# EXPERIMENTAL ANALYSIS OF AN EARLY LIFE-HISTORY STAGE: SELECTION ON SIZE OF HATCHLING TURTLES

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*Abstract.* Life-history evolution in short-lived organisms has been investigated extensively, but little is known empirically about the causes of the different life-history strategies of long-lived organisms. To explore this issue, we conducted experiments to evaluate natural selection acting on key traits during an important life-history stage of the red-eared slider turtle (*Trachemys scripta elegans*). We reared eggs from 56 females in a seminatural common environment and released 356 of the resulting hatchlings in four replicates at a natural nesting area to assess offspring recapture probability as a measure of survivorship during the post-emergence migration. Larger body size of hatchling turtles was strongly favored by natural selection overall ($\beta' = 0.346$, $P < 0.001$) and in each replicate. Although selection on body size was positive in all analyses, the form of selection varied depending on the inclusion of nonrecaptured presumed dead individuals in the statistical analyses. This result indicates that such analytical tools are sensitive to the common assumption in many mark–recapture studies that nonrecaptured individuals have no fitness (i.e., $W = 0$). The most likely explanation for the size-dependent recapture probabilities is differential mortality, because body size at release for survivors was significantly larger than body size at release for hatchlings found dead. This pattern of survivorship appeared to result from size-dependent predation. We suggest that the benefit of larger body size for hatchling turtles may reside in improved locomotor performance that reduces the duration of exposure of larger individuals to predation. This hypothesis is supported by significant negative correlations between measures of body size and time elapsed between release and recapture.

*Key words: body size; hatchling performance; life-history evolution; mark–recapture; natural selection; predation; survivorship;* Trachemys scripta; *turtles.*

## INTRODUCTION

Life-history research is a dynamic area of inquiry in biology (Caswell 1989, Roff 1992, Stearns 1992, Charnov 1993, Charlesworth 1994). Much of the focus has shifted from evaluating the presumed dichotomy of *r*- and *K*-selected taxa (reviewed by Roff 1992, Stearns 1992) toward dissecting the complexity of intraspecific life histories with different approaches. One important direction concerns the role of longevity in shaping patterns of life histories, because life-history theory provides different predictions concerning co-evolving traits in short-lived and long-lived taxa. As a generalization, long-lived organisms are expected to exhibit a suite of characteristics including delayed sexual maturity, high adult survivorship, iteroparity, and increased reproductive effort with age; traits thought to be favored by selection in response to high and variable juvenile mortality (reviewed in Stearns 1992, Charlesworth 1994). Consequently, long-lived organisms represent a complex but important paradigm of life-history evolution.

Most of our empirical knowledge about life-history evolution derives from short-lived organisms, thus thorough evaluations of life-history theory of long-lived taxa have not been well developed. This problem stems largely from the obvious fact that long-lived organisms typically require many years of study to produce satisfactory evaluations of their life histories. Furthermore, the majority of the life-history research that has been conducted on long-lived taxa has focused on mammals (Roff 1992, Stearns 1992). However, many recent empirical life-history studies have concentrated on natural populations of turtles (Wilbur 1975, Tinkle et al. 1981, Márquez et al. 1982*a, b,* Crouse et al. 1987, Frazer et al. 1990, Congdon et al. 1993, 1994, Cunnington and Brooks 1996). Turtles are among the longest lived vertebrates (Gibbons 1987) and thus provide an excellent comparative taxon with which to study the causes of life-history evolution in long-lived organisms.

In addition to high adult survivorship, turtles exhibit many life-history traits that tend to characterize long-lived organisms, including the putative driving force: high and stochastic offspring mortality (reviewed in

Iverson 1991*a*). Despite annual adult survivorship rates consistently in excess of 80% (Wilbur 1975, Galbraith and Brooks 1987, Frazer et al. 1990, 1991*a, b,* Congdon et al. 1993, 1994, Cunnington and Brooks 1996, Tucker and Moll 1997), few individual turtles actually attain a great age. For example, survivorship from oviposition to hatching in natural populations of turtles is variable but uniformly low (<30%) (Galbraith and Brooks 1987, Frazer et al. 1990, Iverson 1991*b,* Congdon et al. 1993, 1994).

Such high and stochastic offspring mortality along with low adult mortality may have influenced the evolution of reproductive life-history traits in turtles. For example, selection for optimal propagule size to maximize the probability of offspring survivorship during early life-history stages may be an important determinant of reproductive allocation (Smith and Fretwell 1974, Brockelman 1975, reviewed in Roff 1992). To yield maximal maternal fitness, optimality theory predicts a trade-off between propagule size and the number of offspring produced. Optimality theory thus requires size-dependent selection on propagules and/or offspring and makes the assumption that larger size is better than smaller size (i.e., survival selection). However, more offspring are also better than fewer (i.e., fecundity selection), thus the trade-off between big-is-better and more-are-better yields optimal propagule size (sensu Smith and Fretwell 1974). Evidence for a trade-off between egg size and clutch size has been documented in turtles (Iverson 1992, Rowe 1992, 1994, Iverson and Smith 1993; F. Janzen, *unpublished data*). Moreover, some turtles whose egg size is apparently limited by morphological constraints appear to produce as large an egg as possible given those restrictions (Tucker et al. 1978, Congdon and Gibbons 1987), which is consistent with optimality theory (Sinervo 1994).

One problem in assessing the biological importance of egg and hatchling mortality rates is that, although high, they are also stochastic and may not be greatly influenced by propagule size or number. However, mortality during critical early life-history stages (e.g., between emergence from the nest and arrival at a hatchling's post-emergence habitat) has been little studied quantitatively (Janzen 1993*a,* Gyuris 1994, Haskell et al. 1996). Mortality during post-hatching migration for aquatic turtles is thought to be high (Wilbur 1975, Wilbur and Morin 1988) because hatchlings may be exposed to extreme environmental conditions and numerous predators (reviewed in Greene 1988, Frazer et al. 1990, Ernst et al. 1994).

To evaluate the patterns and potential consequences of differential recapture probability as a measure of survivorship during a critical life-history stage in a long-lived organism, we conducted a replicated field experiment with offspring of the red-eared slider turtle (*Trachemys scripta elegans*) at a nesting area in west-central Illinois. Our primary objective was to determine whether variation in hatchling size was an important determinant of recapture probability during the post-emergence migration of hatchling turtles in this population. Consequently, we estimated the strength and form of natural selection on hatchling body size, a trait largely determined by egg size at oviposition. We used hatchling turtles produced from eggs incubated in a seminatural common environment to eliminate the influence of among-nest environmental variation (e.g., Cagle et al. 1993). Similar experimental approaches have proven to be exceptionally useful both in dissecting the evolution of life histories and in evaluating the causes of natural selection (e.g., Reznick et al. 1990, Wade and Kalisz 1990, Sinervo and Licht 1991, Sinervo et al. 1992, Janzen 1993*a,* Brodie et al. 1995, Dudley 1996, Kingsolver 1996). The results of our study provide insight into the importance of post-emergence offspring mortality in the life history of a long-lived organism.

## MATERIALS AND METHODS

### *Study system*

*Organism.*—*Trachemys scripta* is a widely distributed aquatic turtle whose 14 subspecies range from Brazil through Central America and Mexico into the United States (Ernst and Barbour 1989). In the United States, the species occurs from Kansas, Oklahoma, and New Mexico, east to northern Florida and southeastern Virginia and north to northern Illinois (Ernst et al. 1994). The red-eared slider (*T. s. elegans*; see Plate 1), the subspecies used in our experiment, ranges up the Mississippi Valley from the Gulf of Mexico to northern Illinois (Conant and Collins 1991, Ernst et al. 1994).

Sliders have been widely studied (reviewed in Ernst et al. 1994). Consequently, a wealth of information exists on the ecology and natural history of the species, particularly for the nominate race (reviewed in Gibbons 1990). At the location of the current study, some sliders have been documented to live at least 30 years (Tucker and Moll 1997). Females become sexually mature when 6–7 yr old and males when 3–4 yr old (Tucker et al. 1995*a, b*). Adult females nest from mid-May to late June, laying 6–30 eggs per clutch with an average clutch size of ~13 eggs and 1–3 clutches per year (Tucker 1996, Tucker et al. 1998*a*). Eggs average 10.6 g (limits = 5.49–16.08 g) ($N$ = 10,017) and hatchling size is strongly dependent on egg size, with heavier hatchlings emerging from heavier eggs ($r$ = 0.84, $N$ = 8070) (Tucker et al. 1998*a, b*). Age at maturity and reproductive output are consistent with previous reports on this species from other Illinois sites (Cagle 1937, 1950, Cahn 1937, Smith 1961, Thornhill 1982).

Neonatal sliders in North America generally remain in the nest over the winter before emerging the following spring (Gibbons et al. 1990, Ernst et al 1994). Emergence activity of hatchling sliders at our study site can be substantial (as many as 60 individuals cap-

PLATE 1. An adult female red-eared slider turtle (*Trachemys scripta elegans*) resting in shallow water shortly after nesting at the field site in Jersey County, Illinois. Photograph by Gary L. Paukstis.

tured in a day) and occurs primarily during daylight (but also in the evening) from mid-April to mid-May (Tucker 1997).

*Field site*.—The study area was a 13 h field in the Mississippi River State Fish and Wildlife Refuge, Jersey County, Illinois (39°18′04″ N, 90°29′42″ W) (Tucker 1997). Located on the eastern edge of the Illinois River, the field has a 3% slope trending west from Illinois Route 100 and is used extensively by *T. s. elegans* as a nesting area (>500 nests in 1994).

### Experimental methods

*Collection and incubation of eggs*.—In May and June of 1994, 56 adult female *T. s. elegans* were captured on their nesting migrations at the field site and transported to the laboratory where oviposition was induced with oxytocin within 48 h (Ewert and Legler 1978, Tucker et al. 1995c). This procedure ensured that all females produced eggs with embryos at the same (i.e., late gastrula) stage of development (Ewert 1979). Eggs were tamped dry, numbered uniquely, and mass was determined to the nearest 0.01 g.

Eggs were placed on moist perlite (54 clutches at −60 kPa and two clutches at −130 kPa) in covered, plastic shoeboxes and were incubated to approximate fluctuating thermal conditions likely to be encountered by turtle eggs in natural nests (Packard et al. 1985, Ratterman and Ackerman 1989, Cagle et al. 1993, Plummer et al. 1994, Weisrock and Janzen 1999). This common-garden experimental design permitted us to expose all eggs to an essentially identical seminatural environment and thereby control the phenotypic influence on hatchlings of substrate moisture, nest temperature, and other environmental clutch effects that would be confounded for hatchlings obtained from natural nests. Shoeboxes were rehydrated once weekly to maintain the initial level of substrate moisture and were then rotated within the incubation room to randomize the influence of possible thermal gradients on hatchling phenotypes. Daily temperatures were recorded with

minimum—maximum thermometers (mean = 29.7°C, limits = 27.6–34.2°C) (Tucker et al. 1998b).

*Hatchling measurement and maintenance*.—Upon hatching in August, neonatal turtles were weighed to the nearest 0.01 g and straight-line carapace length was measured to the nearest 0.1 mm with vernier calipers. Hatchlings ($N = 244$) from 33 clutches were housed separately by clutch in plastic boxes containing moist vermiculite (−150 kPa). A subset of hatchlings ($N = 112$) from the remaining 23 clutches was maintained in four plastic boxes containing moist vermiculite (−150 kPa) but was not kept separate by clutch. All animals were overwintered in a room kept dark except when entered to examine boxes and unheated except when necessary to prevent freezing temperatures (mean = 8.9°C, limits 1.1–20.0°C). Containers were checked weekly to maintain substrate moisture.

*Hatchling preparation*.—Upon removal from the hibernation room on 14 May, all surviving hatchlings appeared healthy. Overwinter mortality was only 2.6% of the total 532 hatchlings that entered hibernation and no hatchling mortality occurred between emergence from hibernation and the experimental releases. The 244 hatchlings that were identified by clutch were systematically assigned to one of four groups ($N = 61$ in each), so that turtles were represented as equally as possible in each group by clutch. Another 112 hatchlings (of unknown parentage because they could not be identified with a specific egg at hatching) were divided randomly into four temporary assemblies ($N = 28$ in each); a set of these 28 hatchlings was then combined with each of the original four groups so that each final group contained 89 hatchlings.

The plastrons of all hatchlings were photocopied for future identification and hatchling body masses (to 0.01 g) and straight-line carapace lengths (to 1.0 mm) were recorded. Hatchlings from each group were marked uniquely as a cohort with correction fluid on the underside of the marginal scutes. Combining cohort identification marks with photocopies of the plastrons of

hatchlings included in the cohort allowed rapid, accurate identification of individual turtles without influencing the probability of recapture. After marking, hatchlings were placed in covered plastic containers with damp paper towels to prevent desiccation and kept at ~10° C for 28–36 h until the first experimental releases.

### Field methods

*Drift fence.*—We constructed a 260-m drift fence of 0.3 m high aluminum flashing parallel to the Illinois River. This fence was located below the known nesting area of *T. scripta* at the field site (Tucker 1997). For pitfall traps, we buried 27 five-gallon (~19 liters) plastic buckets with drainage holes at 10-m intervals along the fence so that the rims were flush with the surface of the soil. Just prior to the experimental releases, vegetation in direct contact with the aluminum flashing was removed so that hatchlings could not climb over the drift fence. No other alterations were made to avoid creation of an ecotonal area adjacent to the fence.

*Release of hatchlings.*—Hatchlings were released as two spatial replicates (designated 1 and 2) and two temporal replicates (designated A and B). The release points for the spatial replicates were 10 m apart with the midpoint of this distance centered perpendicularly to pit 9 on the drift fence (i.e., 90 m south of the start point of the fence at pit 0). The shortest distance from these release points to the fence was 70 m. The first set of the two temporal replicates (A1 and A2) of the experimental releases occurred at 0600 CDT on 16 May. The second set of temporal replicates (B1 and B2) was initiated at 1800 CDT later that same day. Hatchlings were released in the exact locations of the morning replicates. No hatchling turtles from the morning releases were observed, indicating that they dispersed rapidly after the releases. Although hatchlings emerging from natural nests at the site were captured in the drift fence beginning in late April, we waited until 16 May to initiate this experiment, a couple days after the bulk of the hatchlings from natural nests had been recovered (Tucker 1997).

Hatchlings were released by gently emptying turtles for each replicate from their containers onto the ground at the designated location. Turtles were righted if overturned and smoothed into a single layer, but were not oriented in any specific direction. Although unnatural, this protocol exposed all turtles to the same post-emergence environment simultaneously and thus permitted control of this otherwise confounding variable. Once both spatial replicates were arranged for a particular temporal replicate, turtles were released and we departed the area immediately.

*Recapture of hatchlings.*—The drift fence was monitored at 0600 and 1800 CDT daily from 17–24 May. Not until after the fence check at 1800 CDT on 21 May was the field, including the release points, searched for hatchlings because no live individuals had been recap-

tured for 24 h. Thereafter, these field searches were conducted daily at 1800 CDT after the fence check until 25 May when flooding terminated the experiment.

Recaptured hatchlings were identified and reweighed to the nearest 0.01 g. The pitfall trap or the nearest pit for turtles at the fence was also recorded in order to calculate a minimum straight-line travel distance from the release point using the Pythagorean theorem. All live hatchlings were subsequently released in the river. All dead hatchlings could be confidently identified from photocopies even though some individuals had severely damaged plastrons. Neither mass nor exact spatial location was recorded for dead turtles, but none were found at the release points.

*Meteorological and predator observations.*—Meteorological data were recorded during each visit to the site at pit 9 along the drift fence. Ambient temperature was recorded at 30 cm above the ground with a ReoTemp thermometer (Forestry Suppliers, Jackson, Mississippi, USA) and relative humidity was taken at breast height with a Bacharach sling psychrometer (Bacharach, Inc., Pittsburgh, PA, USA). Precipitation and daily high and low air temperatures were recorded nearby at Rosedale and Nutwood, Illinois.

Potential predators on the hatchling turtles were noted at the daily fence checks and intermittently when driving by the site on Illinois Route 100. We scored most potential avian predators as foraging if individual birds were on the ground between the release points and the fence. American Kestrels (*Falco sparverius*) and Loggerhead Shrikes (*Lanius ludovicianus*) were scored as foraging if they were perched directly over this same area. Observations and evidence of other potential predators were noted but were not quantified.

### Statistical analyses

We used Kruskal-Wallis tests (KW) to compare the mass and carapace length of hatchlings recaptured by replicate, date, and pit; Dunn's test (Q) was used to determine statistical significance of these variables from the Kruskal-Wallis tests (Glantz 1992). Comparisons of frequency data were made with the *G* test (Sokal and Rohlf 1981), with turtles being scored either as survivors, not recaptured presumed dead, or known dead.

We further analyzed recapture data in two ways. We first used random-effects logistic regression (Stiratelli et al. 1984) implemented in a Fortran program (H. Stern and A. H. Jones, *personal communication*) to properly account for clutch as a random effect while determining whether body size predicted the likelihood of recapturing hatchlings, an indirect measure of survivorship. Although statistical significance can be assessed appropriately for fixed effects (e.g., body size) in such regression models, the same is not true for random effects (e.g., clutch) (H. Stern, *personal communication*). When clutch is treated as a fixed effect in multiple linear regression models, its impact on the response

TABLE 1. Status of hatchling *Trachemys scripta elegans* from each replicate release (A, B = temporal; 1, 2 = spatial) at the end of the experiment.

| | Replicate A | | Replicate B | | |
| --- | --- | --- | --- | --- | --- |
| Status | Replicate 1 | Replicate 2 | Replicate 1 | Replicate 2 | Total |
| Survivors | 30 | 27 | 32 | 32 | 121 |
| Not recaptured, presumed dead | 47 | 53 | 43 | 49 | 192 |
| Known dead | 12 | 9 | 14 | 8 | 43 |

variable is marginally significant ($P = 0.04$ in the two focal analyses where $N = 244$ and where $N = 124$; *Results*).

The second set of statistical analyses of hatchling recapture data evaluated the strength and form of natural selection on body size (Lande and Arnold 1983, Arnold and Wade 1984*a, b,* Janzen 1993*a,* Brodie et al. 1995). Selection gradients for body size were determined using multiple linear regression in JMP (SAS Institute Inc. 1997). Predictor variables (size and size$^2$) were evaluated for distributional normality and then standardized to a mean of zero and variance of one. Absolute fitness ($W$) was measured by recapture status (i.e., survivors = 1 vs. not recaptured alive = 0) (Lande and Arnold 1983). Relative fitness, the response variable in the linear regression analyses, was then calculated as individual absolute fitness over the mean absolute fitness (Lande and Arnold 1983, Brodie and Janzen 1996). Separate analyses were conducted to estimate the linear (i.e., directional) and nonlinear (i.e., stabilizing/disruptive) selection gradients because multivariate nonnormality of the data can produce inaccurate estimates of linear selection gradients (Lande and Arnold 1983, Phillips and Arnold 1989, Brodie et al. 1995). As in the logistic regression analyses, clutch was included as a random dummy variable. Overall then, we report significance levels of the predictor variables (except for the random variable clutch; see above) from the logistic regression analyses and selection gradients and their standard errors from the multiple linear regression analyses.

Additional linear regression analyses were conducted to test the assumption that individuals not recaptured (and thus presumed dead) could be considered equivalent in fitness to hatchlings that were known to be dead (i.e., does $W = 0$ for both classes of individuals?). We first evaluated selection using only surviving hatchlings and those known to be dead. We then compared these selection gradients to those generated by multiple linear regression analyses of all hatchlings to determine the influence of turtles of unknown fate on the strength, form, and significance of selection (H. Stern and F. Janzen, *unpublished manuscript*). Analyses of covariance (ANCOVA) could not be employed because the data used in the two regression analyses are largely the same, thus violating assumptions of ANCOVA (Sokal and Rohlf 1981). Instead, we used a newly derived statistical technique to determine if selection gradients

from the two linear regression analyses were significantly different (H. Stern and F. Janzen, *unpublished manuscript*). Briefly, the least-squares regression coefficients are estimated as $\hat{\boldsymbol{\beta}}_i = (\mathbf{X}'_s\mathbf{X}_s + \mathbf{X}'_i\mathbf{X}_i)^{-1}(\mathbf{X}'_s\boldsymbol{\gamma}_s + \mathbf{X}'_i\boldsymbol{\gamma}_i)$, where $\mathbf{X}$ is a matrix of predictor variables, $\boldsymbol{\gamma}$ is a vector of responses, $i$ is the regression model ($i = 1$ is the model involving the censored data set, $i = 2$ is the model including all observations), and s refers to observations shared by both regression models. Under the null hypothesis that $\mathbf{d} = \boldsymbol{\beta}_1 - \boldsymbol{\beta}_2 = \mathbf{0}$, then $F = (\hat{\boldsymbol{\beta}}_1 - \hat{\boldsymbol{\beta}}_2)'\hat{\mathbf{V}}_d^{-1}(\hat{\boldsymbol{\beta}}_1 - \hat{\boldsymbol{\beta}}_2)/(p\hat{\sigma}^2)$, where $\hat{\mathbf{V}}_d$ is the estimated variance matrix $\sigma^2(\mathbf{X}'_s\mathbf{X}_s + \mathbf{X}'_i\mathbf{X}_i)^{-1}(\mathbf{X}'_1\mathbf{X}_1 + \mathbf{X}'_2\mathbf{X}_2)(\mathbf{X}'_s\mathbf{X}_s + \mathbf{X}'_2\mathbf{X}_2)^{-1}$, $p$ is the dimension of $\boldsymbol{\beta}_1$ (and $\boldsymbol{\beta}_2$), and $\hat{\sigma}^2$ is the error variance estimate from the complete (i.e., second) model, with $p$ and $n_s + \max(n_1, n_2) - p$ degrees of freedom (H. Stern and F. Janzen, *unpublished manuscript*). Note that the $\boldsymbol{\beta}$ and $\boldsymbol{\gamma}$ notation used here should not be confused with selection gradients.

To aid in visualizing the form of selection on hatchling size, we used the cubic spline technique (Schluter 1988, Brodie et al. 1995). This technique is better able than parametric regression to evaluate the form of selection in great detail. Standard errors for the spline functions were calculated by bootstrapping the original data 100 times. Because both measures of hatchling size (i.e., carapace length and body mass at release) were highly correlated and produced similar patterns in all statistical analyses of survivorship described above, for brevity we only present results for body mass in this paper.

## RESULTS

In all, 121 (34.0%) experimental hatchlings survived, 192 (53.9%) were not recovered and were presumed dead, and the remaining 43 (12.1%) individuals were found dead on the site (Table 1). During the first four days of the experiment (16–19 May), 16 hatchlings that emerged from natural nests at the field site (mean mass ± 1 SE = 6.58 ± 0.21 g, limits = 4.53–7.93 g; mean carapace length ± 1 SE = 31.0 ± 0.40 mm, limits = 27.0–33.0 mm) were also caught at the drift fence along with the experimental hatchlings, indicating that the timing of this experiment was ecologically relevant (see also Tucker 1997). Almost all survivors were recaptured in pits centering around pit 9 (Fig. 1), the pit that was closest to the release points. No hatchlings were captured in the terminal pits (Fig.
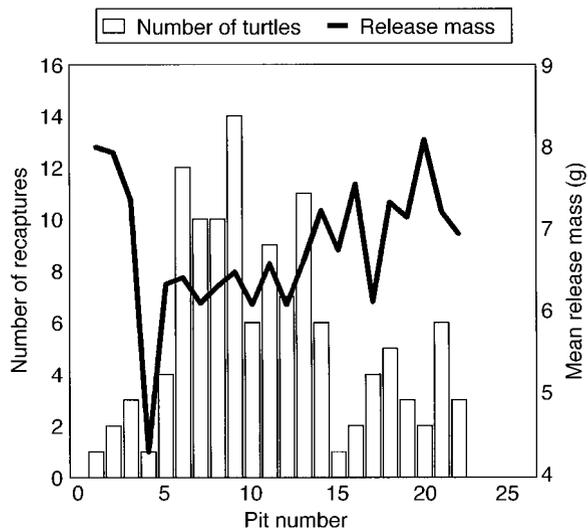
FIG. 1. Relationship between the frequency of hatchling *T. s. elegans* recaptured alive in each pit of the drift fence and the mean mass of those individuals at the time of the experimental releases. Hatchling phenotypes did not vary significantly among pits, although heavier hatchlings tended to be recaptured in the outermost pits of the drift fence, whereas lighter turtles tended to be recaptured in the central pits.

1), suggesting that the bypass rate was essentially zero. Statistical comparison of a normal distribution with the distribution of captures on the fence supports this conclusion (skewness $= 0.519$, kurtosis $= -0.438$, mean pit $= 11.02$, $SD = 5.08$ pits). Thus, the probability of a single hatchling turtle bypassing the fence was $<1\%$.

Both the probability of recapture and measures of hatchling phenotypes did not differ significantly among replicate experimental releases (Tables 1 and 2). Individual spatial and temporal replicates did not differ significantly in the number of survivors, hatchlings not recaptured presumed dead, or those known to be dead ($G = 3.76$, df $= 6$, $P = 0.709$) (Table 1). Replicates were also similar in mass at release (KW $= 2.99$, df $= 3$, $P = 0.393$), carapace length (KW $= 3.42$, df $= 3$, $P = 0.331$), mass at recapture (KW $= 1.30$, df $= 3$, $P = 0.730$), and change in mass from release to recapture (KW $= 4.00$, df $= 3$, $P = 0.261$) (Table 2). Time to recapture was similar between spatial replicates for temporal replicate A (KW $= 0.32$, df $= 1$, $P = 0.574$) and for temporal replicate B (KW $= 0.08$, df $= 1$, $P = 0.771$). However, the time elapsed between release and recapture for temporal replicate A (mean $= 3.27$ d, 1 $SE = 0.16$ d, $N = 57$) was significantly greater (KW $= 10.73$, df $= 1$, $P = 0.001$) than for temporal replicate B (mean $= 2.91$ d, 1 $SE = 0.15$ d, $N = 64$). Despite this temporal pattern, hatchling phenotypes and recapture probabilities did not differ significantly among replicates, so data for all replicates were combined in the following statistical analyses (excepting initial analyses of selection on body size).

Hatchling phenotypes were similar among pits. Mass

at release (KW $= 23.40$, df $= 21$, $P = 0.323$; Fig. 1), carapace length (KW $= 20.41$, df $= 21$, $P = 0.496$), mass at recapture (KW $= 27.12$, df $= 21$, $P = 0.167$), change in mass from release to recapture (KW $= 18.36$, df $= 21$, $P = 0.626$), and time between release and recapture (KW $= 29.64$, df $= 21$, $P = 0.100$) did not differ among pits in which hatchlings were recaptured.

Body size of hatchling turtles at release did vary systematically with date of recapture. Heavier turtles tended to be recaptured alive earlier during the experiment than lighter turtles (KW $= 24.08$, df $= 4$, $P < 0.001$); the same pattern was observed for longer hatchlings compared to shorter individuals (KW $= 22.31$, df $= 4$, $P < 0.001$). The significant negative correlations between the elapsed time from release to recapture and both mass at release ($r = -0.41$, $P < 0.001$, $N = 121$) and carapace length ($r = -0.30$, $P = 0.001$, $N = 121$) are consistent with those observations. Even so, hatchling sliders did not take more time to reach pits at either end of the fence as compared to pits near pit 9 ($=$ the shortest straight-line travel distance) ($r = -0.09$, $P = 0.323$, $N = 121$). Consistent with this finding, more of the larger hatchlings were caught near the ends of the fence than were smaller individuals (Fig. 1), although larger turtles reached the fence more quickly than did smaller turtles. This outcome may be explained by the concentration of smaller hatchlings that took longer to get to the fence near pit 9, where travel distance was shortest. Indeed, the positive correlations between estimated travel distance and both mass at release ($r = 0.26$, $P = 0.004$, $N = 121$) and carapace length ($r = 0.20$, $P = 0.029$, $N = 121$) suggest that body size at release was greater for hatchlings caught in pits farther from the release point than for neonates caught closer to the release point.

The recapture pattern of hatchlings was associated with several daily meteorological parameters recorded during the nine days of the experiment. Relative humidity ($r = -0.22$, $P = 0.572$), precipitation ($r = 0.29$, $P = 0.455$), and daily minimum temperature ($r = -0.65$, $P = 0.057$) presumably did not influence hatchling movement toward the fence. However, fewer hatchlings were recaptured on days with higher temperatures ($r = -0.92$, $P < 0.001$): turtles were less likely to move when ambient temperatures were high. No hatchlings were found at any of the 0600 CDT fence checks, indicating that few if any turtles apparently travel during the evening or after dark.

Although air temperature was associated with the number of hatchlings caught each day, the number of potential avian predators observed between the release points and the fence (Table 3) was not associated with any of the meteorological observations or with the number of recaptures per day ($P > 0.05$ for all correlations). Interestingly, though, the number of potential avian predators observed was positively correlated with the number of hatchlings recaptured on the prior day ($r = 0.85$, $P = 0.007$, $N = 8$). This result suggests

TABLE 2. Hatchling phenotypes by replicate (A, B = temporal; 1, 2 = spatial) and details of recaptures for survivors during experimental releases of 356 offspring of *Trachemys scripta elegans*.

| | Replicate A | |
| | Replicate 1 (mean ± 1 SE, limits) | Replicate 2 (mean ± 1 SE, limits) |
| Variable | | |
| --- | --- | --- |
| Carapace length (mm) | 30.3 ± 0.22, 24–34 | 29.8 ± 0.22, 23–34 |
| Mass at release (g) | 6.25 ± 0.12, 4.02–8.79 | 6.02 ± 0.12, 3.18–8.84 |
| Mass at recapture (g) | 5.95 ± 0.19, 4.27–7.88 | 6.04 ± 0.19, 4.34–8.00 |
| Change in mass (g) | 0.45 ± 0.07, −0.37–1.36 | 0.51 ± 0.08, −0.20–1.27 |
| Recapture time (d) | 3.10 ± 0.12, 1.5–4.5 | 3.46 ± 0.31, 1.5–8.5 |
| Recapture location (pit) | 9.03 ± 0.84, 1–21 | 11.19 ± 0.92, 4–19 |
| Min. distance to pit (m) | 81.9 ± 2.97, 70.0–138.9 | 85.3 ± 3.45, 70.0–122.1 |

*Notes:* $N = 89$ hatchlings for each replicate for the first two variables. For the other five variables, $N = 30$ survivors for replicate A1, $N = 27$ for replicate A2, and $N = 32$ each for replicate B1 and replicate B2.

that the presence of many active hatchlings on one day may have attracted more avian predators on the subsequent day (sensu Horn 1968, Krebs et al. 1972). Other potential predators noted at the field site during the experiment besides birds included red foxes (*Vulpes fulva*), coyotes (*Canis latrans*), and, most commonly, raccoons (*Procyon lotor*).

Hatchling body mass differed systematically and significantly among the three categories of hatchling recapture status (KW = 27.78, df = 2, $P < 0.001$). Mass at release for hatchlings known to be dead (mean ± 1 SE, limits, $N$: 5.49 ± 0.18, 3.83–8.19, 43) was significantly less than mass at release for individuals not recaptured presumed dead (6.12 ± 0.07, 3.18–8.22, 192) ($Q = 3.17$, $P < 0.05$) which, in turn, was significantly less than mass at release for survivors (6.62 ± 0.10, 4.27–8.89, 121) ($Q = 3.22$, $P < 0.05$). The pattern of variation in carapace length of turtles was similar to that of body mass (28.8 ± 0.29, 24.0–33.0 vs. 30.0 ± 0.14, 23.0–34.0 vs. 31.0 ± 0.17, 26.0–35.0, respectively). Note that size of survivors was remarkably similar to that of "natural" hatchlings captured in the drift fence during the experiment (see *Results,* first paragraph). Overall then, hatchling red-eared sliders known to be dead were the smallest turtles at release, those individuals not recaptured presumed dead

were the next smallest at release, and survivors were the largest at release.

Results of logistic regression analyses of hatchling body mass at release for the 89 turtles of known clutch identity that survived and the 155 turtles of known clutch identity not recaptured alive were consistent with the Kruskal-Wallis tests. Mass at release was a significant predictor of probability of recapture ($P < 0.001$) with heavier individuals more likely to be recaptured than lighter hatchlings. Logistic regression analyses of body size of all hatchling turtles used in the study (i.e., 121 survivors vs. 235 hatchlings not recaptured alive) yielded similar results to the analyses on the restricted data set. These analyses of the larger data set, which necessarily excluded clutch as a variable (see *Materials and Methods* for an explanation), again suggested that body mass at release ($P < 0.001$) was a significant positive predictor of the probability of recapturing hatchlings alive.

Multiple linear regression analyses of the strength and significance of natural selection confirmed the results obtained with logistic regression analyses. Significant linear selection was detected on body mass of hatchling turtles at release: larger individuals were more likely to be survivors ($\beta' \pm 1$ SE = 0.346 ± 0.121, $P < 0.001$). Because selection gradients cal-

TABLE 3. Potential avian predators observed in the area during the experimental release of 356 hatchling *Trachemys scripta elegans* (16–24 May 1995).

| | Number of individuals observed | | | | | | | | |
| Avian species | May 16 | May 17 | May 18 | May 19 | May 20 | May 21 | May 22 | May 23 | May 24 |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| American Crow (*Corvus brachyrhynchos*) | 2 | 8 | 3 | 6 | 1 | 2 | 4 | 5 | 0 |
| Red-winged Blackbird (*Agelaius phoeniceus*) | 3 | 23 | 11 | 14 | 0 | 0 | 4 | 8 | 7 |
| Common Grackle (*Quiscalus quiscula*) | 7 | 4 | 18 | 2 | 0 | 1 | 2 | 14 | 0 |
| Loggerhead Shrike (*Lanius ludovicianus*) | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 |
| American Kestrel (*Falco sparverius*) | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| Blue Jay (*Cyanocitta cristata*) | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| Turkey Vulture (*Cathartes aura*) | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| Cattle Egret (*Bubulcus ibis*) | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| Great Blue Heron (*Ardea herodias*) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| Total | 12 | 37 | 36 | 23 | 1 | 3 | 11 | 28 | 9 |

*Note:* Except for 16 May (= evening only), number of birds = sum of morning and evening observations.

TABLE 2.  Extended.

| Replicate B | |
| --- | --- |
| Replicate 1 (mean ± 1 SE, limits) | Replicate 2 (mean ± 1 SE, limits) |
| 30.3 ± 0.20, 26–35 | 30.3 ± 0.23, 25–35 |
| 6.34 ± 0.11, 3.83–8.63 | 6.25 ± 0.12, 4.09–8.89 |
| 6.15 ± 0.15, 4.44–7.99 | 6.15 ± 0.15, 4.57–7.57 |
| 0.63 ± 0.08, −0.45–1.71 | 0.58 ± 0.08, −0.32–1.43 |
| 2.88 ± 0.21, 1.0–8.0 | 2.94 ± 0.30, 1.0–8.0 |
| 11.38 ± 0.97, 2–22 | 12.38 ± 0.88, 3–22 |
| 88.5 ± 4.26, 70.0–147.6 | 88.4 ± 4.53, 70.0–147.6 |

culated using the whole data set ($N = 356$) were very similar to those calculated using only those individuals for whom clutch identity was known ($N = 244$), only the latter results are reported here because of the completeness of the smaller data set. Significant nonlinear selection on body mass was not detected in either multiple linear regression analysis ($\gamma' \pm 1$ SE $= 0.127 \pm 0.075$, $P = 0.243$). The results of these linear regressions were confirmed by cubic spline analyses (Fig. 2A).

Separate statistical analysis of each replicate indicated that the form and strength of selection on hatchling turtles varied little spatially or temporally. Significant selection of similar magnitude among replicates was detected on body size of hatchling turtles (Fig. 3), as was also documented in the overall multiple regression analysis. Although there was some variation among replicates, the general form of selection was largely conserved and indicated that larger hatchlings, particularly the very largest, had the greatest probability of surviving in this experiment regardless of release location or release time (i.e., morning vs. evening release).

Multiple regression analyses comparing survivors to those known to be dead showed that the form and significance of selection on hatchling turtles were generally similar ($\beta' \pm 1$ SE $= 0.159 \pm 0.085$, $P = 0.001$; $\gamma' \pm 1$ SE $= -0.101 \pm 0.060$, $P = 0.306$) to those estimated from analyses in which nonrecaptured individuals were considered dead. Both sets of multiple regression analyses found that larger hatchlings had a significantly greater probability of being recaptured alive at the drift fence than smaller individuals. Nonlinear selection on body size was not statistically significant in either set of analyses. The strength of selection ($\beta'$) on body size, though, was significantly smaller ($P < 0.001$) in the analyses of the restricted data set compared to the analyses that considered nonrecaptured individuals to be dead (H. Stern and F. Janzen, *unpublished manuscript*). These results are not surprising because counting nonrecaptured hatchlings as dead inflates the relative fitness of the known survivors (2.742 for survivors analyzed in the whole data set vs. 1.393 for survivors analyzed in the restricted data set). Nonlinear selection ($\gamma'$) on body size also

differed significantly ($P < 0.001$) between the two analyses from a small positive to a small negative quantity ($\gamma' \pm 1$ SE $= 0.127 \pm 0.075$ vs. $-0.101 \pm 0.060$). Comparison of the two cubic spline analyses, although largely similar in pattern, also suggested that estimates of the probability of recapturing hatchlings from the middle of the size distribution were most sensitive to the assumption that nonrecaptured individuals were dead. In other words, recapture probability estimates for intermediate-sized individuals were smaller when nonrecaptured hatchlings were designated as dead (cf. Figs. 2A and 2B).

## DISCUSSION

The patterns of life-history evolution in long-lived organisms historically have been evaluated by generating life tables for different populations and species and then comparing parameters of these life tables to those of other long-lived organisms. Although insightful for certain demographic questions, this approach has elucidated relatively little about the underlying
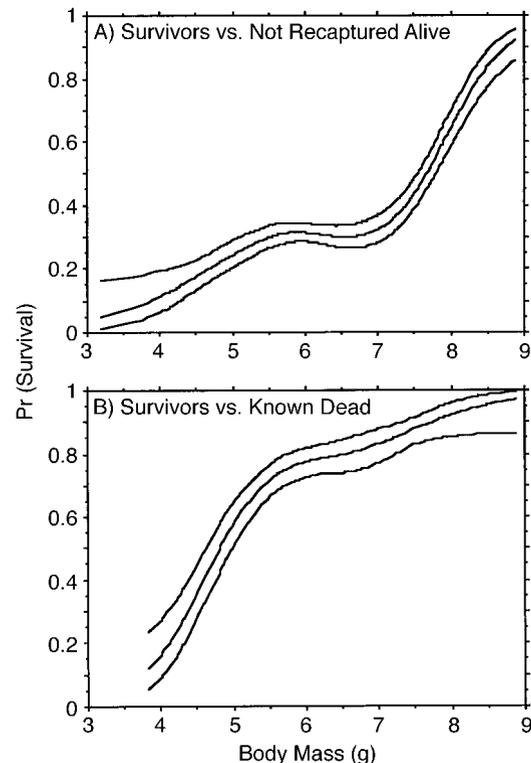


FIG. 2. Probability of hatchling red-eared sliders being recaptured alive in relation to body mass at the initiation of the experimental releases. These selection surfaces were derived from a cubic spline algorithm (Schluter 1988) and are consistent with multiple regression analyses that indicated selection favoring larger body size of hatchlings. The standard error lines flanking each selection surface were generated by bootstrapping the data 100 times. (A) Hatchlings not recaptured during the experiment were considered dead for this analysis. (B) Hatchlings not recaptured during the experiment were excluded from this analysis.
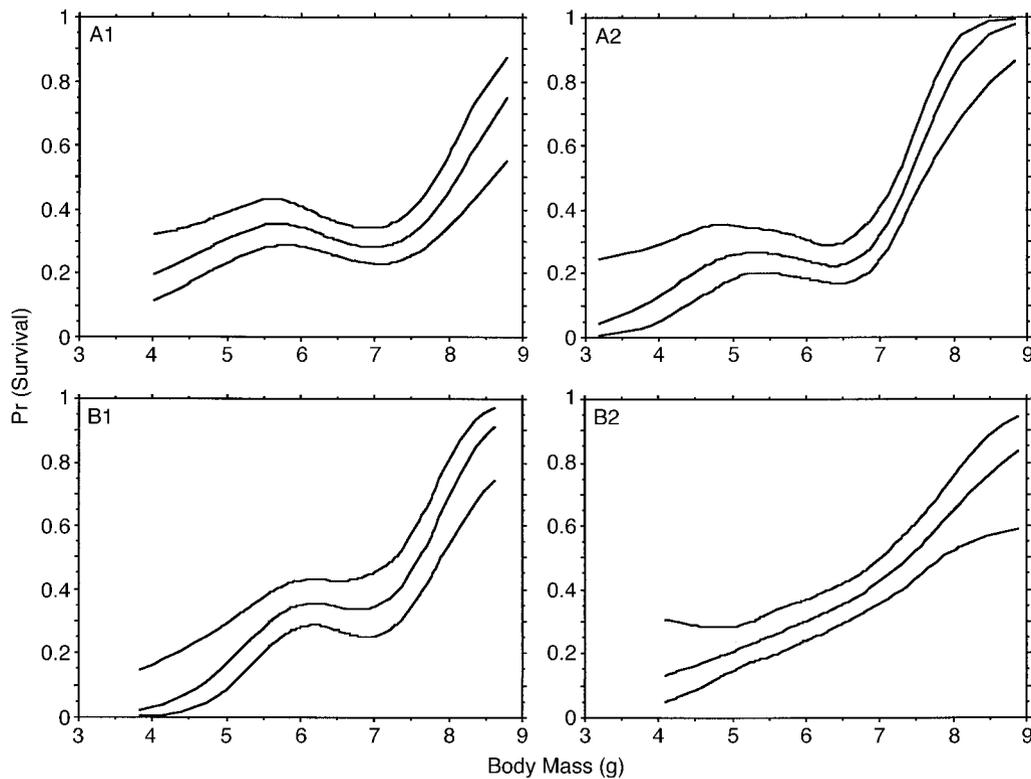
FIG. 3. Probability of hatchling red-eared sliders being recaptured alive in relation to body mass of the turtles at the initiation of four replicate experimental releases (A, B = temporal; 1, 2 = spatial). These selection surfaces were derived from a cubic spline algorithm (Schluter 1988) and are consistent with multiple regression analyses that indicated selection favoring larger body size of hatchlings. The standard error lines flanking each selection surface were generated by bootstrapping the data 100 times.

causes of variation and covariation in life-history traits. In particular, information on juvenile mortality and the patterns of selection acting on juveniles are lacking (e.g., Morafka 1994). Such knowledge is essential to evaluate models of life-history evolution completely (e.g., Cunnington and Brooks 1996). Manipulative studies like the present experiment can play an especially important role in this regard (e.g., Wade and Kalisz 1990, Sinervo et al. 1992). For example, incubating eggs under common seminatural environmental conditions permitted us to evaluate the importance of offspring body size independent of a potentially confounding source of among-clutch variation (i.e., among-nest variation in microclimate). Adopting this methodology, we found in our experimental releases of juvenile turtles that body size (or some correlated trait) exerts significant effects in determining the likelihood of survivorship during a pivotal stage of the life history (i.e., neonatal dispersal) of a long-lived organism.

## Spatial and temporal patterns of offspring recapture rates

Low offspring survivorship (< 30%) seems to characterize natural populations of turtles (Galbraith and Brooks 1987, Iverson 1991b, Congdon et al. 1993, 1994, Cunnington and Brooks 1996). For example, Frazer et al. (1990) found that only 1–27.5% of hatchling *T. scripta* in a South Carolina population survived from oviposition to entering the water in five different years. Such high levels of mortality undoubtedly place a great emphasis on the phenotypes of individual offspring. Although mortality during this postemergence period has been assumed to be high (Wilbur 1975, Wilbur and Morin 1988), surprisingly few experimental studies have examined survivorship of hatchling turtles from emergence from the nest to residence in a subsequent habitat (Janzen 1993a, Gyuris 1994).

We recaptured alive 34% of 356 hatchling red-eared slider turtles that were released. Nearly 60% of the hatchlings released were recaptured alive in a similar experiment using common snapping turtles (Janzen 1993a), although the drift fence in that study was only 50 m from the release point, which may have increased the likelihood of recapturing turtles by reducing their exposure time to predators and adverse environmental conditions. Two alternative explanations for these different recapture rates are that many hatchling *T. scripta* (1) may have headed away from the drift fence or (2) may have circumvented the drift fence. It is unlikely

that many neonates headed away from the drift fence because, at least in *T. s. elegans,* they tend to move downhill and toward water after emerging from nests (Murphy 1970 cited in Ernst et al. 1994, Tucker 1997). We also did not observe any hatchlings near the gravel road to the north of the release site, in the creek to the south, or toward Illinois Route 100 to the east even though we checked these areas at least once daily. With respect to the second idea, the pattern of recaptures among the pits suggests that the drift fence was not too short to catch the vast majority of released hatchlings. No hatchlings were recaptured in the terminal pits of the fence (Fig. 1) and statistical analyses indicated that the probability of any hatchling bypassing the fence was negligible (see *Results*).

Estimating the rate of bypass of the drift fence was also important because hatchlings could exhibit differential dispersion in relation to body size. Hatchling *T. scripta* caught in pits at either end of the drift fence may have had higher mean mass at release than those caught at the drift fence near pit 9, which was closest to the release points, despite the negative result of pit-by-pit comparisons using Kruskal-Wallis tests (Fig. 1). However, recapture probability, an indirect measure of survivorship (above and Fig. 2), and elapsed time from release to recapture were both size-dependent. Thus, the apparently greater dispersion among larger hatchlings may instead reflect increased losses of smaller individuals caused by predation or by increased susceptibility to extreme environmental conditions. Smaller turtles may have been exposed to predation and to the weather for a longer time than were larger turtles due to the slower travel speed of the former.

Hatchling phenotypes, both before and after the release, and the probabilities of recapturing hatchlings did not differ significantly among the replicates (Tables 1 and 2). Thus, the results of this study are robust to the levels of spatial and temporal variation allocated among the replicate experimental releases. Although the average time to recapture varied significantly between the temporal replicates, this difference in time was minimal enough generally not to influence the statistical distributions of hatchling phenotypes or the probabilities of recapture. The selection surface for body mass in replicate B2 differed somewhat from the other three replicates, but both the form and direction of selection were remarkably similar in the other three replicates (Fig. 3). These findings suggest that the diel timing of hatchling emergence from the nests for this population of red-eared turtles might have little impact on hatchling survivorship. Regardless, these results also indicate the importance of replication and sample size in field experiments. A study based solely on the 89 hatchlings used in replicate B2 might have reached different conclusions than the present experiment based on four replicates and 356 individuals. The extent to which such results might differ among years, populations, or species due to environmental, genetic, or phy-

logenetic differences is unclear, although these findings are concordant with those obtained in subsequent release experiments at this site (F. Janzen, J. Tucker, and G. Paukstis, *unpublished data*) and in a similar field experiment using common snapping turtles (Janzen 1993*a*).

### Size-dependent selection: possible causes

The most important result of this experiment concerns the relationship between body size of hatchling *T. scripta* and the probability of recapture. The prevailing hypothesis concerning reptilian offspring is that larger body size confers a greater individual fitness than smaller body size (i.e., bigger is better) (reviewed by Packard and Packard 1988). Nearly all previous studies of this concept in natural populations of reptiles have documented selection favoring larger individuals, especially when resource abundance is low (Ferguson et al. 1982, Ferguson and Fox 1984, Jayne and Bennett 1990, Laurie and Brown 1990, Sinervo et al. 1992, Janzen 1993*a*; Haskell et al. 1996, Bonnet 1997; but see Charland 1989). Also consistent with this hypothesis, survivors in our study were significantly larger than individuals not recaptured presumed dead or those known to be dead. These findings were supported by three separate statistical analyses of the data (see *Results*). Natural selection on body size of the hatchlings was largely linear (i.e., directional) (Fig. 2) and favored a within-generation increase in body size of approximately one-third of a standard deviation. These results suggest that larger hatchling sliders may accrue a significant survival advantage over smaller individuals during the period between emergence from the nest and reaching the aquatic habitat.

The most likely explanation of the size-related recapture probabilities of hatchling sliders is differential mortality. Perhaps the strongest evidence for this statement derives from the relationship between the probability of survival and hatchling body size: larger offspring exhibited a clear survival advantage over the smallest individuals (Fig. 2A). This analysis is especially powerful because it is based only on those hatchlings documented to be either dead or alive and is characterized by tight standard error lines.

The potential causes of size-dependent mortality of neonatal turtles in this experiment are twofold. First, hatchlings that died or disappeared may have succumbed to adverse environmental conditions during the experiment. Movement behavior of hatchling sliders was strongly correlated with daily high temperatures (activity decreased on warmer days), so negative thermal effects on hatchling survivorship are possible. However, there was no evidence of differential dehydration as a size-dependent source of hatchling mortality (see also Janzen 1993*a*).

The more likely mechanism of hatchling mortality in this study is predation. Although the fates of nonrecaptured individuals are unknown, all 43 hatchling

turtles known to be dead at the termination of the experiment were decapitated and/or eviscerated. We also found a significant positive correlation between the number of hatchlings caught at the drift fence and the number of avian predators observed at the site on the following day, suggesting that birds may be cueing on the presence of hatchling turtles. Red-winged Blackbirds (*Agelaius phoeniceus*) and Common Grackles (*Quiscalus quiscula*) kill hatchling turtles of other species (e.g., Vogt 1980) and attack live hatchling *T. scripta* at this field site (J. Tucker, *unpublished data*).

If hatchling mortality in this experiment was caused by predation, the reason for its size-dependence must be explained. Anecdotal reports have suggested that capture and/or ingestion of larger turtles may be difficult for certain predators (Barrows and Schwarz 1895, Bustard 1979, Swingland and Coe 1979). A more likely explanation, however, is differential exposure to predation. Larger hatchlings may have been more frequently recaptured alive than were smaller individuals because they spent less time in the field before reaching the drift fence. This hypothesis is supported by the significant negative relationship between size of hatchling turtles and the time between release and recapture: larger hatchlings were "faster" than smaller neonates. Similar size-dependent locomotor performance has been documented in laboratory studies of hatchling common snapping turtles (Miller et al. 1987, Miller 1993; but see Janzen 1993*a*) and smooth softshell turtles (Janzen 1993*b*). Predators thus may be the mechanism behind directional selection favoring larger hatchlings simply because they are differentially exposed to more of the smaller turtles. Manipulative experiments are nonetheless required to evaluate predation as a clear cause of size-dependent mortality of hatchling sliders in this population.

How this size-dependent fitness advantage is manifested under natural conditions and after this particular life-history stage are unresolved but important questions. Natural nests might experience different environmental conditions during both incubation and hibernation than those to which we exposed eggs and hatchlings in this experiment. However, we used substrate moistures and fluctuating temperatures like those encountered in natural nests (Packard et al. 1985, 1997, Ratterman and Ackerman 1989, Cagle et al. 1993, Plummer et al. 1994, Weisrock and Janzen 1999). Experimental studies of naturally incubated and overwintered hatchlings would be useful to establish more firmly the ecological relevance of the present experiment. In particular, the critical trait of interest may be locomotor performance as it is reflected by body size (Miller et al. 1987, Miller 1993, Janzen 1993*b*).

Once hatchling turtles reach their post-nest emergence environment, size-dependent survivorship may no longer occur. A four-year study of a cohort of painted turtles documented a positive relationship between body size at hatching and longevity in the laboratory (Brodie and Janzen 1996), suggesting persistent fitness benefits of increased offspring size, although a seven-month laboratory study of hatchling common snapping turtles apparently found no such relationship (Brooks et al. 1991). However, juvenile turtles experience much higher mortality rates in nature than in these two enclosure experiments (e.g., Galbraith and Brooks 1987, Frazer et al. 1990, Congdon et al. 1993, 1994), possibly because individuals are exposed to numerous predators in natural habitats (Janzen et al. 1992, Lindeman 1993). Haskell et al. (1996) documented strong size-dependent selection in yearling redbelly turtles that was thought to be due to predation by bullfrogs. On the other hand, neither body size nor running performance was a significant predictor of first-year survivorship in an experimental field study of hatchling common snapping turtles (Janzen 1995). However, few of the predators observed attacking hatchlings in that study are likely to have prey-size limits in this range. Other sources of mortality in the aquatic environment like parasitism are also unlikely to be size-dependent. Experimental studies of the causes and consequences of postmigration mortality in juvenile turtles would provide important insight into another crucial life-history stage for these long-lived organisms. More long-term field studies are also needed to evaluate the generality of these results in terms of individual lifetime fitness. Still, the results of the present experiment are clear: hatchling aquatic turtles have zero lifetime fitness if they do not make it to the water, no matter what happens subsequently.

### Form, strength, and life-history implications of size-dependent selection

One powerful contribution of this study is that the fate of many slider hatchlings not recaptured alive at the drift fence can be documented definitively. This result permits an analysis of the common assumption in selection studies that nonrecaptured individuals are dead (i.e., $W = 0$). If nonrecaptured individuals have zero fitness due to the same causes as those animals known to be dead, then the form of selection should be similar between analyses that include or exclude the former individuals. This assumption was largely borne out by the cubic spline analyses (cf. Figs. 2A and 2B). These analyses did suggest, however, that survival probabilities of medium-sized hatchlings were somewhat underestimated when nonrecaptured animals were considered dead. This result might indicate that medium-sized sliders perished disproportionately due to different predators (e.g., raccoons [*Procyon lotor*], American Crows [*Corvus brachyrhynchos*]), than did individuals of different size classes. Such large predators may have transported hatchlings from the field site or ingested them completely (J. Tucker, *unpublished data*). Regardless, differences in the strength and form of selection between analyses that included and then excluded nonrecaptured presumed dead individuals suggest that caution must be taken in accounting

for the fate of nonrecaptured animals in selection studies.

The strength of natural selection on body size detected in this experiment is relatively large, but whether it would lead to the evolution of larger hatchlings is debatable. Quantitative traits require a heritable component in order to evolve in response to direct selection (e.g., Lande and Arnold 1983) and body size of hatchlings is largely determined by egg size, a maternal effect of unknown genetic basis in turtles. Heritability of body size of hatchling turtles has been suggested to be moderate in magnitude (i.e., 0.72 ± 0.34) (Janzen 1993*a*) which, if accompanied by strong linear selection as documented in this study, could lead to a substantial microevolutionary response (Lande and Arnold 1983). However, a more meaningful quantitative genetic estimate needs to be obtained from multigenerational breeding designs or sibship analyses before adequate predictions about the evolution of offspring body size in turtles can be made. Furthermore, because offspring body size is mainly a maternal effect, it can exhibit evolutionary dynamics unpredictable by standard microevolutionary theory (Kirkpatrick and Lande 1989, Lande and Kirkpatrick 1990, Wolf and Brodie 1998, Wolf et al. 1998). However, even maternal effects on offspring or propagule size can have a large additive genetic component (Cheverud 1984, Byers et al. 1997), which implies that such traits have a significant potential to evolve in response to selection. More complete analyses of these kinds of traits will need to evaluate the impact of evolutionary forces acting on various maternal and offspring phenotypes (reviewed in Bernardo 1996).

This study has significant implications for other aspects of life-history theory as well, including optimal egg/clutch size theory. Larger hatchling sliders, particularly the very largest, were strongly favored by selection, suggesting that production of larger eggs by females might significantly improve their reproductive success. Why then don't red-eared sliders in this population, and turtles generally, produce several large offspring in a single burst of reproduction? One possible answer is that egg size might be constrained by the width of the pelvic girdle (Tucker et al. 1978, Congdon and Gibbons 1987). Thus an increase in adult body size by living longer may be an important route to producing larger eggs and, hence, larger offspring. At the same time, the smaller offspring are likely being produced by younger, smaller females who themselves have a higher probability of mortality during nesting (Tucker et al. 1999). Second, annual and geographic variation in egg size in *T. scripta* is relatively small whereas clutch size varies significantly (Tucker et al. 1998*a*) suggesting that, although larger egg size may be favored by selection for larger offspring, other forces like fecundity selection may favor the production of more eggs at the expense of egg size (sensu Smith and Fretwell 1974). Finally, environmental stochasticity and its impact on the likelihood of offspring survival also selects against "explosive" reproduction (i.e., semelparity). Females may be unable to predict the environmental conditions their offspring experience during either embryonic development or winter hibernation, thereby favoring a bet-hedging reproductive strategy characterized by extended iteroparity (e.g., Galbraith and Brooks 1987).

The results described herein have highlighted the importance of experimental field studies in evaluating size-specific survivorship during a critical life-history stage in a long-lived organism. Larger body size of hatchling red-eared slider turtles, perhaps as a proxy for improved locomotor performance that reduced exposure to predation, was clearly favored by natural selection under various spatial and temporal conditions. The form of selection during migration from the nesting sites toward the postemergence aquatic habitat was mainly linear, but varied somewhat depending on whether nonrecaptured individuals were included as dead in the analyses. The sensitivity of the assumption that nonrecaptured individuals are dead may influence the interpretation of many selection studies based on mark—recapture techniques.

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