interactions (e.g., Gibbons and Lovich, 1990, and references therein). (3) High reproductive frequencies may impose stronger selection for early maturity in males (leading to slower growth and higher mortality in this sex, but see Lovich and Gibbons, 1990), because of the greater potential increase in the numbers of matings that can be obtained in a lifetime.

In summary, our results do not support Fitch's (1981) hypothesis that low reproductive frequencies impose selection for larger per-clutch fecundity and body size in female turtles, such that females have evolved larger body size relative to conspecific males in species with low reproductive frequency. However, the available data are relatively meager. When data on reproductive frequencies become available for a larger number of species, the analysis should be repeated using data from other turtle families and ultimately with a better resolved phylogeny.

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CORRELATIONAL TEST OF MATHIS' HYPOTHESIS THAT BIGGER SALAMANDERS HAVE BETTER TERRITORIES.—*Plethodon cinereus*, the red-backed salamander, is completely terrestrial, and individuals establish territories on the forest floor in eastern North America (Jaeger et al., 1982; Mathis, 1989, 1990). Although *P. cinereus* utilizes a broad diet of small invertebrate prey (Jaeger, 1972; Burton, 1976), food is periodically reduced in availability during dry periods between rainfalls (Fraser, 1976). This limits individual salamanders to foraging in patches of moisture under and around rocks and logs where they can avoid desiccation (Jaeger, 1980). Food is also a "limiting" resource (in terms of energy budgets) during drier, warmer periods when metabolic requirements are raised, and assimilation efficiencies are lowered (Jaeger, 1980). Jaeger (1980) also examined the stomach contents of

P. cinereus before, during, and after rainfalls. He inferred that prey became "limited" in availability during rainless periods because the salamanders were not able to forage outside their retreats in the dry leaf litter on the forest floor.

Both males and females of *P. cinereus* defend these retreats under rocks and logs as territories (Mathis, 1990) during courting and noncourting seasons (Jaeger, 1979; Mathis, 1989). Mathis (1990) demonstrated that cover object size may be one indicator of territorial quality. In a natural forest habitat in Virginia, she found a significant, positive correlation between the snout–vent length of salamanders and the sizes of the cover objects that they occupied; she concluded that intraspecific competition occurs for larger cover objects because such cover objects provide a greater buffer zone from desiccation than smaller cover objects. My study tested Mathis' (1990) hypothesis that bigger salamanders have better territories. I correlated quantities and profitability of prey available within territories of *P. cinereus* to body size and condition of the salamanders holding the territories.

I hypothesized that larger salamanders, based on snout–vent length (SVL) and mass, would be found in more profitable food territories (i.e., both in numbers of prey available and in prey type) than would smaller salamanders. To test this hypothesis, I assayed the invertebrates around the perimeter of cover objects used as territories by *P. cinereus* in their natural habitat.

Methods.—I conducted this research at Hawksbill Gap, Shenandoah National Park, Giles County, Virginia, in a mixed deciduous forest from 0700–1600 h each day during a four-day period from 15–18 July 1992. I performed the research on two 2500 m² sites nine days after 1.96 cm of rain fell (Climatological Data, 1992), because Jaeger (1980) found that no rain for at least three days significantly limited the foraging success of this species. Based on his results, I assumed that the salamanders in my study were limited to foraging under and around their cover objects after a nine-day rainless period and that, therefore, my research assessed food availability of individuals defending territories containing limited resources. These salamanders are presumed territorial residents based on reports of long-term site specificity of individuals under cover objects (Mathis, 1989; Gergits and Jaeger, 1990).

I searched for adult salamanders [males and females under rocks or logs > 50 cm² (*P. cinereus* was not found under smaller objects)] and located 41 individuals. At each of these sites, I placed four 7.6 × 12.7 cm cards made out of

bright yellow plastic sheets coated on both sides with a specially formulated sticky goo (Olson Products, model 5P343). These traps catch mobile invertebrates up to the size of a large cockroach, but salamanders do not stick to them. Each trap was protected from falling leaf litter by placing a 14.5-cm petri dish approximately 3 cm above the trap on sticks pushed into the ground. I placed one trap at the litter-soil interface at each of the four cardinal directions approximately equidistant around a rock or a log where a salamander was found. Any leaves removed from the ground were replaced on top of the petri dish sheltering the trap. I never used sites that had more than one salamander present. I set traps around 21 territories on the first day and collected them 24 h later. The following day, I set traps around 20 more salamander territories in an adjacent area of about the same size and collected them 24 h later. I placed each trap in a separately marked polyurethane bag and froze it until I could examine the trapped invertebrates.

I measured each salamander's SVL to the anterior of the cloaca, tail length (TL), mouth width, and mass and determined its sex. I used only salamanders of ≥ 34 mm SVL based on Sayler (1966), who found this to be the minimum size of male and female sexually mature adults. Cover object size was recorded as greatest width times greatest length. I recorded the number of invertebrates on each trap, identified them to taxonomic order (Borror et al., 1989), and measured the total length and width of each potential prey item using a dissection microscope fitted with an ocular micrometer. The shape of the invertebrates was assumed to be cylindrical (Fraser, 1976; Jaeger, 1980), and their volumes were calculated using the formula for a cylinder. I counted only those prey that were previously determined to be ingested by *P. cinereus* and that were within the size range utilized by *P. cinereus* (0.01–2.5 mm³) based on Jaeger's (1972, pers. comm.) studies at this same site. Prey items were pooled from all four traps within one territory. I attempted to estimate the profitability of a territory by ranking food resources from the lowest profitability (hard bodied prey) to the highest profitability (soft bodied). Soft bodied prey are, in general, more profitable food items than hard bodied prey because the former pass through the salamander's digestive tract faster and are digested more efficiently than are the latter (Jaeger, 1990; Gabor and Jaeger, 1995).

Soil temperatures and cover object volumes were measured at 24 different sites by R. G. Jaeger (unpubl. data) on 1 Aug. 1970 at my site
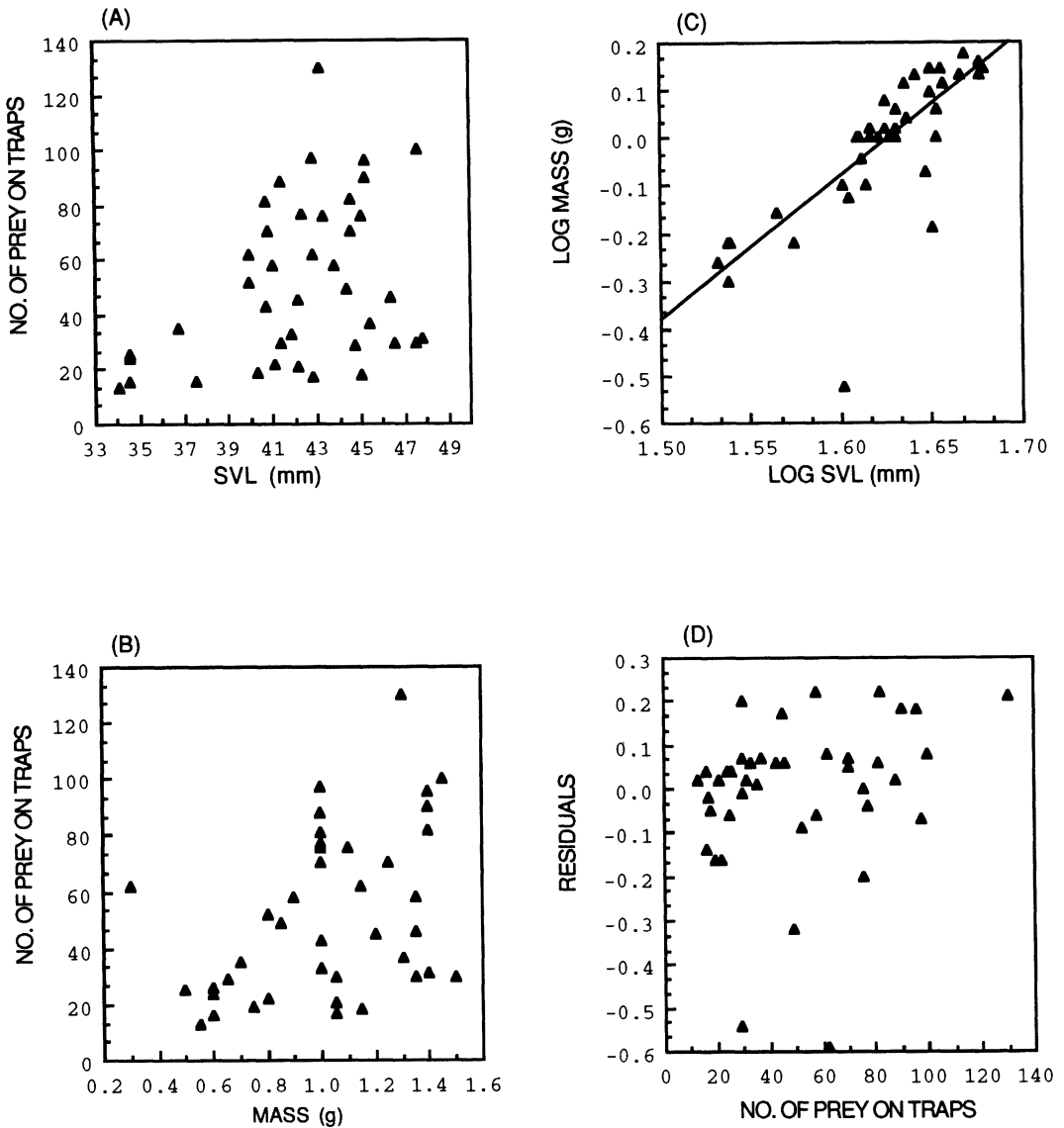
Fig. 1. The number of prey on traps in a territory as a function of (A) salamander size [(SVL) n = 41, r_s = 0.379, P < 0.02] and (B) mass for each salamander in a territory (n = 41, r_s = 0.451, P < 0.005). (C) The log of salamander mass as a function of the log of salamander SVL (n = 41, r_s = 0.853, P < 0.001) and (D) the condition of each salamander as represented by the residual of y (in Fig. 1C) as a function of the number of prey in each salamander's territory (n = 41, r_s = 0.345, P < 0.05). Each point represents one salamander.

in Shenandoah National Park. This is the same date, but different year, as Mathis used to measure the soil temperatures of her cover objects. Jaeger chose a random transect (10 × 100 m) out of numerous predetermined ones and sampled soil temperatures immediately as he raised the first 24 rocks and logs encountered away from the substrate.

The data were analyzed using two-tailed Spearman rank-order correlations with $\alpha = 0.05$ (Siegel and Castellan, 1988). I pooled my data

from the two sites because there was no rainfall on either testing date, the air temperature varied little (27–29 C) on the two testing days (Climatological Data, 1992), and the sites consisted of similar, adjacent habitats. I used the information from the correlation between log of salamander SVL and log of salamander mass to estimate the condition of each salamander using residuals by measuring the distance that each point fell above or below the regression line (Fig. 1C). Salamanders that fell on the line were
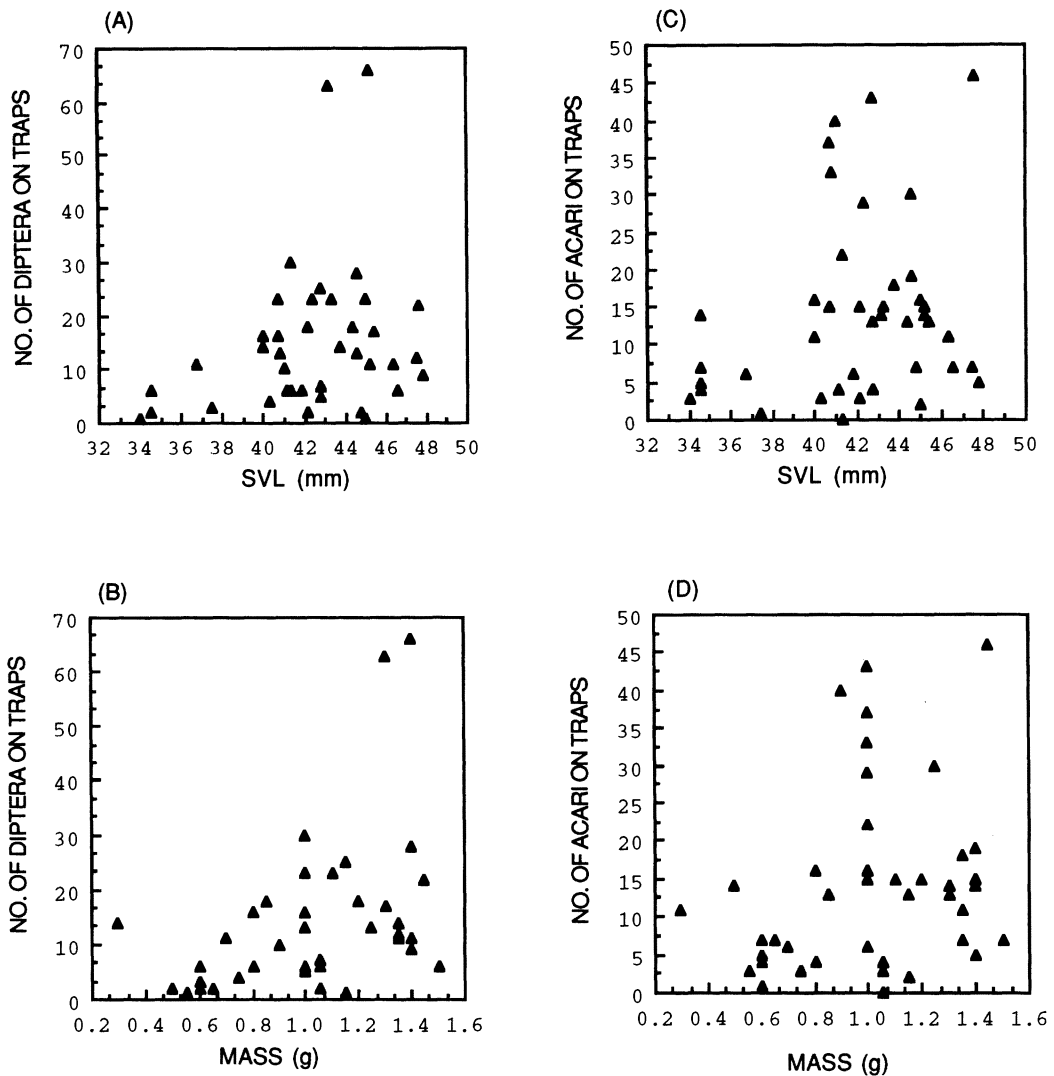
Fig. 2. The number of Diptera on traps in a salamander's territory as a function of the salamander's (A) SVL (n = 41, r_s = 0.326, $P < 0.05$) and (B) mass (n = 41, r_s = 0.437, $P < 0.005$). The number of Acari in a salamander's territory as a function of the salamander's (C) SVL (n = 41, r_s = 0.207, $P > 0.10$) and (D) mass (n = 41, r_s = 0.271, $P > 0.05$).

considered to be of average condition. Those above the line were in above average condition, and those below the line were in relatively poor condition. Note that the methods for testing my hypothesis could not differentiate between whether bigger salamanders are gaining access to better territories or whether salamanders in food-rich territories grow bigger.

Results.—The number of prey on the four traps in each salamander's territory was significantly, positively correlated with that salamander's SVL (Fig. 1A) and mass (Fig. 1B). I found no significant correlations between the total volume of

the prey per territory and salamander SVL (r_s = 0.204, n = 41, $P = 0.20$) or salamander mass (r_s = 0.30, n = 41, $P > 0.05$). There was a significant, positive correlation between log mass of the salamander as a function of log salamander SVL (Fig. 1C). I plotted the residuals from Figure 1C as a function of number of prey found in the territory of each individual and found a significant, positive correlation (Fig. 1D).

I found a significant positive correlation between the number of Diptera, a soft bodied prey, and salamander SVL (Fig. 2A) and salamander mass (Fig. 2B). On the other hand, there was no significant correlation between the number

of Acari, a hard bodied prey, and salamander SVL (Fig. 2C) or salamander mass (Fig. 2D). There was a significant positive correlation between the residuals and the number of Diptera in a territory (Fig. 3A) but not between the residuals and the number of Acari in a territory (Fig. 3B). There was no significant correlation between number of Diptera ($r_s = 0.085$, n = 41, $P > 0.50$) or number of Acari ($r_s = 0.041$, n = 41, $P > 0.50$) on the traps with cover object size. There also was no significant correlation between the size of a salamander's cover object with the salamander's SVL ($r_s = 0.219$, n = 41, $P > 0.10$) or the salamander's mass ($r_s = 0.15$, n = 41, $P > 0.20$). There was no significant correlation between the size of a cover object and the temperature of the soil under the cover object based on Jaeger's study ($r_s = -0.369$, n = 24, $P = 0.08$).

Discussion.—Although these data do not reflect an experimental design, they are based on correlations with a priori predictions and are the first to assess directly the availability of prey at individual feeding territories of *P. cinereus*. They also assess the relationship between prey availability and salamander body condition.

Red-backed salamanders are thought to benefit from territories due to preferential access to a critical resource leading to satisfaction of energy requirements and resulting in a potential increase in fitness (Jaeger et al., 1982). Mathis (1990) inferred that larger, territorial salamanders sequester prey from competitors, because territories are maintained during noncourtship summer months (Jaeger, 1979; Mathis, 1989). Thus, I predicted that larger salamanders should hold more profitable territories.

My data support Mathis' hypothesis that bigger red-backed salamanders have better territories. I found significant, positive correlations between the number of prey in the salamanders' territories and the salamanders' SVLs (Fig. 1A) and masses (Fig. 1B). Mathis (1990) further suggested (but did not test) that larger cover objects may allow salamanders access to a larger number of prey items. My data do not support this inference. There was no significant correlation between a salamander's cover object size and a salamander's SVL, and there was no significant correlation between the size of the cover object and the number of Diptera and Acari. Therefore, although bigger cover objects provide a better buffer zone between the salamander and the extreme environmental temperatures on the forest floor (Mathis, 1990), they do not always provide more or better prey.

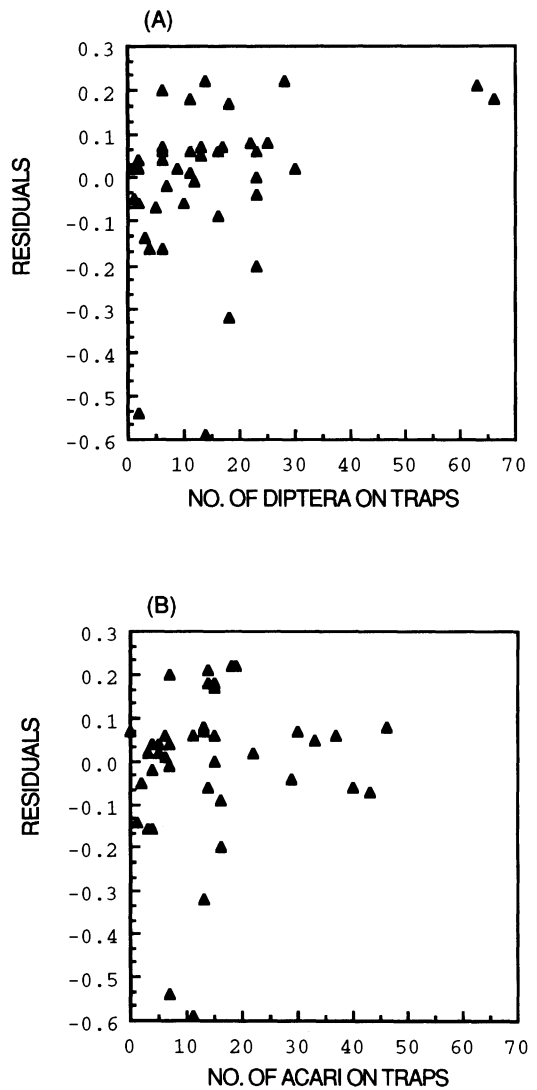Why was cover object size an important factor

Fig. 3. The condition of each salamander as represented by the residual of y (in Fig. 1C) as a function of the number of (A) Diptera (n = 41, $r_s = 0.367$, $P < 0.02$) and (B) Acari on traps in each salamander's territory (n = 41, $r_s = 0.226$, $P > 0.10$).

for the salamanders studied by Mathis but not for the salamanders in my study? The reason may lie in the difference in the forest at Mountain Lake Biological Station (M.L.B.S.) and at Hawksbill Gap. The forest at M.L.B.S. has a broken canopy, allowing sunlight to hit the ground in places, thus heating rocks. Consequently, at M.L.B.S., larger cover objects would be expected to be cooler than smaller cover objects, as Mathis found. At Hawksbill Gap, the canopy is closed, so little or no direct sunlight hits the forest floor. Thus, one might expect that large and small rocks would not differ in

temperature significantly. Mathis found that there was a significant difference between the soil temperature of small and large cover objects whereas R. G. Jaeger (unpubl. data) found no significant difference between the soil temperature of small and large cover objects. Therefore, these results suggest that, where sunlight heats cover objects on the forest floor, salamanders prefer larger objects (Mathis' results), whereas where direct sunlight does not heat cover objects on the forest floor, salamanders do not select cover objects based on their sizes but instead select cover objects based on the quality and quantity of food around them.

By analyzing the residual condition of each salamander as plotted against the number of prey in each territory (Fig. 1D), I infer that either bigger salamanders gain access to food-rich territories or salamanders that happen to be in food-rich territories grow bigger than those in poorer quality territories. Further, my data also suggest that salamander territories serve as feeding areas (Jaeger et al., 1982; Mathis, 1991), but further experiments are needed to test this hypothesis.

I found that the number of Diptera (a profitable food resource) in a salamander's territory was significantly, positively correlated with salamander SVL and mass, supporting the hypothesis that salamanders in food-rich territories grow bigger or that bigger salamanders occupy food-rich territories. The lack of significant correlations between the number of Acari and salamander SVL and mass within a territory provide further support for this hypothesis, because Acari are a more armored (chitinous) prey and thus less profitable to a salamander. In addition, the significant, positive correlation between the condition of each salamander and the number of Diptera in a territory, in contrast with the nonsignificant correlation between the condition of a salamander and the number of Acari in a territory (Fig. 3A–B), further supports the prediction that salamanders in poorer condition occupy less profitable territories. From this study in the natural forest habitat, I infer that larger individuals of P. cinereus occupy territories on the forest floor that contain more and better prey, as predicted by Jaeger (1980), Mathis (1990), and Gabor and Jaeger (1995).

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EFFECTS OF EXTRINSIC LOAD ON LOCOMOTION IN PAINTED TURTLES (*CHRYSEMYS PICTA*).—Numerous studies have examined the costs and effects of mass loading in a number of taxa. Studies with natural loads have been conducted on ants (Nielsen et al., 1982; Lighton et al., 1987; Bartholomew et al., 1988), crayfish (Grote, 1981), crabs (Herreid and Full, 1986), lizards (e.g., Shine; 1980; Bauwens and Thoen, 1981; Schwarzkopf and Shine, 1992), and snakes (Garland and Arnold, 1983; Ford and Shuttlesworth, 1985; Seigel et al., 1987). Several studies examined extrinsic loads on rats, dogs, horses, and humans (e.g., Soule et al., 1978; Taylor et al., 1980; Maloiy et al., 1986).

One of the most obvious forms of loading is a carapace or shell. The shell represents an additional mass carried usually for defense. Although there are numerous invertebrates with shells, among vertebrates only chelonians have shells. One question in regard to shelled animals is how does the shell affect their locomotor performance? Although it is impossible to remove the shell to directly test this in turtles, we can add weight to these animals to examine extrinsic loading. In this way, we can gain insight into the effects of loading on performance. We hypothesized that extrinsic mass loading of turtles will have a direct negative influence on their locomotor performance.

We used turtles as a focus in this study for several reasons. First, because of their shell, turtles are relatively easy to load. In addition, adding extra weight should not distress animals unduly in as much as they normally carry a substantial load in the form of their shell. Finally, female turtles experience natural loading during reproduction and often carry very large clutches of eggs. In *Chrysemys picta*, means of 7.6 eggs per female have been reported (Tinkle et al., 1981; Congdon et al., 1986).

Materials and methods.—We collected juvenile and adult painted turtles, *Chrysemys picta*, from two farm ponds in Belmont County, OH, in the spring of 1991. We maintained turtles at 26 C on a 12L:12D photoperiod for eight weeks prior to testing. All turtles ate mealworms, crickets, and chicken periodically. Adults also ate dry cat food and lettuce. Seven animals participated in this study (mean mass 185.6 g ± 209.6; range 7.6–646.0 g). We included animals from both sexes and all size groups from hatchling to adult in our performance measures.

We conducted all tests at 26 C between 1200 and 1800 h. We attempted only one test per animal per day. To measure performance (locomotion), we used a racetrack consisting of two side-boards approximately 1.75 m long, 0.12 m high, and 0.14 m apart. An additional 1.5-m long board narrowed the track for very small turtles to a width of 0.06 m. Styrofoam on the floor of the racetrack provided adequate traction for all animals. Photocells, positioned at 0.5 m and 1.5 m and connected to an electronic stopwatch, allowed for precise timing of the animals to the nearest 0.01 sec. A remote camera and monitor attached to a VCR provided a stored visual record of each test.

We measured the mass of each animal prior to each test and attached a lightweight flag (mean = 0.25 g for adults and 0.15 g for juveniles) to the center of the carapace of each individual to break a photocell beam during a test. For the loading trials, we attached 60%, 80%, and 100% of the individual's mass to the carapace of each animal. We used plastic tubing filled with sand and water, small lead fishing weights, or a thin coil of lead to load turtles. We then placed the animal in an isolated chamber at the entrance to the track. After a 5-min adjustment period, we opened a gate to allow the animal access to the track. To induce locomotion, an experimenter entered the environmental room housing the racetrack and forced the turtle to run immediately upon opening the gate. Arm waving behind the animal was generally enough to induce running. To increase the likelihood that we were measuring maximal velocity, we obtained three complete trials from each animal running over the last 1.0 m of the track.

We analyzed videotapes of each run to determine the number of strides taken by each animal. For each successful test, we computed