INFLUENCE OF HABITAT AND PREDATION ON POPULATION DYNAMICS OF THE FRESHWATER TURTLE *MYUCHELYS GEORGESI*

Sean J. Blamires[1,2,4] and Ricky-John Spencer[1,3]

[1]*School of Biological Sciences A08, University of Sydney, NSW 2006, Australia.*
[2]*Department of Life Science, Tunghai University, 181 Section 3, Taichung-kan Road, Taichung City, Taiwan 407-04, R.O.C.*
[3]*School of Science and Health, Wildlife and Aquatic Ecology Group (Native and Pest Animal Unit), University of Western Sydney, Locked Bag 1797, Penrith NSW 2751, Australia*

ABSTRACT: Demographic models identify whether animals are vulnerable to local extirpation, but including all ecological parameters across life history stages may be impeded by practical difficulties. When processes acting on certain life stages cannot be measured, extrapolations are often made. A previous study documented that the range of the turtle *Myuchelys georgesi* is restricted to the Bellinger River, New South Wales, Australia, and its population is stable. We assessed whether *M. georgesi* selects certain habitats by comparing their distribution among different water holes. We assessed the threat of catfish predation by examining the stomach contents of catfish specimens. We then evaluated whether threats to *M. georgesi* were likely to have been underestimated by extending our previous demographic model. We did this by revising the previous estimates of adult, juvenile, and hatchling survivorship under hypothetical variations in water hole use and in the presence or absence of catfish predators. We found that *M. georgesi* preferentially uses moderate to deep water holes. We also found that although catfish 250–400 mm consume hatchling or juvenile turtles, those > 400 mm do to a greater extent. By making observations of catfish in the Bellinger River and incorporating their presence into our model, we found catfish presence to influence juvenile, but not adult, water hole use. Our reassessment of λ suggests that it may have been previously underestimated and that the threat to *M. georgesi* may be greater than we thought as the population is sensitive to variations in water hole depth and exposure of juveniles to predators. Events that alter key habitats and expose turtles to fish predators across the river should, accordingly, be evaluated further so they can be accounted for when managing the river.

Key words: Catfish; Demographic modeling; Habitat selection; Hatchling predation; *Myuchelys georgesi;* River turtle

THE HABITATS that animals choose to occupy provide a variety of resources. For example, animals may use specific habitats because they provide refuges from predators (Morris, 2003; Baker and Sheaves, 2009). Other factors such as the availability of food, nest sites, and inter- and intraspecific interactions may also influence how animals respond to changes in the environment and the type of habitats they use (Riechert and Gillespie, 1986; Manly et al., 2002; Morris, 2003, 2005). Understanding habitat use by rare animals enables biologists and managers to assess the vulnerability of animal populations at specific locations (Primack, 1998; Browne and Hecnar, 2007; Edge et al., 2009), and to identify features in the ecosystem integral to their survival (Clements et al., 2006; Newton and Herman, 2009). Specific information on habitat selection and specific vital rates within chosen, or other,

habitats, however, are rarely incorporated into population viability analyses (but see Lomolino and Creighton, 1996; Fryxell, 2001; Pringle et al., 2003).

The widespread degradation of freshwater ecosystems renders their management a high priority. Freshwater turtles are considered indicators of the quality of freshwater ecosystems, but many populations of freshwater turtle are currently threatened with extinction due to habitat loss or introduced predators (Mitchell and Klemmens, 2000; Spencer and Thompson, 2005; Browne and Hecnar, 2007). Stage-based population models are useful for identifying the influences of threatening processes across turtle life-history stages (Heppell et al., 1996; Chaloupka, 2002; Spencer and Thompson, 2005; Peckham et al., 2011), although they have limitations (Taylor, 1995). One limitation is that robust analysis depends on information about the survivorship of a population being equally

[4] CORRESPONDENCE: e-mail, sblamires@thu.edu.tw

available across all life-history stages (Chaloupka, 2002; Spencer and Thompson, 2005). This may not be possible if certain stages are more difficult to sample than others. To mitigate such limitations, population modelers may use extrapolative methods (Taylor, 1995; Boyce, 2002). Detailed examinations of the consequences of using extrapolative methods are, however, seldom done.

Population models usually predict that the stability of turtle populations is sensitive to changes in the survivorship of adults (Chaloupka, 2002; Blamires et al., 2005; Spencer and Thompson, 2005; Enneson and Litzgus, 2008). Information about survivorship across all life stages, however, is often not available (Chaloupka, 2002; Enneson and Litzgus, 2008). Survivorship at the hatchling or juvenile stage is notoriously difficult to assess in turtles because of extremely low encounter rates. Researchers may thus apply one of five extrapolative techniques when hatchling or juvenile survivorship cannot be directly determined: (1) incorporation of the hatchling or juvenile stage with the egg stage (Blamires et al., 2005); (2) estimation of survivorship at the hatchling or juvenile stage from other demographic parameters, such as adult survival or growth (Pike et al., 2008; Mogollones et al., 2010); (3) estimation of hatchling or juvenile survivorship on the basis of that of a phylogenetically or ecologically analogous surrogate (Mitchell, 1988; Blamires et al., 2005; Pike et al., 2008); (4) estimation of hatchling or juvenile survivorship on the basis of assessment of the ecological factors that influence survivorship, e.g., the presence of predators; or (5) extrapolation of survivorship from a measurable population growth parameter (Enneson and Litzgus, 2008).

The freshwater turtle *Myuchelys georgesi* (previously called *Elseya georgesi* by Cann, 1998 and Blamires et al., 2005, and *Elseya latisternum* by King and Heatwole, 1994a,b) has a range confined entirely to a 30-km stretch of the Bellinger River and a few isolated pockets of the nearby Orara River (Cann, 1998) in New South Wales, Australia (152°47′E, 30°26′S to 152°30′E, 30°27′S, datum = AMG66; Fig. 1). A recent population assessment using life table analysis found that the *M. georgesi* population is not likely to decline over 20 generations but its restricted range renders it vulnerable to factors that alter its demographic structure, such as the introduction of foxes (Blamires et al., 2005). In making this assessment, however, few free-swimming hatchling turtles were captured, so hatchling capture data were incorporated into estimates of juvenile survivorship. Additionally, the influence of habitat use across life stages was not considered. Thus, it is possible that the assessment underestimated the extinction threat and may have misidentified threatening processes. Accordingly, we used previously published information (Blamires et al., 2005; Spencer et al., 2007; Georges et al., 2011) to reassess the population dynamics of *M. georgesi* in the Bellinger River taking into account its habitat use, which we assessed using capture–mark–recapture data at water holes with classified depths. We examined the stomachs of catfish specimens to establish if they are potentially a significant predator of turtles. We also counted the number and estimated the size of catfish seen while sampling turtles in the Bellinger River to confirm that they are found in the same locations as turtles.

We used the above information to first determine whether water hole position or depth, used as a proxy of habitat selection, and predator presence influenced survivorship of turtles (stratified by life stage). We then developed a revised population viability model for *M. georgesi* to further explore the consequences of habitat selection and predator presence on population stability.

MATERIALS AND METHODS

We collected *M. georgesi* by snorkel diving or hoop trapping along a 30-km stretch of the Bellinger River upstream from Thora, New South Wales (Fig. 1), during annual or biannual trips lasting 5–21 d to the site between 1988–1991 and 2000–2008 (see King and Heatwole, 1994a,b; Blamires et al., 2005; Spencer et al., 2007; Georges et al., 2011). Individual turtles were marked by a combination of three notches in the marginal scutes to be readily identified when recaptured (Blamires et al., 2005). Straight-line carapace and plastron lengths and widths were measured on each turtle caught using calipers.

Fɪɢ. 1.—Location of the Bellinger River, showing the 30-km stretch along which *Myuchelys georgesi* is found and the divisions between the regions we designated as upstream, midstream, and downstream in our analyses. The numbers (1–16) represent the 16 water holes where > 95% of the marked *M. georgesi* were captured. Redrawn from www.environment.gov.au/ieo/bellinger/maplg.htm

Each turtle was weighed (±1 g) on an electronic balance and sex identified (males identified as turtles > 115 mm plastron length with obviously larger and thicker tails). All turtles < 115 mm plastron length were designated as juveniles (Blamires et al., 2005). We recorded annual capture histories for all individuals, with 0 denoting that the individual was not captured in a given year and 1 denoting that an individual was captured in a given year. From these we calculated capture probabilities (the probability of an animal that is alive at time t being captured at that time $t + 1$) using the program RELEASE (Bailey et al., 2004; Lind et al.,

2005). The capture location for each turtle was recorded as belonging to one of 21 water holes that were identified on a topographic map (Bellinger River Map NC19, ABC Maps, Coffs Harbour, NSW). Much of the demographic data obtained from our surveys has been analyzed and published (NSW National Parks and Wildlife Service, 2001; Blamires et al., 2005; Spencer et al. 2007; Georges et al., 2011). The data used to construct the following models were derived principally from these publications. Catfish observations were based on detailed notes that we made while snorkeling before collecting turtles.

Modeling Habitat Use

The 30-km stretch of the Bellinger River where *M. geogresi* has been sampled is a continuous watercourse with water holes of varying depth interspersed with fast-flowing rocky reaches. Underwater visibility in the Bellinger River is clear to > 10 m, so it is unlikely that individuals of *M. georgesi* were any easier or harder find in any particular water hole. Generally, turtles were found inactive at the bottom of the water holes. There are no physical barriers between the water holes so we have no reason to suspect that *M. geogresi* has difficulty moving between water holes under normal conditions. We identified, numbered (1–16), and estimated the surface area of the 16 most regularly sampled water holes (Fig. 1), in which > 95% of all turtles were found, using a 1:25,000 topographical map. We verified the locations of the water holes by ground-truthing using a hand-held global positioning system (Magellan, Smyrna TN, USA). We used two determinants of habitat selection: (1) water hole position (upstream, midstream, or downstream) and (2) water hole depth (shallow, moderate, or deep).

The Bellinger River flows continuously and is particularly rapid after heavy rains, owing to its elevation at the headwaters ($\sim$1300 m). Accordingly, it might be supposed that it is more common for turtles to disperse from upstream to downstream rather than from downstream to upstream. We thus identified the locations of the 16 water holes as occurring upstream, midstream, or downstream according to their distance from the township of Thora measured on the topographic map. Upstream water holes were located within 10 km from Thora (five locations), midstream water holes were located $\sim$10–20 km from Thora (six locations), and downstream water holes were located > 20 km from Thora (five locations; Fig. 1). The relative density of turtles at each site was estimated, accounting for water hole surface area, by a Jolly–Seber estimate of abundance, on the basis of the recapture rates at each water hole (Borchers et al., 2002). The ratio of male, female, and juvenile *M. georgesi* caught across the 16 sites did not differ significantly from that of the population as a whole (log-likelihood ratio test; $G = 4.70$; df $= 15$; $P = 0.87$), so we did not differentiate between sex or age in our estimates of turtle abundance at each water hole.

To ascertain if water holes were preferably used on the basis of their depths (Haxton and Berrill, 1999), we classified each site as either shallow, moderate, or deep on the basis of visual evaluations while snorkel diving within each water hole. The holes that were classified as shallow were no more than 2 m deep and had a soft sediment substrate and an abundance of river weed and submerged algae. The holes classified as deep sites had a bare and rocky substrate that was barely visible (5–10 m deep) when snorkeling at the surface. Water holes classified as moderate were intermediate of these extremes. All water holes were easily classified into one of these three categories. We considered only depth as a differentiator between water holes.

We performed a Yates-corrected chi-square goodness-of-fit analysis to determine if turtle abundance at each water hole was proportional to the apportionment of total surface area each water hole represented. Standardized selection indices (B_i) were calculated for *M. georgesi* using Neu's method (Manly et al., 2002) for the 16 water holes. Bonferroni-corrected 95% confidence intervals were calculated and B_i values lying outside the confidence intervals were regarded as indicative of preferential use (Manly et al., 2002). Chi-square goodness-of-fit tests were performed and 95% confidence intervals calculated to ascertain if turtles preferentially used either: (1) upstream, midstream, or downstream, or (2) shallow, moderate, or deep water holes (indicated by their distribution difference to the apportionment of surface area of each water hole). We assumed that all water holes were available for all turtles to use and any skew in the distribution of turtles was a result of the turtles preferring to use specific water holes (Hjermann, 2000).

Identification of Water-based Predators

We considered catfish (*Arius graeffei* and *Tandanus tandanus*) the most probable water-based predators of hatchlings and juveniles as they were the most commonly sighted predatory fish in the river. To ascertain whether

catfish prey on turtles, we dissected and removed the stomach contents of 48 catfish (37 *A. graeffei* and 11 *T. tandanus*) at the Australia Museum, Sydney. There were no catfish specimens available from the Bellinger River in the Museum, so we dissected catfish that were caught in the nearby Clarence River as it contains similar-sized turtles (principally *Emydura macquarii*). We removed and preserved (in 90% ethanol) the stomach contents of the catfish at the Australia Museum before weighing (on an electronic balance) and identifying, to make inferences about their feeding, each stomach item as: turtle, other vertebrate, invertebrate, or not animal at the University of Sydney. We categorized the catfish into two size classes: small (length = 250–400 mm) and large (length = 400–500 mm); *T. tandanus* was not represented in the small size class. We separately analyzed and compared (using chi-square tests of homogeneity) the stomach contents of these two size classes to determine if predation threat to turtles varied with catfish size.

We noted the presence and estimated the length, according to their size relative to landmarks of known size, e.g., boulders and logs, of any catfish sighted (all *T. tandanus*) during snorkeling bouts in the Bellinger River and noted the water hole in which they were found. Because all of the catfish observed were estimated at > 250 mm length, we included all catfish observations in our subsequent model. As the water holes were thoroughly examined during surveys and underwater visibility in the river was exceptional at all times, it was unlikely that our surveys failed to detect any catfish that were present in any water hole.

Modeling Habitat Use × Predation

We used a three-way (x,y,z) log-linear model, using the program R (Zeileis et al., 2008), to determine the influence of water hole (x variable), classified as shallow, moderate, or deep (as described above), and catfish presence (y variable) on the response variable "turtle abundance" (z variable), quantified as the number of turtles caught per hour of sampling. As the majority of sites had either a single catfish or no catfish, catfish presence was classified as either "present" or "absent."

The model tested four hypotheses: (1) that catfish presence influences turtle abundance and water-hole depth influences catfish presence ($xy + yz$), (2) that water hole depth influences turtle abundance and catfish presence independently ($xy + xz$), (3) there are three-way interactions between water-hole depth, catfish presence, and turtle abundance ($xy + xz + yz$), or (4) the null hypotheses that water-hole depth, catfish presence, and turtle abundance vary independently. Because hatchlings/juveniles and adults may use habitats differently, have different vulnerabilities to predators, and their survivorship affects population growth differently (Blamires et al., 2005; Spencer and Thompson, 2005; Edge et al., 2009), we separately analyzed the influence of habitat selection × predation on hatchlings/juveniles and adults. We used G^2 goodness-of-fit tests to identify significant interactions in the model and an Akaike information criterion score (AIC_c) to identify the model best fitting the data. We performed Levene's tests and Kolmogorov–Smirnov tests to check for homoscedasticity and conformation to normality of the data before analyses.

Population Assessment

We re-estimated λ using the estimates of maximum and minimum egg survivorship probability made by Blamires et al. (2005), and incorporating the following into the model: (1) survivorship probabilities for adult and juveniles that accord to the conditions implied as important for inducing variations in turtle abundance by the habitat use × predation threat model. (2) Separate estimates of hatchling and juvenile survivorship probability, both in water holes where catfish were present ($n = 11$) and water holes where catfish were absent ($n = 5$), ascertained by separate assessment of the mark–recapture data of all turtles < 60 mm plastron length (predicted to be < 1 yr of age; Blamires et al., 2005) and 60–115-mm plastron length. The survivorship probabilities were calculated from the capture histories for each stage by a Jolly–Cormack–Seber goodness-of-fit model with the model of best fit determined by AIC_c score using RELEASE (Blamires et al., 2005).

We extended the population viability model of *M. georgesi* in the Bellinger River (Blamires

Table 1.—Standardized selection indices (B_i) for *Myuchelys georgesi* according to maximum depth of individual water holes (shallow = maximum depth < approximately 2 m deep; moderate = max. depth approximately 2–5 m deep; deep = maximum depth > 5 m deep).

Feature	Proportion of total area	Turtle abundance (captured/episode)	Habitat index (B_i)	95% CI (upper limit)	95% CI (lower limit)
Depth:					
Shallow	26.31	20.84	0.35	0.44	0.21
Moderate	56.26	25.59	0.20°	0.52	0.28
Deep	17.43	17.50	0.45°	0.38	0.16
Total	100.00	63.93	1.00		

° Denotes selection as values lie outside the 95% confidence interval (CI).

et al., 2005) to incorporate the influence of preferred water-hole use and predator presence. We used the previously estimated fecundity schedules (the average number of female offspring produced by each adult female; $b[x]$) for *M. georgesi* in the Bellinger River (Blamires et al., 2005) and re-estimated survivorship schedules (proportion of individuals surviving to each stage; $\ell[x]$) and generation time (minimum reproductive age; G) from the stage-based survivorship probabilities to estimate the density-dependent population growth rate (λ) of *M. georgesi* using the equation (Gotelli, 2001):

$$\lambda = e^r$$

where r is the intrinsic rate of population growth and is calculated by the equation:

$$r = \frac{\ln(R_o)}{G}$$

The reproductive rate (R_o) was calculated as:

$$R_o = \sum \ell(x)b(x)$$

where $\ell(x)$ and $b(x)$ represent the survivorship and fecundity schedules at each life stage respectively.

Results

We marked 506 turtles (391 adults; 221 females and 170 males, 75 juveniles and 40 hatchlings) and recaptured 204 (156 adults, 33 juveniles and 15 hatchlings) at least once. We estimated capture probability values of 0.45, 0.35, 0.44, and 0.26 adult females, adult males, juveniles, and hatchlings respectively. The different capture probabilities across life stages, thus, may account for some of the variations in capture success between life-

history stages. The number of *M. georgesi* captured per sampling episode was disproportional to the relative surface area of each water hole ($\chi^2 = 76.04$; df = 15; $P < 0.001$) as a consequence of preferential use of sites 1, 2, 10, 11, and 12. Nonetheless, when water-hole use was analyzed according to location (downstream, midstream, or upstream) the number of turtles caught conformed to the degree of surface area available at each location ($\chi^2 = 4.17$; df = 2; $P = 0.12$). Thus, it does not seem to be any more common for turtles to disperse upstream to downstream than downstream to upstream. When water-hole use was analyzed according to depth (shallow, moderate, or deep), there was a disproportionate number of turtles caught relative to the surface area of each water hole ($\chi^2 = 7.58$; df = 2; $P = 0.02$). We interpreted this as resulting from preferential use of the deep and moderate water holes (Table 1).

The stomach contents in the two size classes of catfish differed ($\chi^2 = 107.53$; df = 2; $P < 0.0001$). The stomachs of large fish tended to contain a greater proportional mass of turtle hatchlings and one item was identified as deriving from *Bos taurus*. Turtles were the most abundant items in the stomachs of the large catfish (Fig. 2); hence all catfish > 400 mm in length may be potential predators of hatchling or juvenile turtles. Our log-linear analysis identified the model best fitting our data as a three-way interaction between hatchling/juvenile turtle abundance, water-hole type (deep, moderate, or shallow), and catfish presence. Conversely, adult turtle abundance was affected by water-hole type independent of catfish presence (Table 2).

We re-estimated survivorship under the specific conditions implied by the habitat use × predation model, and recalculated λ for the
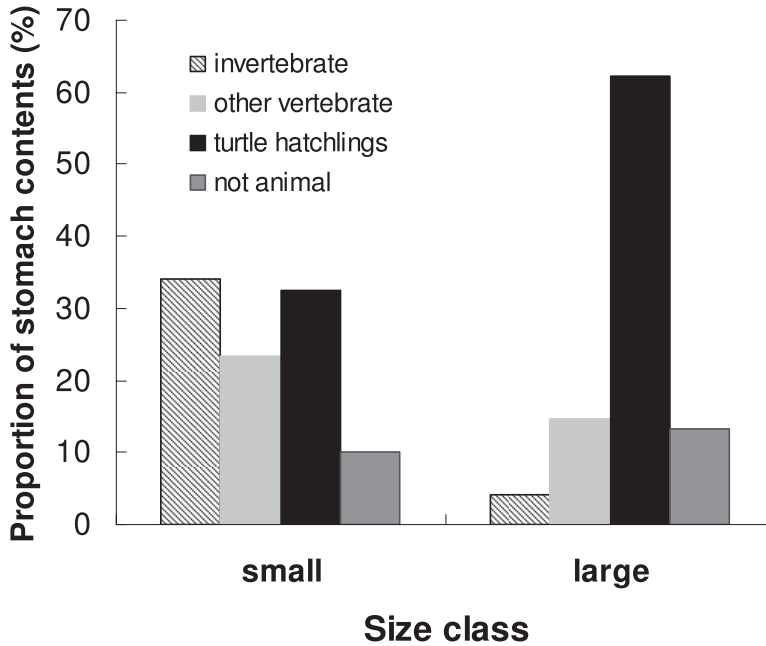
FIG. 2.—Comparative proportion of insects, crustaceans, other invertebrates, fish, turtle hatchlings, and other items found in the stomach of small ($n = 23$) and large ($n = 25$) catfish, *Arius graeffei* and *Tandanus tandanus* (*T. tandanus* represented in "large" group only), from the Clarence River. The proportions between the size classes significantly differed (chi-square test: $P < 0.0001$).

maximal and minimal egg survivorship values calculated by Blamires et al. (2005). For hatchlings in shallow water we estimated a survivorship value of 0.21 ± 0.05, but too few recaptures prevented us from further dividing hatchling survivorship values to account for the presence or absence of catfish. We re-

Table 2.—Results of a three-way log-linear model determining the influence of water-hole depth (x), classified as shallow, moderate, and deep; catfish presence (y), classified as present or absent; on turtle abundance (z), defined as the number of turtles caught per sampling effort.

Model	df	G^2	P	AIC$_c$
Juveniles				
$xy + yz$	6	1.64	0.27	1.21
$xz + xy$	6	2.195	0.20	1.63
$xz + xy + yz$	3	43.39	< 0.0001	32.00*
Null	0	0		
Adults				
$xy + yz$	6	0.84	0.03	0.78
$xz + xy$	6	12.67	0.45	10.92*
$xz + xy + yz$	3	0.36	0.90	0.42
Null	0	0		

* Indicates the model best fitting the data as shown by AIC$_c$.

estimated λ for *M. georgesi* under the following conditions: (A) adults in deep or moderate water holes, (B) adults in shallow water holes, (C) hatchlings and juveniles in deep or moderate water holes in the presence of catfish, (D) hatchlings and juveniles in deep or moderate water holes but not in the presence of catfish, (E) hatchlings and juveniles in shallow water holes in the presence of catfish, and (F) hatchlings and juveniles in shallow water holes but not in the presence of catfish. Deep and moderate water holes were included as a single water-hole type in the analysis because they were equally preferred by turtles over shallow water holes. On all occasions the derived conditional survivorship estimates and λ values were lower than those previously reported (Blamires et al., 2005; Table 3). Only for the highest egg survivorship values, with adults in deep or moderate water holes, or hatchlings and juveniles in deep or moderate water holes in the absence of catfish, did we predict the population to be stable or increasing (Fig. 3). Events that

Table 3.—Survivorship probabilities, with confidence limits in parentheses, and best-case and worst-case (according to maximum or minimum egg survivorship) population growth rate (λ) values under the conditions: no change (= values of Blamires et al., 2005), or if adults are in deep water, adults are in shallow water, juveniles are in deep water with catfish, juveniles in deep water without catfish, juveniles were in shallow water with catfish, juveniles in shallow water without catfish.

		λ	
Condition	Survivorship probabilities	Best-case values	Worst-case values
No change		1.15	0.96
Adults in deep water	0.68 (0.61–0.74)	1.09	0.97
Adults in shallow water	0.63 (0.56–0.69)	0.96	0.92
Juveniles in deep water with catfish	0.50 (0.42–0.58)	0.94	0.88
Juveniles in deep water without catfish	0.58 (0.52–0.63)	1.07	0.95
Juveniles in shallow water with catfish	0.44 (0.37–0.50)	0.89	0.83
Juveniles in shallow water without catfish	0.56 (0.51–0.6)	0.94	0.90

expose adults or juveniles to shallow water or hatchlings and juveniles to catfish, accordingly, may cause the *M. georgesi* population to decline.

Discussion

We extended a derived demographic model for the range-restricted freshwater turtle *M. georgesi* (Blamires et al., 2005) to examine the influences of habitat use and the impact of predatory fish on population dynamics. We also incorporated an estimate of hatchling survivorship and a re-evaluation of juvenile survival in the model. The adjusted model showed that water-hole depth influences adult survivorship and the interaction of water-hole depth and fish predation influences juvenile and hatchling survivorship.

We found that *M. georgesi* prefers to use moderately deep to deep (> 2 m deep) water holes as adults, and hatchlings and juveniles have greater survivorship in moderate to deep water holes devoid of catfish. Our model predicted that should adults, juveniles, or hatchlings become restricted to shallow water or exposed to catfish predators over the long term, the *M. georgesi* population could decline to an extent that it could become extinct (cf. Blamires et al., 2005). We used water surface area to estimate the availability of benthic surface area for turtles as this parameter was estimable from a topographic map. This method may have underestimated benthic surface area availability and, hence, the extent of water-hole use. Nevertheless, the Bellinger River bed is either flat and parallel
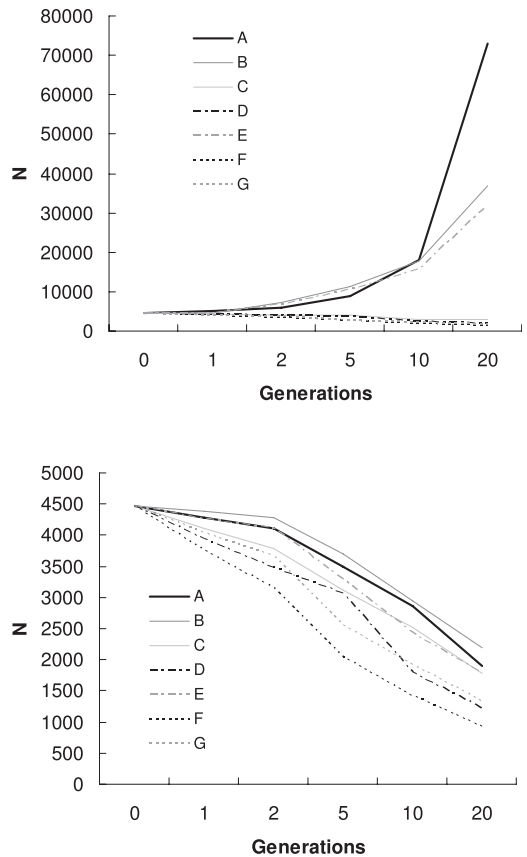

Fig. 3.—Projected population size (*N*) of *Myuchelys georgesi* under the best-case (upper panel) and worst-case (lower panel) scenarios of Blamires et al., 2005. Conditions applied in each instance are: A = projections of Blamires et al., 2005, B = if adults are only in deep water, C = if adults are only in shallow water, D = if juveniles are in deep water exposed to catfish, E = if juveniles are in deep water not exposed to catfish, F = if juveniles are in shallow water exposed to catfish, and G = if juveniles are in shallow water not exposed to catfish.

to the surface, especially among the shallow water holes, or narrower at the bottom than the surface, especially among the deep water holes. Hence the benthic surface area was not likely to have been underestimated for any of the water holes. Since it was evident to us during sampling that there were more turtles present in the deeper water holes than shallower water holes, we are confident that our conclusion that *M. georgesi* selects the deep water holes holds.

We showed here that the previously overlooked impacts of water-hole selection by adult and juvenile *M. georgesi* and the exposure of hatchlings or juveniles to water-based predators may have a negative effect on λ to the extent that the population may decline in certain circumstances. Turtle demographic models, however, usually show λ to be more sensitive to survivorship in the adult life stage than during the juvenile or hatchling stages in turtles (Heppell et al., 1996; Blamires et al., 2005; Enneson and Litzgus, 2008). It is for this reason that efforts to conserve turtles have concentrated on preventing land-based predators, such as foxes, preying on nesting females (Mitchell and Klemmens, 2000; Blamires et al., 2005; Spencer and Thompson, 2005). Hatchling and juvenile survivorship probabilities are, nevertheless, often difficult to estimate because of low capture and recapture rates. Hatchling and juvenile survivorship are often extrapolated from other demographic information, which may be equally problematic in turtles. The true impact of survivorship in the early life stages may thus be misrepresented in some instances. We found that juvenile and hatchling *M. georgesi* had lower capture and survivorship probabilities than adults. However, we sampled only a small number of hatchling or juvenile turtles compared with adults, so the abundance and survivorship probabilities of juveniles and hatchlings may have been underestimated here. Our estimates of hatchling and juvenile survivorship when exposed to catfish should accordingly be considered preliminary until more intensive surveys marking and recapturing more juveniles and hatchlings as well as catfish, are done for verification of the derived values.

Our examination of the stomach contents of catfish specimens from the Clarence River showed that all catfish > 250 mm length are carnivorous, opportunistic predators or scavengers. We used these findings and our observations of catfish to hypothesize that catfish may indeed be consuming hatchling and juvenile turtles in the Bellinger River. One of the species of catfish whose stomach contents we examined, *T. tandanus*, was regularly seen in the Bellinger River, and we see no reason to expect that this catfish does not consume hatchling and juvenile turtles in the Bellinger River. However, the stomach contents of catfish caught in the Bellinger River need to be sampled to test this hypothesis.

This study is one of few to assess freshwater turtle population dynamics by incorporating an availability-based habitat assessment with a categorical habitat model and predator distributions (see also Compton et al., 2002). Our analyses, however, considered water-hole selection only at a course-grained spatial scale (i.e., across water holes). We concede that selection at finer-grained spatial scales may occur (Morin, 1999; Spencer and Thompson, 2003; Carriere and Blouin-Demers, 2010; Rasmussen and Litzgus, 2010), and this may further influence the estimation of *M. georgesi* population dynamics. Within water holes turtles may prefer sites that supply certain food or provide opportunities for thermoregulation or shelter (Carriere et al., 2009; Carriere and Blouin-Demers, 2010; Rasmussen and Litzgus, 2010). *Myuchelys georgesi* is carnivorous as an adult (Allanson and Georges, 1999) and a greater abundance and diversity of insects and fish are likely to be found in the shallower, warmer water holes (Ward, 1982; Declerck et al., 2005). The distribution of food does not appear to drive their water-hole selections. *Myuchelys georgesi* may select the deeper water holes because the rockier substrate provides a refuge from predators or they enable them to better regulate their body temperature. More studies of the specific services supplied by the water holes, however, are needed to ascertain the microhabitat features that turtles select for, or against, and whether such selection affects their population dynamics.

Conservation Implications

We have extended a demographic model for the turtle *M. georgesi* (Blamires et al., 2005) to explicitly ask: what will be the impacts on the population if, hypothetically, all adults or juveniles were to be exposed to certain habitats or predators? We found that if all adults or juveniles were to be exposed to shallow water or catfish predators (or both) the *M. georgesi* population would probably decline. Currently, adults and juveniles seem able to use deep water holes devoid of catfish, so the population is probably stable (as suggested by Blamires et al., 2005). However, the status of *M. georgesi* may change if the conditions were to suddenly change. We did not herein assess the likelihood of adult or juvenile *M. georgesi* becoming suddenly exposed to shallow water or catfish predators, and we are unaware of any projections predicting events, such as changes to the river flow dynamics or topography, that might induce such exposure. Some plausible scenarios, nonetheless, are worth considering so they can be monitored as a component of the river's ongoing management. One threatening scenario might be a shallowing of the river by drought, expansion of nearby towns, flood-induced silting, or landslides off the Dorrigo Range exposing *M. georgesi* adults and juveniles to shallow water or more predators. Another might be an increase in catfish abundance within the river brought about by sudden growth in the catfish population as a consequence of local (e.g., higher water temperature), or global (e.g., changes in oceanic current), conditions favoring enhanced catfish fecundity or recruitment rates (Lake et al., 2010). Further, changes or alterations to the turtle or catfish habitats may force resource overlaps between catfish and turtles and result in greater predation on turtle hatchlings and juveniles.

We conclude that water-hole preference and perhaps catfish predation, factors not incorporated into our initial population model, are potentially detrimental to the freshwater turtle, *M. georgesi*. We also conclude that their true risk of extinction may have been underestimated as survivorship probabilities at the hatchling and juvenile life stage are influenced by water-hole depth and perhaps catfish presence. Our extended model suggests that if adults are exposed to shallow water, or juveniles are exposed to shallow water and catfish, the *M. georgesi* population may decline. The specific threats to *M. georgesi* imposed by these factors should be further assessed in the Bellinger River while identifying and monitoring the availability of *M. georgesi* habitats. More surveys and modeling need to be done to assess the threats imposed by catfish and other water-based predator populations. Broadly, our study emphasizes the importance of habitat use on animal population dynamics, demonstrates how traditional estimates of hatchling survivorship may underestimate λ in long-lived organisms in particular circumstances, and highlights the importance of reassessing demographic data under various scenarios to evaluate the threats to range-restricted or rare animals.

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