

Survival and recruitment of semi-aquatic turtles in an urbanized region

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Abstract Turtles are long-lived organisms that require high survivorship to maintain stable populations. Additionally, turtles are thought to be particularly susceptible to negative effects associated with anthropogenic habitat modification such as increased presence of human-subsidized predators and increased road mortality. Recruitment may also be reduced in populations surrounded by developed landscapes because of high road densities which limits connectivity among habitats or because of limited nesting sites. To address the impacts of habitat development on turtle vital rates, we studied three species of semi-aquatic turtles, yellowbelly sliders (*Trachemys scripta*), eastern mud turtles (*Kinosternon subrubrum*), and common snapping turtles (*Chelydra serpentina*), in the urbanized Charlotte-metropolitan area of North Carolina. Mark-recapture data were analyzed in Program MARK using AIC model selection methods to evaluate models analyzing the effects of pond, sex, and time on both survivorship and recruitment rates. Our results yielded high survivorship estimates for sliders and snapping turtles (73–92.5% and 91.4–99.4%, respectively), indicating that these species were likely not severely affected by habitat modification. In contrast, mud turtles exhibited lower survivorship estimates (56.8–73.6%) than have been previously documented for this species, an observation we attribute to their reliance on terrestrial habitats where they may encounter greater densities of mesopredators in developed areas. Recruitment estimates indicated that most populations were subsidized by sizable additions each year, with the notable exception of snapping turtles whose movement may be limited by increased road densities. Our results suggest that anthropogenic habitat modification has species-specific effects and could imperil certain populations in urbanized areas.

Keywords *Trachemys scripta* · *Kinosternon subrubrum* · *Chelydra serpentina* · Demography · Landscape · Population

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Introduction

Negative effects associated with habitat destruction or degradation are thought to be one of the main factors contributing to wildlife population declines (Sala et al. 2000), especially in reptiles (Gibbons et al. 2000; Gardner et al. 2007). Conservation of semi-aquatic turtles is complicated by the fact that these animals may be affected by alterations to either their aquatic habitats or the surrounding landscape (Marchand and Litvaitis 2004a). Female turtles use upland areas for nesting (Baldwin et al. 2004), and many species exist in metapopulations where movement between populations is critical for species persistence across landscapes (Bowne et al. 2006). Road mortality of turtles in areas of increased road density is known to bias some populations towards males, presumably because of the higher mortality rates of nesting females (Marchand and Litvaitis 2004a; Steen and Gibbs 2004; Gibbs and Steen 2005; Steen et al. 2006). Although female turtles may reduce their susceptibility to road mortality by nesting closer to the edges of aquatic environments, those nests are more likely to suffer predation because of increased predator activity in such areas (Baldwin et al. 2004; Marchand and Litvaitis 2004b). Despite the apparent challenges to nesting and movement imposed by habitat modification, some turtles are able to persist in developed habitats (Mitchell 1988; Conner et al. 2005; Failey et al. 2007).

The life-history characteristics of turtles, including long life span and delayed sexual maturity, can make them particularly sensitive to the negative effects associated with habitat development (Congdon et al. 1993). High rates of nest predation and juvenile mortality result in turtles having variable annual reproductive success which must be offset by multiple reproductive events over an individual's life (Gibbons 1987). As such, turtle populations may become imperiled by increased mortality in any age class of a population (Congdon et al. 1993). Additionally, because of their long life spans, the status of turtle populations is often difficult to assess using simple abundances, the method of analysis used in many turtle studies (e.g. Marchand and Litvaitis 2004a; Rizkalla and Swihart 2006). Abundances may be misleading indicators of habitat quality because they do not incorporate detection probabilities nor do they directly address factors responsible for population declines (Todd and Rothermel 2006). Thus, mark-recapture studies may provide a more complete assessment of population status by estimating vital rates such as survivorship and recruitment (Van Horne 1983; Todd and Rothermel 2006).

Our objectives in this study were to estimate survivorship and recruitment rates for three species of semi-aquatic turtles, the yellowbelly slider (*Trachemys scripta*), the eastern mud turtle (*Kinosternon subrubrum*), and the common snapping turtle (*Chelydra serpentina*) from an increasingly urbanized region, the Charlotte-metropolitan area of North Carolina. Studies in areas lacking significant urban land-cover have estimated adult survivorship to be approximately 80–90% for these three species (Parker 1996; Frazer et al. 1991; Congdon et al. 1994; Flaherty et al. 2008). Based on studies that have noted the potential negative impacts of anthropogenic habitat modification on turtles (Baldwin et al. 2004; Marchand and Litvaitis 2004a; Gibbs and Steen 2005), we hypothesized that these three turtle species would likely exhibit lower survivorship and recruitment rates in the urbanized Charlotte-metropolitan region than have been reported in other studies. Additionally, based on the assertion of Gibbs and Shriver (2002) that larger-bodied turtles may be more susceptible to road mortality than smaller turtles because of their increased range of movement, we predicted that snapping turtles would have lower survivorship and recruitment rates when compared with the relatively ubiquitous yellowbelly slider (Cagle 1950; Ernst et al. 1994). We predicted that mud turtles would also exhibit lower survivorship and recruitment values in developed areas than in largely unaltered habitats because of their dependence on upland

habitat for use in overwintering (Harden and Dorcas 2008; Harden et al. 2009). Finally, based on studies that have found skewed sex ratios in turtle populations, presumably as a result of road mortality (Marchand and Litvaitis 2004a; Gibbs and Steen 2005), we predicted that all three turtle species would show sex-specific survivorship rates with females having lower survivorship than males.

Methods and materials

Collection and processing methods

From 2005 to 2008 we collected mark-recapture data on semi-aquatic turtle populations in the Charlotte-metropolitan area of North Carolina, USA. According to the 2008 US census results, the Charlotte metropolitan statistical area is home to approximately 1.7 million people in an area of roughly 8,000 km², and the region is one of the fastest growing in the United States (Ewing et al. 2005). Turtles were captured at five ponds: two were located within residential housing developments that were constructed after the first year of sampling (Christenbury and Glen Grove), one was on a golf course (Mallard Head), and two were farm ponds with an undisturbed habitat buffer \geq approx. 100 m immediately surrounding the ponds (Robbins Park 1 and 2; Failey et al. 2007). All ponds were greater than 10 km apart except for Robbins 1 and 2 which were separated by approximately 300 m. Each year we sampled the ponds using 10 hoop-net traps (model MHNIA, 2.54 cm mesh, Memphis Net and Twine, Memphis, TN) set along the edges of the ponds in shallow water (Failey et al. 2007). We checked traps every other day for a 20-day period, and all new turtles captured were returned to the lab for data collection before they were released on the next trap checking occasion. We individually marked all turtles by filing the marginal scutes with a unique three-letter code (Sexton 1959). We determined the sex of sliders by examining foreclaw length, shell shape, and tail length, and for mud turtles we judged sex by tail length and plastron size/shape (Ernst et al. 1994). We used the formula of Mossimann and Bider (1960) to determine the sex of snapping turtles. Juvenile turtles that we were unable to accurately sex were excluded from our analyses.

Data analysis

For mark-recapture analyses we combined all capture events within years to create encounter histories with four capture events (one per year). We then used open population models in Program MARK because we assumed our study populations were not static from one year to the next.

To test the hypotheses that survivorship of the three turtle species varied among sites and among sexes, we constructed a Cormack–Jolly–Seber (CJS) model set (Lebreton et al. 1992) for each species in Program MARK (White and Burnham 1999). We used attribute groups to classify encounter histories according to both the pond where the turtle was captured and the gender of the turtle. Based on our previous turtle research (Eskew et al. unpublished data), we assumed that recapture rates (p) were likely to depend on the pond where the turtle was captured, its sex, and the effect of time (notated Pond and Sex * t) or simply pond and the effect of time (notated Pond * t). Therefore, we used these two recapture rate structures and generated models for each species where apparent survivorship (Φ) depended on different parameter combinations of pond, sex, and time. Because sufficient data for mud turtles and snapping turtles were only available from one pond for

each species, it was not necessary to generate models that included pond effects and thus model sets for those species contain fewer candidate models than the model set for sliders.

To estimate recruitment rates (f) for each species we used Pradel models within Program MARK (Pradel 1996). As with the CJS models, encounter histories were organized with attribute groups representing both the pond where a turtle was captured and its sex. We used survivorship and recapture rate structures from the most parsimonious model in the CJS model sets and then generated models where recruitment varied depending on combinations of pond, sex, and time effects. Survivorship estimates from the CJS models were used in Pradel models to fix survivorship parameters and thus improve estimation of recruitment parameters. It should be noted that recruitment in this context represents any addition to a population, for example by birth or immigration. However, because we suspect that our hoop-net traps were less effective at trapping juvenile turtles than adults, recruitment in our study likely stems from one of two sources: turtles growing into size/age classes that we were able to catch in our traps and immigration of adult turtles into our study populations.

We based our model selection on Akaike Information Criterion (AIC) values calculated by Program MARK (White and Burnham 1999). We used values corrected for small sample sizes (AIC_c) with lower values identifying greater parsimony. The AIC_c selection method evaluates model parsimony based on a combination of both fit and precision, and Akaike weights (w_i) represent the weight of evidence that a given model is the best in the model set (Burnham and Anderson 2002). Goodness-of-fit for all CJS models were evaluated using a parametric bootstrapping procedure with 1,000 iterations (described in Cooch and White's "Program MARK: 'A Gentle Introduction'" available at <http://www.phidot.org/software/mark/docs/book/>). The overdispersion factor, \hat{c} , was calculated as the observed global model deviance divided by the mean expected model deviance from the bootstrapping results. If overdispersion was evident from goodness-of-fit testing (e.g. $\hat{c} > 1$) we used AIC_c values adjusted for overdispersion (QAIC_c; Burnham and Anderson 2002). If goodness-of-fit testing reveals that $\hat{c} < 1$, no changes were made in model selection methods. We used model averaging to obtain parameter estimates if our model selection methods indicated similar support for multiple models.

Results

At some ponds, we captured limited numbers of some species, thus limiting our ability to include data from those ponds in our analyses. We analyzed capture data of sliders from three ponds (Christenbury [18 turtles], Glen Grove [33 turtles], and Robbins 1 [15 turtles]), mud turtles from one pond (Mallard Head [31 turtles]), and snapping turtles from one pond (Glen Grove [21 turtles]).

Cormack–Jolly–Seber pond and sex models

Yellowbelly Sliders Goodness-of-fit testing did not indicate any overdispersion for slider capture data. The best candidate model (approximately 41% of the support in the model set) included a sex effect on survivorship and a pond and time effect on recapture rate (Table 1). The next best model (approximately 38% of the support) included a pond effect on survivorship and identical recapture rate structure to the top model (Table 1). Because the best supported models did not include time effects on survivorship, we used model averaging to generate

Table 1 Model set analyzing effect of pond and sex on survivorship and recapture rate of the yellowbelly slider (*Trachemys scripta*) using Cormack–Jolly–Seber models. The number of parameters in each model is shown in the np column

Model	AIC _c	ΔAIC _c	w _i	np
Φ(Sex) p(Pond * t)	187.54	0.00	0.41	11
Φ(Pond) p(Pond * t)	187.72	0.18	0.38	12
Φ(Pond and Sex) p(Pond * t)	190.42	2.88	0.10	15
Φ(Sex * t) p(Pond * t)	190.76	3.22	0.08	14
Φ(Pond * t) p(Pond * t)	193.03	5.49	0.03	15
Φ(Sex) p(Pond and Sex * t)	197.65	10.11	0.00	20
Φ(Pond) p(Pond and Sex * t)	203.06	15.53	0.00	21
Φ(Sex * t) p(Pond and Sex * t)	206.86	19.32	0.00	23
Φ(Pond and Sex) p(Pond and Sex * t)	207.56	20.02	0.00	24
Φ(Pond and Sex * t) p(Pond * t)	208.88	21.34	0.00	25
Φ(Pond * t) p(Pond and Sex * t)	213.20	25.66	0.00	25
Φ(Pond and Sex * t) p(Pond and Sex * t)	216.65	29.11	0.00	28

only one survivorship estimate for each gender at each pond (Fig. 1). These estimates varied from 92.5% (Glen Grove males) to 73.0% (Christenbury females; Fig. 1).

Eastern Mud Turtles Goodness-of-fit tests indicated overdispersion for the mud turtle data and thus a \hat{c} correction of 2.64 was used in the QAIC_c formula for model selection. The two best candidate models (47% and 34% of the model support, respectively) both showed a time effect on recapture rate while the best model included a constant survivorship rate and the second best assumed sex differences (Table 2). Model averaging procedures (as above)

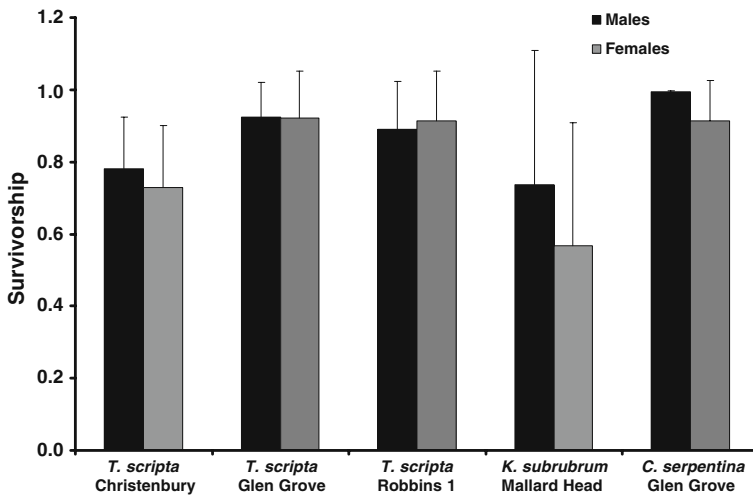


Fig. 1 Model-averaged survivorship (Φ) estimates for three species of semi-aquatic turtles. Bars represent the estimated yearly survival rates for each group of turtles indicated. Estimates were generated using Cormack–Jolly–Seber models in Program MARK and error bars represent one standard error above the estimate

Table 2 Model set analyzing effect of pond and sex on survivorship and recapture rate of the eastern mud turtle (*Kinosternon subrubrum*) using Cormack–Jolly–Seber models. The number of parameters in each model is shown in the np column

Model	QAIC _c	ΔQAIC _c	w _i	np
$\Phi(\cdot) p(t)$	33.57	0.00	0.47	4
$\Phi(\text{Sex}) p(t)$	34.24	0.68	0.34	5
$\Phi(t) p(t)$	36.07	2.51	0.13	5
$\Phi(\cdot) p(\text{Sex} * t)$	38.38	4.81	0.04	7
$\Phi(\text{Sex}) p(\text{Sex} * t)$	40.81	7.24	0.01	8
$\Phi(\text{Sex} * t) p(t)$	43.78	10.21	0.00	9
$\Phi(t) p(\text{Sex} * t)$	44.53	10.96	0.00	9
$\Phi(\text{Sex} * t) p(\text{Sex} * t)$	47.18	13.61	0.00	10

resulted in survivorship estimates of 73.6% and 56.8% for males and females, respectively (Fig. 1).

Common Snapping Turtles A goodness-of-fit bootstrapping test revealed slight overdispersion of the data and therefore we used QAIC_c model selection techniques with a \hat{c} of 1.21. The best candidate model (approximately 55% of the model support) included constant survivorship rate and a time effect on recapture rate (Table 3). Model averaging resulted in survivorship estimates of 99.4% and 91.4% for males and females, respectively (Fig. 1).

Recruitment models

Recruitment parameter structure varied among the three turtle species. The best candidate model for sliders (96% of the model support) included both a pond and sex effect on recruitment while the top models for both mud turtles (56% of the model support) and snapping turtles (74% of the model support) assumed equal recruitment between the sexes. The best models in each model set did not include time effects on survivorship, so as with the CJS models, we used model averaging to generate only one recruitment estimate for each gender at each pond. Estimates for sliders ranged from 2.00 for females at

Table 3 Model set analyzing effect of pond and sex on survivorship and recapture rate of the common snapping turtle (*Chelydra serpentina*) using Cormack–Jolly–Seber models. The number of parameters in each model is shown in the np column

Model	QAIC _c	ΔQAIC _c	w _i	np
$\Phi(\cdot) p(t)$	54.40	0.00	0.55	4
$\Phi(\text{Sex}) p(t)$	56.04	1.64	0.24	5
$\Phi(t) p(t)$	57.33	2.93	0.13	5
$\Phi(\cdot) p(\text{Sex} * t)$	59.15	4.75	0.05	7
$\Phi(\text{Sex}) p(\text{Sex} * t)$	60.85	6.44	0.02	8
$\Phi(\text{Sex} * t) p(t)$	64.94	10.54	0.00	9
$\Phi(t) p(\text{Sex} * t)$	67.29	12.89	0.00	9
$\Phi(\text{Sex} * t) p(\text{Sex} * t)$	68.03	13.63	0.00	10

Christenbury to <0.01 for males at Christenbury and Robbins 1 (Fig. 2). Male mud turtles were estimated to have recruitment rates of 0.33 while female recruitment was estimated at 0.32 (Fig. 2). Snapping turtles had low rates of recruitment with males at 0.02 and females at 0.03 (Fig. 2).

Discussion

Turtles in suburban environments are thought to be negatively affected by increased road mortality (Marchand and Litvaitis 2004a; Gibbs and Steen 2005) and increased nest predation (Baldwin et al. 2004; Marchand and Litvaitis 2004b). In our study, both survivorship and recruitment rates showed considerable variability both among species, and for sliders, among ponds, suggesting that the impacts of urbanization may be species- and site-specific and that generalizations regarding the effects of urbanization should be made with caution.

Survivorship estimates for sliders agreed closely with previous studies that found 77–86% survival rates for this species (Parker 1996; Frazer et al. 1991), suggesting that habitat development at our study sites did not significantly lower the vital rates of these populations. However, these results may also be interpreted as an indication that the negative effects of habitat modification on turtles do not manifest themselves in the years immediately following development. At two of our three ponds (Glen Grove and Robbins 1) analyses showed similar survivorship estimates for both sexes (Fig. 1), indicating little support for the hypothesis that females would be heavily impacted by road mortality in developed areas. However, females did have somewhat lower survivorship estimates at Christenbury (78% for males, 73% for females) where a road closely borders the pond. Increased road mortality may explain the reduced survivorship estimates at this pond when compared with our other study sites where road mortality does not appear to have impacted the populations. Recruitment estimates for sliders varied widely by both pond and sex.

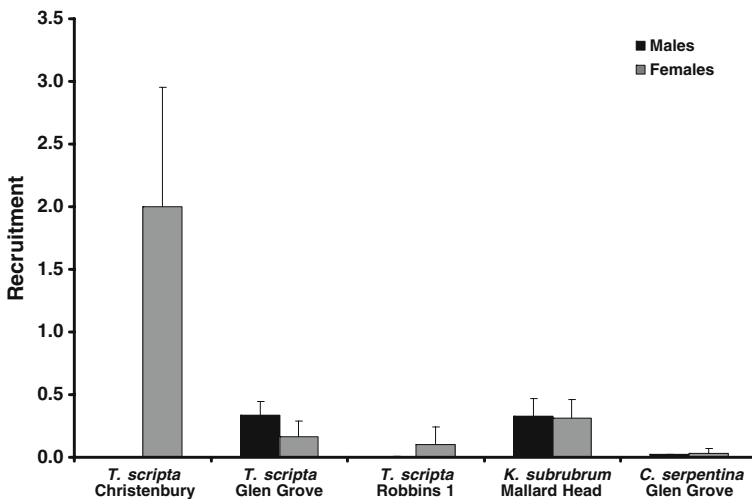


Fig. 2 Model-averaged recruitment (f) estimates for three species of semi-aquatic turtles. Bars represent the estimated yearly recruitment rates for each group of turtles indicated. Estimates were generated using Pradel models in Program MARK and error bars represent one standard error above the estimate

Estimates of 33% and 17% for males and females respectively at Glen Grove indicate that many new turtles are entering the population at this developed site, probably through both birth and immigration. Note that the very high recruitment estimates for females at Christenbury is the result of a relatively small population at this pond and many captures of female turtles in the latter study years.

In contrast to sliders, mud turtles from our study showed decreased survivorship rates when compared with previous research. At Mallard Head golf course male survivorship was 74% and female survivorship was 57% whereas previous studies have found very high survival (88–100%) in this species in natural wetland environments (Buhlmann and Gibbons 2001; Frazer et al. 1991). Previous research that used radio telemetry to monitor mud turtles at Mallard Head documented the death of 2 of 11 study animals during overwintering in a single year (Harden et al. 2009). Their deaths were attributed to mammalian mesopredators which may be more abundant in urbanized environments (Riley et al. 1998; Smith and Engeman 2002). Additionally, mud turtles are known to make extensive upland movements which may render them more vulnerable to those predators (Harden et al. 2009) or to road mortality. Despite the low survivorship estimates in this golf course environment, our recruitment estimates (Fig. 2) show that both male and female populations are being subsidized by significant additions each year (nearby ponds may provide sources of immigration at this site).

Although our data on snapping turtles were gathered from a pond surrounded by single-family housing (Glen Grove) we observed relatively high survival rates at this site. Our findings of 99% and 91% annual survivorship for males and females, respectively, fall within or exceed previous estimates of 88–97% for snapping turtles in natural habitats (Congdon et al. 1994; Flaherty et al. 2008). These estimates suggest limited mortality of snapping turtles at this site, at least among the age classes that we captured. However, our low recruitment rates (2–3%) indicate limited additions to the population, which could be problematic for the population in the future. Such low recruitment rates may indicate reduced nesting success at this habitat or perhaps that snapping turtles, which can reach large sizes, are more negatively affected by high road density than other species as some researchers have hypothesized (Gibbs and Shriver 2002). In either case, sliders at the same pond do not show the same pattern of very limited recruitment to the population (Fig. 2).

Overall, our survivorship results for sliders and snapping turtles indicate relatively high survivorship rates for these turtle species in the rapidly developing Charlotte-Metropolitan area. Mud turtles seem to be more vulnerable to habitat alteration, likely because of their extensive terrestrial movements. Based on our findings of limited recruitment in snapping turtles, road mortality may also be more of a factor for larger-bodied pond turtles as has been suggested previously (Gibbs and Shriver 2002). We suggest more long-term studies that focus on estimating the vital rates of turtle populations as a means to more fully understand turtle species' responses to anthropogenic habitat development as well as research efforts that examine populations across broad spatial scales in order to sample in a variety of developed and more pristine habitats.

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