Effects of Slope, Substrate, and Temperature on the Locomotion of the Ornate Box Turtle, *Terrapene ornata*

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Ornate box turtles, from the Sand Hills of Nebraska, live in a habitat character-ized by slopes, a fine sand substrate, and temperatures that can vary greatly, both diurnally and seasonally. We examined the locomotor responses of these turtles to slope, substrate, and temperature. Only 25% of the turtles could successfully walk on slopes as steep as −40°. They were better at walking upslope, but their speed progressively decreased as slope increased. As grade increased, they primarily ad-justed stride frequency on upslopes but stride length on downslopes. Turtles appear to be much more affected by slopes than are lizards. Speed was significantly reduced on sand substrates in comparison to Styrofoam, and this was primarily because of a reduction in effective stride length. Speed increased with increasing temperature from 20 to 35 C, almost entirely resulting from an increase in stride frequency; however, the Q_{10} for locomotor performance was low. Turtle speeds in the field averaged 0.05 m/s and, although there was a tendency for higher speeds at higher operative environmental temperatures, this was not statistically significant. Within their natural Sand Hill habitat, these turtles are often active under conditions of slope, substrate, and temperature that are suboptimal for locomotion. However, locomotor performance is not adversely affected to any appreciable degree by the potential constraints of their habitat.

E FFECTIVE locomotion under a variety of environmental conditions is essential for the survival and well-being of essentially all an-imals. For terrestrial ectotherms, these condi-tions include terrain slope, the nature of the substrate, and ambient temperature. Locomo-tor performance can be categorized in a num-ber of ways but perhaps most basically by the speeds that animals use, or are able to achieve, under a specific set of conditions. Because speed is the product of stride length and stride frequency, one can easily examine not only the effects of environmental factors on speed but also the nature of the adjustments in leg move-ments.

The great majority of locomotor studies have been conducted on a horizontal surface. Many animals, however, live in hilly terrain, and must contend with the consequences of moving up and down slopes. This has been given some lim-ited attention for lizards (Huey and Hertz, 1982; Irschick and Jayne, 1998; Jayne and Irschick, 2000) and turtles (Muegel and Claussen, 1994; Finkler and Claussen, 1997), but only a handful of species have been examined.

Most laboratory studies have also used a rel-atively firm and unyielding substrate for loco-motion. However, sand and some other natural substrates are quite compliant. The conse-quences of a compliant substrate for animal lo-comotion have only rarely been examined, al-though a few studies have considered the effects

of tundra (White and Yousef, 1978), snow (Park-er et al., 1984), or sand (Lejeune et al., 1998) on mammalian locomotion.

Although many ectotherms are capable of ef-fective behavioral thermoregulation, their body temperatures nonetheless reflect, to at least some degree, the existing ambient tempera-tures. In reptiles, locomotor performance, as expressed by maximal speed, typically increases with increasing temperature up to some optimal body temperature (or a narrow optimal range), beyond which performance begins to decline (Bennett, 1980, 1990). The effects of tempera-ture on animal speed have been well docu-mented for many lizards (e.g., see Bennett, 1980; Hertz et al., 1983) and a few snakes (Ste-venson et al., 1985; Haily and Davies, 1986; Finkler and Claussen, 1999). Corresponding data for turtles are, however, quite sparse, al-though Adams et al. (1989) found that volun-tary speeds of eastern box turtles (*Terrapene car-olina*) tend to increase with increasing temper-ature.

We designed the present study to examine the effects of slope, substrate, and temperature on the locomotor performances of ornate box turtles, *Terrapene ornata*. Our animals were col-lected from the Sand Hills of Nebraska—a hab-itat where slopes are more common than flat land, where the substrate consists primarily of highly compliant loessal sand and where tem-perature can vary markedly, both seasonally and

diurnally. We hypothesized that (1) speed would decrease as slope (either up or down) increased and that these changes would primarily result from altered stride length, (2) speed would be slower on a more compliant substrate because of a reduction in both stride length and stride frequency, and (3) speed would increase with increasing temperature up to some optimal temperature and that the changes in speed would primarily be based on changes in stride frequency.

MATERIALS AND METHODS

We collected 25 ornate box turtles in June of 1996 and an additional 32 animals in June of 2000. All animals were collected within the Sandhills in Cherry County, Nebraska. The 1996 animals were used for the slope and substrate studies, whereas the 2000 animals were used to examine the effects of temperature. The turtles were housed in an environmental chamber on a 12:12 L:D photoperiod at 25 ± 1 C, but they were also provided with full spectrum lights 12 h per day for basking. Water was provided at least once a week, and the turtles were fed, two or three times a week, crickets or fruits (apples, peaches, plums) and calcium and vitamin supplements.

The turtles were tested on a racetrack approximately 1.8 m long and 0.14 m wide with sideboards 0.12 m high. Slope and substrate studies were conducted at 26 C with one meter of the track marked off and divided into thirds. Infrared emitting diodes and IR detecting photocells were positioned on opposite sideboards at 0 m, 0.33 m, 0.67 m, and 1.0 m and connected to an electronic stopwatch. This allowed precise timing to the nearest 0.1 sec for each 0.33-m segment. During temperature studies, one meter of track was divided into five 0.05-m segments, followed by one 0.25-m and one 0.5-m segment. The eight photocells were connected to a custom designed computer-based timer accurate to the nearest 0.01 sec. For all experiments, the turtles were weighed and lightweight flags were attached to their carapaces to break the infrared beams. Each measurement period consisted of three consecutive trials, but no turtle was tested in more than one measurement period per day. All trials were videotaped for subsequent analysis and determination of stride lengths and frequencies. Stride length (m) for each measurement was computed from a count of the number of strides per meter, estimated to the nearest half stride. Stride frequency (Hz) was then calculated by dividing speed by stride length. The turtles in the slope and substrate

studies were motivated to move by a piece of fresh peach tied to a string and moved along just fast enough to keep it approximately 3 cm in front of the animal. For the temperature studies, the peach slices were placed in a sliding plastic weighing boat pulled along by a string connected to a pulley at the end of the track. To increase motivation, food was withheld for two or three days prior to each measurement period.

For the slope studies, the racetrack was positioned at various angles ($-40°, -20°, 0°, +20°, +40°$) using a stepladder platform. Twenty turtles were tested at the various slopes in a predetermined random order. A slope trial was considered successful only if the turtle completed the one meter using an apparently normal gait. For the substrate studies (all conducted at a slope of 0 degrees), the Styrofoam base, used for all other experiments, was replaced by a 2.5–3.0 cm depth of either coarse (riverine) or fine (loessal) sand. These substrates were tested in a predetermined random order. We quantified the sand sizes by using an ocular micrometer to measure the maximum lengths and minimum widths of 100 randomly selected grains of each type of sand. The coarse sand grains were 0.49 ± 0.44 (mean $\pm$ SD) mm long and 0.39 ± 0.36 mm wide, whereas the fine sand grain averaged only 0.35 ± 0.09 mm long and 0.26 ± 0.06 mm wide. These size differences were highly significant statistically ($P = 0.002$ and $P = 0.0005$ for length and width, respectively). The approximate mean volumes of the sand grains, estimated as the cube of half the sum of the length plus the width, were 0.085 mm^3 and 0.028 mm^3 for coarse and fine sand, respectively.

For the temperature tests, turtles were tested in groups of five animals in a repeating 25, 30, 40, 20, 35, 25 C sequence staggered so that one group started at 25 C, the next at 30 C, the third at 40 C, and so on. The turtles were placed at the test temperature for approximately one hour prior to the first trial to allow them to equilibrate to the test temperature. Although we did not directly measure body temperatures, a one-hour equilibration should be adequate inasmuch as larger box turtles (*T. carolina*) heat and cool at 0.15 and 0.34 C /min, respectively, under roughly comparable conditions (Spray and May, 1972).

During June of 2000, we collected field data in the Sandhills to quantify the relationship between ambient temperature and voluntary speed of box turtles. The probes of three StowAway XTI data loggers (Onset Computer Corp.) were inserted into carapaces of dead box turtles stuffed with aluminum foil. These three

operative environmental temperature models were then positioned in full sun, partial shade, and full shade, respectively. Turtles were located in the field and fitted with thread trailing devices as described by Claussen et al. (1997). The end of the thread was attached to a flag to mark the starting point and the turtle was released. The human observer moved at least 5 m away from the turtle and remained motionless while viewing the animal. The turtles usually began moving after remaining stationary for a few minutes after release. An observation period was terminated if the turtle remained inactive for as long as 60 min. Active animals were subsequently timed by stopwatch from when they began to move until they came to a stop for more than 5 sec. Each stopping point was marked with a flag. After three such movements, the turtle was weighed on a field balance and sexed. The string between each set of flags was collected and measured for length. The operative environmental temperatures (i.e., the median temperature recorded by the three data loggers) were subsequently matched to the corresponding times of the trials.

For the purposes of statistical analysis, we excluded the racetrack data for the −40° slopes (because of a 75% failure rate). We also excluded data for those turtles with incomplete data (i.e., those missing data for other slopes, temperatures, or substrates). We then used repeated measures analyses of variance (ANOVA) and Tukey-Kramer posttests for multiple comparisons of the remaining data. SAS was used to perform a repeated-measures ANOVA of speed in relation to platform slope with mass as a covariate. Results are considered significant at $P < 0.05$.

RESULTS

Only five (25%) of 20 turtles successfully navigated the steepest downslope (−40°). The other tests were failures because of the tumbling down, sliding, or turning around of the animals. Data from the 19 turtles completing all of the remaining slopes were used for statistical analysis. The mean velocities for the three trials were significantly affected by slope ($P < 0.0001$). The differences for all comparisons were significant ($P < 0.001$) except for that between 0° and −20° (Fig. 1A). There was also a significant relationship between stride length and slope ($P < 0.0001$). The mean stride length at +40° was significantly less than that at the other three slopes ($P < 0.001$; Fig. 1B). Mean stride frequency was likewise affected significantly by slope ($P < 0.0001$). The differences
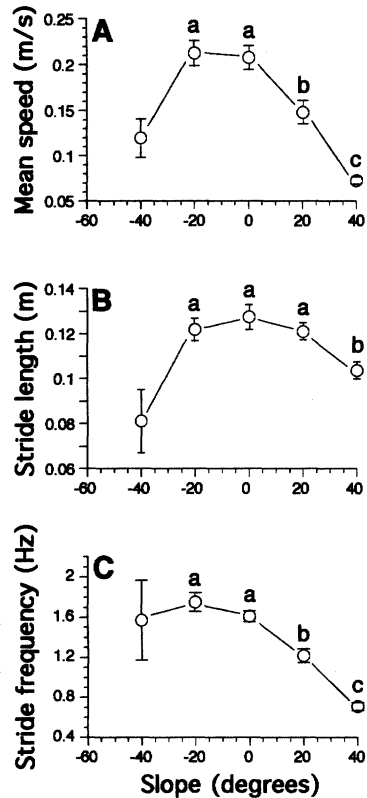

Fig. 1. The effects of slope on mean speed (A), stride length (B), and stride frequency (C) of ornate box turtles. Open circles depict the means and vertical lines one standard error above and below the mean. Sample size was five for the −40° slope and 19 for all other slopes. Within each graph, for slopes of −20° and above, symbols with a lower case letter in common do not differ significantly ($P > 0.05$).

for all comparisons were significant ($P < 0.001$) except for that between 0° and −20° (Fig. 1C). The relative contributions of stride length and stride frequency to the effects of slope on speed can be best visualized by plotting the mean values as a percentage of the values at 0° (Fig. 2). The adjustment for up slopes appears to be mainly in terms of stride frequency whereas the adjustment for down slopes appears to be mainly in terms of stride length.

Speed generally increased with increasing body mass (Fig. 3), although apparently less so as platform slope increased. The relationship between speed and mass is statistically significant ($P < 0.01$) only for the horizontal (0° platform slope) data. There are significant differences among the regression slopes ($P < 0.05$), although only the regression slope for the horizontal trials differs significantly ($P < 0.0005$) from the others (Fig. 3).
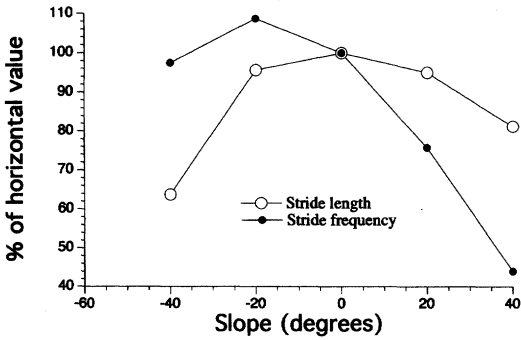
Fig. 2. A comparison of the relative effects of slope on stride length and stride frequency of ornate box turtles. All values are expressed as a percentage of the values on a horizontal surface.

There was a significant relationship between mean speed and substrate type ($P < 0.0001$). Speeds on both coarse and fine sand were significantly slower than those on Styrofoam ($P < 0.001$), but there was no difference between the two sand types (Fig. 4A). There was also a significant effect of substrate type on stride length ($P < 0.0001$). Again, there was no difference between the sand types but both were associated with significantly shorter stride lengths ($P < 0.001$; Fig. 4B). There was no apparent effect of substrate type on stride frequency (Fig. 4C).

Some of the observed variation in speed can be attributed to variation in body size (Fig. 5). The scaling exponents (regression slopes) for the three substrates did not differ significantly and were similar at about 0.18; nevertheless, the correlation between speed and body mass was statistically significant only for fine sand ($P = 0.02$), though nearly so for coarse sand ($P = 0.06$).

Fig. 4. The effects of substrate on speed (A), stride length (B), and stride frequency (C) of ornate box turtles. Sample size was 21. See Figure 1 for further explanation of symbols.

The mean velocities of the box turtles were significantly affected by temperature ($P < 0.0001$). The speeds at 20 C were significantly lower than those at 30 C or higher ($P < 0.01$), and those at 25 C were significantly lower than those at 35 C ($P < 0.01$; Fig. 6A). There was no statistically significant relationship between
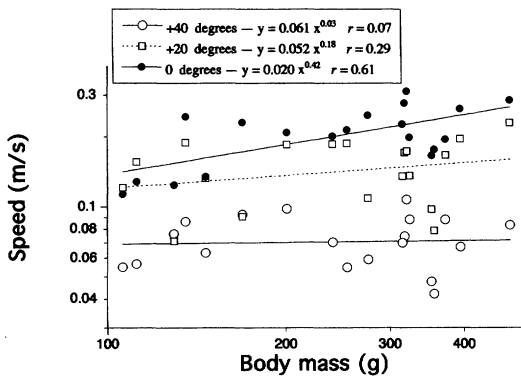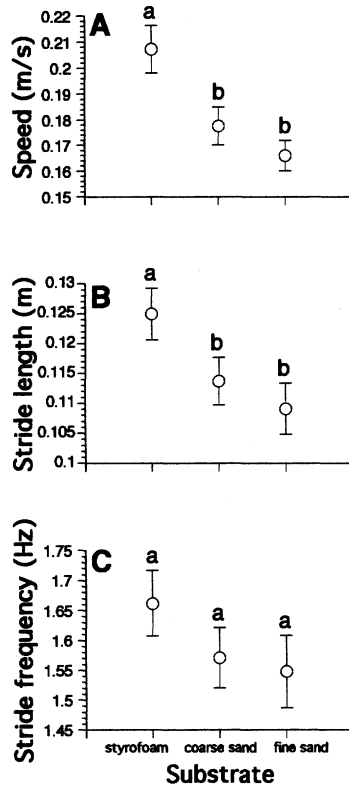

Fig. 3. The relationship between body mass and the speed of 19 ornate box turtles on horizontal surfaces and upslopes. The correlation for 0 degrees is statistically significant ($P < 0.01$).
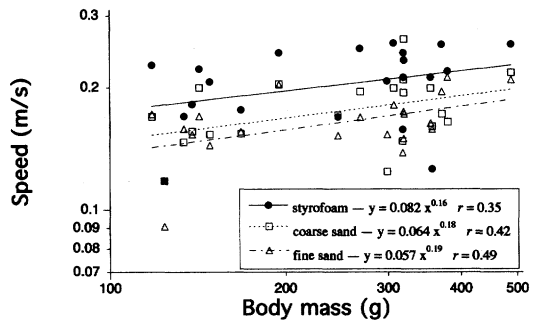

Fig. 5. The relationship between body mass and the speed of ornate box turtles on three different substrates. The correlation for the fine sand data is statistically significant ($P < 0.01$).
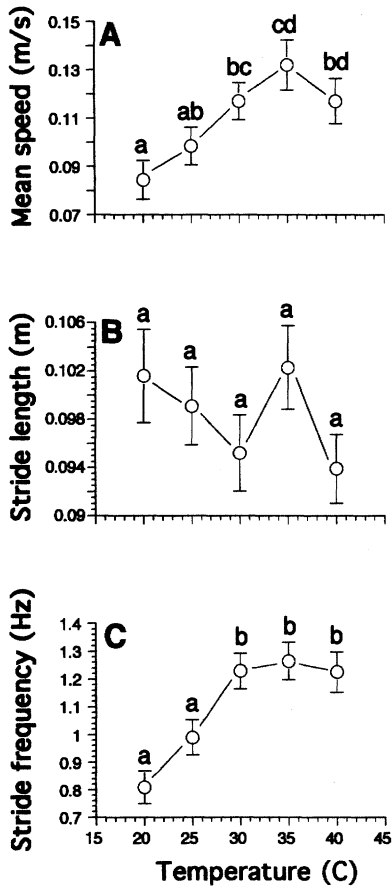
Fig. 6. The effects of temperature on speed (A), stride length (B), and stride frequency (C) of ornate box turtles. Sample size was 22. See Figure 1 for further explanation of symbols.
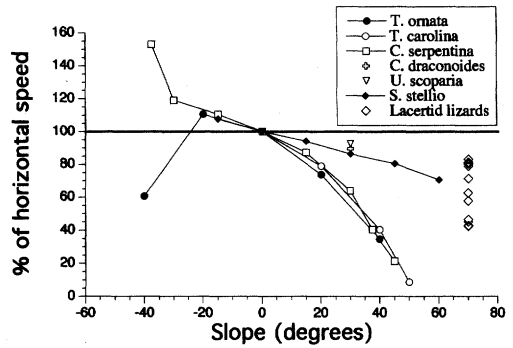

Fig. 7. The effects of slope on the speed (relative to horizontal) of three species of turtles and 16 species of lizards. Sources of data: *Terrapene ornata*, present study; *Terrapene carolina*, Muegel and Claussen, 1994; *Chelydra serpentina*, Finkler and Claussen, 1997; *Callisaurus draconoides*, Irschick and Jayne, 1998; *Uma scoparia*, Jayne and Ellis, 1998; *Stellio stellio*, Huey and Hertz, 1982. Lacertid lizards (the symbols represent the values for 13 different species), Vanhooydonck and Van Damme, 2001. Except for *S. stellio*, all lizards depicted were tested on only one upslope.

stride length and temperature ($P = 0.10$; Fig. 6B). Temperature significantly affected stride frequency ($P < 0.0001$). Stride frequencies at 20 C were significantly lower than those at 30 C or above ($P < 0.001$), and stride frequencies at 25 C were also significantly lower than those at higher temperatures ($P < 0.01$; Fig. 6C).

We obtained field data for 14 adult turtles (42 movement segments). The speeds averaged 0.05 ± 0.02 m/s, and ranged from 0.02–0.09 m/s. The associated field operative environmental temperatures, while these turtles were active, averaged 31.2 ± 1.0 C, and ranged from 21.9–41.4 C. Although there was a slight tendency for faster speeds at higher temperatures, the correlation between these variables was not statistically significant ($P > 0.05$).

DISCUSSION

Box turtles are frequently found in hilly regions, and field observations suggest that their movements are little affected by shallow slopes. Nonetheless, the locomotor performance of *T. ornata* is significantly influenced by slope (Fig. 1), and their speed decreases on upslopes and steep downslopes. The reduced speed on upslopes primarily, though not entirely, results from a reduced stride frequency (Fig. 2). In contrast, it appears that the speed reduction on steep downslopes largely reflects a decreased stride length. It should be noted that we determined stride length from a count (to the nearest half stride) of the number of strides per meter. There is some round-off error here (though likely less than 5%, given the typical stride counts). Our method also assumes constant stride length, which appeared from videotape analysis to be the case over these short distances. Stride frequency is, of course, subject to these same potential errors inasmuch as it is computed from stride length.

The relative effects of upslope on speed are remarkably similar for ornate box turtles, eastern box turtles, and juvenile snapping turtles (*Chelydra serpentina*; Fig. 7), in spite of the differences in body mass and terrestrialism among these turtles. For all three species, moderate slopes (i.e., 20° or less) decrease speed by only 20–30%, whereas slopes greater than 35° reduce speed by 50% or more. Among other reptiles, lizards appear to be less affected by upslopes than are turtles. Some lizards can run effectively on upslopes of 60° or more (Huey and Hertz, 1982; Vanhooydonck and Van Damme, 2001). In contrast, the upper slope limit for turtles ap-

pears to be around 50° (Muegel and Claussen, 1994; Finkler and Claussen, 1997).

The superior performance of lizards probably results from their body shape (relatively long legs and absence of a carapace). Their performance on slopes may also be affected by a lower center of gravity. Additionally, the lizards that have been studied are much smaller than box turtles, and size does make a difference. Huey and Hertz (1982) found that small *Stellio stellio* are much less affected by slope than are larger individuals. Nevertheless, body mass can explain only a portion of the apparent difference between lizards and turtles, because the juvenile snapping turtles (Finkler and Claussen, 1997) were mostly smaller than the *S. stellio*.

Although lizards may be able to locomote on steep slopes, nonarboreal species such as *Callisaurus draconoides* (Irschick and Jayne, 1999) and *Uma scoparia* (Jayne and Irschick, 2000) generally avoid doing so within their natural environment. Comparable field data for turtles are lacking.

The effects of downslope on turtle locomotion seem less consistent among species (Fig. 7). Downhill speeds of juvenile snapping turtles progressively increase up to their maximum angle ($-35°$) for normal walking (Finkler and Claussen, 1997). In contrast, the speeds of ornate box turtles decreased at $-40°$, although many animals were unable to locomote normally on a slope this steep. The 25% success rate that we observed for *T. ornata* is quite similar to the successful completion rate of 22% reported by Muegel and Claussen (1994) for *T. carolina* at this same slope.

Larger animals appear to be more affected by upslopes than are smaller turtles (Fig. 3). Although the scaling exponent of 0.42 relative to body mass for speed on a horizontal plane is higher than the values reported in most turtle studies (see Wren et al., 1998), the suggested size effect is consistent with the observations of Huey and Hertz (1982) on the lizard *S. stellio*. It is interesting to note that turtle speeds on steep slopes appear to be essentially size independent.

The slowing associated with walking on sand resulted primarily from a shortened effective stride length (Fig. 4). It should be noted, however, that our method of determining stride length (i.e., as the reciprocal of strides per meter) was based on the distance moved forward rather than on the actual extension of the limbs during a stride. It is quite possible that the turtles extended their limbs as far on sand as on Styrofoam but that, because of the highly compliant nature of this substrate, their forward progress per stride was considerably reduced. Marked reductions in speed (to 85.6% and 80.1% of the Styrofoam values for coarse and fine sand, respectively) were not unexpected. Sand is an energy-absorbing damper (Lejeune et al., 1998) and, for humans, requires more than twice the energy needed for walking at the same speed on a firm surface. Herreid and Full (1986) reported that hermit crabs (*Coenobita compressus*) are about twice as fast on wet sand as on dry sand; however, few other studies have compared speeds on sand relative to those on firmer ground.

Although the substrate experienced by turtles in the Sandhills is fairly consistent, this is not necessarily the case for other populations of box turtles. Future studies should examine the effects of alternative substrates, such as loose gravel or rock, which might cause drag when in contact with the plastron, and should determine the difference between wet and dry sand on turtle locomotion.

The scaling exponents for speed relative to body mass (Fig. 5) are quite low, averaging about 0.18, which is identical to the value reported by Wren et al. (1998) for this species, and similar to the value of 0.16 reported by Marvin and Lutterschmidt (1997) for *T. carolina*. These values on different substrates (Fig. 5) are also all quite similar, and there is thus no evidence that heavier animals are relatively more affected by walking on sand, at least at a slope of zero degrees, than are their lighter counterparts.

The range of variation within our results was large. This was apparent throughout but was especially noticeable for the substrate study (Fig. 5). While testing, we did note considerable variation in apparent motivation both among individual animals and in the same individuals from time to time. We cannot explain these differences. Although some individual turtles were markedly slower or faster than expected for their size (e.g., in Fig. 5), ANOVA revealed no extreme outliers. Also, these same individuals were not consistently slower or faster in other tests (e.g., Fig. 3).

The speeds of the turtles collected in 2000 and tested at 25 C were markedly slower (on average only about half as fast) than the corresponding speeds for animals collected in 1996 and tested at a similar temperature (i.e., compare Fig. 1A with 6A). We are not certain of the reason for this, but it probably reflects procedural differences in training and testing rather than physiological differences between the two populations of turtles. The turtles in 1996 were tested by two investigators after a more regular

(and probably a more effective) training regimen, and the peach slice was kept at a near constant distance in front of the animal. The 2000 turtles were tested by a single investigator and the peach slices were in a plastic weighing boat less visible to the animal. Also, the frequent temperature changes during the 2000 tests might have disrupted the conditioning process and, by affecting food digestion, might also have altered the feeding motivation of the turtles.

In spite of the slower speeds in 2000, there was a significant effect of temperature, which was almost entirely attributable to changes in stride frequency (Fig. 6). The thermal dependence of box turtle locomotion was quite low, with a Q_{10} of 1.35 between 25 and 35 C. This is similar to the corresponding Q_{10} value of 1.23 for the eastern fence lizard, *Sceloporus occidentalis* (Marsh and Bennett, 1986), and the value of 1.4 for the snakes, *Nerodia sipedon* and *Regina septemvittata*, between 20 and 30 C (Finkler and Claussen, 1999). In contrast, some lizards have Q_{10} values above 3, especially over lower temperature ranges (Bennett, 1980, 1990) and voluntary speeds of eastern box turtles, *T. carolina*, have a Q_{10} of 3.3 between 10 and 32 C (Adams et al., 1989). Our observed Q_{10} of 1.35 between 25 and 35 C is close to the value (between 1.4 and 1.5) reported by Gatten (1974a) for active metabolic rates of *T. ornata* at these temperatures but well below corresponding values for standard metabolic rates.

Ornate box turtles have been reported to be active in the field at body temperatures ranging from 13 to 36 C (Fitch, 1956) and to have preferred body temperatures in a laboratory thermal gradient close to 30 C (Gatten, 1974b). The locomotor performance of ornate box turtles is near optimal at 30 C but appears to peak closer to 35 C (Fig. 6). There is little evidence, however, of the abrupt performance decline at the highest temperatures exhibited by some (but not all) lizards (see Bennett, 1990).

The mean speed of 0.05 m/s from our field study is similar to voluntary speeds reported from laboratory studies for *T. carolina* (Adams et al., 1989; Muegel and Claussen, 1994) but well below (i.e., less than one-third of) the speeds in our laboratory study on a fine sand substrate at comparable temperatures (Fig. 4). A literature review by Adams et al. (1989) revealed that voluntary speeds of lizards and snakes are, on average, much slower than forced speeds, and Irschick (2000) similarly reported that *Anolis* lizards typically move at preferred speeds of 40% or less of their maximal capacity. Nevertheless, because the field turtles

had been disturbed a few minutes prior to data collection, we cannot be certain that their locomotion was entirely voluntary. Studies of movements of truly undisturbed turtles in the field are needed.

Overall, our original hypotheses were generally, though not entirely, supported by our results. As we hypothesized, (1) speed did decrease as upslope increased and at the steepest (−40°) downslope; however, there was no difference between 0° and −20°. Stride length adjustments were important on steep downslopes, but changes in stride frequency appear to be more important on upslopes. (2) Speed was indeed reduced on more compliant substrates, but adjustments in stride length were more important than those in stride frequency. (3) Speed did increase with increasing temperature up to an apparent optimal temperature around 35 C, and these changes in speed were almost entirely due to changes in stride frequency.

Ornate box turtles in the Sand Hills of Nebraska live in a habitat composed of sloping terrain and loessal sand substrate where temperatures are sometimes extreme and where rapid temperature changes are commonplace. The turtles are thus often moving about under slope, substrate, and thermal conditions that are clearly far from optimal for locomotor performance. Box turtles are nonetheless able to adjust to such conditions and to sustain effective, even if suboptimal, movement in the field. They live in the "slow lane," and they do not appear to be adversely affected to any major degree by the potential constraints of their habitat on their locomotor performance.

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