

Estimates of adult survival and migration for diamondback terrapins: conservation insight from local extirpation within a metapopulation

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Abstract: As a case study we analyze a recent extirpation within a metapopulation of diamondback terrapins (*Malaclemys terrapin*) in a South Carolina salt marsh. Survival and migration probabilities were estimated by means of a multistratum approach in Cormack–Jolly–Seber mark–recapture models to obtain transition probabilities among four tidal creeks adjoining a river. Terrapins showed high fidelity to each subpopulation and the low migration rates were insufficient for recolonizing a creek that had suffered extirpation. Annual survival rates for adult female terrapins averaged 0.84 across all creeks, ranging from 0.748 to 0.971. Survival rates were converted to instantaneous mortality rates (M) for the purpose of calculating the mean life-span as $1/M$. When re-expressed in terms of mean life-span, the results confirmed that the average female terrapin did not survive to its estimated age at maturity, as might be predicted if additional mortality of females in crab pots was implicated. The results emphasize that incidental mortality of terrapins in crab pots is a conservation concern. Simple modifications of crab-pot design, such as an entrance reducer, can successfully mitigate this threat to the survival of terrapin populations.

Résumé : Nous avons analysé l'histoire d'un cas récent de disparition d'une population de Terrapènes (*Malaclemys terrapin*) de la métapopulation d'un marais salé de Caroline du Sud. Les probabilités de survie et de migration ont été estimées selon une approche multi-stratifiée, d'après les modèles de marquage–recapture de Cormack–Jolly–Seber, ce qui a permis de calculer les probabilités de passage entre quatre ruisseaux de marée adjacents à une rivière. Les tortues se sont montrées très fidèles à chacune des sous-populations et les faibles taux de migration se sont révélés insuffisants pour assurer la recolonisation du ruisseau d'où les tortues avaient disparu. Les taux annuels de survie des femelles adultes ont été évalués à 0,84 (0,748–0,971) en moyenne dans les quatre ruisseaux. Les taux de survie ont été convertis en taux instantanés de mortalité (M) en vue du calcul de la durée moyenne de la vie ($1/M$). Exprimés sous forme de durées de vie moyennes, les résultats confirment que la femelle terrapène moyenne ne survit pas jusqu'à l'âge estimé de sa maturité, comme on aurait pu théoriquement le prédire si l'on avait tenu compte de la mortalité additionnelle attribuable à la présence de casiers à crabes. Ces résultats démontrent que la mortalité des terrapènes dans les casiers est un phénomène dont les responsables de la conservation doivent se préoccuper. Des modifications simples des casiers à crabes, par exemple une réduction de l'ouverture, peuvent minimiser cette menace à la survie des populations de terrapènes.

[Traduit par la Rédaction]

Introduction

Diamondback terrapins (*Malaclemys terrapin*) are locally common in salt marshes of the eastern and Gulf coasts of the United States (Ernst et al. 1994). Although terrapins were abundant and exploited commercially through the 1920s, many of the localized population declines within recent decades have been linked to incidental capture by crab-pot fisheries (Bishop 1983; Seigel 1983; Seigel and Gibbons 1995; Roosenburg et al. 1997, 1999; Wood 1997; Hoyle and

Gibbons 2000; Roosenburg and Green 2000). Crab pots for commercial and recreational use are deployed in waters that coincide with zones frequented by terrapins (Bishop 1983; Roosenburg et al. 1999), resulting in terrapin capture and subsequent drowning.

Male and juvenile female terrapins are the size classes most frequently captured in crab pots (Hoyle 1997; Roosenburg 1991). Because turtles in these life-history stages are sensitive to exploitation, the impact of low adult survivorship on population dynamics is severe (Brooks et al. 1991; Congdon et al. 1993, 1994; Heppell 1998). There is abundant and indisputable evidence that terrapins suffer mortality from a variety of human influences (Roosenburg 1991; Burger and Garber 1995; Wood and Herlands 1997), yet few estimates of natural survival exist against which to measure the effect of additional mortality.

The present paper addresses two objectives by estimating vital parameters for the diamondback terrapin. First, we employ 17 years of mark–recapture data to calculate survival and capture probabilities for a metapopulation of terrapins in

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a system composed of multiple tidal creeks along an estuarine river. Hence, independent estimates of survival and capture from each creek's subpopulation will contribute to an overall view of population parameters for the area. Second, terrapins show high fidelity to specific creeks (Gibbons et al. 2001) or sections of river (Roosenburg et al. 1999), yet there is little quantitative evidence concerning rates of interchange among subpopulations. We use the probability of transition among subpopulations to evaluate migration among creeks, using the multistratum approach implemented in recent advances of Cormack–Jolly–Seber (CJS) population models (Nichols and Kendall 1995). From a source–sink perspective (Pulliam 1998), the findings will illustrate whether the levels of migration between subpopulations are sufficient to reestablish terrapins in creeks that become demographically vacant because of either local population extirpation or abandonment.

As a case study we analyze a dramatic local-scale decline that occurred in one of the four creeks. We evaluate the level of interchange among creeks and a river where commercial and recreational crabbing occurs. The empirical estimates of survival, capture, and migration will generate a more thorough understanding of impacts on terrapin populations at a metapopulation scale, particularly when they may be subject to incidental capture in crab pots (Seigel and Gibbons 1995).

Materials and methods

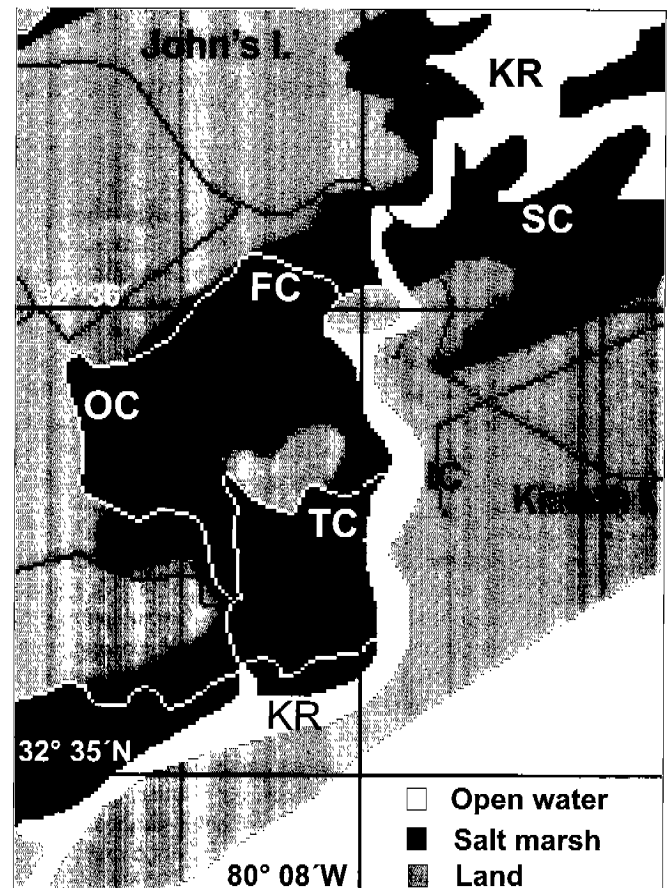
Study site

The study site encompasses an extensive salt marsh of *Spartina alterniflora* bordering the Kiawah River northwest of Kiawah Island, South Carolina (80°08'W, 32°36'N). Specific site descriptions are given in reports of the numerous studies conducted there (Gibbons and Harrison 1981; Lovich and Gibbons 1990; Lovich et al. 1991; Zimmerman 1992; Tucker et al. 1995; Hoyle 1997; Hoyle and Gibbons 2000; Gibbons et al. 2001). Commercial crab pots are operated regularly in the Kiawah River and recreational crab pots were introduced when a community dock was completed in 1983 opposite Terrapin Creek (Fig. 1). For terrapins these areas constitute population sinks because of incidental mortality in crab pots (Hoyle 1997; Hoyle and Gibbons 2000; Gibbons et al. 2001).

We investigated subpopulations in Terrapin Creek (1982–1999), Oyster Creek (1986–1999), Fiddler Creek (1987–1999), and Sandy Creek (1992–1999), as spatially discrete tidal creeks adjoining the Kiawah River (Fig. 1). The study was initiated in Terrapin Creek and the Kiawah River and as logistics allowed, expanded to adjacent creeks upstream and downstream while surveys continued in Terrapin Creek. Thus, creeks were replicate sampling sites rather than expansions of the original study area. This design avoided the practical problem of internal expansion of a study to meet the assumptions of an open-population model.

Annual surveys of each subpopulation produced the majority of terrapin captures between 1988 and 1994 (Fig. 2), when multiple seine pulls per year were conducted in Oyster Creek in 1990–1994, Terrapin Creek in 1983–1991, Fiddler Creek in 1988–1997, and Sandy Creek in 1992–1994. Variable sample effort is a breach of the assumptions of CJS models that does not cause survivorship estimates to suffer. As the population in Terrapin Creek began to dwindle rapidly between 1990 and 1991, sampling was continued with equivalent thoroughness in order to monitor the population status in adjacent creeks. After 1997, efforts in Terrapin Creek were curtailed to an annual visual survey and a single seine pull because of the low catch per unit effort (two turtles taken in 5 years).

Fig. 1. A salt marsh to the northwest of Kiawah Island, South Carolina, that hosts subpopulations of diamondback terrapins (*Malaclemys terrapin*) in the tidal creeks of the Kiawah River. FC, Fiddler Creek; IC, Inlet Cove; KR, Kiawah River; SC, Sandy Creek; and TC, Terrapin Creek.



General methods

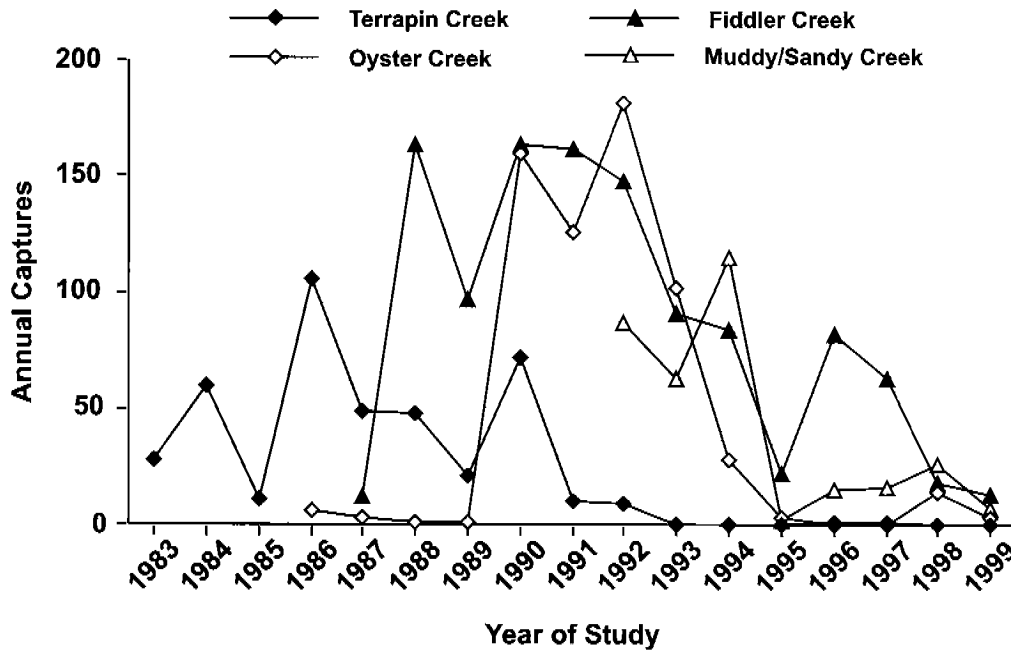
Terrapins were collected by the combined use of trammel nets and seines during mid-ebb through mid-flood tides (Lovich and Gibbons 1990; Tucker et al. 1995), with some additional collecting by hand. The net mesh targeted large juvenile and adult terrapins, i.e., the same size classes that entered crab pots (Fig. 3; see also Bishop 1983; Hoyle 1997; Roosenburg and Green 2000; Gibbons et al. 2001). We measured the carapace length, plastron length, and body mass of each turtle, determined its age, and determined its sex from the position of the cloaca. The cloaca is anterior to the rear carapace margin in females and posterior to the rear carapace margin in males. We marked all turtles individually and permanently by making notches in the carapace margin. Terrapins were returned within 24 h to the same creek where they had been collected.

Survival and recapture analysis

Any terrapins that died during the study were accounted for as a negative number in the encounter–history format (Cooch and White 2000). Twenty deaths resulted from crab-pot drowning, 8 specimens were sacrificed for genetic study, 6 deaths resulted from net drowning, 5 carcasses were discovered on land, 2 deaths resulted from laboratory experiments, and 1 death was due to a boat strike.

We estimated population parameters directly from mark–recapture encounter histories by an iterative process of model selection with

Fig. 2. Captures of turtles from four subpopulations in tributaries of the Kiawah River as an index of annual encounter effort.



maximum-likelihood methods (Burnham et al. 1994). Survival (ϕ) and capture (p) parameters for two groups (male and female) were estimated in the CJS open-population module of the program MARK (White 2000). Given the variable nature of encounter effort across years (Fig. 2), a priori we included models with time-dependence of capture probability. For any years during which a subpopulation was not sampled, the capture probability was constrained as zero. We further evaluated sample effort (i.e., the number of turtles captured annually in a creek) as a covariate to assess whether a linear function of the covariate could achieve lower standard errors for p in the models.

We began with a fully saturated model for two groups (male and female) with time-dependence in both survival and capture and successively fitted reduced parameter models. The corrected Akaike Information Criterion (AICc) was used to assess the relative probabilities of competing models, and the highest AICc weight indicated the most parsimonious model (Anderson and Burnham 1994; Burnham et al. 1995). We tested for potential overdispersion in the data by dividing the model deviance, $\hat{\epsilon}$, of the log-likelihood estimate by a $\hat{\epsilon}$ value estimated from 1000 bootstraps to yield a quasi-likelihood estimator, QAICc (Burnham and Anderson 1998). All parameter estimates were made by model averaging, based on AIC weightings to reflect model uncertainty (Burnham and Anderson 1998). Model averaging allowed unconditional estimates of variances and standard errors to be made for each parameter.

To better interpret how survival related to size or age classes that were commonly captured in crab pots, we derived instantaneous mortality (M) from annual adult survival (S) by the equation $S = e^{-M}$. Mean life-span for each mortality rate was calculated as $1/M$ (Charnov 1993). We determined the life-spans of terrapins at the low, average, and high survival estimates from CJS models.

Multistratum analysis

Multistratum models estimate the conditional probability of survival, capture, and transition among strata (Jolly 1965; Hestbeck et al. 1991; Brownie et al. 1993). In our study, the transition probability (ψ) represented the likelihood of movement among the four creeks and the Kiawah River. The high site fidelity of terrapins predicted that transition probabilities among subpopulations would

be lower among the distant creeks and higher for nearby creeks. The net transition probability was calculated as the sum of movements between pairs of subpopulations. For example, a 0.10 probability of transition between A and B (A:B), combined with a 0.03 probability of transition from B to A (B:A), excluding fidelity of A:A and B:B, yielded a 0.07 net vector from A to B (A:B).

The probabilities of transition among creeks were developed on the basis of a dataset discussed previously by Gibbons et al. (2001). However, it should be clarified that Gibbons et al. (2001) reported numbers and proportions of terrapins found in a different creek following an initial capture location, whereas the present analysis was conditioned on survival and capture probabilities to determine transitions among creeks.

Results

Survival probabilities

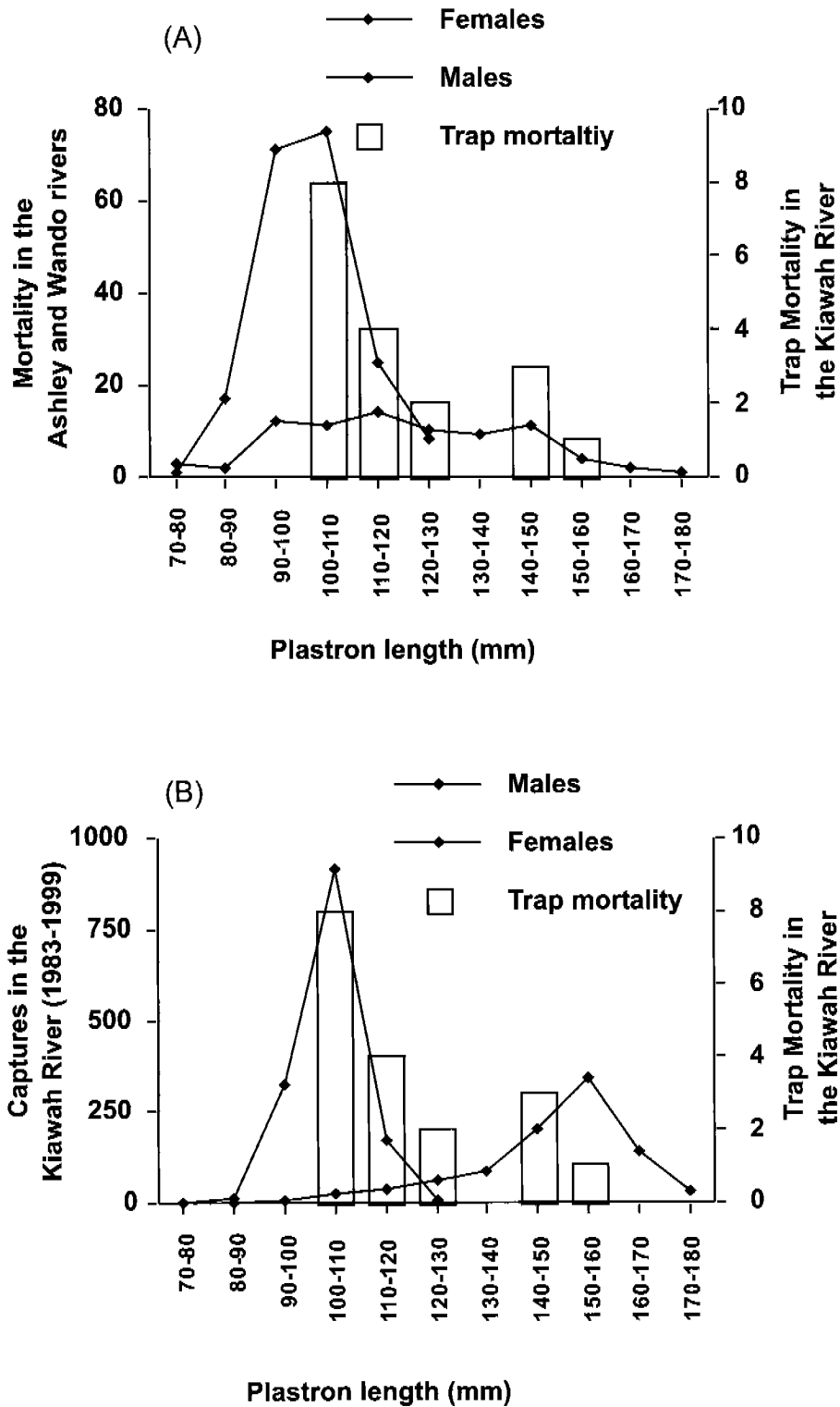
The estimated range of annual survival (ϕ) was more variable for females than for males (Table 1). Female survival estimates ranged from 0.748 to 0.971, whereas male survival ranged from 0.788 to 0.901. The average survival estimates across the four subpopulations were 0.835 (SE = 0.045) for males and 0.840 (SE = 0.054) for females, with lowest estimates found in Oyster Creek and highest estimates in Sandy Creek (Table 1).

When these annual survival estimates were expressed as instantaneous mortality rates (Table 2), the values for females corresponded to mean life-spans ranging from a shortest life-span of 3.4 years to a longest life-span of 34.0 years, with a mean of 5.7 years.

Capture probabilities

Given the efficiency of seining and trammel-netting techniques in catching turtles, a correlation of sample effort and capture probability was not surprising. Indeed, all of the most parsimonious models estimated by MARK included some form of time-dependency in capture probability (Table 3). However, the best model obtained for Terrapin Creek

Fig. 3. Comparison of known crab-pot mortality with sizes of trapped terrapins in the Ashley and Wando rivers in South Carolina, summarizing data from Bishop (1983) (A), and of mortality rates with sizes of terrapins captured in the Kiawah River (B). Pooled trap-mortality data from a partial commercial catch in the Kiawah River (unpublished data for 1990) and two ghost pots in Fiddler Creek (Hoyle 1997) are also shown.



included only two parameters related to capture probability because of the stark difference in pre- and post-1992 periods, despite that being the longest time series and thus po-

tentially yielding the greatest number of parameters to be estimated by a fully parameterized model.

Ranges of capture probabilities were slightly lower for

Table 1. Survival (ϕ) and capture (p) probabilities for male (M) and female (F) diamondback terrapins (*Malaclemys terrapin*) in the Kiawah River system.

| Subpopulation | Sex | Parameter | Estimate | SE | 95% CI |
|----------------|-----|-----------|----------|-------|-------------|
| Oyster Creek | M | ϕ | 0.788 | 0.033 | 0.716–0.846 |
| | F | ϕ | 0.748 | 0.039 | 0.663–0.817 |
| | M | p | 0.409 | 0.038 | 0.337–0.484 |
| | F | p | 0.569 | 0.052 | 0.465–0.668 |
| Terrapin Creek | M | ϕ | 0.830 | 0.040 | 0.737–0.895 |
| | F | ϕ | 0.847 | 0.057 | 0.699–0.929 |
| | M | p | 0.243 | 0.033 | 0.185–0.314 |
| | F | p | 0.259 | 0.049 | 0.175–0.366 |
| Fiddler Creek | M | ϕ | 0.819 | 0.016 | 0.785–0.849 |
| | F | ϕ | 0.792 | 0.022 | 0.746–0.831 |
| | M | p | 0.401 | 0.022 | 0.359–0.445 |
| | F | p | 0.342 | 0.029 | 0.288–0.401 |
| Sandy Creek | M | ϕ | 0.901 | 0.091 | 0.553–0.985 |
| | F | ϕ | 0.971 | 0.098 | 0.038–0.999 |
| | M | p | 0.156 | 0.027 | 0.109–0.217 |
| | F | p | 0.224 | 0.038 | 0.158–0.307 |
| Mean | M | ϕ | 0.835 | 0.045 | 0.554–0.878 |
| | F | ϕ | 0.840 | 0.054 | 0.175–0.967 |
| | M | p | 0.302 | 0.030 | 0.267–0.457 |
| | F | p | 0.349 | 0.042 | 0.079–0.404 |

males than for females ($p = 0.156$ – 0.409 for males; $p = 0.224$ – 0.569 for females). Capture estimates averaged 0.349 ($SE = 0.042$) for females and 0.302 ($SE = 0.030$) for males, with lowest estimates occurring in Sandy Creek and highest estimates in Fiddler Creek (Table 3). The mean values gave little evidence of the annual variation in captures for each subpopulation (Fig. 4). In particular, the crash of the Terrapin Creek population was initially obscured by mean values. There was a general pattern of lower survival rates in males in Fiddler Creek and Terrapin Creek lagging declines in survival of females by a year (Fig. 4); equivalent lags were not so evident for Oyster Creek or Sandy Creek.

Movement among creeks

The net transition probabilities among the four subpopulations reflect high site fidelity, the exception being transitions between Terrapin Creek and the Kiawah River (Table 4). For males, the highest transition probabilities were 0.102 for Terrapin Creek to the Kiawah River and 0.058 for the converse movement, even though net movement probabilities between subpopulations ranged from 0 to 0.044 . For females, the highest transition probabilities were 0.398 between the Kiawah River and Terrapin Creek and 0.183 for the converse movement. Net movement probabilities for females between subpopulations ranged from 0 to 0.215 (Fig. 5). The net movement probabilities were highest between the Kiawah River and Terrapin Creek (0.215), which were twice the next closest transition probabilities (see the largest arrows in Fig. 5). Overall, females were more likely than males to move among the tidal creeks (Table 4). Furthermore, females in upstream creeks showed higher site fidelity than females in downstream creeks. In contrast, males showed equally high fidelity regardless of the creek's position in relation to the river. Nevertheless, the low net rates of ex-

Table 2. Demographic estimates of the mean life-span of female terrapins.

| S^* | M | $1/M$ (years) |
|--------------|-------|---------------|
| 0.748 | 0.290 | 3.4 |
| 0.76 | 0.274 | 3.6 |
| 0.80 | 0.223 | 4.5 |
| 0.84 | 0.174 | 5.7 |
| 0.88 | 0.128 | 7.8 |
| 0.92 | 0.083 | 12.0 |
| 0.96 | 0.041 | 24.3 |
| 0.971 | 0.029 | 34.0 |

Note: Instantaneous adult mortality rates (M) were calculated from annual adult survival rates (S) using the equation $S = e^{-M}$. The mean life-span for each mortality rate is calculated as $1/M$ (Charnov 1993).

*Values in boldface type are the lowest, average, and highest estimates estimated from CJS analysis in Table 1.

change among subpopulations were unlikely to lead to the reestablishment of adjacent populations that were extirpated.

Discussion

This study dealt only with adult survival estimates and did not address juvenile survival. Turtles display a type III survival pattern characterized by low juvenile survival followed by high adult survival (Iverson 1991). We readily acknowledge that any estimates of life-span which are based on the assumption of constant survival rates (Charnov 1993) will overestimate a population's capacity to withstand additional mortality. Hence, these conservative estimates of adult survival probably foreshadow a declining population dynamic for many of the creeks (Fig. 4, Table 2).

Recent reviews confirm that survival of most adult

Fig. 4. Time-dependence in survival ($g \times t$) and capture (t) probabilities for male and female terrapins in four subpopulations in the Kiawah River (○, surviving females; ●, surviving males; ▼, capture probabilities). Linear regressions are given only as an overall indication of the trend.

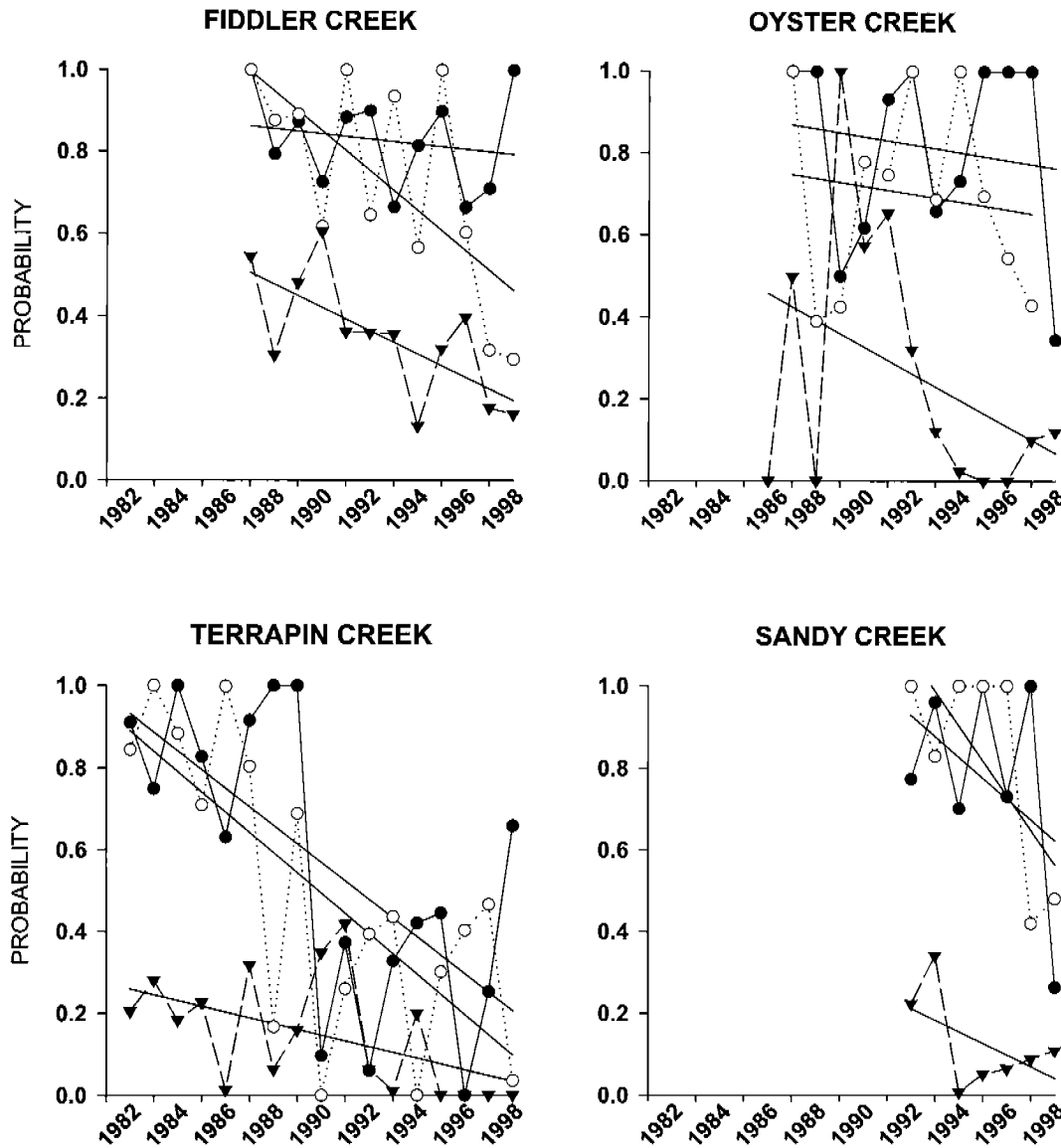


Table 3. Parsimonious models selected for four subpopulations of terrapins in the Kiawah River, based on the corrected Akaike Information Criterion (AICc).

| Subpopulation | Model | AICc | AICc weight | No. of parameters | Deviance |
|----------------|--------------------------------------|---------|-------------|-------------------|----------|
| Oyster Creek | $\phi(\cdot)p(t)$ | 1027.37 | 0.605 | 14 | 152.907 |
| Terrapin Creek | $\phi(\cdot)p(1992 \text{ decline})$ | 715.33 | 0.736 | 11 | 219.703 |
| Fiddler Creek | $\phi(g)p(t)$ | 2426.07 | 0.982 | 14 | 833.417 |
| Sandy Creek | $\phi(\cdot)p(t)$ | 479.65 | 0.593 | 8 | 66.160 |

Note: There was no effect of gender on survival in the most parsimonious models (denoted as $\phi(\cdot)$), except for Fiddler Creek, which reflected the tighter confidence intervals for annual survival in Fiddler Creek (refer to the standard errors listed in Table 1). Time-dependence for capture probability was evident (denoted as $p(t)$) in all models, but for Terrapin Creek took the form of a pre- and a post-1992 probability, reflecting the stark change in capture probability.

chelonians approaches or even exceeds >90% (Iverson 1991). The mean annual survival of female terrapins (0.840) ranked in the lower 30% percentile of the 25 annual survival rates

listed by Shine and Iverson (1995, their Table 1). For Maryland terrapins to remain stable or increase, a minimum estimated adult survival of >0.87 was necessary, depending

Table 4. Transition probabilities of movements within and between creeks, derived from multistratum CJS models.

| Recapture location | Point of origin | | | | |
|--------------------|-----------------|---------------|----------------|---------------|----------------|
| | Kiawah River | Oyster Creek | Terrapin Creek | Fiddler Creek | Sandy Creek |
| Males | | | | | |
| Kiawah River | 0.907 | <0.001 | 0.102 (0.094) | <0.001 | <0.001 |
| Oyster Creek | 0.028 (0.30) | 0.928 | 0.043 (0.018) | 0.009 (0.004) | <0.001 |
| Terrapin Creek | 0.058 (0.061) | 0.065 (0.054) | 0.830 | <0.001 | <0.001 |
| Fiddler Creek | 0.007 (<0.001) | 0.007 (0.005) | 0.016 (0.008) | 0.986 | <0.001 |
| Sandy Creek | 0 | <0.001 | 0.009 (0.010) | 0.005 (0.004) | 0.999 |
| Females | | | | | |
| Kiawah River | 0.447 | 0.108 (0.056) | 0.183 (0.153) | 0.011 (0.012) | 0.003 (<0.001) |
| Oyster Creek | 0.043 (0.032) | 0.774 | 0.022 (0.016) | 0.027 (0.011) | <0.001 |
| Terrapin Creek | 0.398 (0.316) | 0.061 (0.099) | 0.789 | <0.001 | <0.001 |
| Fiddler Creek | 0.112 (0.131) | 0.045 (0.016) | 0.006 (0.006) | 0.957 | <0.001 |
| Sandy Creek | <0.001 | 0.012 (0.012) | <0.001 | 0.005 (0.006) | 0.997 |

Note: Values in parentheses are standard errors. For estimated probabilities <0.001, no standard errors are given.

upon clutch size and age at maturity (Roosenburg and Niewiarowski 1998). By comparison, the mean survival (0.84) of Kiawah terrapins (Table 2) extrapolates to an average life-span that is less than the estimated age at maturity in the population (7 years for the smallest female; cf. Lovich and Gibbons 1990), as might be predicted for additive mortality of females. Incidental female mortality often exceeds a turtle species' demographic capacity to cope with natural hazards (Congdon et al. 1993, 1994), since there is no reproductive compensation for an increase in mortality risk.

We expected that natural survivorship might be lower for females than for males because their nesting migrations may extend considerable distances beyond the usual activity range (cf. Gibbons et al. 2001). Such migrations may impose greater exposure to mortality risk if a female passes through regions of active boat traffic. Thirteen Kiawah River individuals (6 males, 7 females) had propeller scars on the carapace (Gibbons et al. 2001). While it appeared that boat strikes were a minor hazard (1% of the population, or 13/1266), the incidence was probably underestimated if turtle carcasses were not noticed within the relatively brief time frame of a field trip. Boat traffic was relatively infrequent in the Kiawah River until the installation of the Inlet Cove Dock. Further monitoring will determine if increasing water traffic is associated with boat-strike injury. Other studies of terrapins have recorded a higher incidence of prop scars in females than in males (19.7% of females vs. 2.2% of males; Roosenburg 1991) that relates to different habitat use by each sex, with females using deeper water channels in common with boat traffic.

As females emerge to nest, they encounter humans and natural predators. Nesting females that crawl onto coastal causeways risk being killed by vehicular traffic (Wood 1997). In addition, raccoons (*Procyon lotor*) and foxes (*Urocyon cinereoargenteus*, *Vulpes fulva*) are common predators of females or their nests. For example, >10% of female terrapins in Florida were killed in 1 year by raccoons during nesting excursions (Seigel 1980); raccoon predation is also prevalent on populations in New York (Burke and Feinburg 2000) and Maryland (Roosenburg 1992). At the Kiawah River, the carcasses found on land ($n = 5$) were of both adult male and

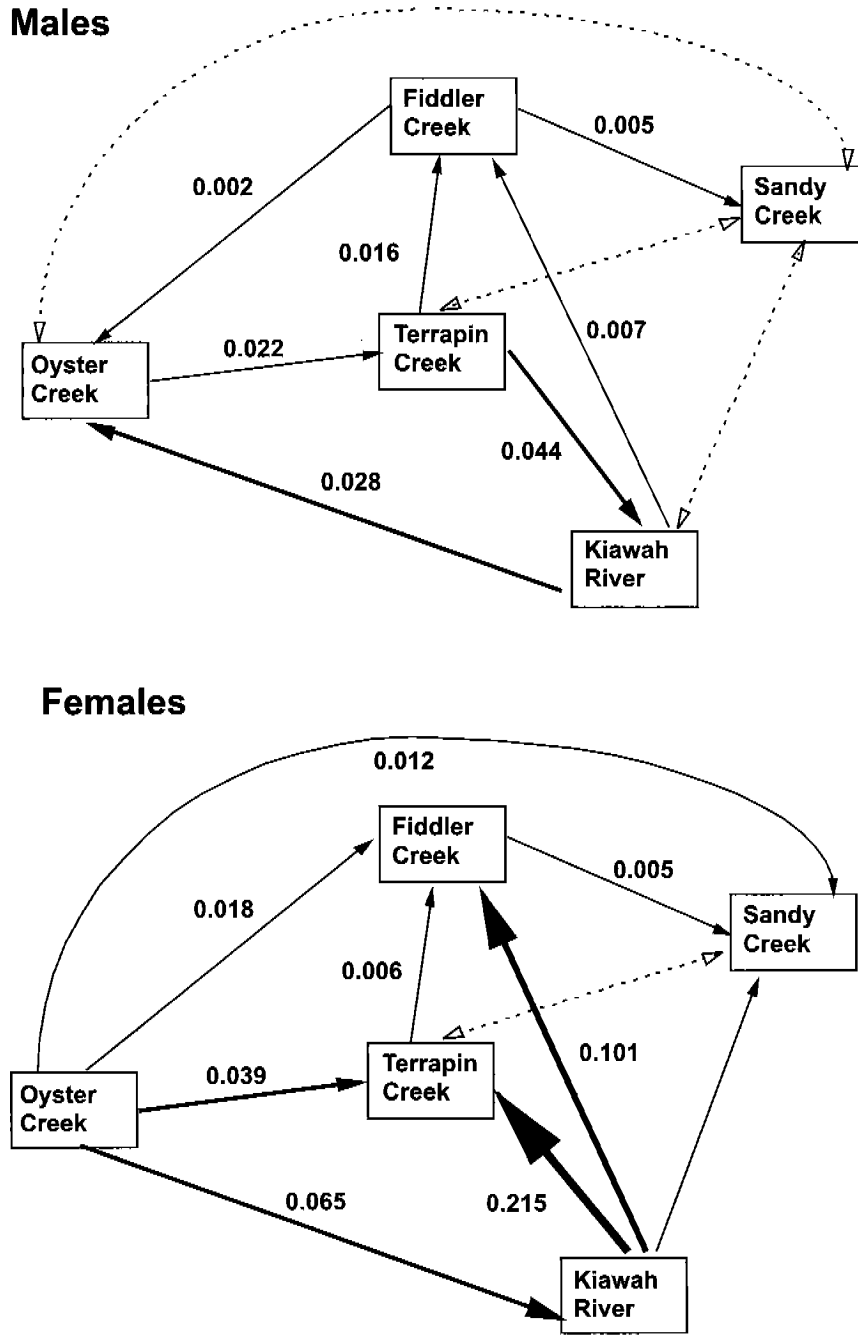
female sizes. Since male turtles would only be vulnerable to an aquatic predator, this may suggest that otters (*Lutra canadensis*) also feed on terrapins (Brooks et al. 1991). Although there is no direct evidence, we conclude that otters were probably unrelated to the Terrapin Creek decline because (i) they are generally rare in the marsh but also (ii) they are likely to avoid the disturbance at the nearby dock.

Injuries are evidence of sublethal predation and herein lies an overlooked concern regarding incidental capture in crab pots. Insofar as the incidence of limb injury to Kiawah River terrapins is concerned, 17 females (12%) and 20 males (8%) had missing feet (Lovich and Gibbons 1990). A decade later, the cumulative records indicate a comparable rate of injury: 8.6%, or 44/510, of females and 5.4%, or 40/742, of males had one or more missing feet. As both sexes incurred loss of limbs at similar frequencies, whether the injuries were sustained as juveniles or adults is equivocal. We cannot conjecture about rates of injury to juveniles because they are encountered so rarely. However, adult terrapins have been noted to risk injury from the chelae of large crabs while feeding on them (Davenport et al. 1992). It is reasonable to infer that within the confines of a crab pot a terrapin could receive limb injuries from large blue crabs (*Callinectes sapidus*). It is debatable whether terrapins were attracted to the crab pots to forage on the blue crabs within or to the bait that initially attracted the crabs. The frequency of terrapin captures within peeler crab pots, which are unbaited, suggests that the former is the case (Bishop 1983; Roosenburg et al. 1997; Wood 1997). A further concern is whether the activity of the first turtle within a pot would attract other individuals that would then become trapped (Frazer et al. 1990). It is important to understand the specific foraging decisions made by terrapins in order to reduce incidental captures in crab pots.

Fidelity

The sampling methods (seining and trammel nets) were unbiased in terms of body size, so an overall lack of a sex difference in capture probabilities was not an artifact of variation in sample size. However, time-dependence in capture probability was evident, in that years of increased sampling effort (multiple samples per year) coincided with higher capture

Fig. 5. Net movement among four creeks by male and female terrapins in the Kiawah River system. Values were calculated from the movement vectors between pairs of subpopulations given in Table 3.



rates, even though the coverage areas remained similar. The high fidelity to a creek signifies that at least in the short term, low migration rates between adjacent subpopulations are unlikely to reestablish extirpated subpopulations as long as the Kiawah River remains a population sink because of incidental captures in crab pots.

The marginally higher transition probabilities for females than for males are likely related to two factors. One aspect is the reproductive migration from tidal creeks to suitable nesting habitats that females undertake. A separate factor is habitat selection. Adult female terrapins appear to spend more

time than adult males in deeper water (Roosenburg et al. 1999), which probably indicates foraging behavior.

Conservation implications

Terrapins display strong site fidelity, but this does not imply that they are immobile during the shifts of daily tidal flow. (Roosenburg et al. 1999). Tidal creeks impose only limited physical structuring when terrapins swim along with tidal currents. Creek drainages that are isolated at low tide become a continuous wetland as incoming tides flood the marsh. On inflows, terrapins use creeks and drains as ave-

Table 5. Summary of studies that have documented capture rates (number of terrapins per trap-day) and mortality rates of terrapins in unmodified crab pots versus pots fitted with entrance-reduction devices.

| U.S. State | Capture rate | | Mortality rate | Reference |
|------------|----------------------|--------------------|----------------|-------------|
| | Unmodified crab pots | Modified crab pots | | |
| S.C. | 0.02–0.18 | — | 0.10 | Bishop 1983 |
| N.J. | 0.153 | — | 0.20 | Wood 1997 |
| | 0.486 | — | 0.24 | |
| | 0.075 | 0.075 | — | |
| | 0.071 | 0.011 | — | |
| | 0.229 | 0.010 | — | |
| | 0.106 | 0 | — | |
| | 0.0005 | 0 | — | |
| | 0.092 | 0.015 | — | |
| | 0.054 | 0.005 | — | |
| | 0.075 | 0.008 | — | |
| | Md. | 0.17 | — | |
| S.C. | 0.022–0.050 | — | 0.31 | Hoyle 1997 |

Note: Values are decimal percentages.

nues to swim through the salt marsh (Tucker et al. 1995). During outflows, terrapins depart the draining creeks to deeper water, where crab pots are often set. An obvious resource conflict arises when the spatial and seasonal distribution of crab pots corresponds to zones of terrapin activity.

The use of contrasting terrapin populations, where some are exposed to additional mortality from crab pots, is a quasi-experimental design to partition fishing mortality from natural mortality (Pitcher and Hart 1982). The case study of population extirpation in Terrapin Creek clarified that crab-pot mortality may cause the collapse of local terrapin populations within a short time frame. As Bishop (1983) pointed out, a major need exists for quantitative data on incidental captures in areas where crabbing activities and terrapin populations overlap. Recreational crabbing has a spotty spatial distribution, but commercial pots are set extensively along tidal rivers and estuaries. Crab pots are primarily operated in spring, when terrapins are active in courtship and likely to be caught (Bishop 1983; Wood 1997). Terrapin populations are therefore at risk both spatially and temporally throughout much of their Atlantic and Gulf distributions.

The mortality of terrapins in unmodified crab pots can range from 10 to 78% (Table 5). The minimum–maximum values for unmodified crab pots yield capture rates (range = 0.0005–0.486) and mortality rates (range = 0.10–0.78) that extrapolate to a low value of 0.00005 turtle deaths per crab pot (at low capture rates and low mortality) and a high of 0.379 turtle deaths per pot (for high capture rates with high mortality). In contrast, mortality is generally reduced by an order of magnitude when crab pots are modified to narrow the entrance to exclude terrapins (Table 5).

Our empirical estimates of survival establish that mortality in crab pots is a detriment to the long-term persistence of terrapins in zones of high fishing pressure. The case study at Terrapin Creek proves that population declines can be sudden and that recolonization will be uncertain as long as a population sink persists nearby. Crab pots can be fitted with an entrance reducer that alleviates the incidental mortality of

terrapins without affecting the efficiency of crab capture (Roosenburg et al. 1997; Wood 1997; Guillory and Prejean 1998; Roosenburg and Green 2000). Use of the device avoids a management alternative of imposing spatial or temporal restrictions on crabbing activity. We advocate that this simple modification of crab pot design receive wider recognition and promotion to enhance the survival prospects of terrapins throughout their range.

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