

Reproductive and Nesting Ecology of the Yellow-Blotched Map Turtle, *Graptemys flavimaculata*: Implications for Conservation and Management

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We studied the reproductive and nesting ecology of the Yellow-Blotched Map Turtle (*Graptemys flavimaculata*) from 1993–1994 and from 1996–1997 on the Pascagoula River in southeastern Mississippi. This species has undergone a recent decline leading to its listing as Threatened under the U.S. Endangered Species Act. We found three distinctive features of the biology of this population: a relatively low reproductive frequency compared with most other map turtles (maximum of 1.16 clutches/female), a very high level of nest mortality caused by river flooding and fish crow predation (90% mortality in some years), and an unexpectedly high level of nesting in shaded areas along the riverbank, perhaps in response to human disturbance on and near sandbars. Our data suggest that, in the absence of extraordinarily high adult survival, this population will decline because of low recruitment. We suggest a series of specific strategies to reverse these declines, including better law enforcement to protect adult turtles, public education, and possibly, protection of nests on the nesting beaches.

LIKE other species of turtles around the world, many of the 12 species of the North American genus *Graptemys* are impacted by both habitat alteration and collecting for the pet trade (Ernst et al., 1994; Lindeman, 1998). In addition, only three species in this genus (*Graptemys geographica*, *Graptemys pseudogeographica*, and *Graptemys ouachitensis*) are geographically widespread; the other species have a geographical range limited to one or a few river systems, a factor that may also contribute to their decline. The U.S. Fish and Wildlife Service has already listed two species with such a restricted range (*Graptemys flavimaculata* and *Graptemys oculifera*) as Threatened under the Endangered Species Act, and other species in this genus might also warrant such protection (Lindeman, 1998).

The Yellow-Blotched Map Turtle (*G. flavimaculata*) occurs only in the Pascagoula River in southern Mississippi and its major tributaries, the Leaf, Chickasawhay, and Escatawpa Rivers. The preferred habitat appears to be characterized by moderate currents, abundant basking structures, sandbars for nesting, and an open canopy that allows sunlight to penetrate to the water's surface for several hours per day (Federal Register, 1991). The Yellow-Blotched Map Turtle is absent from some areas of the Pascagoula River system where it formerly occurred in abundance. As a result, the species was listed as Threatened in 1991 (Federal Register, 1991). The reason(s) for this apparent decline is not known, but it may have involved a disruption of the reproductive biology of local populations (Federal Register, 1991). Other potential causes

of a decline include flooding of the sandbars where map turtles nest, extremely high rates of nest predation, and water quality degradation (Federal Register, 1991; Ernst et al., 1994).

Until the mid-1990s, relatively little published information was available on the life history and ecology of *G. flavimaculata* (Cagle, 1954; Cliburn, 1971). Detailed information is now available on population structure (R. Jones, unpubl. data), movement patterns via radiotelemetry (Jones, 1996), habitat use (Lindeman, 1998), and female and male hormonal cycles (Shelby et al., 2000; Shelby and Mendonca, 2001). In this paper, we examine the nesting and reproductive ecology of the largest known population of *G. flavimaculata*. Our primary goals are to determine whether (1) there are unusual features of the reproductive and nesting ecology of this species that may have led to the apparent decline and (2) to use these data to help formulate a management plan for this species.

MATERIALS AND METHODS

All research was conducted on the Pascagoula River in Jackson County, Mississippi, mainly in and adjacent to the Ward Bayou Wildlife Management Area (Fig. 1), from May 1993 to August 1994 and from April 1996 to August 1997. As far as is known, this area contains the largest concentration of Yellow-Blotched Map Turtles in any river system (R. Jones, pers. comm.). In all, we examined female reproductive biology and nesting during four separate reproductive seasons (1993, 1994, 1996, and 1997).

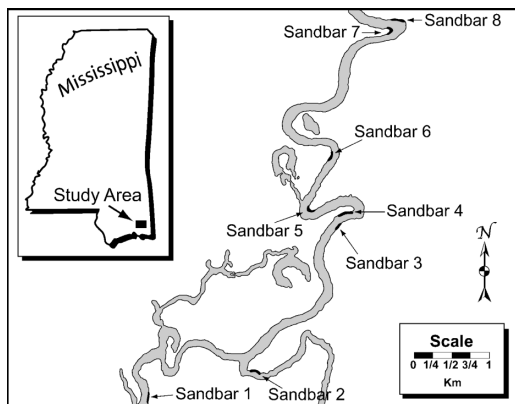


Fig. 1. Map of the study area, showing the major sandbars mentioned in the text.

Capture and processing methods.—Turtles were captured primarily with basking traps, which consisted of 2.54-cm black plastic crawfish wire. Traps were approximately $100 \times 50 \times 45$ cm in size and were nailed or tied just below the water's surface under logs and branches that *G. flavimaculata* used as basking sites. We recorded straight-line maximum carapace length, maximum carapace width, midline plastron length, and carapace height to the nearest 0.1 cm using aluminum calipers. Body mass was recorded to the nearest 0.5 g using Pesola scales. (For brevity, only carapace length is reported here, but data on other measurements are available upon request.) All turtles were given a permanent mark using the method of Cagle (1939) and released at the point of capture.

Reproductive ecology.—We used radiography (X-rays) to determine the clutch size of living turtles without sacrificing them. All females captured in the field were palpated to determine whether they were gravid. Any females suspected to be gravid were taken to a local veterinarian for radiography. Clutch frequency was determined in two ways. First, we used radiography of individual females captured on multiple occasions. Gibbons and Greene (1979) and Hinton et al. (1997) both reported no detrimental effects on the females, eggs, or embryos subjected to this treatment. In addition, we used ultrasound analysis in 1997 as a means of comparing our data from radiography. Using equipment at the Auburn University Veterinary School, we examined a series of adult-sized females from Ward Bayou every two weeks from May through August 1997. Each female was marked and measured, then examined via ultrasound to determine the presence of either de-

veloping follicles or shelled eggs or both. We classified follicles by size as follows: follicles larger than 15 mm diameter were classed as large follicles that would almost certainly be shelled and laid as eggs during 1997. Follicles between 10 and 15 mm were medium follicles that would likely result in eggs during 1997, and follicles smaller than 10 mm were classified as small follicles, which may or may not be shelled and laid during 1997. The simultaneous presence of shelled eggs and large or medium-sized follicles was taken as evidence of a female, which would produce more than one clutch during 1997. We caution that this is an overly optimistic scenario, since Licht (1984) has noted that even the presence of developing follicles does not mean that those follicles will be laid as eggs during a particular year. Thus, our classification scheme likely overestimates the probability of multiple clutches in *G. flavimaculata*.

Nesting ecology.—Intact (nonpredated) nests of *G. flavimaculata* were located primarily by following the distinctive track of this species along sandbars to sites where a concentrated ground disturbance occurred, then carefully excavating the nest chamber. Nest surveys were conducted 1–3 times per day, usually starting in the mid-morning. In addition, we observed nesting females from a blind located either on the nesting beaches or across the river from the nesting beaches and used a spotting scope and binoculars to observe both nesting behavior and the presence of any predators. After oviposition the nest chamber was excavated (if necessary) and the following variables recorded for each intact nest: date, location, distance of nest from water and vegetation, height above water, substrate type, number of eggs, air temperature, surface temperature, and shade condition (e.g., full sun, partial shade, full shade). Nest depth was recorded from the soil surface to the top each of each clutch. In addition, partial or complete measurements were taken on freshly destroyed nests, the amount of data depending on the time elapsed since the nest was destroyed. For determination of predation rates in 1996–1997, some nests were left completely undisturbed except for a stake to indicate position. Finally, a selected number of freshly constructed nests were covered immediately with wire mesh cages (1 cm² hardware cloth) to deter predators. These cages were buried several centimeters below the sand to lessen the probability of disturbance by humans.

We calculated two measures of nest survival: Nesting success is the percent of total nests that pro-

TABLE 1. DATES FOR FINDING THE FIRST AND LAST GRAVID FEMALES, THE FIRST AND LAST FRESH NESTS, AND THE OVERALL LENGTH OF REPRODUCTIVE SEASON FOR YELLOW-BLOTCHED MAP TURTLES, *Graptemys flavimaculata* ON THE PASCAGOULA RIVER IN MISSISSIPPI. The reproductive season is defined as the longest period between the first fresh nest or gravid female and the last fresh nest or gravid female.

Year	First gravid female	First fresh nest	Last gravid female	Last fresh nest	Reproductive season
1993	18 May	26 May	3 August	8 August	83 days
1994	24 May	20 May	9 August	9 August	82 days
1996	18 May	22 May	31 July	5 August	80 days
1997	28 May	20 May	14 August	12 August	87 days

duced at least one hatchling; Hatching success is defined as the percent of eggs that hatched divided by the total number of eggs monitored in successful nests. Thus, hatching success is a measure of the percent of total eggs that have survived flooding and predation. All nests were monitored through the late summer and early fall until all nests had hatched or were determined to be nonviable.

Data processing and statistical analysis.—Data were entered on a spreadsheet and statistical analysis was done on SYSTAT 10.0 (SPSS Inc., Chicago, IL). We used either analysis of covariance (ANCOVA), regression analysis, or contingency table analysis to compare variables among years or sites. In all ANCOVA results reported, differences among groups are caused by differences in γ -intercepts and not differences in slopes. Where necessary, data were transformed to a log base 10 scale to satisfy assumptions for parametric tests. All means are followed by ± 1 SD. Alpha level is 0.05 unless stated otherwise.

RESULTS

Length and timing of the reproductive season.—Sampling was conducted from 6 May through 10 August 1993, 20 May through 30 August 1994, 11 April through 18 October 1996, and 9 April through 17 October 1997. During that time, we examined 641 adult females (> 14.9 cm carapace length) for reproductive condition or fecundity or both (1993 = 117 females, 1994 = 144, 1996 = 204, 1997 = 176). The length of the reproductive season (defined as the longest period between the first fresh nest or gravid female and the last fresh nest or gravid female) was consistent among years, with both the first gravid female and the first fresh nest found between 18 and 28 May (Table 1). The last gravid female and the last fresh nest were found from 31 July through 14 August. Thus, the reproductive season of *G. flavimaculata* lasted 80–87 days (Table 1).

Fecundity.—We determined the clutch size (CS) of 134 individual turtles from 1993–1996 (clutch size was not determined in 1997 since ultrasound could not be used to accurately count numbers of eggs). The overall mean CS for the three study years was 4.7 ± 1.07 (range = 3–9, $n = 134$). Mean CS was 4.8 ± 0.92 ($n = 22$) in 1993, 4.8 ± 1.06 ($n = 44$) in 1994, and 4.7 ± 1.14 in 1996 ($n = 68$). There was no significant difference in CS among years with the effects of female size removed via ANCOVA ($F = 0.13$, $df = 2, 130$, $P = 0.88$).

The mean carapace length (CL) of gravid females varied little among years (19.1 ± 1.58 cm [$n = 22$] in 1993, 19.1 ± 1.29 [$n = 44$] in 1994, and 19.0 ± 1.37 [$n = 68$] in 1996). The smallest gravid female had a CL of 15.7 cm, which is slightly larger than the smallest adult female (14.9 cm CL) reported by Cagle (1954). For 1993, 1994, and 1996 combined, we found a positive and significant relationship between CS and female size ($r^2 = 0.44$, $F = 101.6$, $df = 1, 132$, $P < 0.001$). The regression equation was as follows; $CS = -5.099 + 0.517(\text{CL in cm})$. Thus, there was an increase of approximately one additional egg for each 2 cm increase in CL.

Reproductive frequency via radiographs.—Of the 37 occasions when females were captured at least twice during a single reproductive season from 1993–1997, only six (16.2%) were definitely found to produce multiple clutches as evidenced either by different sized egg counts among captures or, if egg counts was the same, by changes in the numbers of eggs in the left and right oviduct. Thus, even if all females were reproductively active in a given year (see below), the reproductive frequency would be 1.16 clutches/per year. However, of 27 females captured in at least two separate reproductive seasons, only six (22.2%) were gravid in at least two years, 10 (37.0%) were gravid in only one year, and 11 (40.7%) were never found while gravid. Thus, it seems likely that at least some females were not gravid each year.

TABLE 2. SUMMARY OF NEST SURVIVAL IN *Graptemys flavimaculata* DURING 1993, 1994, 1996, AND 1997. Intact nests refers to nests we found by trailing females to nest sites and monitoring the fate of that nest from that point forward. Nests found destroyed refers to nests we located after predators had already destroyed the nest. All intact nests in 1994 were caged to protect them from predators; thus, the predation rates from 1994 are not comparable to other years. See text for explanation of flooding mortality in 1997.

Year	# intact nests monitored	# destroyed by predators	# destroyed by flooding	# successful nests	# nests found destroyed
1993					
uncaged	31	13 (41.9%)	15 (48.4%)	3 (9.7%)	84
1994					
caged	51	0	44 (86.3%)	7 (13.7%)	218
1996					492
caged	19	0	0	15 (78.9%)	
uncaged	13	13 (100%)	0	0	
1997					633
caged	16	0	6 (37.5%)	10 (62.5%)	
uncaged	11	8 (72.7%)	0	3 (27.2%)	

The overall proportion of females found gravid using radiographs varied significantly among years, with 1993 having a significantly lower reproductive frequency than either 1994 or 1996 (contingency table analysis, $\chi^2 = 17.0$, $df = 2$, $P < 0.001$; 1993: 0.263, $n = 95$; 1994: 0.496, $n = 115$; 1996: 0.483, $n = 149$). Because determination of reproductive condition was done using radiographs in 1993–1996 and ultrasound in 1997, we cannot directly compare those data-sets.

Reproductive frequency via ultrasound.—We examined 97 females using ultrasound in 1997. Eight females were classified as nonreproductive, although five of these were collected near the end of the reproductive season. Of the remaining females, 76 (78.3%) had either shelled eggs or one set of developing follicles and were considered to produce only one clutch, 12 (12.4%) had either both eggs or one set of developing follicles or two sets of follicles, and were considered to produce two clutches, and one female (1.0%) was considered to have the potential to lay three clutches. Thus, if all enlarged follicles were actually ovulated and laid, these 97 females had the potential to produce 103 clutches, a clutch frequency of 1.06. If the nongravid females are excluded, the reproductive frequency is 1.15, almost exactly that calculated using radiographs (also see Shelby et al., 2000). However, we recognize that, because ultrasound was used only in 1997, it cannot be compared directly to the remaining years.

Nest site location.—We located 1509 intact or freshly predated nests of *G. flavimaculata* from

1994–1997 (1994 = 115 nests, 1995 = 269, 1996 = 492, 1997 = 633). Of these, 1198 (79.4%) were located along one of six major (large numbers of nests) and three minor (small numbers of nests) sandbars (see Fig. 1), whereas 311 nests (20.6%) were located in small clearings along the banks of the river, usually on a clay bank with a steep slope. However, this overall percentage of nests located along the riverbanks may be misleading, because we did not make a directed effort to search for such nests until 1996. The percent of non-sandbar nests was 19.5% in 1996 and 32.5% in 1997. During 1993, nests along sandbars were built between 1.3–17.1 m from the edge of the water (mean = 8.0 ± 4.00 m, $n = 70$). Nests were built at a mean height above the water of 94.9 ± 28.3 cm (range = 34.2–134.6, $n = 32$; sample sizes differ for different variables owing to the use of intact versus destroyed nests). Mean nest depth from the surface to the top egg was 9.2 cm (range = 5.2–12.4 cm, $n = 50$).

Nest and hatching success.—Of 55 unprotected nests located on sandbars, 34 (61.8%) were destroyed by predators (mainly fish crows, see below) and 15 were destroyed by flooding (27.3%). Only six (10.9%) unprotected nests successfully hatched (Table 2). Sources of mortality of unprotected nests varied among years, with predation rates of 41.9–100% and nest flooding rates of 0–48.4% (Table 2). Nests protected from predators but still exposed to flooding had success rates of 13.7–79.8%. However, the relatively high nest success in 1997 is misleading, since most of these nests were

caged later in the season, after most flooding had subsided. All nests caged prior to early July were destroyed by the effects of Hurricane Danny, so mortality from flooding was still a major problem in 1997. Digging up nests to determine nest depth did not seem to impact predation rates, because predation rates in 1993 (when nests were dug up) were much lower than in 1996 or 1997, when nests were left undisturbed (Table 2).

Hatching success in the wild (percent of eggs from successful nests producing hatchlings) was much higher in 1996 (82.8%, $n = 70$ eggs monitored) than in 1997 (56.1%, $n = 66$ eggs monitored), and the differences between years were significantly different ($G = 11.8$, $df = 1$, $P = 0.001$). Hatching success for 25 eggs (from fresh nests) incubated in our laboratory in 1996 at a constant 27.5 C was 80%, comparable to that seen under natural conditions.

Nest predators.—We found over 1500 predated nests from 1993–1997. The only nest predators directly observed were fish crows (*Corvus ossifragus*), nonnative fire ants (*Solenopsis invicta*), and Speckled Kingsnakes (*Lampropeltis getula*; Brauman and Fiorillo, 1995). Although not observed directly, other signs of predators included raccoons (*Procyon lotor*) and feral pigs (*Sus scrofa*). Because fish crows were the most common predator, we present data on their behavior in some detail.

Typically, fish crows flew over the beach several times an hour. When nesting turtles were on the beach, crows often perched in a tree near the beach. The fish crows patrolled the beach from sunrise to sunset, in both rain and sunshine, but their efforts appeared to be somewhat reduced during rain events (M. Moore, pers. obs.). Frequently the crows targeted their search along the vegetation line (areas that previously contained nests) or along fresh turtle tracks. They were sometimes persistent enough to randomly search the beach in a hit-or-miss fashion for nests by sweeping their beaks across the sand and probing for nest cavities. Fish crows were highly aggressive in attacking nests, sometimes driving away nesting females before they could finish nesting (on two occasions, crows were tenacious enough to grab an egg from a nesting turtle [one *G. flavimaculata* and one *Pseudemys* spp.] before they completed oviposition). Once female map turtles left the nest site, crows often reopened it before she was able to reenter the water only a short distance away (for range and mean distance of nest from shore, see Nest site location).

Nesting and human disturbance.—About 182 hours of observations on nesting behavior were made from 28 May to 13 August 1997, effectively covering the nesting season. Observations were equally divided between those from a blind on Beach 7 (Fig. 1; 28 May through 9 July) and those from a blind located across the river from the beach (10 July through 11 August). Our data suggest that map turtles are highly sensitive to the presence of humans on the nesting beach. The number of nesting attempts made on Beach 7 was over three times lower, whereas the blind was on Beach 7 compared to when it was removed (before removal = 0.136 ± 0.289 attempts/hour, $n = 18$ days; after removal = 0.497 ± 0.706 , $n = 19$ days; Mann-Whitney U -test, $U = 228.0$, $df = 1$, $P = 0.047$). By contrast, the presence of the observer/blind did not significantly affect the completion of nesting once the female began digging her nest ($G = 0.13$, $df = 1$, $P = 0.718$). These data indicate that even the very low-level disturbance from an observer trying to remain inconspicuous in a blind still impacted females and reduced the number of nest attempts at a given nesting beach. Other, more common forms of disturbance at these sandbars (e.g., boats passing by sandbars at high speeds, camping, and picnics on the nesting beaches), caused an even more dramatic effect, with turtles observed to wait several hours for humans to leave a nesting beach before attempting to nest. Indeed on weekends in June and July, most sandbars had human activity on them most of the day, making these sites effectively unusable by nesting females. Humans also directly impacted nests by trampling them and by digging up eggs and nest covers.

DISCUSSION

One of the primary reasons for listing *G. flavimaculata* as Threatened under the U.S. Endangered Species Act was speculation that the decline in population size was related to a disruption in reproductive ecology (Federal Register, 1991). We identified three distinctive features of the reproductive ecology of this population; low annual reproductive potential, high mortality rates among nests, and higher-than-expected use of riverbanks for nesting. Taken together, these factors may at least partially explain the apparent decline of this species and indicate what management steps might be needed to stabilize the population.

Reproductive frequency.—Based on data from both ultrasound and radiographs, *G. flavimaculata* ap-

TABLE 3. SUMMARY OF REPRODUCTIVE CHARACTERISTICS OF VARIOUS SPECIES OF *Graptemys*.

Species	Location	Clutch size	Clutch frequency	% gravid	Source
<i>G. barbouri</i>	GA, AL, FL	6–11	4	—	Cagle, 1952
<i>G. ernsti</i>	AL	7.2	4–6	—	Shealy, 1976
<i>G. flavimaculata</i>	MS	4.8	1–2	62	This study
<i>G. geographica</i>	CN	9–17	—	—	Gordon et al., 1980
<i>G. geographica</i>	MO	10.1	2–3	100	White and Moll, 1990
<i>G. nigrinoda</i>	AL	5.5	3	—	Lahanas, 1982
<i>G. ouachiensis</i>	WS	10.5	2–3	100	Vogt, 1980
<i>G. ouachiensis</i>	WS	11.3	—	—	Janzen et al., 1995
<i>G. pseudogeographica</i>	WS	14.1	2–3	100	Vogt, 1980
<i>G. pseudogeographica</i>	WS	12.8	—	—	Janzen et al., 1995

pears to have a low rate of multiple clutches, and there is a high likelihood that some females were not reproductively active during some years. Even assuming that all females produced at least one clutch per year, the average number of clutches produced per female using either method is only 1.15–1.16 (i.e., all females produced one clutch and 15–16% produced two). We acknowledge that our reliance on radiographs in most years, combined with the long nesting season of *G. flavimaculata*, suggests that some females classified as nonreproductive may, in fact, have laid eggs either before or after the individual was radiographed (for comments on radiographs for determining reproductive frequency, see Tucker, 2001). Unfortunately, dissection and examination of female reproductive tracts was not available to us because of the legal status of the species. However, the value for reproductive frequency noted above is almost identical to that found by using ultrasound methods on the same population (see also Shelby et al., 2000).

In contrast with our data, estimates of reproductive frequency and potential in most other species of map turtles are much higher (Table 3). Although not all studies specified the proportion of females that were reproductively active, the consensus is that female map turtles generally produce at least one clutch per year and many produce multiple clutches (up to four in *Graptemys barbouri* and six in *Graptemys ernsti*). Thus, the reproductive frequency and total reproductive potential of our population of *G. flavimaculata* appear to be very low in comparison to other map turtles. The cause of this apparent low reproductive potential is not known; possible explanations include smaller maternal body size in *G. flavimaculata* (we are grateful to an anonymous reviewer for this suggestion) and disruption of the hormonal system of the species as a result of chemical pollution

upstream of our study site (see summaries in Ernst et al., 1994; Shelby et al., 2000). Furthermore, R. Vogt (pers. comm.) used dissection data to suggest that *G. flavimaculata* laid up to three clutches per year in the late 1970s upstream from our study site. This low reproductive potential, when combined with low nest survival, makes maintenance of a viable population problematic (see below).

Nest and egg survival.—Of over 1500 nests we found during this study, only 38 hatched successfully (Table 2): The rest were destroyed by predators or flooding before we could protect them. Of the 55 nests monitored from laying to hatching, only six hatched (10.9%). Even nests protected from predators via caging had low rates of success because of flooding in some years (e.g., 86% of nests destroyed in 1994; Table 2). Thus, current nesting success at this site is extremely low. However, it is difficult to determine whether these high mortality rates represent a recent change (leading to population decline) or whether these sites normally have low nesting success. Although egg viability was measured in the lab only in 1996, the high rate of hatching success we observed (80%) suggests that when protected from predators and flooding, hatching success can be quite high.

Of the two factors that cause nest mortality (predation and flooding), long-term data are available only on rates of river flooding. Historical data on river levels on the lower Pascagoula River were available from 1931–1994 and were used to determine how commonly the river reached levels high enough to flood nests between mid-May and late July each year. These data showed that flooding is a common occurrence along the Pascagoula River, with floods high enough to cover nesting beaches occurring in 17 summers between 1931 and 1994, and in five of the six summers from 1989–1994

(Brauman, 1995). Flooding also occurred again in 1997 when Hurricane Danny struck the Gulf Coast of Mississippi and Alabama. Thus, high mortality from flooding appears likely at this site, especially in recent years. However, our data cannot determine whether increased flooding is the cause of the apparent decline.

As far as we can determine, there are no historic data on nest survival for this species (Ernst et al., 1994). However, high predation rates on map turtle nests may be the result of recent changes in fish crow populations, which are apparently increasing as a result of overwintering near garbage dumps (Madge and Burn, 1994: 155). Whether this apparent increase in fish crow populations has resulted in higher than normal predation rates cannot be determined with our data.

Nest site selection.—Most species of riverine map turtles, including *G. flavimaculata*, are known to nest primarily on sandbars (Ernst et al., 1994); thus, we concentrated our initial survey efforts on those habitats in 1993–1994. However, by 1996 we were aware of large numbers of nests being constructed along the steep clay banks of the Pascagoula River and occasionally observed turtles attempting to nest in such areas, sometimes on angles as steep as 65 degrees (B. Horne and M. Moore, pers. obs.). In addition to dramatic changes in soil type and slope as compared to sandbars, nesting along the riverbank also exposes nests to much lower incubation temperatures. We measured the incubation temperatures of four nests along the riverbank using Hobo Data Loggers in 1997 and found that the mean nest temperature was 25.9 ± 0.420 C, compared with a mean temperature of 28.7 ± 0.756 C for six nests on sandbars ($t = 6.67$, $df = 8$, $P < 0.001$). Although lab experiments on temperature-dependent sex determination have not been conducted with *G. flavimaculata*, incubation data from other map turtles (Vogt and Bull, 1984) indicate that, (if this species has TSD), nests built along the riverbank would produce almost exclusively male hatchlings, whereas those from sandbars will likely produce a mixture of males and females. In addition, a number of recent studies have shown that incubation conditions (temperature and hydric environment) significantly affect a variety of phenotypic traits of turtles, including incubation time, body size at hatching, and hatchling growth, survival, and endurance (Guttske et al., 1987; Miller et al., 1987; Brooks et al., 1991; Janzen, 1993a,b).

Why Yellow-Blotched Map Turtles at our study site use these unusual nest sites is not known. A

possible explanation is that females are prevented from nesting on sandbars because of high levels of human recreational use. On numerous occasions we have seen boaters setting up long-term camps on sandbars, especially on weekends. Our observational data indicate that female map turtles are highly susceptible to disturbance before nesting and will avoid beaches where humans are present (see section on Nesting behavior). In addition, some nesting beaches became increasingly encroached with non-native vegetation during our study, making them less suitable for nesting (Horne, 1999). Other explanations are that (1) some females are preprogrammed to produce male hatchlings by seeking out cooler nest sites, or (2) nests along the riverbank are a normal, but previously unobserved, aspect of the nesting ecology of these turtles, especially if riverbank nesting produces higher levels of nest survival. However, because only male hatchlings are likely produced from riverbank nests, females cannot be returning to neonatal nesting sites for nesting (i.e., using natal homing) to find riverbank nests. Thus, how and why females use these sites remains unknown.

Population viability.—Our data show that Yellow-Blotched Map Turtles from this site (1) have a relatively low annual reproductive output, (2) have a very high rate of nesting mortality, and (3) use an unusual nesting location, riverbanks. The combined effects of these findings on population viability can be illustrated by determining how many eggs a female turtle would have to lay to replace herself in the population (resulting in a stable population with $R_0 = 1.0$). Using our data and those from the literature, we used a spreadsheet to construct models with varying levels of nest mortality (for details, see Table 4). These simulations show that when nest mortality is greater than 90%, a female would have to produce 153 eggs during her lifetime to replace herself in the breeding population. At a mean clutch size of 4.8 and assuming a 1:1 primary sex ratio, a female would have to produce approximately 64 clutches over her lifetime to replace herself. Our data suggest that this is demographically improbable; with an average clutch frequency of 1.16 clutches per year, the average female would have to survive 55 reproductive seasons, requiring adult survival rates far in excess of those observed in turtle populations in the wild (Congdon et al., 1993, 1994; J. Congdon, pers. comm.). Even if females averaged two clutches per year, females would still have to survive more than 32 years after the onset of maturity, a condition which may only

TABLE 4. EFFECT OF NEST MORTALITY ON THE NUMBER OF EGGS FEMALE MAP TURTLES MUST PRODUCE OVER THEIR LIFETIME TO REPLACE THEMSELVES IN THE BREEDING POPULATION. The model assumes annual juvenile survival rates of 0.80, an average clutch size of 4.8 (this study), 1.16 clutches/year (this study), a 1:1 primary sex ratio, and an age at maturity of 10 years (using data from the closely related *Graptemys oculifera*; R. Jones, pers. comm.). Based on prior studies (e.g., Heppell et al., 1996), juvenile survival is likely to have a major impact on this model, and the figure used here is intentionally optimistic. The ranges of nest mortality values are broadly representative of the calculated hatchling success for monitored nests from 1993–1997 (for details of calculations, see text).

Nest mortality	# eggs for replacement	# clutches for replacement	Required years of reproduction
50%	19.0	7.9	6.8 years
82%	52.0	21.6	18.6 years
94%	153	63.8	55.0 years

be possible under the best of circumstances. Such circumstances are unlikely to apply at our site since females are frequently killed via anthropogenic causes, including being shot by local campers, killed by propellers by speeding boats, and drowned in commercial hoop traps (R. Jones, pers. comm.). Finally, females nesting along riverbanks almost certainly produce male-biased hatchling sex ratios, requiring even more eggs than indicated above.

Management implications.—Despite marking over 1100 turtles since 1993, recapture rates were too low to permit population size estimates that could be used to estimate population trends. However, our data on reproduction and nesting indicate a population that is likely declining because of low recruitment and (possibly) abnormally low reproductive frequency. Because one possible cause of low reproductive frequency (dioxin contamination; see Shelby et al., 2000) is difficult to address in a practical way, we concentrate here on methods for increasing recruitment by enhancing either female or nest survival.

Numerous turtle populations suffer from high predation rates on nests, and often ambitious attempts have been made to increase recruitment by enhancing nest survival, either in situ or in artificial hatcheries (for review, see Seigel and Dodd, 2000). However, from a demographic perspective, increasing nest or hatchling survival is inefficient, since turtle populations usually are most susceptible to changes in subadult or adult survival, not that of hatch-

lings (Congdon et al., 1993, 1994; Heppell et al., 1996). Thus, efforts at maintaining this population should first focus on increasing adult survival. This would require a combination of enhanced law enforcement at the site (to prevent illegal shooting of basking turtles) combined with an aggressive program to inform the public regarding the plight of this species, with specific attention to the effects of random shootings and disturbances to the nesting beaches. Some recent progress has been made, because commercial hoop traps have been prohibited in this area (R. Jones, pers. comm.). We suggest that a well-designed public relations campaign is essential in implementing a comprehensive conservation plan; only with public cooperation can appropriate conservation steps be implemented.

Our data suggest that, in the absence of flooding, caging intact natural nests is an effective means of increasing nest survival at our study site. Of 86 caged nests from 1993–1997, 32 (37.2%) were successful, compared with 10.9% success rate for unprotected (six of 55 monitored). Because caging natural nests does not alter incubation conditions (and, hence, sex ratio and phenotypes), this is a relatively unobtrusive conservation tool (Seigel and Dodd, 2000). However, the overall impact of caging natural nests is limited by several factors, most notably manpower to monitor nesting beaches (and remove cages later in the season) and the impact of flooding on nest survival. Although eggs are not as important as adults in managing turtle populations (e.g., Congdon et al., 1993, 1994; Heppell et al., 1996), this method may be more easily and quickly implemented than protection of adults. However, we emphasize that protection of natural nests, by itself, is insufficient as a management procedure. Only a combined approach, focusing on enhanced law enforcement, public relations, and increasing nest survival is likely to prevent future declines of this species.

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