based on previous findings for the escape locomotion of *U. scoparia* (Jayne and Ellis 1998), we expected the speeds of undisturbed locomotion will be fastest for paths that have the least turning and are horizontal (i.e., not inclined). (4) Increased amounts of vegetation will decrease the speed and increase the amount of turning during voluntary locomotion since increased amounts of exploration and foraging seem more likely in these areas.

METHODS

Study site.—All field observations were in the area studied previously by Jayne and Ellis (1998) in the Kelso dune system of the Mojave Desert ~13 km southwest of Kelso in San Bernadino County, California, USA. The overall study area was 1.08 × 0.20 km with the longer axis oriented directly towards the highest peak in the Kelso dunes. The upper end of the study
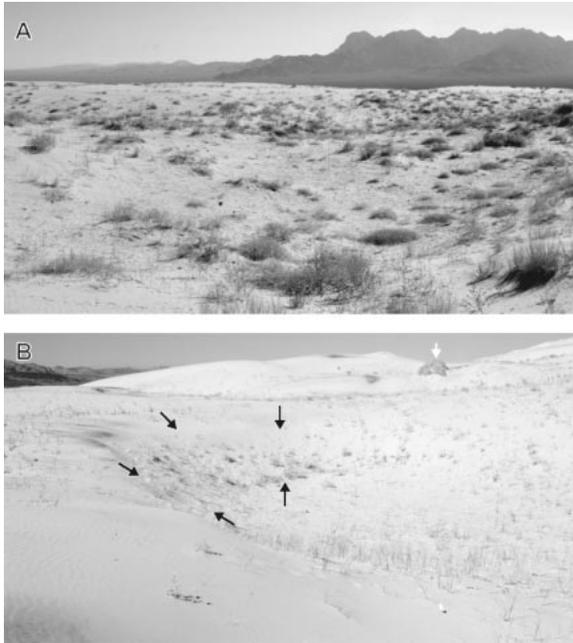
FIG. 1. Photographs of the (A) low and (B) high areas of the study site in the Kelso dunes of southern California, USA, showing the differences in vegetation and topography of the dune surface (see Fig. 2). The height of the tallest vegetation in the foreground of (A) approximates 60 cm. The foreground in (B) shows a large depression, with steep sides 2–3 m long (between black arrows) where inclines are ~30°, and the white arrow indicates a large clump (4 m wide) of sand paper plants (*Petalonyx thurberi*) ~90 m from the foreground and at the far side of a second large depression.

area was midway between the edge of the creosote flat (just outside of the study area) and the highest point in the dune which is nearly devoid of vegetation. Thus, the length (*y*-axis) of the site was parallel to gradients of variation in the vegetation (Fig. 1) and in the topographic features of the dune surface (Fig. 2). The origin of our *x*–*y* coordinate system in the site was at the lower, southernmost corner of the rectangular study area, and we express all coordinates in meters. Jayne and Ellis (1998) provide additional details on the site location and co-occurring species of organisms.

To provide points of reference for quantifying habitat and the locomotion of lizards, we used surveyors flags to mark 20-m intervals along the length of the entire site at $x = 100$ and at 10-m intervals inside of each of three 40 m $\times$ 100 m plots within the study site. The 100 m edge of each study plot was perpendicular to the *y*-axis. Hereafter, we use low, middle, and high to refer to the locations of plots in order of successively greater *y*-coordinates (Fig. 2).

Habitat measurements.—To quantify angles ($\pm 0.1°$) of inclination of the surface of the sand dune, we used a digital level (Smart Tool Builder's Angle finder, Macklanburg-Duncan, Oklahoma City, Oklahoma, USA) mounted on a 1-m rod. To facilitate visualizing the topography of the dune surface, we measured angles of inclination for each meter ($n = 1080$) of the line at $x = 100$ m for the length of the entire study area and for the 100-m lines through the middle of each of the 40 m $\times$ 100 m plots. We calculated values of rise (vertical distance gained per 1-m interval of the dune
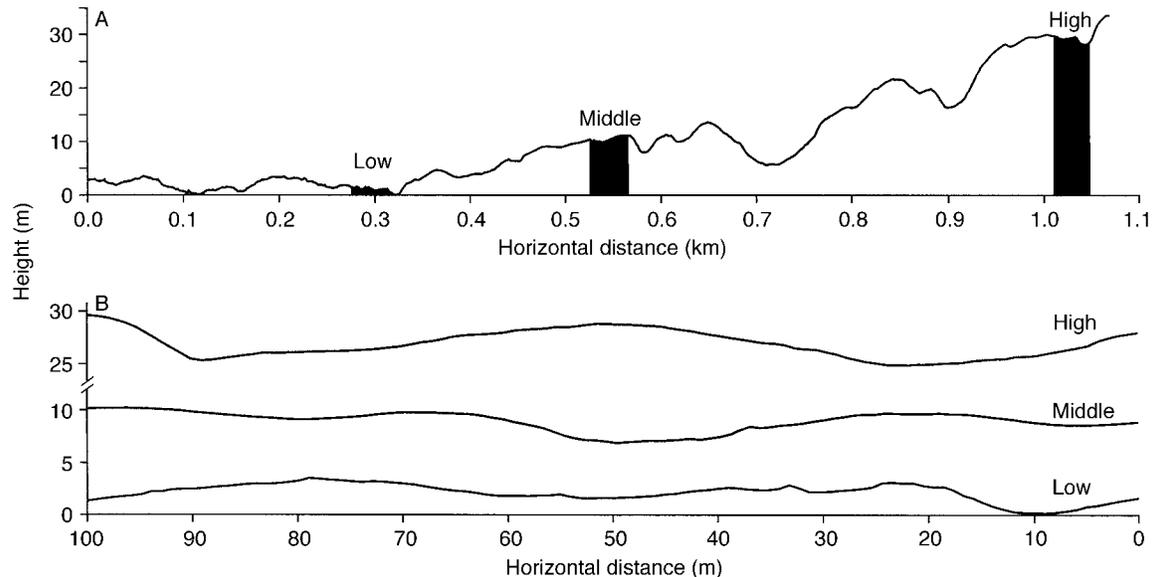

FIG. 2. Elevation profiles of the study side. (A) A transect ~1 km long extending from the base of the dune directly toward its highest point. A value of zero for height indicates the lowest point along the transect. The shaded areas indicate the locations of the three 40 m $\times$ 100 m plots. (B) Three 100-m transects perpendicular to the 1-km transect and through the middle of each plot in which we quantified habitat and lizard tracks. The axes of (A) are not to the same scale, and hence slope of the graph appears steeper than the actual slope of the dune surface, whereas in (B) the slope of the graph is visually identical to the actual slope of the dune surface.

surface) as the sine of each angle of inclination. For each 1-m interval measured, we then summed successive values of rise and of the cosine of the angle of inclination to determine vertical and horizontal position, respectively, which enabled us to reconstruct detailed topographic profiles along the major axes of the entire study area (Fig. 2A) and the three plots within it (Fig. 2B). To quantify the occurrence of inclines in the habitat, we measured maximum values of rise at 5-m intervals along the edges and in the interior ($n =$ 189) of each of the 40 m $\times$ 100 m plots. Unlike the procedures for taking measurements used for reconstructing topographic profiles, the measuring rod was oriented in whatever direction yielded a maximum incline rather than in a single direction.

We quantified the vegetation along three 100-m transects 10 m apart and including the middle of each of the 40 m $\times$ 100 m plots. From a direct overhead view of a 1.3-cm wide tape measure, we determined the amount of overlap with vegetation to the nearest centimeter and then calculated the cumulative percentage of each of the transects that was covered by vegetation.

Field measurements of lizard movement.—The primary goals of the study were to obtain an unbiased sample of the undisturbed locomotion of *U. scoparia* and relate the speed of movement to variation in incline and vegetation. We use the term ''undisturbed'' as the most convenient way to refer to a lack of disturbance by humans and to contrast these observations with our other methods of observing locomotion of lizards in their natural environment wherein humans deliberately elicited escape behavior (Jayne and Ellis 1998, Irschick and Jayne 1999*a*). We were able to distinguish the tracks of *U. scoparia* from those of the few co-occurring species of lizards, and we ignored tracks made by any lizard that we observed directly since our presence might have affected the speed of locomotion.

From 15 to 22 June 1998, we used leaf blowers to erase tracks within the 40 m $\times$ 100 m plots early (before 0700) in the morning before lizards were active. We erased only one plot per day, and we waited until midafternoon to begin gathering data. For the first sample of each plot, we erased the entire 40 m $\times$ 100 m area, but we were only able to mark and measure all of the paths in continuous areas ranging from 40 m $\times$ 40 m to 40 m $\times$ 60 m before the late-day winds prevented further tracking and measuring. After obtaining the first sample from all three plots, we then erased and measured paths in the remainder of each plot three to four days after the first sample. To minimize disturbance to the plots, we made all habitat measurements only after the completion of all of the measurements of lizard paths within an entire 40 m $\times$ 100 m plot.

We used surveyors flags to mark 1-m straight-line distances along the paths made by *U. scoparia*, and we determined the *x–y* coordinates for the beginning of each path. We then determined the following seven quantities for each 1-m interval of a path. (1) Stride length equaled the distance traveled between successive footprints of a particular foot and was measured for strides that were nearest the 25, 50, and 75 cm locations within each 1-m interval. Sometimes, erasure by the wind or overlapping tracks of lizards did not allow us to obtain the lengths of three strides for each 1-m segment. (2) The appearance of each measured stride was recorded as one of four categories[2] similar to those of Jayne and Ellis (1998). Briefly, category 1 indicates rapid bipedal locomotion, whereas the remaining categories (2–4) are different types of quadrupedal locomotion. The slowest category (4) of tracks had distinct impressions of individual toes, and tail drag marks were frequently visible. We collected the remaining data the day after we had measured stride lengths. (3) Rise for the path of the lizard (rise$_p$) and (4) the maximum rise of the habitat (rise$_h$) at the midpoint of each 1-m segment of the path were calculated from angles of inclination measured with a digital level mounted on a 1-m rod. (5) The orientation ($\pm 2°$) of each 1-m segment was measured from a compass mounted on the measuring rod. (6) Turning angles equaled the difference between the successive values of orientation for the 1-m intervals of the lizard path. (7) Indices of vegetative cover (maximum possible value = 3) equaled the sum of values for 30-cm wide swaths along each third of a 1-m interval (1 = presence, 0 = absence of vegetation that was sufficiently large to provide cover; 0.2 = only sparse grass).

We did not have sufficient time to follow and measure the portions of paths that extended beyond the boundaries of plot, and additional factors that prevented us from determining the exact start and end points of some paths included overlapping paths and shifting sand. Thus, the measured lengths of paths frequently underestimate actual distances traveled, but in all other respects, our methods provided a robust, representative sample of the total surface locomotor activity of *U. scoparia*.

To determine the size of the lizards that were making tracks in the field as well as an appropriate size to use for laboratory measurements, we captured, measured, and released a total of 55 *U. scoparia*. The snout–vent lengths (SVL) ranged from 5.6 to 10.0 cm (7.4 $\pm$ 0.9 cm, mean $\pm$ 1 SD). Individuals with SVL >9 cm or <6 cm were rare as indicated by 47 of the 55 individuals having values of SVL between 6.3 and 8.3 cm.

Laboratory measurements of lizard locomotion.—To determine the relationship between stride length and speed we used a similar test arena and procedures as described in more detail in Jayne and Ellis (1998). However, in the present study the stride lengths measured in the laboratory were from fairly steady speeds of locomotion of lizards that were not startled by the investigators, whereas values in Jayne and Ellis (1998)

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[2] URL: http://www.biology.uc.edu/faculty/jayne/bcjhi10.htm for illustrations.

were for lizards that had been startled and were accelerating maximally from a standstill. In brief, we used a NAC HSV 500 high-speed video system (NAC Image Technology, Simi Valley, California, USA) to determine durations of stride to the nearest 4 ms for seven *U. scoparia* (SVL range = 6.6–7.9 cm; 7.5 ± 0.5 cm, mean ± 1 SD). Overhead 35-mm slides of the tracks in the sand were used subsequently to determine stride length and track category. We then divided stride length by stride duration to obtain the average forward velocity of each stride.

Data analysis.—For straight-line paths traveled on a single inclined plane, the rise of the paths can have an infinite number of values, but their range is limited by the positive (steepest uphill) and negative (steepest downhill) maximal values of rise for the inclined surface. Thus, for each plot, we randomly sampled values (as in Jayne and Ellis 1998 and Irschick and Jayne 1999*a*) drawn from the positive and negative maximal values of each rise measured to characterize the habitat. We used four random draws per value of maximal rise since this provided a robust characterization of the null distribution, and the resulting total sample size per plot ($n = 756$) was also very similar to the numbers of 1-m intervals of lizard paths that were measured in each plot. Each frequency distribution generated by this random sampling procedure thus represents the probability that a 1-m vector located randomly on the surface of a plot will have a particular value of rise.

Unless stated otherwise we used $P < 0.05$ as the primary criterion for statistical significance. We used Systat version 5.0 (Wilkinson 1992) to perform one-way analyses of variance (ANOVA) with the Tukey hsd procedure to test for significant differences in vegetation and whole-path variables among the low, middle, and high plots. To make global tests of whether or not particular pairs of frequency distributions differed significantly from each other, we used two-sample Kolmogorov-Smirnov (K-S) tests.

We used linear least-squares regressions to relate stride length to forward velocity for each category of tracks made by the lizards in the laboratory, and we used an analysis of covariance (ANCOVA) to test for significant differences among the regressions for each of the categories of footprints. We then used these regressions to estimate the velocity of each stride length that was measured in the field.

For each 1-m interval of the lizard paths, we calculated the mean of the values of stride speed ($n = 1$–3) and then used these average values of velocity per 1-m interval as the dependent variable in multiple regressions for which the independent variables included measurements of rise, vegetation, and turning angle. We used a forced-fit regression procedure and only retained independent variables that had significant partial regression coefficients. Using entire paths as the unit of replication for statistical analyses had limited utility for relating speed to variation in habitat because many

individual paths, especially short ones, lacked a combination of uphill and downhill locomotion or had similarly limited ranges in values of other independent variables such as turning angle and the amount of vegetation.

RESULTS

Habitat

The amount of vegetative cover per 100-m transect differed significantly among the three 40 m × 100 m plots (one-way ANOVA, $F_{2,6} = 29.1$, $P = 0.001$). The mean value of total percentage of vegetative cover of the low plot (15.3%) was significantly greater than those of both the middle (6.3%, $P = 0.003$) and high (3.7%, $P = 0.001$) plots (Fig. 1). Although the high plot had the least vegetative cover, it was not significantly less than that of the middle plot ($P = 0.30$). The percentage of vegetation that was grass increased from the lowest (54.3%) to highest (95.5%) location (Fig. 1). A large (3 m diameter) cluster of *Petalonyx thurberi* bushes was near (10 m) but not within the high plot (Fig. 1A).

The inclines of the dune surface changed in several respects from the lowest to highest locations within the study area. Although steep surfaces (angle = 15°, rise = 0.25) were scattered throughout the entire study area, they rarely extended >2 m in the lower regions. In contrast, the upper areas of the site had many large depressions with steep sides that commonly extended >10 m (Figs. 1 and 2). The lowest region of the site did not have a net gain in elevation in any direction, but average elevation did increase conspicuously for the middle and high regions (Fig. 2A).

Relatively shallow and steep inclines were most abundant for the lowest and highest 40 m × 100 m plots, respectively (Fig. 3A–C). For example, for the low, middle, and high plots the cumulative percentages of values of maximum rise <0.1 were 42%, 37%, and 19%, respectively, and those for values >0.25 were 19%, 9%, and 31%, respectively. Each of the three frequency distributions of maximal rise of the habitat (Fig. 3A–C) had highly significant overall differences from each other (K-S test, $P < 0.001$).

For the frequency distributions of the random samples of inclines (Fig. 4A–C) drawn from the measurements of maximal incline (Fig. 3A–C) within each of the 40 m × 100 m plots, the high plot differed (K-S test) from both the middle ($P = 0.001$) and low ($P < 0.001$) plots, but the middle and low plots were similar ($P = 0.59$). The 95% confidence limits of all means and values of skewness, g_1, of the random samples of rise (Fig. 4A–C) included zero, and hence did not differ significantly from a normal distribution (Table 1). However, for all plots the values of kurtosis, g_2, were all significantly greater than zero, the value of a normal distribution (Table 1). The decline in values of kurtosis from the low to high plots indicates, in part, a decrease
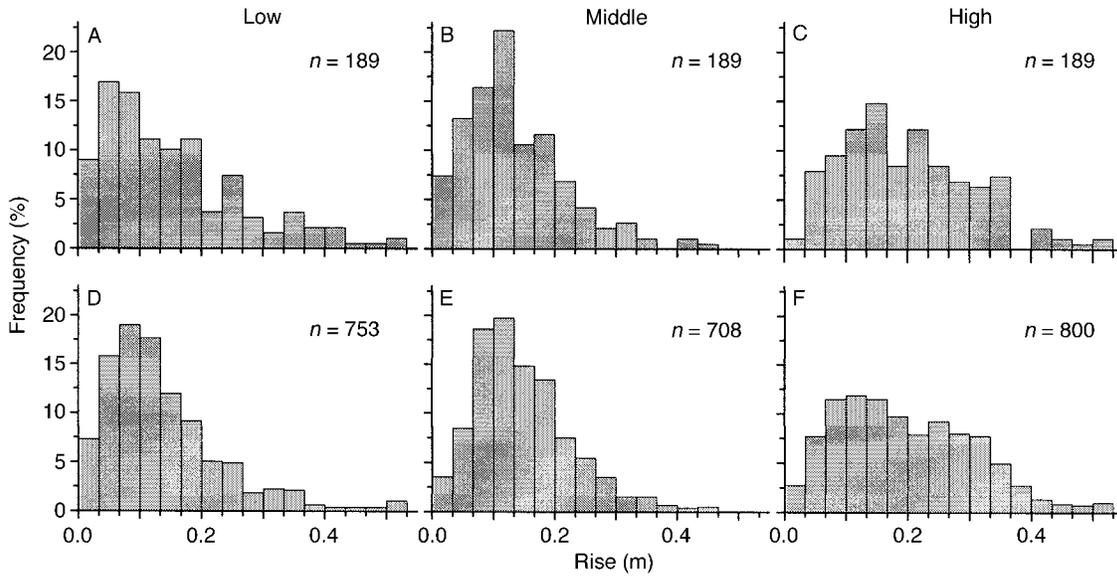
Fig. 3. Frequency distributions for values of maximal rise of the (A–C) habitat measured at 5-m intervals along the edges and interior of each 40 m × 100 m plot (see Fig. 2) and of the (D–F) dune surface ($rise_h$) at the midpoint of each 1-m interval of the paths traveled by the lizards.

in the frequency of shallow inclines expected for paths (Fig. 4A–C, Table 1).

Habitat use

The frequency distributions for the maximal values of rise ($rise_h$) of the surfaces upon which locomotion occurred (Fig. 3D–F) were statistically indistinguish-able (K-S tests; low plot, $P = 0.052$; high plot, $P = 0.77$) or differed only marginally (middle plot, $P = 0.024$) from those measured every 5 m in the corresponding 40 m × 100 m plot (Fig. 3A–C). Thus, habitat use was effectively random with respect to the inclines of the surfaces upon which locomotion occurred. In addition, all of the frequency distributions of $rise_h$ for
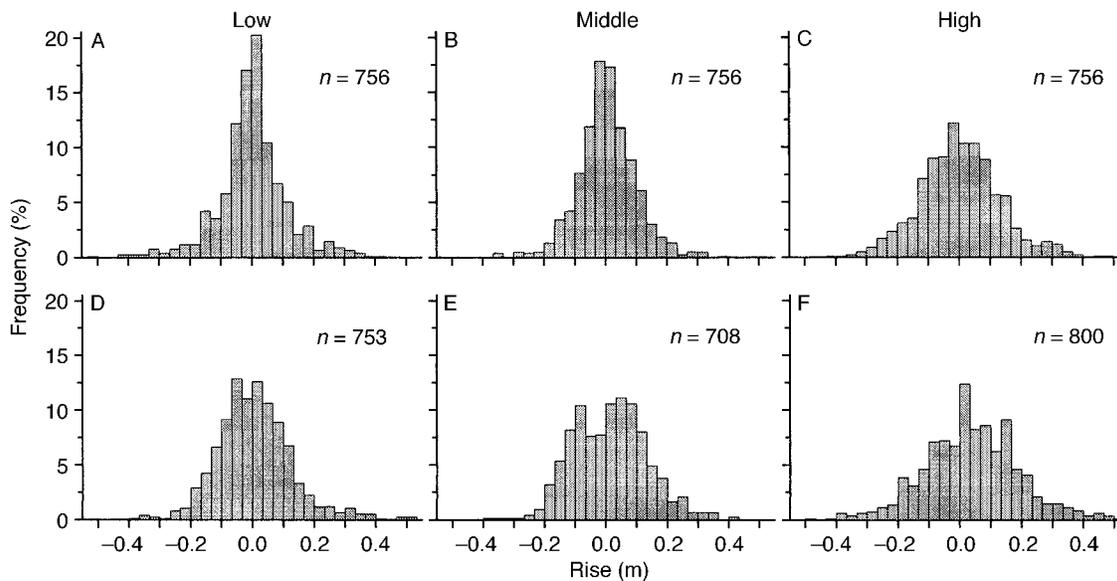

Fig. 4. Frequency distributions (A–C) for values of rise expected if the orientation of paths was random with respect to the orientation of the steepest incline at a particular point, and (D–F) for each 1-m interval of the paths ($rise_p$) traveled by *Uma scoparia* in each of the three 40 m × 100 m plots (see Fig. 2). Negative, zero, and positive values indicate downhill, horizontal, and uphill, respectively. We obtained the expected frequency distributions (A–C) by taking a random sample of the data shown in Fig. 3A–C.

TABLE 1. Descriptive statistics for rise in a random sample from each 40 m × 100 m plot in the 1998 experiments and values of rise of the paths (rise$_p$) traveled by *Uma scoparia* in the Kelso dunes of southern California, USA, and rise$_p$ for escape data from Jayne and Ellis (1998).

Sample	n	Mean	Median	Range	SD	$g_1 \pm$ 95% CL	$g_2 \pm$ 95% CL
Rise random sample							
Low	756	0.0019	0.0017	−0.522–0.412	0.111	−0.14 ± 0.17	2.43 ± 0.35
Middle	756	0.0056	0.0025	−0.357–0.380	0.095	0.05 ± 0.17	1.56 ± 0.35
High	756	0.0031	0	−0.409–0.497	0.130	0.17 ± 0.17	0.57 ± 0.35
Rise$_p$							
Low	753	0.0066	0	−0.390–0.530	0.122	0.60 ± 0.17	1.76 ± 0.35
Middle	708	0.0145	0.0165	−0.390–0.415	0.121	0.21 ± 0.18	0.04 ± 0.36
High	800	0.0373	0.0314	−0.475–0.545	0.153	0.08 ± 0.17	0.48 ± 0.34
Low, middle, high run	2261	0.020	0.016	−0.475–0.545	0.134	0.31 ± 0.10	0.81 ± 0.20
Escape	550	0.016	0.017	−0.415–0.462	0.123	−0.05 ± 0.20	0.82 ± 0.41

Notes: Low, middle, and high refer to the three different locations of plots (Fig. 2); g_1 and g_2 are skewness and kurtosis, respectively.

each plot (Fig. 3D–F) had highly significant differences from each other (K-S tests, all $P < 0.001$) such that progressively more locomotion occurred on steeper surfaces from the low to the high plot.

Steep slopes could be traversed obliquely. Hence, an important but subtly distinct issue is whether or not the inclines (rise$_p$) of the paths made by lizards (Fig. 4D–F) conform to the random expectation based on surface inclines (Fig. 4A–C). The frequency distributions for rise$_p$ from the 40 m × 100 m plots (Fig. 4D–F) differed significantly from their corresponding null distributions (Fig. 4A–C; K-S tests; low plot, $P = 0.004$; middle plot, $P < 0.001$; high plot, $P < 0.001$) and from each other (K-S tests; low–middle, $P = 0.022$; low–high, $P < 0.001$; middle–high, $P < 0.001$). The frequency distributions of rise$_p$ had unexpectedly few 1-m intervals with shallow inclines (Fig. 4, D–F vs. A–
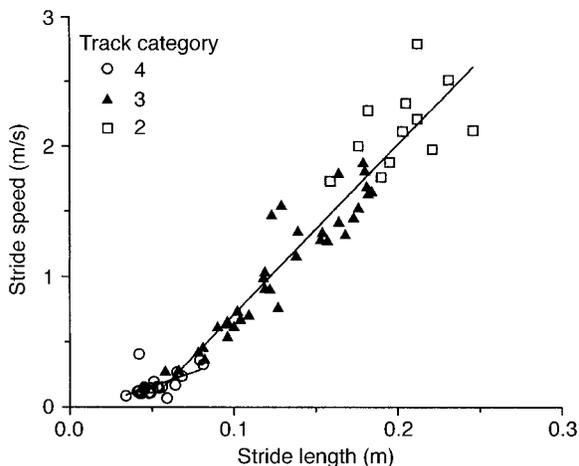

FIG. 5. Least squares regressions used to estimate field stride speed from laboratory observations of speed and stride length (*L*) of *Uma scoparia* moving on sand. For category 4 tracks, speed = $4.31L - 0.055$ ($r^2 = 0.33$, $P < 0.001$, $n = 22$), and for the other categories of tracks, speed = $13.0L - 0.59$ ($r^2 = 0.89$, $P < 0.001$, $n = 48$). For descriptions of track categories, see *Methods: Field measurements of lizard movement.*

C; Table 1: compare kurtosis). For the low, middle, and high plots, the expected (Fig. 4A–C) percentages of rise magnitudes of paths <0.1 were 72.5%, 75.4%, and 59.8%, respectively, whereas the corresponding observed values for rise$_p$ (Fig. 4D–F) were 65.2%, 58.2%, and 50.4%, respectively. For the low, middle, and high plots, the percentages of the values of rise$_p$ that were >0 (uphill) were 48.9%, 54.1%, and 59.9%, respectively. Thus, after allowing for differences in habitat among the three plots, *U. scoparia* had a consistent bias in the orientation of its paths that decreased the proportion of values of rise$_p$ near zero and increased the amounts of uphill locomotion in the upper two plots.

The cumulative distances of lizard paths were similar among the low (753 m), middle (708 m), and high (800 m) 40 m × 100 m plots, but the amounts of activity per unit area differed substantially on a finer spatial scale. For example, we obtained the following ranges and standard deviations for cumulative path distance per 20 m × 20 m subsample in the 40 m × 100 m plots: low, 0–176, SD = 1208; middle, 5–144, SD = 979; high, 35–140, SD = 430. Although the high plot had the lowest variance in activity per 20 m × 20 m subsample, the heterogeneity in variance among the plots was not quite statistically significant ($F_{max\ 2,9} = 2.8$, $P > 0.1$). All three plots had areas nearly devoid of vegetation and the high plot was most homogeneously barren, but the cumulative path distances per subsample were not significantly correlated ($r = 0.053$, df = 28, $P = 0.77$) with the score of vegetative cover for each corresponding 20 m × 20 m subsample along the vegetation transects ($y = 10$ or 30 m).

Locomotion

Laboratory observations.—We used two different regressions (Fig. 5) to relate stride length to speed because the slope of the regression for category 4 tracks was significantly less than that of the regression for the remaining categories of tracks (ANCOVA, $F_{1,65} = 6.5$, $P = 0.014$). For all category 4 tracks and for all strides
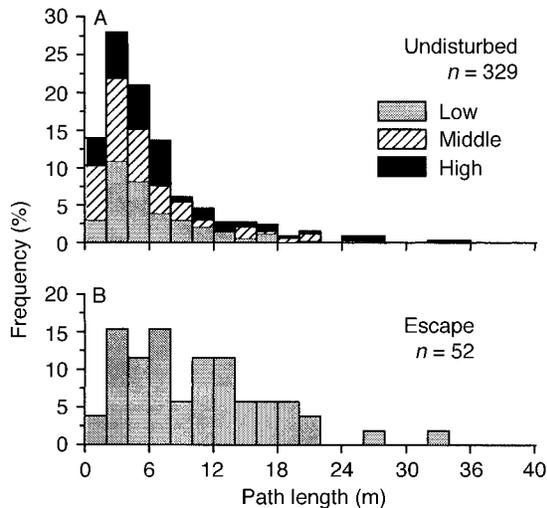
FIG. 6. Frequency distributions of the lengths of paths quantified for the (A) undisturbed and (B) escape (Jayne and Ellis 1998) locomotion of *Uma scoparia* in the Kelso dunes. Data in (B) were not graphically subdivided, but they included all regions of the dune.
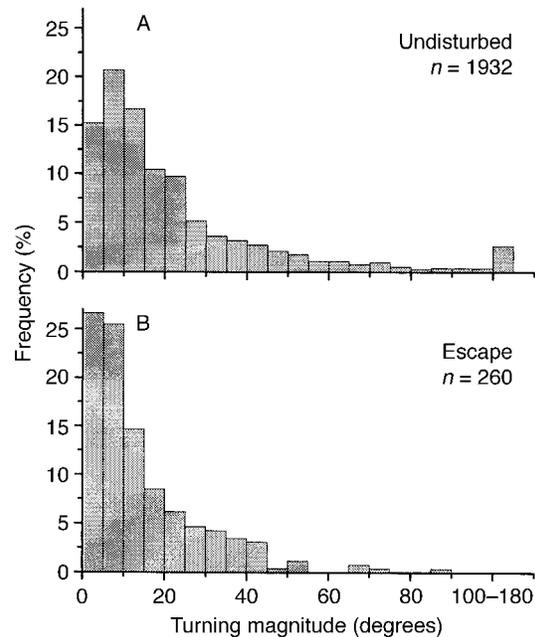

FIG. 7. Frequency distributions of the magnitude of turning angle between successive 1-m intervals of lizard paths for the entire sample of (A) undisturbed locomotion and (B) escape locomotion that Jayne and Ellis (1998) elicited from *Uma scoparia* in the same area of the Kelso dunes. For graphical clarity, the last bin in the histogram in (A) indicates the frequency of all values pooled from 100° to 180°.

with speeds <0.7 m/s, the proportion of the stride cycle for which a particular foot was on the ground (duty factor) was always >50%, indicating a walking gait. All category 2 tracks and strides with speed >1.3 m/s had duty factors <50%, indicating a running gait. The rank order of track categories corresponded well with the rank order based on speed (Fig. 5).

Whole-path variables and variation among plots.—For the total of 329 paths measured, the median, mean, maximum, and standard deviation of path lengths were 5.00, 6.87, 36, and 5.59 m, respectively, and only 10.3% of these path lengths were >12 m (Fig. 6A). The straight-line distances from the beginning to end of paths averaged a high percentage (83%) of path length indicating low amounts of turning in many paths. For the magnitude (absolute value) of the turning angle between successive 1-m intervals, the modal bin was from 5° to 10°, and only 12.4% of the values were ≥45° (Fig. 7A). The mean speed per path ranged from 0.18 to 3.42 m/s, and the median, mean, and standard deviation were 1.77, 1.70, and 0.71 m/s, respectively (Fig. 8).

The average magnitude of turning angle was the only whole-path variable for which a one-way ANOVA did not detect significant differences among the 40 m × 100 m plots (Table 2). The low plot had significantly greater vegetative cover per 1-m interval of path than the other two plots. The high plot had significantly greater average values of path length, rise$_h$, and magnitude of rise$_p$ per path. The average speed per path in the high plot was significantly lower than that of the middle plot and almost significantly lower than that of the low plot (P = 0.07). The average speed per path had a significant positive correlation with path length

and significant negative correlations with all remaining variables (Table 3). The average magnitude of turning angle per path was not significantly correlated with vegetative cover per 1-m segment of path (Table 3).

Variation within paths and correlations with habitat.—In contrast to the average speed per path (Fig. 8), the speed of locomotion per stride had two remarkably distinct modes (Fig. 9). For convenience, we use walk and run to refer to the lower (0.09–0.68 m/s) and higher (0.85–4.75 m/s) ranges of speeds, respectively (Table 4) even though a few of the "run" strides <1.3 m/s
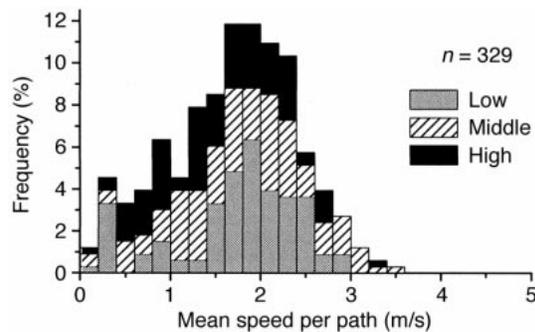

FIG. 8. Frequency distributions of average speed per 1-m interval for each length of path (i.e., *n* = the number of paths) quantified for the 40 m × 100 m plots at the low, middle, and high areas.

TABLE 2. Mean plot values and results from one-way ANOVAs testing for differences among plots in the whole-path variables for all paths ($n = 316$) that were >1 m.

Whole-path variable	Among-plot comparisons and mean plot values			One-way ANOVA	
	Low	Middle	High	$F_{2, 313}$	P
Length (m)	6.65	6.46	8.41	3.8	0.024
Speed (m/s)†	1.76	1.80	1.54	3.8	0.023
Cover†	0.203	0.083	0.100	8.3	<0.001
Turning angle (degrees)†	18.9	20.7	24.2	2.0	0.131
Rise$_h$†	0.143	0.150	0.194	12.6	<0.001
Rise$_p$†	0.100	0.099	0.122	4.2	0.016

Notes: Mean values of different plots with a common underline were not significantly different (Tukey hsd test, $P < 0.05$). Rise$_h$ is the maximal value for the habitat (dune surface) at the location of the path measurement; Rise$_p$ is the vertical gain per 1-m interval of the lizard path. To calculate whole-path averages, we used absolute values of turning angle and rise$_p$. For an explanation of indices of vegetative cover, see *Methods*: *Field measurements of lizard movement.*
† Mean value per path.

probably did not involve a running gait. Walk strides consisted exclusively of category 4 tracks, and no category 4 tracks occurred for run strides. For the entire sample of 5993 strides, only 28 (0.5%) were bipedal, and the percentages of strides belonging to categories 2, 3, and 4 were 8.8%, 78.0%, and 12.8%, respectively. For tracks belonging to categories 1–4, 0%, 3.0%, 2.0%, and 5.4%, respectively, of the strides occurred in 1/3-m segments with vegetative cover other than sparse grass.

The low, middle, and high plots had extremely similar percentages of walk strides (13.2%, 12.1%, and 12.9%, respectively) with the mean values of stride speed approximating 0.25 m/s (Table 4). Overall, the frequency distributions of speeds for the walk strides of the middle and high plots were similar (K-S test, $P = 0.183$), but those of the middle and high plots differed significantly from that of low plot ($P = 0.005$ and $P < 0.001$, respectively) for which parameters indicating the central tendency (mean, median) of the sample were slightly higher (Table 4).

For the entire sample, 5228 run strides had a mean value of stride speed of 2.00 m/s. The frequency distributions of speeds for the run strides differed significantly for all pair-wise comparisons among plots (K-S tests, $P < 0.001$), and the mean value of stride speed of the high plot was substantially lower than those of

the middle and low plots (Table 4). The modes for stride speed were similar among all three plots (Fig. 9), but the left tail of the distributions differed substantially as progressively greater amounts of run strides with speed <1.5 m/s occurred from the low (16.0%) to middle (20.5%) and high (27.1%) plots.

The frequency distributions of turning angles between successive 1-m intervals of paths did not differ significantly for any of the pair-wise comparisons among the three 40 m × 100 m plots (K-S tests, $P > 0.4$ for all comparisons). The highly significant positive value of kurtosis for turning angles for the pooled data (Table 4) indicates the preponderance of angles near zero.

We used average speed per 1-m interval (in meters per second) as the dependent variable in multiple regression analyses for the 1862 m of paths measured that did not have missing values for any the variables. To clarify whether or not the incline of the dune surface had an effect on speed independent of rise$_p$, we calculated Δrise as the difference between the absolute values of rise$_h$ and rise$_p$, which is proportional to the amount of lateral tilting of a lizard. The regression explaining the most variance in speed ($r^2 = 0.164$) and for which each independent variable had a significant regression coefficient was: speed = $2.36 - 0.00648$ turn magnitude $- 5.61$ rise$_p^2 - 1.35$ Δrise $- 0.680$ rise$_p -$

TABLE 3. Simple Pearson correlation coefficients between whole-path variables for all paths ($n = 316$) > 1 m.

Variable	Cover	Turning angle	Rise$_h$	Rise$_p$	Length
Speed	−0.236***	−0.338***	−0.312***	−0.255***	0.171*
Cover		0.066	0.122	0.134	−0.078
Turning angle			0.199*	0.141	−0.038
Rise$_h$				0.766***	0.005
Rise$_p$					−0.036

Note: Except for length (measured in meters), all variables are averages per 1-m interval of path.
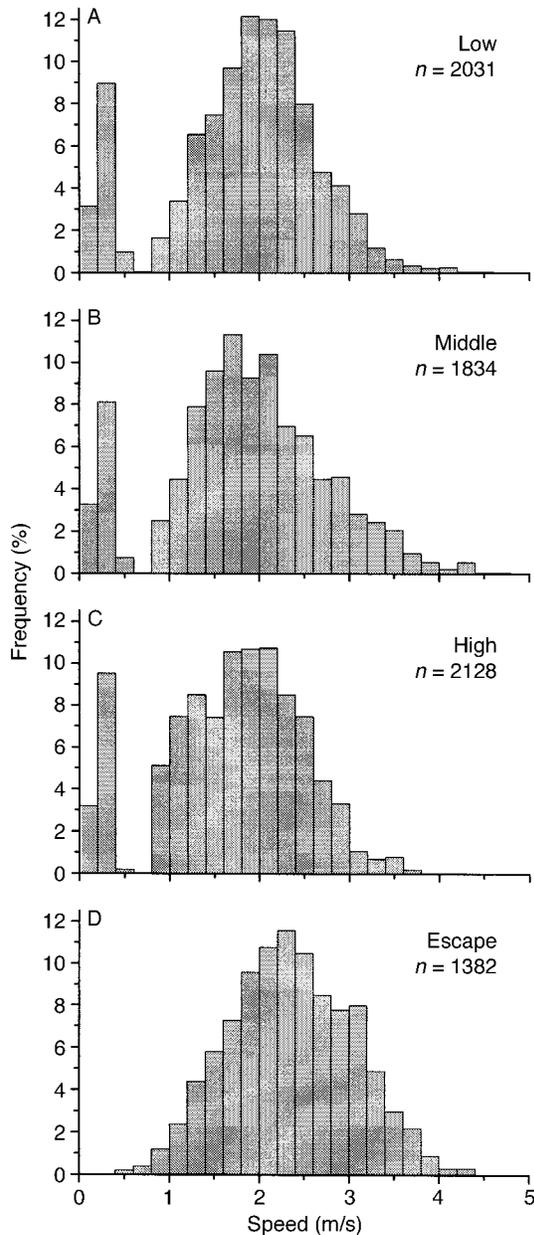* $P < 0.05$, *** $P < 0.001$ (using Bonferroni statistics).

Fig. 9. Frequency distributions of speed per stride for (A–C) undisturbed and (D) escape locomotion of *Uma scoparia* in the Kelso dunes. The undisturbed locomotion data are from all three of the plots (see Fig. 2), and the escape data from Jayne and Ellis (1998) were reanalyzed to facilitate direct comparisons with undisturbed locomotion. The stride speeds of undisturbed locomotion were strikingly bimodal, unlike the average speeds for entire paths (see Fig. 4).

0.335 cover. Each of the five regression coefficients above had $P \ll 0.001$, and the terms in the equation are given in order from most to least significant. Thus, several environmental and behavioral factors had highly significant negative effects on the preferred speed of locomotion. A lizard traveling a straight path on a flat surface with no vegetation has a predicted speed

of 2.36 m/s. Furthermore, predicted speed is maximized for a shallow downhill path with $rise_p = -0.06$, but this value of $rise_p$ only increases the expected value of speed by 0.02 m/s compared to that for a level surface. For this study, biologically meaningful values were as follows: turn magnitude, 0–180; $rise_p$, −0.54–0.54; $\Delta rise$, 0–0.54; cover, 0–3. When maximal values were entered for only one independent variable and all others equaled zero, the predicted speeds ranged from 0.62 to 1.69 m/s. When the experimentally observed value of the independent variables were entered into the regression equation, the frequency distribution of the predicted speeds was not bimodal and only 0.4% of the 1-m intervals had speeds <0.7 m/s, whereas the frequency distribution of observed average speeds per 1-m interval for the same sample ($n = 1862$) was bimodal, grossly similar to those for stride speed (Fig. 9), and 11.0% of the values were <0.7 m/s.

A potential criticism of our multiple regression analysis of average speed per 1-m interval is that different numbers of 1-m intervals came from different individuals. However, similar regression analyses of long individual paths, comparing entire frequency distributions among plots, and comparing average attributes per path among plots, all confirm that environmental variation affects the speed of locomotion.

To clarify the potential interactive effects of speed, incline, and the orientation of the paths traveled by lizards, we calculated the frequency distributions of $rise_p/rise_h$ for subsamples of 1-m intervals with average speeds less than or greater than the mean speed of run strides (2 m/s) and for three ranges of $rise_h$ (Fig. 10). The quantity $rise_p/rise_h$ indicates the extent to which the paths of the lizards were oriented directly uphill (1), directly downhill (−1), or horizontally (0) and hence perpendicular to the incline of the surface. The lack of nearly horizontal locomotion on all inclined surfaces was striking (Fig. 10). Thus, a large fraction of the shallow path inclines were the result of traveling on surfaces with shallow inclines rather than traversing steep surface obliquely relative to the steepest trajectory.

For relatively shallow surface inclines (Fig. 10A), more locomotion was oriented nearly directly downhill ($-1.0 \leq rise_p/rise_h < -0.9$) than directly uphill (26.2% vs. 18.5%), and 2 m/s was exceeded by more (58.3%) of the directly downhill locomotion than by the directly uphill locomotion (47.2%). For surfaces with intermediate slope (Fig. 10B), the percentages of locomotion directly downhill and uphill were nearly equal (18.8% and 15.7%, respectively), and the majority (68.6%) of the directly uphill locomotion was slower than 2 m/s whereas the directly uphill locomotion had nearly equal amounts of locomotion faster (47.3%) and slower (52.7%) than 2 m/s. For the steepest surfaces (Fig. 10C), the amount of locomotion directly uphill (22.8%) greatly exceeded the amount for directly downhill (6.9%), and only a small fraction of both di-

TABLE 4. Descriptive statistics for stride speed and turning angle between successive 1-m intervals of paths for the 1998 experiments and escape data from Jayne and Ellis (1998).

Sample	n	Mean	Median	Range	SD	$g_1 \pm 95\%\,\text{CL}$	$g_2 \pm 95\%\,\text{CL}$
Stride speed (m/s)							
Low walk	267	0.27	0.26	0.09–0.68	0.092	0.90 ± 0.29	1.52 ± 0.59
Middle walk	223	0.25	0.24	0.10–0.53	0.081	1.06 ± 0.32	1.15 ± 0.64
High walk	275	0.24	0.22	0.12–0.50	0.064	0.81 ± 0.29	0.91 ± 0.58
Low run	1764	2.06	2.02	0.85–4.49	0.578	0.46 ± 0.11	0.38 ± 0.23
Middle run	1611	2.07	1.97	0.85–4.75	0.700	0.73 ± 0.12	0.22 ± 0.24
High run	1853	1.89	1.89	0.85–3.78	0.587	0.31 ± 0.11	−0.34 ± 0.22
Low, middle, high run	5228	2.00	1.96	0.85–4.75	0.627	0.56 ± 0.07	0.31 ± 0.13
Escape	1382	2.65	2.61	0.78–4.60	0.688	0.07 ± 0.13	−0.37 ± 0.26
Turning angle (degrees)							
Low, middle, high	1932	−0.05	0	−172–180	33.5	0.40 ± 0.11	7.29 ± 0.22
Escape	260	−0.54	0	−88–67	19.4	−0.42 ± 0.30	2.80 ± 0.60

Notes: Low, middle, and high refer to the three different locations of plots. Turning angles include positive and negative angles, whereas the magnitudes of turning angle (Fig. 7) are absolute values; g_1 and g_2 are skewness and kurtosis, respectively.

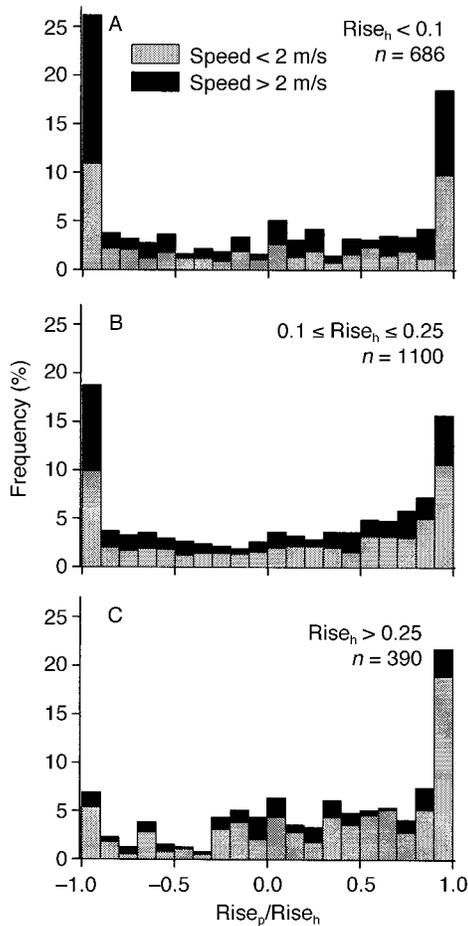FIG. 10. Frequency distribution for values of rise of each 1-m interval of the lizard paths (rise_p) relative to the steepest rise of the habitat (rise_h) at the midpoint of each 1-m interval of the lizard path. We pooled data from all three plots and subdivided the entire sample according to speed and the steepness of the surface upon which the lizard was traveling (rise_h). Values of −1, 0, and 1 for rise_p/rise_h indicate that the path of the lizard was directly downhill, horizontal, and directly uphill, respectively. *Uma scoparia* tended to move directly up or down rather than traversing inclines horizontally.

rectly uphill (12.9%) and directly downhill (22.2%) locomotion had speed exceeding 2 m/s.

DISCUSSION

Comparisons with escape locomotion

More than a decade ago, Hertz et al. (1988) discussed the need for information regarding how routinely animals use their maximum locomotor capabilities. To address this issue, data are needed for both the maximal speed of locomotion and for a comprehensive, unbiased sample of the animal's locomotion in nature. Numerous studies of lizards have documented maximal speeds (reviewed in Garland and Losos 1994) but not of the locomotion in nature. The few studies (Pennycuick 1985, Kenagy and Hoyt 1989) with frequency distributions of the speeds for other groups of vertebrates in their natural habitats lack additional data on where locomotion occurred in the habitat or how habitat structure affected locomotion.

Several comparisons are possible between the undisturbed and escape (Jayne and Ellis 1998) locomotion of *Uma scoparia* in the Kelso dunes. The stride speed of escape locomotion had a nearly normal distribution (Fig. 9D, Table 4) with unexpectedly high overlap with the undisturbed speeds (Fig. 9). Thirteen percent of all undisturbed strides and 14.9% of undisturbed run strides exceeded the mean value (2.65 m/s) of stride speed for escapes, and 14.3% of the escape strides had speeds less than the mean value for undisturbed run strides. The mean speed per escape stride was >0.5 m/s greater than that of the undisturbed run strides (Table 4), and these two frequency distributions had highly significant differences (K-S test, $P < 0.001$). The mean value of speed for the fastest stride per escape path of *U. scoparia* was 3.62 m/s (Jayne and Ellis 1998), and 20.6% of escape strides and 3.3% of the undisturbed strides were within 10% of this maximal value of performance.

TABLE 5. Comparisons between undisturbed and escape locomotion in *Uma scoparia* (Jayne and Ellis 1998).

Comparison	Escape vs. undisturbed
K-S test, frequency distributions	
Rise$_h$	similar ($P = 0.98$)
Rise$_p$	similar ($P = 0.24$)
Turning angle	different ($P < 0.001$)
Percentage of 1-m intervals†	
Category 1	10.0% vs. 0.6%
Category 2	85.1% vs. 9.4%
Category 3	12.5% vs. 79.2%
Category 4	0.9% vs. 16.4%
Maximum path length (m)	34 vs. 146§
Path length (m)‡	10.6 ± 6.8 vs. 5.0 ± 5.6
	($n = 52$; $n = 329$)‖
Turning angle magnitude per 2 m‡	13.3° ± 14.1° vs. 20.5° ± 26.5°
	($n = 260$; $n = 1932$)‖

† Due to the fact that some 1-m intervals of paths had more than one category of track, the percentages do not sum to 100. Category 1 = bipedal run; category 2 = fast quadrapedal run; category 3 = medium speed quadrapedal run; category 4 = slow quadrapedal walk.
‡ Values are means ± 1 SD.
§ From preliminary observations (not 40 × 100-m plots).
‖ Sample sizes for escape locomotion and undisturbed locomotion, respectively.

Bipedal locomotion was much more common for escape than for the undisturbed locomotion of *U. scoparia* (Table 5), and the bipedal strides of escapes are most common near the beginning of the paths where lizards accelerate rapidly (Jayne and Ellis 1998). Category 2 and 3 tracks were most common for escape and undisturbed locomotion, respectively (Table 5). With increased speed, lizards often change from a plantigrade (flat-footed) to a digitigrade (heel does not touch ground) foot posture (Fieler and Jayne 1998, Irschick and Jayne 1999*b*). All category 4 tracks were plantigrade, but all the circular-shaped category 1 and 2 tracks and many category 3 tracks resulted from digitigrade foot posture. This high proportion of digitigrade foot posture contradicts the common assertion that lizards use plantigrade foot posture and further emphasizes the need for ecomorphological studies on the rapid running of terrestrial lizards to account for the functional importance of the distal limb (Irschick and Jayne 1999*b*) instead of relying only on measurements of entire limb length.

Compared to escapes, the frequency distributions of rise$_h$ and rise$_p$ for undisturbed locomotion were similar, whereas those for turning angles differed significantly (Table 5). For both types of locomotion, rise$_h$ conformed to random habitat use, but rise$_p$ had fewer shallow path inclines than randomly expected. Undisturbed locomotion had greater magnitudes of turning angles than escapes (Table 5), and this trend persisted for a subsample of 1-m intervals of undisturbed locomotion that lacked category 4 tracks.

For escapes, a multiple regression predicted that average speed per 1-m interval was maximized for horizontal running rather than on shallow downhill paths as in undisturbed locomotion. In light of these detrimental effects of steep path inclines on speed and as-

suming that rapid speed would be of utmost importance during escape, the identical use of inclines for escape and undisturbed locomotion was contrary to our expectations. For both escapes and undisturbed locomotion of *U. scoparia,* turn magnitude had a significant negative effect on speed.

During escapes the most conspicuous use of vegetative cover was near the end of paths where *U. scoparia* commonly used vegetation to hide from observers (Jayne and Ellis 1998). For undisturbed locomotion the category 4 (low speed) tracks had the greatest probability of being near vegetative cover, and we frequently observed lizards near cover when they were basking or remaining still. However, faster undisturbed locomotion showed little conspicuous association with vegetative cover. Interestingly, in a nearby dune site, escapes of a closely related species of lizard, *Callisaurus draconoides,* oriented more towards vegetative cover than those of *U. scoparia,* which frequently escapes to heavily used burrows (Irschick and Jayne 1999*a*).

For *U. scoparia,* the mean length of escapes exceeded that of undisturbed locomotion, whereas the longest escape path was a small fraction of the longest observed undisturbed path (in preliminary experiments; Table 5). Several of the undisturbed paths were truncated by the borders of the experimental plots, whereas none of the escape paths were truncated.

Incline use

An important issue in ecology is whether the habitat use of animals is biased. In our study of *U. scoparia,* the occurrence of locomotion in the habitat was a random sample of surfaces with respect to their inclines. However, on a fine spatial scale, lizards utilized some areas of the dune more than others. Four key conclu-

sions regarding the effects of habitat structure on preferred speed emerged from our work with *U. scoparia*. First, rather than a uniform response to surface inclines, the effects of incline had some complicated threshold and interactive effects on path orientation and the speed of locomotion. Second, downhill locomotion was only more frequent than uphill locomotion when lizards were on surfaces with relatively shallow inclines which enhanced downhill speed. Third, all locomotion on steep surfaces had diminished amounts of fast speeds regardless of path orientation. Finally, locomotion directly downhill was only avoided when surfaces were very steep.

Physiological considerations

The mean values of the walk and run modes of *U. scoparia* were 9.4% and 75.5%, respectively, of the mean maximal stride speed per field escape (Jayne and Ellis 1998). Furthermore, the best estimates of the physiologically maximum speeds of *U. scoparia* appear to be field values because they averaged approximately one-third more than values obtained with standard laboratory methods (Jayne and Ellis 1998). In contrast to relatively rapid speed of the predominant running mode of *U. scoparia*, several species of *Anolis* lizards have mean speeds of undisturbed locomotion in the field that are relatively low compared to their maximal sprinting capacities (mean = 33.4%, range = 16.7%–58.3%) (Irschick and Losos 1998).

Besides maximal speed, additional physiological descriptors of locomotion characterize the sustainability (endurance) and energetics of movement (Bennett 1985, Garland 1994). Moving intermittently can enhance endurance capacity (Weinstein and Full 1992, 1998), and some of the longer paths of *U. scoparia* had tracks that clearly indicated a pause. We have commonly observed intermittent running by *U. scoparia* that allowed the lizards to stay on a treadmill for >20 s and >1 min, for constant treadmill speeds of 3 and 2 m/s, respectively (Irschick and Jayne 1999b). The mean endurance capacity for a similar sized and closely related species, *Uma inornata*, moving at 0.28 m/s is ~8 min (Garland 1994). Ninety percent of the undisturbed paths measured were <15 m, and traveling a path of this length would only take 60 or 7.5 s, respectively, for a *U. scoparia* traveling with the modal speeds of walking and running. Thus, we rarely observed paths that suggested that the endurance capacity of *U. scoparia* was regularly taxed.

For the entire sample of undisturbed locomotion of *U. scoparia*, 12.8% of the strides belonged to the walk mode, but because of the short length and slow duration of these strides, they represented a small percentage of the total distance (4.9%) but a larger percentage of the total time (29.3%), of all strides measured. Some laboratory studies of lizards (Van Damme et al. 1998) and small mammals (Perry et al. 1988) have found unimodal frequency distributions of speed, but two thorough field studies of mammals have found bimodal frequency distributions of voluntary speed (Pennycuick 1975, Kenagy and Hoyt 1989). For the golden-mantled ground squirrel, *Spermophilus saturatus,* in its natural habitat, Kenagy and Hoyt (1989) also found distinct walking (0.21 m/s) and running (3.63 m/s) modes, and walking comprised the bulk (88%) of the time spent moving but only 29.8% of the average distance traveled per day (5 km). This small mammal differs from *U. scoparia* by having a running mode that is aerobically sustainable and relatively much faster than its walking mode, and the running mode of *S. saturatus* may be important for minimizing total time spent traveling because such great distances are traveled (Kenagy and Hoyt 1989).

For two small species of lizards (<5 g) on a 50° slope (77% grade) the net cost of locomotion increases >80% compared to locomotion on a level surface (Farley and Emshwiller 1996), but the cost of downhill locomotion is presently unknown for lizards. Although the net cost of transport decreases with animal size (Taylor et al. 1982), some insights may still be gained from studies of large mammals. For example, the energetic cost of locomotion for humans is minimized on a 10% downhill grade, and additional studies of large mammals have also found that the cost of locomotion down steep inclines is greater than that on a level surface (e.g., Dailey and Hobbs 1989). Thus, our finding from the multiple regression analysis that *U. scoparia* had maximal undisturbed speeds on a 6% downhill grade might reflect environmental conditions that minimize the energetic cost of locomotion.

Besides inclines, *U. scoparia* also must cope with moving on very loose sand, and several aspects of its morphology appear well-suited for this task (Stebbins 1944). For instance the expanded scales on the toes of *U. scoparia* create fringes that enhance maximal speed on sand (Carothers 1986). For humans, much of the increased energetic cost of locomotion on sand results from work being done on the environment by moving the sand (Lejeune et al. 1998). Perhaps for *U. scoparia* the lesser amounts of sand displaced by the predominant category 3 tracks compared to the large divots of category 1 and 2 tracks indicate selection of a preferred speed for which considerably less work is performed on the environment. Loose sand also might exacerbate the effects of inclines on the energetic cost of locomotion. Whether or not the fringed toes of *U. scoparia* reduce the energetic cost of locomotion remains an open question.

An issue related to the energetic cost of transport is preferred speed. For example, does *U. scoparia* have lower preferred speeds on inclines because it tends to use a constant fraction of some maximal capacity such as maximal aerobic capacity or maximal speed? Perhaps *U. scoparia* modulates speed to retain a particular safety factor to ensure its ability to escape because even

its escapes are often well below physiologically attainable speeds (Fig. 9D).

Behavioral and ecological considerations

Although the multiple regression was very useful for determining some features of environment and behavior that had statistically significant effects on speed, it did not adequately predict either the extremely fast or slow locomotion. Focal animal observations could help to resolve some of the sources of this unexplained variation in speed. For example, we have commonly observed that when one lizard escaped from us it would come near another lizard which would in turn run quickly in an apparent response to an intruder. Similarly, if one observed *U. scoparia* capturing prey, as has been done for *Anolis* lizards (Irschick and Losos 1998), some of the rapid locomotion might be associated with this behavior. However, even focal animal observations often have difficulty in determining the purpose of movements.

We had not expected a positive correlation between path length and speed, but the thermal conditions and open habitat of the dune site may partially explain this and the occurrence of speeds at either extreme. Jayne and Ellis (1998) found *U. scoparia* in the Kelso dunes active when temperatures of the sand surface and air (~1.3 m above the surface) were as high as 56.3° and 41°C, respectively. Thus, even though *U. scoparia* commonly has high active body temperatures ranging from 40° to 45°C (Jayne and Ellis 1998), they often may be in danger of quickly exceeding their critical thermal maximum or sustaining localized thermal damage to their feet as they move across exposed sand. We have also personally sighted or observed tracks of coachwhip snakes, sidewinder rattlesnakes, and several species of mammals and birds (Stebbins 1944) that are potential predators for *U. scoparia*. Thompson (1985) suggested that heteromyid rodents traveled rapidly between clumps of vegetation in similar open desert habitats to minimize exposure to visually oriented predators. Thus, rapid locomotion of *U. scoparia* across relatively open areas ultimately may reduce either adverse thermal conditions or risk of exposure to predators. At the other extreme, the slowest (category 4) tracks had the closest association with vegetative cover. When *U. scoparia* emerge in the morning prior to being active they often bask at the entrances of burrows or near or under vegetation as they increase their body temperature. Thus, many of the slow, convoluted category 4 tracks may have been made when the lizards were substantially below their preferred active body temperature and inconspicuous to predators.

Our finding that may best illustrate the importance of behavior was the striking lack of locomotion down steep inclines (Fig. 10C). Moving up steep inclines should have the most adverse effects with respect to the energetic cost and speed of movement based on biomechanical considerations. In contrast, no aspect of biomechanics or the physiological capacity of *U. scoparia* adequately explains the scarcity of movement down steep inclines. This reluctance of *U. scoparia* to move down steep surfaces can profoundly affect how the lizards travel through their environment. For example, along the upper rim of a large depression near the high plot, we discovered a path of *U. scoparia* with four places where the lizard had just begun to go down the steep surface and then abruptly reversed direction back uphill to continue an overall trajectory along the rim of the depression rather than traveling down the steep face of the depression.

U. scoparia is physiologically capable of moving on virtually every sand surface of the Kelso dune system. Remarkably, we have even found of tracks of this species along the barren, wind-swept crest of the dune which rises nearly 200 m. Thus, the spatial variation that we found in both the amounts and speed of locomotion of *U. scoparia* vividly illustrates the importance of attempting to integrate the behavior of organisms with their physiology and environment.

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