Effects of Temperature on Voluntary Locomotion of the Eastern Box Turtle, *Terrapene Carolina Carolina*

Nadine A. Adams, Dennis L. Claussen and John Skillings

We examined voluntary locomotion of *Terrapene c. carolina* in a laboratory racetrack at six temperatures ranging from 9.7–31.9 C. The mean number of strides and stops, velocity, fastest non-stop velocity, total time stopped and body mass were recorded for each turtle. We did not observe acclimation or training effects and neither time of year nor prolonged captivity affected locomotor performance. Stride length increased with body mass. The mean number of strides, and the mean total time stopped in the first meter, decreased as temperature increased. Both the mean velocity and the mean fastest non-stop velocity increased with increasing temperature. Body temperatures of turtles in the field, monitored via radiotelemetry, ranged from −1.4–34.9 C (rarely exceeding 31.9 C) and clustered about the simultaneous ambient temperatures. Both laboratory and field data suggest that locomotion is strongly temperature dependent. Voluntary locomotion in the laboratory appeared to be maximal at body temperatures between 24 and 32 C; however, the existence of an 'optimal' temperature remains uncertain. Although the voluntary speeds of turtles are much slower than the sprint velocities of squamates, they are comparable to the speeds of urodele amphibians and to voluntary speeds of lizards and snakes.

ECTOTHERMIC animals must contend with low and variable body temperatures which strongly affect both physiological processes (Crawshaw, 1979) and behavioral performance (Huey and Stevenson, 1979; Bennett, 1980). Many reptiles, however, behaviorally thermoregulate to achieve some degree of homeothermy (Cowles and Bogert, 1944). Eastern box turtles, *Terrapene c. carolina*, reportedly thermoregulate by varying their activity period and selecting favorable microenvironments to maintain a body temperature between 29 and 38 C (Ernst and Barbour, 1972). Such high body temperatures, however, are attained only in the summer and are not characteristic of all populations of box turtles. Russo (1972) found the mean body temperature of a New Jersey population to be 26–28 C in the summer. Spring, fall, and winter mean body temperatures of these turtles were 9.0, 17.1, and 1.5 C, respectively. Ernst and Barbour (1972) defined the box turtle's natural condition as an ambient temperature range between 10 and 29 C. According to Hutchison (1979) the mean preferred body temperature of *T. c. carolina* is 25.6 C. This was derived, however, from a single observation by Brattstrom (1965). Erskine and Hutchison (1981) reported that box turtles, acclimated to 25 C and tested within a laboratory thermal gradient, select mean temperatures ranging from 21.2–24.8 C with no significant diel variation.

Temperature strongly influences the locomotor performance of animals. The effect of temperature on locomotion has been widely studied in lizards (Bennett, 1980; Hertz et al., 1983), and many species exhibit an 'optimal' temperature for locomotor performance. Comparable data for chelonians are lacking, although some investigators have examined swimming in sea turtles or have determined the speed of hatchling turtles on land (Dial, 1987; Miller et al., 1987). Most of the work conducted on turtles involved forced locomotion induced by nociceptive (i.e., injurious or potentially injurious) stimuli, and previous studies have not specifically examined the effects of temperature on the terrestrial locomotion of chelonians.

This study combined field and laboratory investigations to elucidate the effects of temperature on box turtle locomotion. We expected to find clear evidence of behavioral thermoregulation in the field and we hypothesized that turtle locomotion should be strongly temperature dependent with maximal performance near the preferred temperature.

METHODS AND MATERIALS

Locomotor studies.—Twenty-four turtles were captured in the area surrounding Oxford, Ohio between May and Aug. 1986. They were transported to the laboratory where they were maintained in a stock tank (1.14 m × .58 m) con-

taining 5 cm of commercial rodent bedding. We kept the turtles under standard conditions of temperature and light (24 h/d at 22 C, 12L: 12D), and changed their food (a variety of fruits, vegetables, earthworms and crickets) and water daily.

We moved the turtles, 24 h prior to the initiation of testing, to a second stock tank located within an environmental chamber maintained at a specified temperature (± 0.5 C). They remained in this chamber throughout the subsequent 5 d testing sequence. We conducted the definitive tests from 21 Jan.–17 April 1987. The turtles were tested, in order, at temperatures of 14.0, 9.7, 28.4, 19.0, 31.9, and 24.0 C. We conducted two additional experiments to test the null hypotheses that conditioning and duration of captivity do not affect locomotor performance: from 28 April–2 May 1987, 11 of the original 24 turtles were retested at 14.0 C and on 17 May 1987, 10 additional turtles were collected in the Oxford area and then tested at 14.0 C and 28.4 C. For all testing, we placed each turtle individually on the racetrack, within the environmental chamber, once per day on each of five consecutive days. The turtle walked down the track independent of external stimuli. If the turtle did not move forward after 1 h had passed or if the turtle turned around before completing the run, we removed it from the track. We weighed each turtle immediately after testing, if any locomotion data were collected.

We designed a wooden 3.66 m U-shaped racetrack (20.32 cm wide × 15.24 cm high) to measure the speed of the turtles. Foam plastic sheeting cut to size and placed in the bottom of the track provided adequate traction. Each turtle was required to walk the distance of the track. They then continued to walk off the track and entered a cardboard box (51.5 cm × 41 cm) positioned at the end of the track. Once a turtle had entered the box, it was prevented from reentering the track by a hinged plexiglass gate.

Infrared and visible light systems, connected to digital stopwatches, were used together to measure the speed of each turtle. We positioned detectors at 0.5, 1.0, 1.5, 2.0, and 3.5 m from the beginning of the track. Each turtle had a lightweight flag (4.7 g) made of styrofoam board taped to its shell in order to trip the detectors which were placed 9.5 cm (infrared) and 14 cm (visible light) above the bottom board.

We used a remote VHS observation system to monitor turtle locomotion. Locomotor patterns were observed at all temperatures and various gait parameters (e.g., strides/m and number of stops) were measured. Wire switches, positioned at 0.5, 1.0, 1.5, and 3.5 m from the beginning of the track, turned on low wattage bulbs positioned on a light board that was remote from the visual field of the turtle. This light system aided in accurately counting the number of steps taken by a turtle per meter on the track. We counted the number of strides by observing the back left leg of each turtle.

Testing was done on five consecutive days to investigate the effects of thermal acclimation on voluntary locomotion. We noted the effect of acclimation time on: 1) the total time stopped in the first meter; 2) the total time taken to walk the first meter; 3) the mean number of strides; 4) stops in the first meter; 5) change in weight; and 6) the fastest non-stop speed of the turtle at the differing temperatures. We ran an ANOVA with factors turtle and day on the data from the 5 d and compared the data statistically using a least significant difference multiple comparison. Because of missing cells, this was performed by means of a least squares means test on statistical analysis system (SAS) (SAS, 1982) and all means reported below represent least squares means. We also used this test to compare the data on each locomotor variable collected at the six different temperatures. Correlations were computed when significance was evident in order to elucidate any existing trends.

Field study.—We conducted this study within the Hamilton County Park District at Miami Whitewater Forest (the Braille Trail Area) from May 1986–April 1988. The study site of approx. 19.4 ha, containing both grassland and woodland habitats, was surveyed and mapped.

To monitor the body temperatures (Tb's) of turtles in the field, we captured six *T. c. carolina* and took them to the laboratory. We had previously calibrated temperature sensitive radiotransmitters (Model L Mini-Mitter) in a series of water baths of known constant temperature. While each turtle was under cold anesthesia, we drilled a hole of approx. 3 mm in diameter through the seventh lateral scute from the front on the right side. We inserted the transmitter probe approx. 1.5 cm into the peritoneal cavity through this hole in the carapace. The turtles were restrained with strapping tape, and transmitters were secured with fiberglass on their

TABLE 1. THE LOCOMOTOR VARIABLES OF ELEVEN CAPTIVE *Terrapene c. carolina* TESTED IN JANUARY 1987 AND RETESTED IN MAY 1987 AT 14.0 C. *P* values obtained from Wilcoxon matched-pairs signed-ranks test.

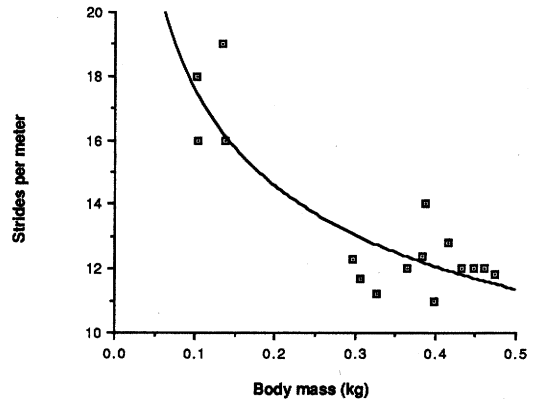| Variable		Mean ± 95% confidence interval
Body mass (g)	Jan	368.6 ± 92.1
	May	380.2 ± 91.9
Number of strides in 1st meter	Jan	13.1 ± 2.0*
	May	12.4 ± 1.6
Number of stops in 1st meter	Jan	1.0 ± 0.6
	May	1.4 ± 0.42
Mean fastest non-stop velocity (m/sec)	Jan	0.017 ± 0.006
	May	0.016 ± 0.002

* *P* < 0.05.

Fig. 1. The effects of body mass (X) on the mean number of strides within the first meter (Y) at a testing temperature of 28.4 C ($Y = 9.4X^{-0.27}$; $P < 0.001$; the correlation coefficient (r) = 0.88; the sample size [n] = 16). Similar relationships were observed at 9.7 C ($Y = 11.0X^{-0.25}$; $P = 0.008$; r = 0.75; n = 11) and 19.0 C ($Y = 9.4X^{-0.29}$; $P < 0.001$; r = 0.73; n = 20).

posterior carapace. We then released the turtles in the woods at the location of capture within 24 h.

An antenna and receiver were used to locate the turtles, at regular (i.e., every 7–14 d) intervals. When each turtle was found, we recorded the number of transmitter clicks per 100 sec and later converted these counts to Tb's based on the calibration curves for the individual transmitters. We also recorded ambient temperatures (Ta's) by measuring the shaded air temperature on the ground beside each turtle, or the adjacent soil temperature for animals buried within a hibernaculum. In addition, we noted the location of each turtle, the time of day, and a description of the microhabitat.

RESULTS

Least significant difference multiple comparisons revealed little evidence of a training or of an acclimation effect, because for captive turtles, 33 of the 36 comparisons (i.e., the six variables listed above times the six test temperatures) did not vary significantly ($P > 0.05$) over the 5 d period. For the newly captured turtles tested at 14.0 and 28.4 C, nine of the 12 tests (i.e., six variables times two temperatures) showed no significant difference ($P > 0.05$) during the 5 d period. For all turtles tested, when the variables did show a significant day effect, there was no clear trend associated with day of testing. Accordingly, we pooled the data over the 5 d testing period.

We found little indication of a seasonal effect because three of the four locomotor variables of turtles retested at 14.0 C in May did not differ

significantly from comparable values obtained earlier in Jan. (Table 1). The only significant difference was in the number of strides taken in the first meter. Although significant, the percent difference between the number of strides taken in Jan. and May was small (5.3%) and may have been partly due to the 3.1% increase in mean body mass over the time period, even though this mass change was not itself statistically significant. Finally, the locomotor variables of turtles held for up to 9 mo in captivity did not differ significantly from those of other newly captured animals tested at 14.0 and 28.4 C.

At 9.7, 19.0, and 28.4 C, the number of strides taken in the first meter was significantly correlated ($P < 0.05$) with body mass (Fig. 1). No significant correlation existed between body mass and the other locomotor variables. All locomotor variables of captive turtles differed significantly ($P < 0.05$) over the six testing temperatures, though neither mean mass nor mean number of stops in the first meter was significantly correlated ($P > 0.05$) with increasing temperature. The mean number of strides taken in the first meter (Fig. 2A) and mean total time stopped in the first meter (Fig. 2B) both decreased significantly with increasing temperature, whereas the mean fastest non-stop velocity (Fig. 2C) and mean velocity computed from the total time taken to walk one meter (Fig. 2D) significantly increased.
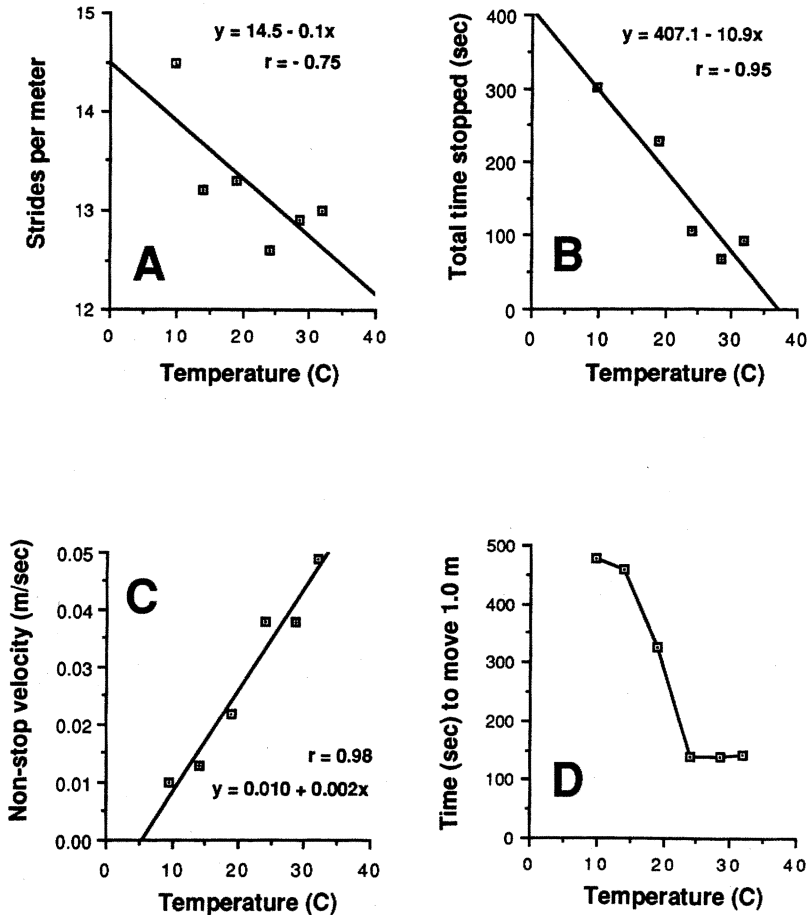
Fig. 2. A) The effects of temperature (x) on the mean number of strides within the first meter (y). $P = 0.018$. Each point represents the mean for 11 (9.7 C) to 20 (19.0 C) turtles. B) The effects of temperature (x) on the mean total time stopped within the first meter (y). $P = 0.003$. Each point represents the mean for 11 (9.7 C) to 20 (19.0 C) turtles. C) The effects of temperature (x) on the mean fastest non-stop velocity within the first meter (y). $P < 0.001$. Each point represents the mean for 5 (9.7 C) to 17 (28.4 C) turtles. D) The effects of temperature (x) on the mean total time to travel the first meter (y). $P = 0.004$. Each point represents the mean for 11 (9.7 C) to 20 (19.0 C) turtles.

The body temperatures of the field Eastern box turtles ranged from $-1.4–34.9$ C and were clustered about the corresponding ambient temperatures (Fig. 3). The relationship was linear ($r = 0.97$) and the points are clustered about the isotherm.

DISCUSSION

Because our box turtles were tested repetitively and the acclimation time-course was unknown, we examined the data for training or acclimation effects. Miller et al. (1987) reported

that hatchling snapping turtles, *Chelydra serpentina*, are faster during a second performance test. In contrast, we found little evidence of a consistent day of testing effect for either long-term captive or newly captured turtles. This difference may be partly due to the method of testing. The tails of the Miller et al. (1987) turtles were pinched to force locomotion whereas our turtles moved voluntarily. The apparent lack of an acclimation effect on locomotor performance is consistent with the results of some (Putnam and Bennett, 1981; Else and Bennett, 1987) but not all (Miller and Zoghby, 1986;

Londos and Brooks, 1988) studies. Prolonged captivity also appeared to have little or no effect on the locomotor performance of our box turtles.

We maintained the captive turtles in the laboratory from Aug.–May. They were tested at differing temperatures over this time period. The body masses of the turtles ranged from 94.8–498.0 g and also gradually changed over this time period. Although body mass varied with test temperature, the only mass significantly different ($P < 0.05$) from the mean mass at 9.7 C was that at 24.0 C. This probably was affected by the order in which the temperatures were tested. Overall, the turtles gained mass over the 6 mo testing period. The turtles, however, ate very little while being tested at 9.7 C. The mean masses were the lowest at the testing temperature (28.4 C) that followed 9.7 C, but the turtles did gain mass over this 5 d testing period. The mass of the turtles was most likely not directly dependent on temperature to any large degree but rather gradually increased over time with a transient decrease induced by inanition during exposure to 9.7 C.

We evaluated locomotor performance in relation to the body masses of the captive turtles at test temperatures of 9.7, 19.0, and 28.4 C. The number of strides taken in the first meter was the only locomotor variable which was significantly correlated with body mass. A similar relationship was observed at all three temperatures (Fig. 1). The scaling exponents derived from log-log plots of stride length vs body weight ranged from 0.23–0.29. For mammals, the scaling exponent of stride length with body mass is 0.38 (Heglund et al., 1974). For the lizard, *Amphibolurus nuchalis*, the scaling exponent of stride length for hind limb span is 0.3 (Garland, 1984), which is closer to the values of the present study.

Body mass of our box turtles did not significantly affect the total time stopped or the number of stops. The lack of correlation of speed (mean fastest non-stop velocity) with body mass disagrees with some lizard studies. Maximum speeds of the agamid *A. nuchalis* (Garland, 1985) and of lacertids (Avery et al., 1987b) increase with body mass. The burst speed of the iguanid, *Ctenosaura similis*, is, however, mass independent (Garland, 1984).

Our turtles took significantly more strides per meter (i.e., had smaller stride length) at the 9.7 C testing temperature than at the other temperatures (Fig. 2A). This could be due to the fact that the turtles stopped frequently at this
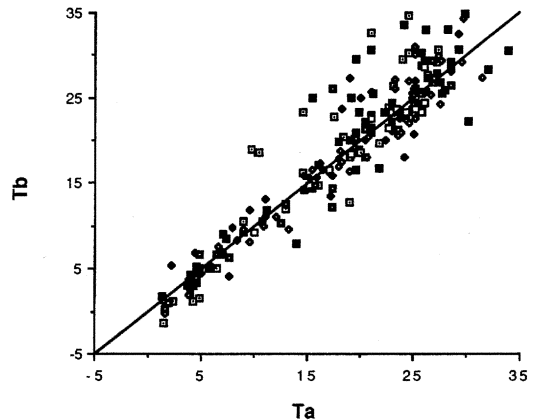

Fig. 3. The relationship between the body temperatures of five field Eastern box turtles and the corresponding ambient temperatures. Ambient temperature values represent shaded air temperatures for non-hibernating turtles or soil temperatures for hibernating turtles. The line depicts the isotherm or line of equality between body temperature and ambient temperature. The correlation coefficient (r) is 0.97.

temperature. They took small steps between stops, and they often moved only one leg before again stopping. Marsh and Bennett (1986) obtained quite similar results for the iguanid lizard, *Sceloporus occidentalis*.

The total time the turtles stopped within the first meter also was dependent on temperature (Fig. 2B). Disregarding the highest temperature, as the temperature decreased, the total time the turtles stopped increased. At 31.9 C the total time the turtles stopped was greater than at 28.4 C. This suggests that the 'optimal' temperature for voluntary locomotion may be below 32 C. However, the mean fastest nonstop velocity of the box turtles increased with increasing temperature (Fig. 2C) and reached a maximum value of 0.049 m/sec at 31.9 C.

The thermal dependence of box turtle velocity between 10 and 20 C was quite high (Fig. 2C). The thermal coefficient (Q_{10}) of mean fastest non-stop velocity in captive turtles equals 3.3. The lizards *Gerrhonotus multicarinatus* and July tested *S. occidentalis* have comparable Q_{10} values of 3.6 and 5.5 respectively between 10 and 20 C (Bennett, 1980). The thermal dependence of amphibian locomotion over a comparable temperature range appears to be lower. Q_{10} values for *Bufo marinus* (Miller and Zoghby, 1986), *Ambystoma tigrinium* (Else and Bennett,
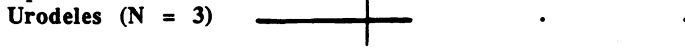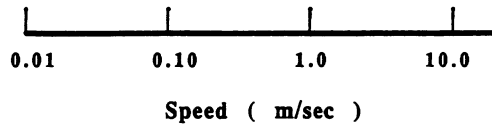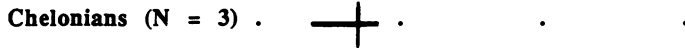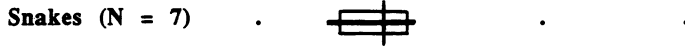
Fig. 4.   A comparison of forced and voluntary locomotion in amphibians and reptiles. A log scale is used to better depict the data span. Sample size (n) is indicated for each group. The means are indicated by the vertical lines and the ranges by the horizontal lines. The rectangles depict the 95% confidence limits about the means for those groups having a relatively large (≥7) sample size. See Table 2 (Appendix) for the data sources.

1987), *B. boreas* and *Rana pipiens* (Putnam and Bennett, 1981) approximate 1.9, 1.4, 2.3, and 1.8, respectively.

The relationship between speed and temperature is apparently linear for the Eastern box turtle (Fig. 2C). This is similar to the responses of the anurans, *B. boreas* and *R. pipiens* (Putnam and Bennett, 1981), and of garter snakes (Heckrotte, 1967; Stevenson et al., 1985), but contrasts with the locomotor responses of lizards, which typically exhibit a clear optimum temperature range. It is possible that tests at higher temperatures would have revealed a decrease in velocity and, indeed, the data on mean velocity, which incorporates total time stopped (Fig. 2D) suggest an optimum temperature be-

tween 24.0 and 31.9 C. The motivational component of voluntary locomotion is considerably greater for total distance moved per unit time than for maximal non-stop velocity. The absence of a clear optimum temperature range for maximum voluntary speed (Fig. 2C) makes it difficult to neatly categorize box turtles as either thermal specialists or generalists. However, their voluntary locomotor activity over a broad range of body temperatures, coupled with field observations on turtle movements, argues for classification as generalists.

The field data (Fig. 3) reveal that box turtles in our study population rarely attained body temperatures in excess of 31.9 C (the highest temperature tested in the laboratory). On many

occasions, the turtles could have achieved higher temperatures, yet failed to do so. Although we occasionally observed turtles basking in the field, we saw little evidence of well-developed behavioral thermoregulation comparable to that observed in many lizards (Cowles and Bogert, 1944). The body temperatures of our turtles varied seasonally and were generally similar to those reported by Russo (1972) but were markedly lower than the values suggested by Ernst and Barbour (1972) for this species.

Our field observations generally are consistent with our laboratory findings. A comparison of sequential sightings revealed that box turtles rarely moved at body temperatures averaging 10 C or less. Locomotor behavior at higher temperatures was frequent, but highly individualistic. Some turtles moved at high (>30 C) body temperatures, but most individuals remained inactive (half-buried within a deep form) on very hot days.

The maximum speed of 0.049 m/sec for *Terrapene carolina* is slower than the mean voluntary speed of 0.108 m/sec reported by Dial (1987) for hatchling sea turtles, *Caretta caretta*, moving in a frenzy from their nests to the sea at 30 C. The box turtle value is quite similar to the maximum forced running speeds of 0.04 m/sec at 23 C and 0.033 m/sec at 30 C respectively for hatchling *Chelydra serpentina* (Miller et al., 1987) and *Pseudemys scripta* (Dial, 1987). The maximum forced swimming velocity of *C. serpentina* is likewise similar at 0.04 m/sec; however, young *Chelonia mydas* can be forced to swim at 0.35 m/sec (Prange, 1976). Voluntary swimming in sea turtles is also faster, with reported maximum values of 0.30 (O'Hara, 1980) and 0.38 m/sec (Salmon and Wyneken, 1987)

for *Caretta caretta* hatchlings and values ranging from 0.44–2.0 m/sec for hatchling to adult *Chelonia mydas* (Carr et al., 1974; Frick, 1976; Ireland et al., 1978). Green (1984) reported long-distance swimming of adult *C. mydas* at minimum velocities of 0.06–0.15 m/sec.

The maximum velocities of running urodeles seem quite comparable to the voluntary and forced data for turtles, whereas the forced locomotion speeds of terrestrial anurans are somewhat greater (Fig. 4). Lizards, not surprisingly, run much faster than turtles, with sprint velocities ranging over about two orders of magnitude, from a chelonian-like 0.11 m/sec for a chameleon (Abu-Ghalyun et al., 1988) to 9.61 m/sec for an individual *Ctenosaura similis* (Garland, 1984). In spite of this large range, the variance for lizards is quite low, with 34 out of 37 observations (see Appendix) falling between 0.7 and 2.7 m/sec. The mean of 1.67 m/sec is 34 times the maximum voluntary velocity of box turtles. The mean sprint velocity for snakes is 13.5 times our turtle value. However, these squamate sprint velocities (Fig. 4) were recorded under stressed conditions whereas locomotion in the present study was voluntary and presumably non-stressed.

The few reports of voluntary locomotion in lizards and snakes (Fig. 4; Appendix) yield values not markedly different from those of box turtles and other chelonians but differing from the forced locomotion data by about one order of magnitude. Although voluntary locomotion is more difficult to monitor in the laboratory than is forced locomotion, such data provide a more realistic reflection of routine locomotor performance in the field.

APPENDIX

Terrestrial locomotion in amphibians and reptiles. The listed values are the mean maximum values reported under forced (spring) or voluntary conditions.

Species	Speed (m/sec)		Source
	Forced	Voluntary	
Amphibians			
Urodeles			
Family Ambystomatidae:			
Ambystoma tigrinum	0.14	—	Else and Bennett, 1987
Family Plethodontidae:			
Plethodon jordani	0.07	—	Full, 1986
Desmognathus ochrophaeus	0.01	—	Feder, 1986
Anurans			
Family Bufonidae:			
Bufo boreas	0.18	—	Putnam and Bennett, 1981
B. marinus	0.14	—	Miller and Zoghby, 1986
B. woodhousei	0.81	—	Londos and Brooks, 1988
Family Ranidae:			
Rana pipiens	0.38	—	Putnam and Bennett, 1981
Reptiles			
Lizards			
Family Agamidae:			
Stellio stellio	2.70	—	Hertz et al., 1983
Agama savignyi	2.70	—	Hertz et al., 1983
Amphibolurus nuchalis	2.46	—	Garland, 1985
Family Chamaeleonitidae			
Chamaeleo senegalensis	0.11	—	Abu-Ghalyun et al., 1988
Family Iguanidae			
Sceloporus undulatus	1.73	—	Crowley, 1985
S. occidentalis	2.03	—	Bennett, 1980
Dipsosaurus dorsalis	2.16	—	Bennett, 1980
Uma inornata	2.63	—	Bennett, 1980
Amblyrhynchus cristatus	2.50	0.28	Gleeson, 1979
Family Gekkonidae			
Phyllodactylus marmoratus	1.61	—	Daniels, 1983
Family Teiidae			
Cnemidophorus sexlineatus	1.91	—	Ballinger et al., 1979
C. murinus	2.45	—	Bennett, 1980
C. tigris	—	0.05	Anderson and Karasov, 1981
Ameiva festiva	2.20	0.04	Van Berkum et al., 1986
Family Lacertidae			
Lacerta vivipara	0.55	0.17	Avery et al., 1987b
L. viridis	1.66	0.17	Avery et al., 1987a
L. trilineata	2.39	0.36	Avery et al., 1987a
Podarcis muralis	1.39	0.21	Avery et al., 1987a
P. pityusensis	1.59	0.24	Avery et al., 1987a
Eremias lineoocellata	2.63*	0.13	Huey and Pianka, 1981
E. lugubris	1.58*	0.16	Huey and Pianka, 1981
E. namaquensis	2.68*	0.14	Huey and Pianka, 1981
Nucras tessellata	2.05*	0.20	Huey and Pianka, 1981
Meroles suborbitalis	—	0.13	Huey and Pianka, 1981
Ichnotropis squamulosa	—	0.11	Huey and Pianka, 1981

APPENDIX. CONTINUED.

Species	Speed (m/sec)		Source
	Forced	Voluntary	
Family Scincidae			
Eumeces obsoletus	1.57	—	Bennett, 1980
Trachydosaurus rugosus	0.75	—	John-Alder et al., 1986
Tiliqua scincoides	1.07	—	John-Alder et al., 1986
Egernia cunninghami	2.69	—	John-Alder et al., 1986
E. whitii	1.10	—	Huey and Bennett, 1987
Ctenotus regius	1.01	—	Huey and Bennett, 1987
C. taeniolatus	1.24	—	Huey and Bennett, 1987
C. uber	1.81	—	Huey and Bennett, 1987
Eremiascincus fasciolatus	0.83	—	Huey and Bennett, 1987
Hemiergis decresiensis	0.70	—	Huey and Bennett, 1987
H. peronii	0.52	—	Huey and Bennett, 1987
Sphenomorphus kosciuskoi	1.02	—	Huey and Bennett, 1987
S. quoyi	1.52	—	Huey and Bennett, 1987
S. tympanum	1.22	—	Huey and Bennett, 1987
Family Anguidae			
Gerrhonotus multicarinatus	1.12	—	Bennett, 1980
Snakes			
Family Boidae			
Lichanura roseofusca	0.10	0.04	Mosauer, 1935
Family Colubridae			
Thamnophis sirtalis	0.37	0.04	Heckrotte, 1967
T. elegans	0.82	—	Stevenson et al., 1985
T. marcianus	0.65	—	Seigel et al., 1987
Coluber flagellus	1.61	0.13	Mosauer, 1935
Salvadora hexalepis	0.64	0.10	Mosauer, 1935
Pituophis catenifer	0.53	0.06	Mosauer, 1935
Lampropeltis multicinta	0.32	0.08	Mosauer, 1935
Family Viperidae			
Crotalus cerastes	0.91	0.14	Mosauer, 1935
Chelonians			
Family Chelonidae			
Caretta caretta**	—	0.11	Dial, 1987
Family Chelydridae			
Chelydra serpentina**	0.04	—	Miller et al., 1987
Family Emydidae			
Pseudemys scripta**	—	0.03	Dial, 1987
Terrapene carolina	—	0.05	Present Study

* Data from Huey et al., 1984.
** Hatchlings.

LITERATURE CITED

ABU-GHALYUN, Y., L. GREENWALD, T. E. HETHERING-TON AND A. S. GAUNT. 1988. The physiological

basis of slow locomotion in chamaeleons. J. Exp. Zool. 245:225–231.

ANDERSON, R. A., AND W. H. KARASOV. 1981. Contrasts in energy intake and expenditure in sit-and-wait and idly foraging lizards. Oecologia 49:67–72.

AVERY, R. A., C. F. MUELLER, S. M. JONES, J. A. SMITH AND D. J. BOND. 1987a. Speeds and movement patterns of European lacertid lizards: a comparative study. J. Herpetol. 21:324–329.

———, ———, J. A. SMITH AND D. J. BOND. 1987b. The movement patterns of lacertid lizards: speed, gait and pauses in Lacerta vivipara. J. Zool. (Lond.) 211:47–63.

BALLINGER, R. E., J. W. NIETFELDT AND J. J. KRUPA. 1979. An experimental analysis of the role of the tail in attaining high running speed in Cnemidophorus sexlineatus (Reptilia: Squamata: Lacertilia). Herpetologica 35:114–116.

BENNETT, A. F. 1980. The thermal dependence of lizard behavior. Anim. Behav. 28:752–762.

BRATTSTROM, B. H. 1965. Body temperatures of reptiles. Amer. Midl. Nat. 73:376–422.

CARR, A., P. ROSS AND S. CARR. 1974. Internesting behavior of the green turtle, Chelonia mydas, at a mid-ocean island breeding ground. Copeia 3:703–706.

COWLES, R. B., AND C. M. BOGERT. 1944. A preliminary study of the thermal requirements of desert reptiles. Bull. Amer. Mus. Nat. Hist. 83:261–296.

CRAWSHAW, L. I. 1979. Responses to rapid temperature change in vertebrate ectotherms. Amer. Zool. 19:225–237.

CROWLEY, S. R. 1985. Thermal sensitivity of sprint running in the lizard Sceloporus undulatus: support for a conservative view of thermal physiology. Oecologia 66:219–225.

DANIELS, C. B. 1983. Running: an escape strategy enhanced by autotomy. Herpetologica 39:162–165.

DIAL, B. E. 1987. Energetics and performance during nest emergence and the hatchling frenzy in loggerhead sea turtles (Caretta caretta). Herpetologica 43(3):307–315.

ELSE, P. L., AND A. F. BENNETT. 1987. The thermal dependence of locomotor performance and muscle contractile function in the salamander Ambystoma tigrinum nebulosum. J. Exp. Biol. 128:219–233.

ERNST, C. H., AND R. W. BARBOUR. 1972. Turtles of the United States. The University Press of Kentucky, Lexington, Kentucky.

ERSKINE, D. J., AND V. H. HUTCHISON. 1981. Melatonin and behavioral thermoregulation in the turtle, Terrapene carolina triunguis. Physiol. & Behav. 26:991–994.

FEDER, M. E. 1986. Effect of thermal acclimation on locomotor energetics and locomotor performance in a lungless salamander, Desmognathus ochrophaeus. J. Exp. Biol. 121:271–283.

FRICK, J. 1976. Orientation and behaviour of hatchling green turtles (Chelonia mydas) in the sea. Anim. Behav. 24:849–857.

FULL, R. J. 1986. Locomotion without lungs: energetics and performance of a lungless salamander. Amer. J. Physiol. 251:R775–R780.

GARLAND, T., JR. 1984. Physiological correlates of locomotory performance in a lizard: an allometric approach. Amer. J. Physiol. 247:R806–R815.

———. 1985. Ontogenetic and individual variation in size, shape, and speed in the Australian agamid lizard Amphibolurus nuchalis. J. Zool. (Lond.) 207:425–439.

GARLAND, T., AND S. ARNOLD. 1983. Effects of a full stomach on locomotory performance of juvenile garter snakes (Thamnophis elegans). Copeia 1983:1092–1096.

GLEESON, T. T. 1979. Foraging and transport costs in the Galapagos marine iguana, Amblyrhynchus cristatus. Physiol. Zool. 52:549–557.

GREEN, D. 1984. Long-distance movements of Galapagos green turtles. J. Herpetol. 18:121–130.

HECKROTTE, C. 1967. Relations of body temperature, size, and crawling speed of the common garter snake, Thamnophis s. sirtalis. Copeia 1967:759–763.

HEGLUND, N. C., C. R. TAYLOR AND T. A. MCMAHON. 1974. Scaling stride frequency and gait to animal size: mice to horses. Science 186:1112–1113.

HERTZ, P. E., R. B. HUEY AND E. NEVO. 1983. Homage to Santa Anita: thermal sensitivity of sprint speed in agamid lizards. Evolution 37(5):1075–1084.

HUEY, R., AND A. BENNETT. 1987. Phylogenetic studies of coadaptation: preferred temperatures versus optimal performance temperatures of lizards. Ibid. 41:1098–1115.

HUEY, R. B., A. F. BENNETT, H. JOHN-ALDER AND K. A. NAGY. 1984. Locomotor capacity and foraging behaviour of Kalahari lacertid lizards. Anim. Behav. 32:41–50.

———, AND E. R. PIANKA. 1981. Ecological consequences of foraging mode. Ecology 62(4):991–999.

———, AND R. D. STEVENSON. 1979. Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. Amer. Zool. 19:357–366.

HUTCHISON, V. H. 1979. Thermoregulation, p. 207–228. In: Turtles perspectives and research. M. Harless and H. Morlock (ed.). Wiley Interscience, New York, New York.

IRELAND, L. C., J. A. FRICK AND D. B. WINGATE. 1978. Nighttime orientation of hatchling green turtles (Chelonia mydas) in open ocean, p. 420–429. In: Animal migration, navigation, and homing. K. Schmidt-Koenig and W. T. Keeton (eds.). Springer-Verlag, New York, New York.

JOHN-ALDER, H. B., T. GARLAND, JR. AND A. F. BENNETT. 1986. Locomotory capacities, oxygen consumption, and the cost of locomotion of the shingle-back lizard (Trachydosaurus rugosus). Physiol. Zool. 59:523–531.

LONDOS, P. L., AND R. J. BROOKS. 1988. Effect of temperature acclimation on locomotory performance curves in the toad, Bufo woodhousii woodhousii. Copeia 1988:26–32.

MARSH, R. L., AND A. F. BENNETT. 1986. Thermal dependence of sprint performance of the lizard *Sceloporus occidentalis*. J. Exp. Biol. 126:79–87.

MILLER, K., G. C. PACKARD AND M. J. PACKARD. 1987. Hydric conditions during incubation influence locomotor performance of hatchling snapping turtles. *Ibid.* 127:401–412.

———, AND G. M. ZOGHBY. 1986. Thermal acclimation of locomotor performance in anuran amphibians. Can. J. Zool. 64:1956–1960.

MOSAUER, W. 1935. How fast can snakes travel? Copeia 1935:6–9.

O'HARA, J. 1980. Thermal influences on the swimming speed of loggerhead turtle hatchlings. Copeia 1980:773–780.

PRANGE, H. 1976. Energetics of swimming in a sea turtle. J. Exp. Biol. 64:1–12.

PUTNAM, R. W., AND A. F. BENNETT. 1981. Thermal dependence of behavioural performance of anuran amphibians. Anim. Behav. 29:502–509.

RUSSO, P. M. 1972. Behavioral thermoregulation and energy budget of the Eastern box turtle, *Terrapene carolina carolina* (Linne). Unpubl. Ph.D. dissert., Rutgers University, New Brunswick, New Jersey.

SALMON, M., AND J. WYNEKEN. 1987. Orientation and swimming behavior of hatchling loggerhead turtles *Caretta caretta* L. during their offshore migration. J. Exp. Mar. Biol. Ecol. 109:137–153.

SAS INSTITUTE, INC. 1982. *SAS User's Guide: Statistics*, 1982 Edition. SAS Institute, Inc., Cary, North Carolina.

SEIGEL, R., M. HUGGINS AND N. FORD. 1987. Reduction in locomotor ability as a cost of reproduction in gravid snakes. Oecologia 73:481–485.

STEVENSON, R., C. PETERSON AND J. TSUJI. 1985. The thermal dependence of locomotion, tongue flicking, digestion, and oxygen consumption in the wandering garter snake. Physiol. Zool. 58:46–57.

VAN BERKUM, F., R. HUEY AND B. ADAMS. 1986. Physiological consequences of thermoregulation in a tropical lizard (*Amieva festiva*). *Ibid.* 59:464–472.

(NAA, DLC) DEPARTMENT OF ZOOLOGY AND (JS) DEPARTMENT OF MATHEMATICS AND STATISTICS, MIAMI UNIVERSITY, OXFORD, OHIO 45056. Accepted 1 Nov. 1988.

Are All Females Welcome? Agonistic Behavior of Male Red-backed Salamanders

JANET S. THOMAS, ROBERT G. JAEGER AND EVA A. HORNE

Males of the red-backed salamander, *Plethodon cinereus,* court during the autumn and spring of every year while females apparently court biennially. Our laboratory experiment examined the agonistic behavior of territorial males, during the courtship season, toward four intruder types: gravid females, nongravid females, males, or control surrogates. Resident males did not exhibit a significant difference in threat display toward gravid females, nongravid females or male intruders, but all of these were threatened significantly more than the control. Male intruders were bitten more frequently than were female intruders. Residents were significantly more aggressive toward male intruders after exposure to gravid female intruders but did not alter their response to nongravid female intruders. These results indicate that territorial males do not differentially defend their territories against gravid vs nongravid females. Because nongravid and gravid females also exhibit territorial behavior, we hypothesize that territorial males allow nongravid females access to their territories because these same females may be in close proximity the following year when they will be potential mates.

W ELLS (1977) postulated that some spacing mechanism should evolve among males as a result of male-male competition for mates in species exhibiting prolonged breeding.

The red-backed salamander, *Plethodon cinereus* (Plethodontidae), has prolonged breeding in that courtship occurs over several months (Sayler, 1966) and individuals are territorial (Jaeger,