Nesting Ecology of the Alligator Snapping Turtle (*Macroclemys temminckii*) along the Lower Apalachicola River, Florida

FINAL REPORT

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Submitted as final report for
Nongame Wildlife Program project NG89-020

March 1994

This report is the result of a project supported by the Florida Game and Fresh Water Fish Commission's Nongame Wildlife Program. It has been reviewed for clarity, style, and typographical errors, but has not received peer review. Any opinions or recommendations in this report are those of the authors and do not represent policy of the Commission.

Suggested citation:

Ewert, M.A. 1994. Nesting Ecology of the Alligator Snapping Turtle, *Macroclemys temminckii*, along the Lower Apalachicola River, Florida. Fla. Game and Fresh Water Fish Comm. Nongame Wildl. Program Final Rep. 45pp + vi. Tallahassee, Fla.

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Abstract: The alligator snapping turtle (*Macroclemys temminckii*), a species with temperature-dependent sex determination, nests along the banks of the lower Apalachicola River. Building from 8 years of observations initiated during the 1970s, we conducted an expanded 2-season field and laboratory study on the distribution and dynamics of the nests. A 2-year total of 105 nests (63 intact, 42 predated) was located along the Apalachicola mainstem from just south of Liberty County to just above its confluence with the Jackson River. Most of the nests (87 of the 105) occurred on prominent dredged spoil substrates that have accrued from channel maintenance for barge traffic. For all years of observation, mean clutch size of 130 nests at 35.1 (range 17-52) eggs has remained stable and appears to represent the natural value for a largely undisturbed population. We estimate nesting to occur between 20 April and 11 May but to vary annually by about a week within this period. Hatching extends throughout August. In protected nests, hatching success averaged 66 % (for 26 nests) in 1991 and 78% (for 24 nests) in 1990. The lower hatching success in 1991 is likely a consequence of asphyxiation in response to abnormally wet conditions.

Estimates of sex ratios in individual nests varied from all males to all females; however, overall sex ratios were roughly 1 male:2 females in both years (34.8% male in 1991, 32.5% in 1990). This bias toward females is associated with nesting in open areas, the mounds and beaches of dredged spoil. These sites provide warmer environments for incubation than those within wooded areas and produce mostly to exclusively females as a consequence. Alternative warm environments may have been unavailable in presettlement times when probably the floodplain and levees were continuously forested. Continued presence of these places should not obviously harm alligator snapping turtles. The population appears to contain sufficient phenotypic plasticity (temperature response polymorphisms) to adjust hatchling sex ratio to the new conditions and should not suffer decline as long as some open shoreline remains. The open areas may have favored population growth in some other species of turtles and may even have been critical to colonization by still others.

Hence, management of the river system should consider a very modest maintenance of some of the existing beaches by perpetuating an early successional vegetation of sparse herbs and by slightly increasing the heights of the beaches above the water. However, to understand better the value of the banks of the mainstem for the nesting of alligator snapping turtles and other turtles, additional study is needed (1) on more seasons of sex ratios of hatchling recruitment, as the 2 study seasons appear to have been wetter and warmer than average, (2) on home ranges of female adult alligator snapping turtles that nest along the mainstem, allowing that some other females may be nesting elsewhere, and (3) on sex ratios of hatchling recruitment in other (including protected) species of turtles and their relevance to the open areas for nesting.

ACKNOWLEDGMENTS

We thank the staff of the Apalachicola National Estuarine Reserve (Woody Miley, Director) for their encouragement and appreciable support, and especially, Lee Edmiston for making a boat and motor available to us and Chip Bailey for keeping it working. We thank Jon Dodrill for permitting us to use Ft. Gadsden State Historical Site for camping and as a general base of operations. Many people gave physical assistance with the field work: from the Florida Department of Natural Resources, Jon Dodrill, Catherine Florko, Hank Smith, and Isbon Teuton; from the Game and Fresh Water Fish Commission, Dave Cook, Jeff Gore, Larry Perrin, and Jim Ruhl; from the Florida Natural Areas Inventory, Tom Ostertag and John Palis; and from other places, Harry Andrews (Madras Crocodile Bank), John Allsteadt and Jeff Lang (University of North Dakota), James Dobie (Auburn University), Rosélis Ramor de Sousa (INPA, Brazil), and Bob Walker. We especially thank Isbon Teuton for cordially finessing our many needs about Ft. Gadsden (as well as on the river) and for assuring that our stays would be pleasant.

We thank Helen Leitman (U.S. Geological Survey) for providing us with hydrological data and Steve Leitman (Florida Defenders of the Environment) for sending us many kinds of information on man-made modifications to the Apalachicola River. We thank Fred Rhodes of the Qunicy Agricultural Experiment Station for instructing us about soil temperatures and Jan Smith for giving us data on soil temperatures in advance of publication.

Craig Nelson helped with various facilities at Indiana University. Maxine Watson loaned us incubators, as did Jack McCoy (through a loan from the Carnegie Museum of Natural History). Pat Clark assisted with incubation of the eggs.

The Florida Game and Fresh Water Fish Commission has provided several permits over the years for the taking of alligator snapping turtles. The 2 most recent permits for material in this report are WX91071 and WX90038. Funding for the study was provided by the Florida Game and Fresh Water Fish Commission's Nongame Wildlife Program (contracted project NG89-020).

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INTRODUCTION

The alligator snapping turtle (*Macroclemys temminckii*) is a unique and exclusively North American representative of our natural heritage (Ernst and Barbour 1989). The species also has commercial value and has been exploited at least sporadically, principally for its meat. This harvest, together with habitat degradation and probably accidental taking, are reasons given for an apparent decline in populations throughout much of its natural range (Pritchard 1989). However, knowledge by which to plan management and protection of the species is limited to 1 major paper on reproductive biology (Dobie 1971), 1 short paper on movements of adults (Sloan and Taylor 1987), and informal evidence from turtle trappers on declines in their harvests (Pritchard 1989).

Observations in 1972 and 1973 indicated that nests of the alligator snapping turtle could be located fairly easily along the lower Apalachicola River in Franklin and Gulf counties, Florida (Ewert 1976). Nesting females voluntarily and frequently selected (Ewert 1976) various spoil mounds that have accrued from modification of the Apalachicola River to serve as an inland waterway for barge traffic (Eichholz et al. 1979, S. Leitman et al. 1990). Locally, these mounds and some similarly generated riverside sandbars represent large gaps in an otherwise mostly closed forest canopy.

Studies on the determination of sex in reptiles (Bull 1980, Vogt and Bull 1984, Ewert and Nelson 1991) suggest that use of the unnatural open areas by alligator snapping turtles could affect their population structure by skewing sex ratio. Alligator snapping turtles, like sea turtles, sliders and cooters, and alligators, acquire their genders during embryonic development within their eggs. Nest temperatures, as elevated by direct sunlight or cooled by shade, determine gender during roughly the middle third of development (Yntema, 1976, Pieau and Dorizzi 1981). Preliminary evidence on alligator snapping turtles indicates that warm temperatures produce only females, mild temperatures produce mostly males, and cool temperatures produce, again, mostly females (Ewert and Nelson 1991). Hence, as potential nesting sites, the mounds and sandbars, which have their substrates heated by direct sunlight, should provide greater proportions of females than would develop in naturally available environments, the shaded soils of natural levees. Given these concerns, objectives focus on the status of the local population, its use of natural and man-made features of riverine habitat, and a mechanistic approach to understanding potential problems.

Study Objectives

1. To document (map) the distribution and abundance of nests of the alligator snapping turtle, primarily along the mainstem of the Apalachicola River, from below the mouth of the Chipola River into tidewater above Apalachicola Bay, and to attempt to locate any other concentrations of nests that may contribute to local populations.

2. To determine various life history parameters for local alligator snapping turtles; these should allow an estimate of local population health by comparison with 1 other population (in Louisiana: Dobie 1971) and with turtles in general.

3. To document and evaluate the use of spoil mounds and other spoil areas for nesting and to contrast this with the use of natural levees and other natural areas.

4. To document and evaluate the use of spoil mounds and other spoil areas for nesting by other species of turtles so that the value of the spoil areas to the overall community of turtles can be assessed.

5. To determine any effect that nesting by alligator snapping turtles on the spoil areas may be having on hatchling sex ratios.

6. To conduct studies on incubation temperatures vs. hatchling sex ratios that will allow comparison of laboratory and field data. Of importance is understanding the varying nature of temperatures in field nests vs. constant or controlled temperatures in the laboratory vs. other factors, such as temperature response polymorphisms in the progeny of individual turtles. This last factor may provide some indication of potential adaptability of the alligator snapping turtle population to man's inadvertent provision of unnatural nesting substrates.

STUDY AREA

Overall, the study area includes the mainstem of the Apalachicola River as it courses through portions of Gulf, Liberty, and Franklin counties, Florida, from the mouth of the Chipola River into tidewater (the intracoastal waterway). Also included are a few local features of relevance to the nesting of alligator snapping turtles (from west to east: Cypress Creek, Saul Creek Road, Brothers River, and Ft. Gadsden Creek) but which lie apart from the mainstem. A more focused portion of the study area is limited to the mainstem and its banks from the "Brickyard area" (just upstream from Forbes Island) to the southern tip of Forbes Island. The most immediate core of the study covers the upper half of this area (about 8 km of the mainstem). This portion is the site of historical as well as current observations.

A detailed and current description of physiography and forest vegetation of the Apalachicola River and its floodplain are given in a recent hydrologic study (H. Leitman et al. 1983). Generally, the whole region is flat with alluvial deposits of clay, silt, and sand. The floodplain that borders the river varies from 4 km to more than 6 km in width. Data on relevant U.S.G.S. quadrangles (Kennedy Creek, Forbes Island, Jackson River) indicate that no naturally occurring land within the floodplain rises more than 3 m above average river level. Personal observation and data from the Sumatra hydrologic (surface water monitoring) gage generally support this aspect, and most of the natural levees rise under 1.5 m above the average level. Such land is subject to periodic spring flooding during the late April to mid-May nesting season. Small regions of high banks (ca. 3-4 m) occur at the latitude of Brushy Creek and at Ft. Gadsden Historical Site, where the river courses along the eastern border of the floodplain (from Brickyard Creek to Ft. Gadsden Creek). A third very local area lies just inland from the river at Bloody Bluff. Across the core of the study area, surface waters of the mainstem of the Apalachicola River are higher than those in a companion channel, the Brothers River, to the west across Forbes Island. Numerous small channels from the mainstem breach its levees along Forbes Island and show obvious flow for ca. 400 m to the west. During periods of low flow, tidewater influence has been measured near the southern tip of Forbes Island (H. Leitman et al. 1983). As tidal marsh crustaceans occur along the mainstem up to 4 km upstream from its confluence with the intracoastal waterway, marine salinization evidently penetrates at least this far.

More than 95% of the vegetated floodplain within the study area can be placed within 3 major forest types (H. Leitman 1984). From least to most often saturated or actually flooded, these types are: Type AB) water hickory (*Carya aquatica*) - sweetgum (*Liquidambar styraciflua*) - overcup oak (*Quercus lyrata*) - green ash

(*Fraxinus pennsylvanica*) - sugarberry (*Celtis laevigata*) (6-8% of floodplain area); Type C) tupelo (mostly *Nyssa aquatica* and *N. ogeche*) - bald cypress (*Taxodium distichum*) with mixed hardwoods (ca. 55% of area); and Type DE) tupelo - bald cypress (ca. 36% of area). Forest Type AB narrowly lines both banks of the mainstem at the level of Forbes Island. Very locally, along the shoreline of the lower insides of bends, willow (*Salix nigra*) is common.

Very sandy substrates artificially created from dredged spoil deposition occupy <1% of the floodplain but perhaps 3-4% of forest Type AB (estimated from Eichholz et al. 1979; H. Leitman 1984; Ewert, unpubl. data.) These substrates are distinguished by their relatively coarse textured sand (typically with inclusion of shells of Asiatic clams [*Corbicula manilensis*]) in contrast to the very fine sand deposited on the levees during natural flooding. Artificial substrates are disproportionately prominent along the mainstem. Terrestrial spoil areas occur as mounds along levees and as raised areas partially within the river. The mounds rise 3 - 6 m above normal river level and often extend 150-250 m inland from the river (Eichholz et al. 1979). Nearly all mounds present 1 or more barren areas. However, typically half or much more of the surface of a mound supports at least sparse vegetation. Vegetation close to areas used by turtles includes laurel oak (*Quercus laurifolia*), overcup oak, cabbage palm (*Sabal palmetto*), American beautyberry (*Callicarpa americana*), and wild grape (*Vitus* sp.). Terrestrial spoil areas that extend into the river form sandy beaches and sandbars. They are lower and appear more natural than the mounds because the river submerges and contours them during floods. Although a portion of the surface may be barren, prominent areas support river birch (*Betula nigra*), grasses (*Andropogon* sp. and *Panicum* sp.), or brushy borders with grape vine and poison ivy (*Rhus radicans*) being prominent.

The mounds and sandbars are fairly recent features in the region. Dredging began in 1957, and terrestrial deposition continued at least through 1973 (S. Leitman et al. 1984). Fig. 1 matches recorded locations and periods of dredging and volumes of dredged materials (U. S. Army Corps of Engineers, unpubl. data, current through 1989) with personally observed sites of onshore deposition (as located on composite aerial photographs for assignment of locations). Although this match is only approximate, it appears to concur with direct observation. Thus, mounds currently supporting the largest trees occur adjacent to sites of the earliest dredging (e.g., at kilometer 23.8). Also, large and small locations of dredging activity roughly match large and small areas of mounds and sandbars (e.g., at kilometer 22.5, 23.8, 30.3, and 33.3 vs. kilometer 26.7 and 31.1). Fig. 1 indicates that most of the dredging occurred during the early 1970s. In the earliest years of direct observation (1972, 1973), many onshore piles of spoil were fresh. After 1976, onshore deposition was phased out (S. Leitman et al. 1984), but evidently not suddenly, as dredging at kilometer 26.1- 27.0 in 1976 matches a

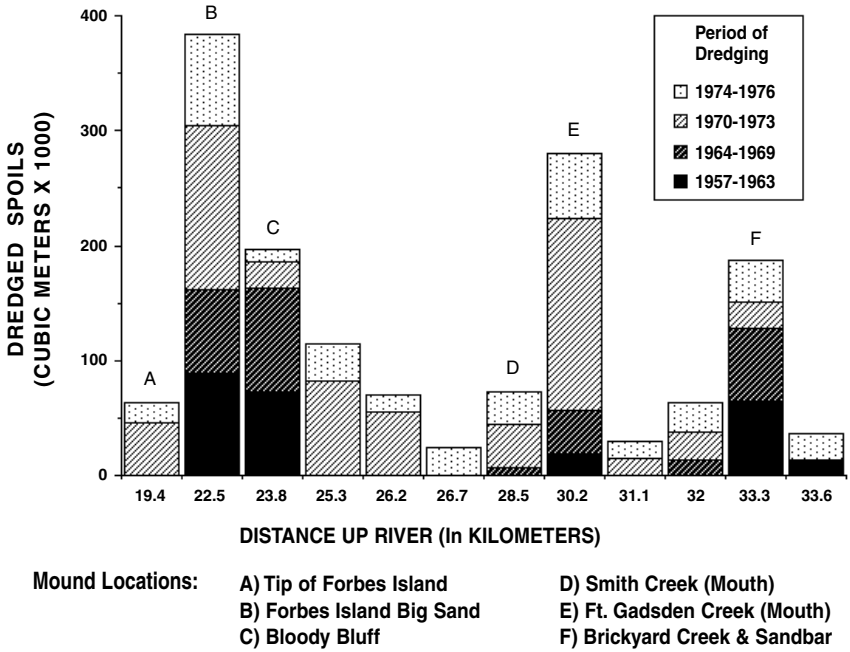

Fig. 1. Summation of recorded volumes of dredged spoil according to known sites of onshore and along shore deposition. Spoil deposition sites are ordered linearly with increasing distance upstream; however, distances along the horizontal axis are not evenly proportional. The association is implied rather than positively known (sources for quantification: U. S. Army Corps of Engineers, unpublished chart current through 1989; composite aerial photographs). Letters approximately associate deposition sites with 6 obvious geographic features, as named at the bottom of the figure.

spoil known mound at kilometer 26.7. Generally, by 1976 bald cypress protruding from deposition piles had died but had only just begun to decay and drop small branches. In 1991 only main trunks and major branches of a few trees remained standing. At the sandbar sites, open faces to the water are becoming smaller. In some places, the river is eroding the face back against pioneering brushy vegetation, whereas elsewhere, emergent vegetation in shallow water is screening off the open face. The average annual discharge cycle of the Apalachicola River has peak high flows in March, with high discharge beginning in January or February and continuing into April. During May the discharge tends to decrease rapidly (but with exceptions that will be addressed below). Low discharge is common in late summer and most typical of October and November (H. Leitman et al. 1983). A similar discharge pattern in the adjacent drainage of the Ochlockonee River (H. Leitman et al. 1991) suggests that the pattern is regional.

METHODS

Survey

Based on fortuitous discovery of recent nesting in 1972 (Ewert 1976) and subsequent refinement in later years (Ewert, unpubl. data), we estimated that all local nesting by alligator snapping turtles would occur between 23 April and 14 May. Hence, all nests could be censused during this period. For censusing in 1990, we visited nearly all "high" (least often flooded) ground along the mainstem from the mouth of the Chipola River to just below the confluence with Jackson River (the intracoastal waterway). Nesting female alligator snapping turtles seek the highest places on the floodplain. We used topographic quadrangles and a composite aerial photograph as guides to locate mounds and other high ground. During 1991, searching along the mainstem was more limited to the core study area and just beyond. However, we visited several points along the west side of the floodplain in hopes of estimating nesting activity away from the mainstem. In connection with locating nests to protect and to monitor, we searched first at places of known nesting (especially certain mounds and sandbars) and next at very similar looking places. However, even though we visited all of the mounds, overall we searched somewhat greater areas of levees than of obvious deposits of spoil.

A recently completed alligator snapping turtle nest presents a 1-2 m long by 0.5-0.75 m wide track of churned earth, often with small paired cavities at 1 end. It tends to cover a larger area than other animal diggings except those of feral hogs and others associated with obvious burrows. Eggshells strewn about depredated nests tend to facilitate location. Also, eggshells of alligator snapping turtles are distinguishable as being larger than those of other sympatric turtles.

The locating of nests and nesting by turtles other than alligator snapping turtles was somewhat limited to chance finds. However, we did search specially under bushes for nests of the common snapping turtle (*Chelydra serpentina*) and in open places for nests of the Barbour's map turtle (*Graptemys barbouri*). Females of some species could be found nesting during the day. Eggshells from depredated nests of common snapping turtles and softshell turtles (*Apalone* sp.) are distinguishable from each other and from those of other species.

Nest Protection

We needed to take data on intact (unpredated) nests and to protect most of them for an analysis of nest productivity in the absence of predation and of

nest temperature vs. hatchling sex ratio. Our system of protection required not only that we exclude predators but also that we retain hatchlings and keep them safe from overheating and desiccating near the ground surface. This protection consisted of an inverted "basket" of hardware cloth (a 29 cm diam x 30 cm high cylinder with a 30 cm square of hardware cloth attached across an end) about the eggs and a 90 cm square sheet of chicken wire over the basket and adjacent ground. The uppermost portion of the basket was kept 15-18 cm below the ground surface to prevent emerging hatchlings from coming closer to the surface. The sheet of chicken wire was also buried but in an arched curve with its shallowest point over the basket (3-5 cm below the ground surface) and its edges curved downward (buried to 10-15 cm). A predator could scrape the earth from above the chicken wire, but emerging hatchlings would still be protected by 12-15 cm of overburden.

In 1990 we were able to provide immediate full protection on approximately a third of the nests. As haste usually dictated that we protect many nests during a very short period of time, we temporarily installed just the chicken wire over these nests. We followed this procedure for $^2/_3$ of the protected nests in 1990 and on all but 1 in 1991. Then, at greater leisure, we could return to take data on the nest and eggs and to install the basket before replacing the chicken wire.

The first step in installing protection was to dig down to the clutch of eggs and to measure the distance from the top egg to the substrate surface. Then, we measured temperatures (with a thermistor soil probe) adjacent to the top and along the sides of the egg chamber. If we were in a hurry, we resealed the nest. If there were time to continue, we lifted the eggs from the nest and measured the depth to the bottom of the egg chamber. These values would tell us how deep to sink the basket and how deep to place the eggs within the basket. We next measured temperatures at the bottom of the egg chamber and replaced the egg chamber with a cylindrical pit to receive the whole vertical section of the basket at least 15 cm below the original ground surface. We then partially filled the basket with nesting substrate (usually nearly pure coarse sand) and carefully formed an artificial egg chamber such that it would lie at approximately the same depth below the substrate surface in the reconstructed nest as in the original, natural nest. Lateral to the egg chamber, just outside the basket, we inserted a maximum-minimum thermometer sealed within a plastic bag. The temperature indices of the thermometer were set just a bit warmer than the originally measured temperatures of the nest side walls. We then returned most of the eggs (all except 6-8 eggs for laboratory work and any pierced eggs) to the chamber, placed a small piece of plastic screening on top (to assure an air space within the nest), and covered this with more earth. We attached the top of the basket with wire or tie-wraps, added more earth, and set

the chicken wire. We tacked down the margins of the chicken wire with 6 to 8 metal stakes and rebuilt the nest surface to approximately the original contour. If there had been vegetation or debris on the original surface, we approximately reconstituted it. Some nest surfaces were so well reconstituted that they were hard to relocate 3 months later, even with flagging on adjacent trees.

We reopened nests with only temporary protection and then followed much the same procedures as above except that we used data on the original depth of the egg chamber as a guide in reconstruction, and we set the max-min thermometer to ambient nest side wall conditions.

We recorded nest clutch size in 1990 and 1991. In 1990 we also dusted debris off the eggs and weighed them as a group. This process proved tedious if the eggs were not fresh because we had to restore the original upright orientation of each egg (Ewert 1979, 1985). As the need to protect nests in 1991 was more hurried, we discontinued weighing clutches. However, in 1991, most fertile eggs were becoming chalked (a distinct whitening of the eggshell that accompanies early development; Ewert 1985) in nests reopened for installation of full protection. This enabled an assessment of egg fertility.

We could assume that eggs in several of the nests had hatched by mid-August. At this time, we removed the chicken wire, opened the basket and removed the nest contents. We also recorded the maximum and minimum temperatures for the duration of incubation and the ambient temperatures in the nest sidewalls as well as on the nest bottom. We recorded the outcome of incubation (live hatchlings, eggs containing healthy term embryos, the status of the remaining eggs). If the living contents of a nest included only hatchlings, we took a random sample of 6 turtles for diagnosis of sex and freed the rest of the hatchlings. If we found the eggs unhatched or only partly hatched, we took all of them from the nest and let them hatch in plastic containers. We then took samples from these groups and freed the rest after they had hatched.

Laboratory Work

Although some data are available on sex ratios that result from incubation at a few constant temperatures, we needed more precise data from these and some additional constant temperatures. One aspect of precision is detection of any variation among clutches in the sex ratios that result at a given temperature. It is possible for a given constant incubation temperature to make only females in 1 clutch and only males in another. Hence, the response to temperature is polymorphic among embryos with different parentage

(temperature response polymorphism). Knowledge of polymorphisms can assist in predicting how perturbations in the environment, such as the creation of mounds and sandbars, might affect sex ratios in a population as a whole. Possibly superimposed on a temperature response polymorphism are complex responses to temperature in which fluctuating temperatures, such as occur in nests, determine sex in a manner that cannot be predicted from a series of constant temperatures that represents the range of fluctuation. Evidence to support a complex response comes from application of a graded series of increasingly warm temperatures applied to eggs of a crocodile (Webb et al. 1987). We tested for both types of effects.

For laboratory incubation, eggs were placed in plastic boxes (generally measuring 33 x 23 x 9 cm and containing 18-24 eggs per box) that contained sufficient damp vermiculite (dry vermiculite mixed with an equal weight of water) to just cover the eggs. In 1990, 6 eggs from each of 32 clutches were incubated at 22.5°C. The 8 boxes of eggs were shifted several times among different places in the incubator to guard against very local differences in temperature within the incubator. In 1991 6 eggs from each of 26 clutches were apportioned to 25, 26, and 27°C (1 egg to each temperature) and to a series of step shifts in temperature (3 eggs per clutch). The regimen for the step shifts had eggs at 24°C until stage 14-15 (Yntema 1968; as estimated by candling), then at 25°C for 10 days, then at 27°C through pipping. As the eggs had been developing in the field and varied from stage 6^+ to stage 12^- when we set up the experiment, we divided clutches among 5 boxes according to similarities in stage and took them through the steps of warming a box at a time in a staggered sequence. In addition to the several small samples, we took 1 entire clutch through the step series. Any eggs that were not used for these experiments were placed at some other constant temperature (e.g., 24°C, 28°C, or 29°C).

Diagnosis of Sex

In nearly all cases, sex of hatchling alligator snapping turtles can be diagnosed from the gross appearance of the gonads and accessory structures as viewed under a dissecting microscope. The gonads of females vary from white through gray to nearly black. Often, they show a mosaic of shading and typically, the 2 gonads of the same individual differ markedly in color. The male gonads vary only from nearly white to light gray and are similarly colored in the same individual. Gonads of females tend to be larger and longer than those of males, have slightly greater opacity, and occasionally show primary follicles. Females possess prominent mullerian ducts (oviducts), whereas in males these usually are absent, occasionally are small, and only very rarely (2 cases in 740 specimens diagnosed) appear even moderately large as in females.

Because the gonads continue to differentiate after hatching, we kept the young turtles for about 2 months before euthanizing them. We have kept turtles from 22.5 C (the most difficult group to diagnose) for 8 months following hatching and have found appreciable development of primary follicles in females and loss of any trace of mullerian ducts in males.

Releases of Hatchlings

Because the alligator snapping turtle is listed in Florida as a Species of Special Concern, sacrifices were kept to the minimum number that we felt necessary for the research. Hence, from a total of 1046 eggs known to have hatched successfully within nests, 743 hatchlings (71%) were released during 1990 and 1991. We took most of the hatchlings to various small channels associated with the mainstem (from Brushy Creek to East River) and dispersed them at about 30 hatchlings per channel, or about 1 turtle per 3 m over 100 m stretches. A few were released into dense beds of emergent vegetation along the mainstem.

RESULTS

Nest Survey

Alligator Snapping Turtles.—We located 41 nests during 1990 and 65 nests during 1991 (Fig. 2). The most complete search in any previous year, in 1976, was confined to the core of the study area (7.5 km of the mainstem from Van Horn Landing to the Brickyard Area). This reach yielded 29 nests (18 intact, 11 depredated) in 1976, 32 nests (25, 7) in 1990, and 44 nests (23, 21) in 1991. As the time spent searching in 1976 was briefer than in 1991 (2 vs. 14 days) and involved 1 rather than 2 or more persons, it is possible that the 15-nest difference between 1991 and 1976 can be attributed to differences in sampling effort. However, the moderately advanced status of predation in 1976 (38% of the nests found already destroyed) would suggest that the nesting season was nearly complete, and thus easy to census. Still, more abundant local nesting seems to have occurred in 1991 than in the 2 earlier years. Less intensive searches in other years (1972, 1973, 1978, 1779, 1980, 1981, 1986) yielded a total of 70 nests (48 intact, 21 depredated, 1 hatched; mostly within the core study area). However, other than in 1972 and 1973 (Ewert, 1976) the record of depredated nests is fairly casual.

The distribution of nests in 1990 and 1991 nearly spans that of all previous years and generally includes all local sites (Fig. 2). However, in 1972 1 nest was found upriver from the Brickyard area, approximately across the mainstem from the mouth of Brushy Creek. A search in 1991 of roads along ditches west of the river and leading to the Apalachicola floodplain yielded 1 intact nest along Saul Creek Road (south of Howard Creek as shown) and an apparent attempted nest about 2 km to the south. West of Howard Creek, where Hwy 387 crosses Cypress Creek (T6S R9W, Sec 34, SW1/4), an intact nest was on the NE embankment of the bridge. Cypress Creek empties into Lake Wimico, which once emptied into the Apalachicola River via the Jackson River. In 1976, tracks of an adult alligator snapping turtle were found on a sandy road near Ft. Gadsden Creek, about 300 m west of Hwy 65 (T6S R8W, Sec 25). As the only terrestrial activity known in adult alligator snapping turtles is nesting, the tracks strongly suggest an instance, although no nest was found. Hence, alligator snapping turtles nest at widely scattered locations away from the mainstem but still close enough to contribute to the population of the floodplain.

Along the Apalachicola mainstem, we have found most of the nests on spoil mounds. These include 44 (69%) of 64 nests in 1991, 25 (61%) of 41 nests in 1990 and 54 (72%) of 75 nests in the earlier years when records often were incomplete. The sites of next most frequent use appear to have been used

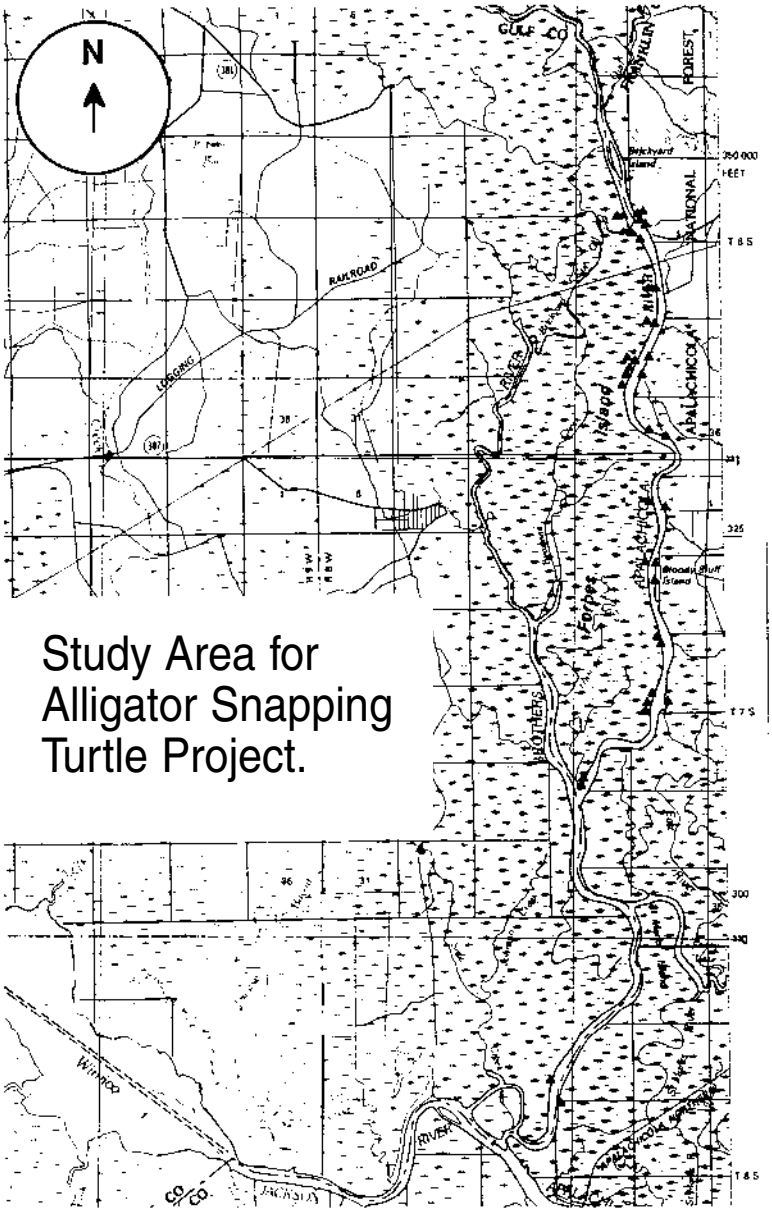

Fig. 2. Map of the study area and local surroundings showing locations of alligator snapping turtle nests found during 1990 and 1991. The core of the study area begins just south of Brickyard Island (near the upper right corner) in the mainstem of the Apalachicola River and extends south almost to Bloody Bluff Island (far right of center). Each plotted (▲) point represents 1 to several nests.

for "within bank" spoil deposition (S. Leitman et al. 1984) that in some places has spilled over onto natural levees and in others has extended these levees into the river as high sandbars or beaches. Only 6 nests in 1990-1991 and 8 nests from earlier years occurred in substrates of completely natural levees.

Other Turtles.—*Chelydra serpentina*: We located 25 nests (3 intact, 22 depredated) and 2 nesting female common snapping turtles during 1991. During 1990, we found 20 nests (9 intact, 11 depredated) and 1 nesting female. These nests are more difficult to find than those of the alligator snapping turtle, and we probably missed finding several, especially in 1990. For the earlier years, 54 nests (28 intact, 26 depredated) are recorded, but many predated nests went unrecorded. We suspect that common snapping turtles begin nesting earlier than alligator snapping turtles, perhaps by 15 April, but we lack exact records. During 1991, the last nesting was by 28 April (vs. 9 May for an alligator snapping turtle). During 1978, the peak of nesting activity occurred on 4 May, the day after a heavy rain.

Common snapping turtles frequently nest on the spoil mounds. This preference includes 21 (78%) of 27 nests (including 2 searching females) in 1991 and 12 (57%) of 21 nests (including 1 searching female) in 1990. During 1978, 9 fresh nests were recovered from a single mound. However, during the unusually dry spring of 1986, several nests were located along the normally low, natural banks of channels crossing Forbes Island up to 200 m from the levees, and few could be located on the spoil mounds. Over the years, several nests have been found on the levees, sometimes in fine sand and sometimes in silty sand.

Graptemys barbouri: Only intact nests of Barbour's map turtles can be positively identified; the eggs are similar to those of the river cooter (*Pseudemys concinna*). Of 20 Barbour's map turtle nests, 17 were in the large sandy areas created from within banks spoil deposition. Usually, these nests have been in areas of sparse herbaceous vegetation at the edges of trees or brush. In 1991, we found 2 females at their completed nests on 2 different spoil mounds. One female was more than 200 m inland from the mainstem, on a mound that itself is separated from the mainstem by 30 m of floodplain forest. Numerous eggshells from depredated nests found on several mounds in August suggest that Barbour's map turtles may frequently use the mounds. During August 1991, we found 1 nest in fine sand in a mostly shady treefall gap on a natural levee.

Other species: Although we have records of nests or activity associated with nesting for 6 additional species, we have only casual quantification or just a few observations on each. We have found at least 10 sliders (*Trachemys scripta*; nesting or searching females, or nests) on spoil mounds and at least

5 in other situations (1 on a natural levee, 1 on a levee with spoil, 3 on sandy beach areas). We found 1 nest of the Gulf Coast box turtle (*Terrapene carolina major*) on the low edge of a spoil mound on 29 April 1991. Non-nesting adults frequent the mounds during springs with high water. Four intact and many depredated nests of spiny softshells (*Apalone spinifera*) have been located only on open sandy beaches, usually in areas well away from any vegetation. We found 1 nest of the Florida softshell (*Apalone ferox*) on the sandy beach at Van Horn Landing on 9 May 1991. For the loggerhead musk turtle (*Sternotherus minor*), we have found 5 searching or nesting females or nests (1 on a spoil mound on 3 May 1981, 2 on levees with spoil, 1 on a natural levee, 1 on the upland river bank at Brickyard Landing). On 3 May 1979, a spent female common musk turtle (*Sternotherus odoratus*) was found leaving a spoil mound.

Life History Features

Alligator Snapping Turtles.—We estimate from the stage of development in nest eggs that the earliest annual date for nesting is ca. 20 April (1991) and the last date is 11 May (1976). Durations of single seasons are 20 April (ca.) - 9 May 1991 and 23 April - 7 May 1990. Although we have never been present for an entire nesting season, we can tell, at least, that peak laying occurs earlier in some years than in others. The known extremes are pre-27 April 1991 and post-1 May 1978, and the probable range is 24 April - 3 May. Known dates with many fresh nests (typically from pre-dawn to dawn nestings) or with some turtles found nesting are 28 April 1990, 3 May 1980, and 3 May 1979. By contrast, we found only 3 fresh nests (of 63 nests) after 1 May 1991. In summary, the phenological range of fluctuation in nesting appears to be about a week.

The overall period of hatching probably is more prolonged than for nesting but is much less well documented. In 1991, the first eggs in warm nests probably began hatching about 5 August, and eggs taken from the coolest nest completed hatching in a comparably cool incubator (26°C) on 29 August. Most nests contained recent hatchlings still in their egg chambers on 15 August. In 1990, the first eggs appear to have hatched about 1 August, and the last egg hatched in the laboratory on 27 August. Most nests had been hatched for several days by 15 August, and the hatchlings had burrowed to the the tops of their baskets. Estimates based on the condition of the umbilical scar suggest that several days pass between pipping and beginning to leave the nest chamber. In 1990, hatchlings in 2 of the warm nests had begun to deteriorate from confinement. Comparable experience under laboratory incubation and subsequent confinement, together with recorded nest temperature, suggest that the earliest hatching had begun about 2 weeks before we began opening baskets.

The mean clutch size in 130 nests is 35.1± 6.6 (range = 17-52 eggs), with most clutches ranging from 28-44 eggs (Fig. 3). A group of small clutches (17-21 eggs) set apart from the main distribution suggests that some females might be depositing only half of a clutch in a given nest (Pritchard 1989). One of these small clutches was associated with a narrow trackway (i.e., tracks from the nesting female) and a small area of disturbance. This could have been the nesting of a young female. However, another very narrow trackway was associated with an above-average sized clutch (38 eggs) of very small eggs. Apportionment of the overall sample according to decade of laying fails to suggest any variation over time (Fig. 3).

Only 10 nesting females were directly encountered during the 10 seasons of study and only carapace length (CL) and plastron length (PL) were recorded from all. Mean CL is 45.0±2.8 (range = 41.8-51.0) cm, and mean PL is 34.1± 2.4 (range = 30.0-38.5) cm. Measurements of these females generally equal or exceed those of the few largest females from Louisiana (Dobie 1971), and the clutch size of the Apalachicola population averages half again larger (35.1 vs. 24.5 eggs). In addition to large size, some of the Apalachicola females

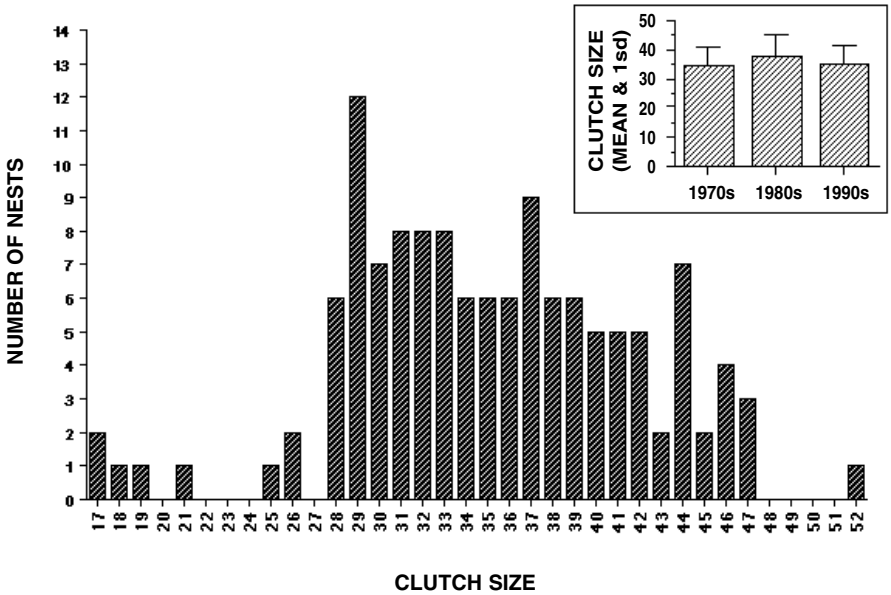

Fig. 3. Distribution of clutch sizes (numbers of eggs per nest) of alligator snapping turtles over 10 years of sampling. Inset: mean clutch size according to decade of sampling. Sample sizes are 45 nests for the 1970s, 21 for the 1980s, and 64 for the 1990s.

have very smooth shells, which suggests that they are quite old. Although we did not actually see any young females, narrow trackways associated with 2 nests in 1991 indicate small individuals, which most likely are young.

In 1990, clutch mass in nests built on spoil mounds averaged larger than nests built elsewhere (1,062 ± 146 vs. 915 ±183 g) but not significantly so ($t = 2.14$, 11 df, $p > 0.05$). Both egg mass and egg number were significantly correlated with clutch mass ($r = 0.65$, $p < 0.01$; $r = 0.792$, $p < 0.01$, respectively, $n = 24$ clutches). In 1991, when clutches were not weighed, clutch size from mounds averaged nearly the same as elsewhere (33.4 vs. 34.0 eggs). Hence, turtles choosing to nest on mounds seem unlikely to differ from other turtles in clutch mass.

Other Turtles.—With exception of the common snapping turtle, we expect that all other species have prolonged nesting seasons that our methods can only partly define. However, we have witnessed or estimated the beginning of the nesting season for Barbour's map turtles (29 April 1991, ca. 5 May 1990, 30 April 1986, 2 May 1981, 3 May 1979, after 5 May 1978, by 10 May 1976) and for spiny softshells (after 9 May 1991, after 8 May 1990, 10 May 1976). Common snapping turtles appear to have completed nesting on 28 April 1991 and on 30 April 1990. There was appreciable nesting activity on the previous few days. Females were still nesting on 2 May 1981 and on 3 May 1980, and the peak in nesting activity in 1978 occurred on 3-4 May, before which few nests were seen. Scattered nesting was still occurring on 9 May 1976.

Clutch sizes for 7 species of turtles are given in Table 1. Clutch sizes in the common snapping turtle averaged significantly smaller (29.9± 7.5 vs. 37.6 7.8 eggs; $p < 0.003$) before 1980 than more recently.

Table 1. Primary nesting habitat and clutch size (mean ± 1 standard deviation) of 7 species of turtles that nest along the mainstem of the Apalachicola River.

Species	No. of Clutches	Principal Nesting Habitat	Clutch Size ± s.d.	Range
Chelydra serpentina	46	Spoil Mounds	33.2 ± 8.5	17-52
Graptemys barbouri	18	Sandbars & Beaches	8.5 ± 2.3	4-14
Trachemys scripta	14	Spoil Mounds	6.9 ± 1.7	4-11
Terrapene carolina	5		3.4 ± 1.1	3-5
Apalone ferox	1	Sandbar	27	
Apalone spinifera	4	Sandbars	21.5 ± 1.7	20-24
Sternotherus minor	6		2.7 ± 0.5	2-3

Fates of Eggs in Nests

Predation.—Most eggs eventually succumb to predation. However, the predators (mostly if not exclusively raccoons) seem seldom to take eggs of alligator snapping turtles until they have been in the ground for several days. This delay has allowed us time to find and protect nests. Hence, in 1990 we arrived almost at the beginning of the nesting season and encountered 35 of 41 nests (85%) as still intact, whereas late arrival in 1972 and 1973 found only 5 of 15 nests (33%) still intact.

In 1991, we had opportunity to compare predation pressures on spoil mounds vs. elsewhere, including a small natural levee. We believe that most of the nests in 1 group (generally near Bloody Bluff) were over 10 days old when we located them. We found proportionately more depredated nests (12 of 13) on mounds than elsewhere (4 of 7 nests), but the trend is weak ($p= 0.07$ for the comparison). In 1990, 3 clutches of eggs that we reburied on spoil mounds lacked protection. We used fill untouched by female turtles (or our hands or clothes) and found in August that only 1 of these nests had been depredated.

Egg Fertility and Viability.—Eggs can be diagnosed as fertile if they show a clear subgerminal space or if a chalky white spot has appeared on the eggshell. During development, formation of the subgerminal space precedes any chalking. Eggs in a few fresh nests have not advanced to either stage and yet have done so within a few days. The delay in finding some nests in 1991 and in providing full protection to others allowed fertile eggs to become distinguishable from infertile eggs. As several nests were protected in 1990 while they still contained early eggs, diagnosis of fertility was grossly incomplete. In 1991, overall fertility of 27 nests was 91% (or 829) of 909 eggs. However, if 1 entire clutch (43 eggs) that was infertile is deleted, fertility becomes 96%.

Although we believe that infertile clutches are rare, we did find 1 in 1986 in addition to the 1 in 1991. In 1990, 1 clutch (38 eggs) contained a mixture of 36 infertile eggs and fertile eggs that died at very early stages (prior to chalking), and only 2 eggs that hatched.

Table 2 categorizes hatching success within nests and the developmental fates of the failing eggs according to year and 2 classes of habitat (spoil mounds and other). In considering the various proportions, it is important to realize that nearly all nests each forfeited a sample of 6-8 eggs for laboratory work. As only apparently viable eggs were selected for laboratory work, true hatching success could be 4-6% higher than noted.

Table 2. Fates of eggs and embryos of alligator snapping turtles in nests according to habitat. The category "other" includes sandbars, levees with spoil, and natural levees.

Year & Habitat		No. Eggs (%) Dying Prior to Hatching as:				
(No. of Nests)	No. of Eggs	Embryo not found	Early Embryo	Advanced Embryo	Term, Pipped	No. Hatched (%)
1991 Mounds	495	109	22	14	11	339
(19)		(22)	(4)	(3)	(2)	(69)
1991 Other	225	63	24	1	2	135
(8)		(28)	(11)	(0.4)	(0.9)	(60)
1991 All	720	172	46	15	13	474
(27)		(24)	(6)	(2)	(2)	(66)
1990 Mounds	408	62	3	20	5	318
(13)		(15)	(0.7)	(5)	(1)	(78)
1990 Other	329	69	0	3	3	254
(11)		(21)	(0)	(0.9)	(0.9)	(77)
1990 All	737	131	3	23	8	572
(24)		(18)	(0.4)	(3)	(1)	(78)
All Mounds	903	171	25	34	16	657
(32)		(19)	(3)	(4)	(2)	(73)
All Other	554	132	24	4	5	389
(19)		(24)	(4)	(0.7)	(0.9)	(70)
All Nests	1457	303	49	38	21	1046
(51)		(20.8)	(3.4)	(2.6)	(1.4)	(71.8)

However, increases of 2-2.2% (from 65.8% to 67.8% in 1991; from 77.6% to 79.8% in 1990) are more likely, as many seemingly viable eggs do succumb within nests. Hatching success was clearly lower in 1991 than in 1990. The distinction between spoil mounds or other substrates is small; however, advanced embryos do seem a little more likely to fail within spoil mounds (Table 2). Still, all of the eggs within 1 nest on a spoil mound as well as in another on a sandbar hatched. The only 2 nests in completely natural substrates had hatching successes of 77% and 97%. As a consequence of low fertility (see above) or apparent flooding (see below), 6 nests had unusually low hatching. If these 6 nests are removed from the overall calculations (leaving 45 nests for 1990 and 1991), hatching success becomes 80.8%, an increase of 9% (Table 2).

In 1991, all or nearly all of the eggs failed in 4 nests that had been diagnosed as 100% fertile in May. Although 2 of these nests were on a spoil mound and 2 were on sandbars, all were in locally completely flat places as well as in seemingly low situations relative to the river. Nearly all of the dead embryos that we could find in August had died at stages that would have required about 3 weeks of moderately cool incubation to be achieved in the laboratory. Data from the Sumatra hydrologic gage show that the

mainstem rose abruptly when the moribund nests would have been about 3 weeks old (Fig. 4). Thus, the nests could have been flooded by a rising water table. Alternatively, there could have been swamping from a locally heavy rain (as in sea turtles, Kraemer and Bell 1980). Such a storm did occur at Wewahitchka to the NW but not at Apalachicola to the south (NOAA data). Either way, the most likely cause of death is asphyxiation brought on by excessive moisture.

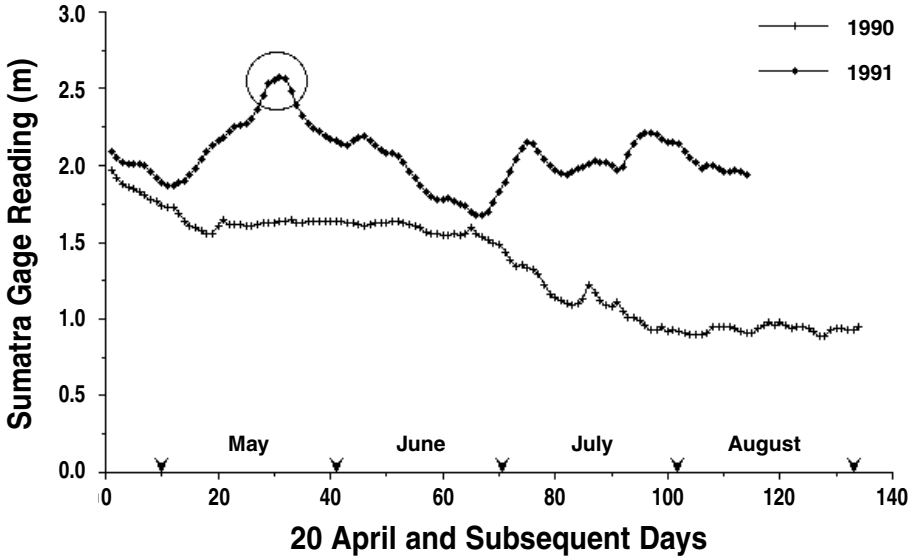

Fig. 4. Water levels in the Apalachicola River mainstem as gaged near the upstream end of the study area during 2 seasons of nesting and embryonic development. The circled peak in water level in May 1991 is coincident with early embryonic death in 4 nests.

Sex Ratios and Environments within Nests

The Seasonal Pattern in Soil Temperatures.—Ambient temperatures in the sidewalls of fresh nests in 1981, 1980, 1979, and 1976 were consistently cool (20.5-23.5°C). Such temperatures must sustain early development. However, we would expect soil temperatures to rise during periods of intense sunlight in June and as a general consequence of the hot summer weather. As we wanted to know general seasonal trends in soil temperature but did not have our own automated recorder, we examined published records from the closest source of NOAA records, the Quincy

Agricultural Experimental Station, 86 km NE of the study area. Published data provide daily maxima and minima at ca. 20 cm (8 inches), which is just a little shallower than the center of the average nest. We compared records for 1991 and 1990 (Fig. 5a), which gave quite similar patterns, with those for 1979, 1978 and 1976 (Figs. 5b, 5c, 5d) to give us more perspective on variation among seasons.

In general, soils at the beginning of incubation are cooler than at any other time. Although there are occasional short term, day-to-day decreases in successive maxima (and minima), the trend is for these measurements to rise until late in incubation. In some years, appreciable cooling may precede the expected time of hatching (Figs. 5c, 5d); in other years, little cooling occurs (Figs. 5a, 5b). Differences between daily extremes are smaller in wet soils (ca. 1-2°C) than in dry soils (ca. 2-4°C).

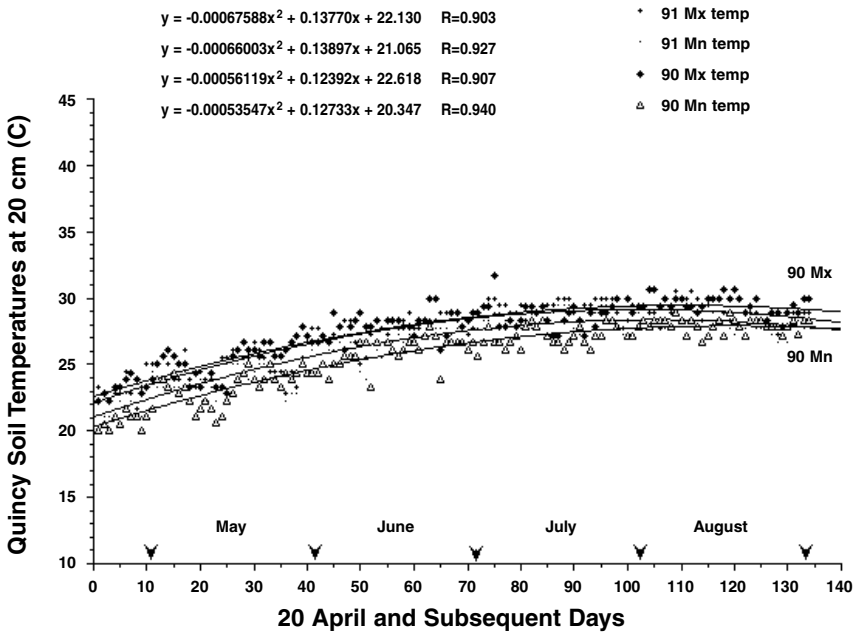

Fig. 5a. Soil Temperatures at 20 cm during 1991 and 1990, Quincy Agricultural Experimental Station

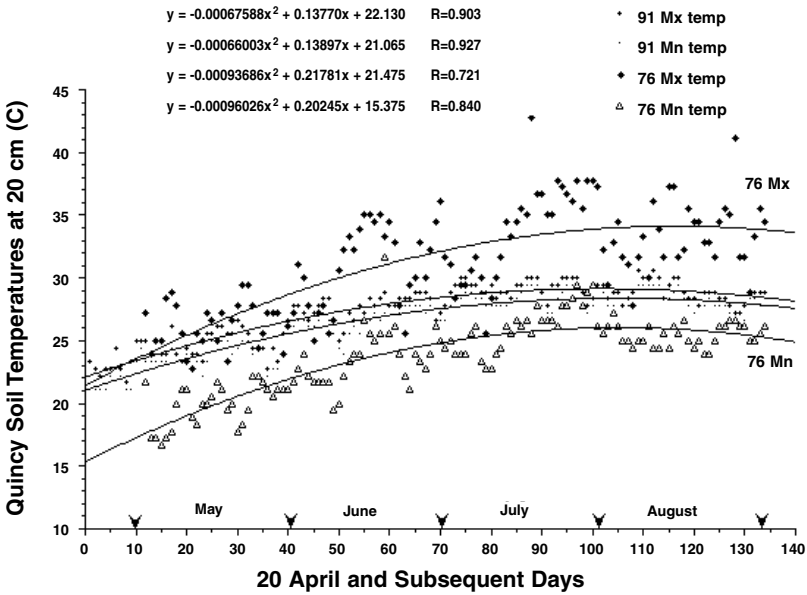

Fig. 5b. Soil Temperatures at 20 cm during 1976, Quincy Agricultural Experimental Station.

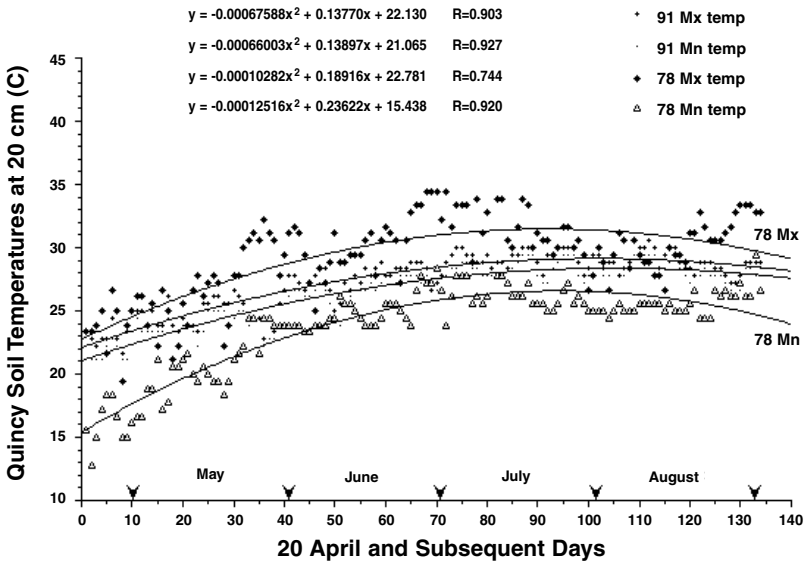

Fig. 5c. Soil Temperatures at 20 cm during 1978, Quincy Agricultural Experimental Station.

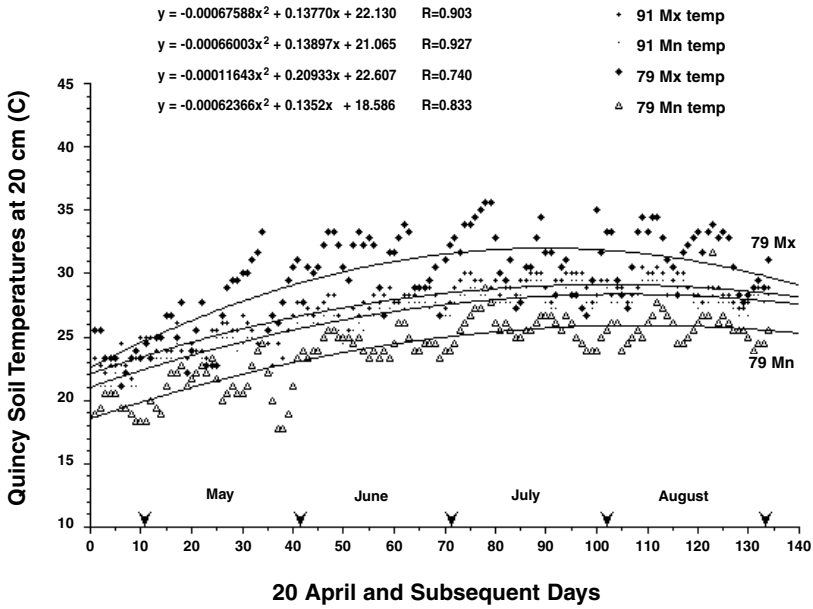

Fig. 5d. Soil Temperatures at 20 cm during 1979, Quincy Agricultural Experimental Station.

Figs. 5a,b,c,d. Soil temperatures (in degrees Celsius recorded at a depth of 20 cm) at Quincy Agricultural Experiment Station, Quincy, Florida, concurrent with the season of nesting in alligator snapping turtles and incubation of their eggs along the Apalachicola River. The Experiment Station is located 86 km NE of the study area. The measurements are daily maxima and minima as reported in the monthly U. S. Natl. Oceanic & Atmos. Adm. Climatological Data (Vols. 83, 85, 86, 95, and 96). All fitted curves are second order polynomials. As 1991 differs most among the 5 years, it is used as a basis for comparison. (a) 1991 and 1990 are similar years with shallow diel as well as longer term variation. The long trend has temperatures rising until early August. (b) 1976 shows great diel fluctuation between daily maxima and minima as well as over longer periods. Overall, temperatures tended to rise until late July. (c,d) 1978 & 1979 are similar years with large diel variation and somewhat irregular longer term variation. The warmest temperatures were in early-mid July.

Soil Temperatures within Nests.—Our records of ambient temperatures within nests show that on average only slight gradients of 1°C or less extend between the tops and bottoms of the egg chamber (Table 3). In a few late afternoon gradients the tops were 3°C warmer than the bottoms. There were several reversals (bottoms warmer than tops) in August, when generally, gradients were smaller than in the spring.

The 4 measurements of temperature (minimum, maximum, initial ambient, final ambient) that we took in the sidewalls of nests are summarized in Table 4. Some of the nest maxima were higher than the highest temperature recorded at Quincy during the same period. Since some nests were in open places, even with a slight southerly slope, high temperatures were to be expected. However,

Table 3. Ambient substrate temperatures (C ± 1 s.d.) 1-3 cm above, below, and in the sides of the egg chambers of natural or reconstructed nests of alligator snapping turtles.

Dates (No. of Nests)	Position Relative to the Egg Chamber		
	Top	Sides	Bottom
26 April-7 May 1991 (23)	24.5 ± 1.7	24.2 ± 1.4	23.8 ± 1.1
27 April-9 May 1990 (24)	24.6 ± 2.2	24.3 ± 2.0	23.6 ± 1.6
14-17 August 1991 (23)	26.4 ± 0.95	26.2 ± 0.7	26.0 ± 0.5
14-18 August 1990 (24)	28.8 ± 1.6	28.6 ± 1.4	28.5 ± 1.4

Table 4. Substrate temperatures (C) in or immediately adjacent to the egg chamber sidewalls of natural or reconstructed nests of alligator snapping turtles. The category "other" includes sandbars, levees with spoils, and natural levees.

Year & Habitat	Type of Temperature	No. Obs.	Mean ± 1 s.d.	Highest	Lowest
1991: Mounds	Minimum	16	22.3 ± 0.5	23.1	21.5
	Maximum		30.7 ± 1.7	33.0	28.1
	Starting ambient		23.8 ± 0.8	25.2	22.3
	Final ambient		26.3 ± 0.7	27.7	25.4
1991: Other	Minimum	7	21.7 ± 0.3	22.3	21.7
	Maximum		30.4 ± 2.5	35.0	27.0
	Starting ambient		23.8 ± 1.7	26.4	21.7
	Final ambient		25.8 ± 0.5	26.4	25.2
1991: All nests	4-Temperature				
	Mean	23	25.7 ± 0.9	27.5	24.0
	Mean of Max. & Min.	23	26.5 ± 1.0	28.6	24.3
1990: Mounds	Minimum	13	21.5 ± 1.1	23.0	19.5
	Maximum		32.1 ± 2.5	36.5	28.5
	Starting ambient		24.6 ± 1.8	26.9	22.2
	Final ambient		29.0 ± 1.3	29.9	26.1
1990: Other	Minimum	11	20.9 ± 1.0	23.0	20.0
	Maximum		30.2 ± 2.5	34.4	26.5
	Starting ambient		23.9 ± 2.3	27.9	21.0
	Final ambient		28.1 ± 1.3	29.9	26.1
1990: All nests	4-Temperature				
	Mean	24	26.3 ± 1.5	28.8	23.7
	Mean of Max. & Min.	24	26.2 ± 1.0	29.2	23.2

2 of the warm records at 35.0°C and 36.5°C approach the lethal level ("critical thermal maximum" = 39.3; Hutchison et al. 1966). The final ambient temperatures show greater departures from the seasonal maxima in warm nests than in cool nests (Fig. 6). However, in 1990 the final ambient temperatures were strongly associated with the maximum temperatures (Fig. 7), whereas in 1991 the association was weak because less variation occurred among the ambient temperatures. In 1991, we felt that heavy rains were periodically leveling temperatures throughout the study area. However, expression of the same relationship in 1990, which lacked such heavy summer rains, suggests that the decreasing solar exposure on warm nests with the passing of summer may foster declining temperatures, while cool nests are still warming against conductive cooling losses to deeper in the earth.

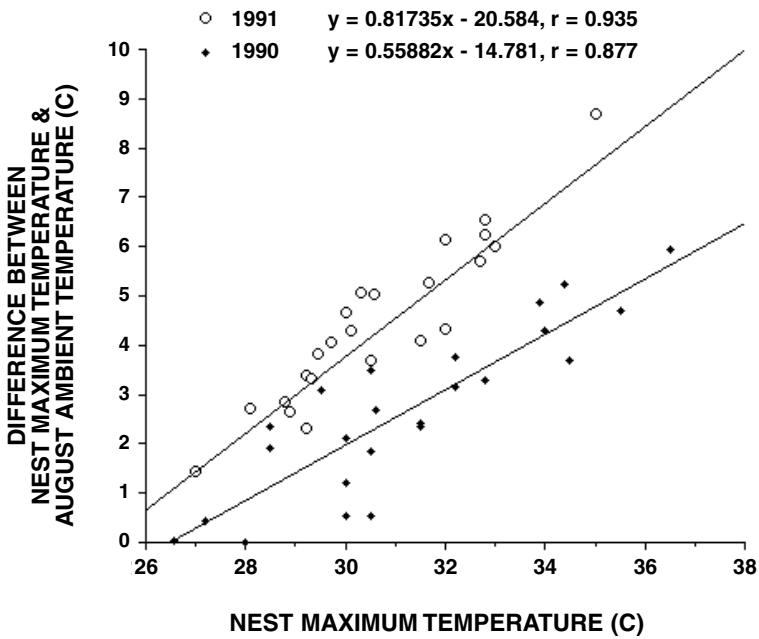

Fig. 6. Soil temperatures in or closely adjacent to the sidewalls of nests of alligator snapping turtles. The August ambient temperatures have cooled to a greater extent in warm nests (with high maximum temperatures) than in cool nests.

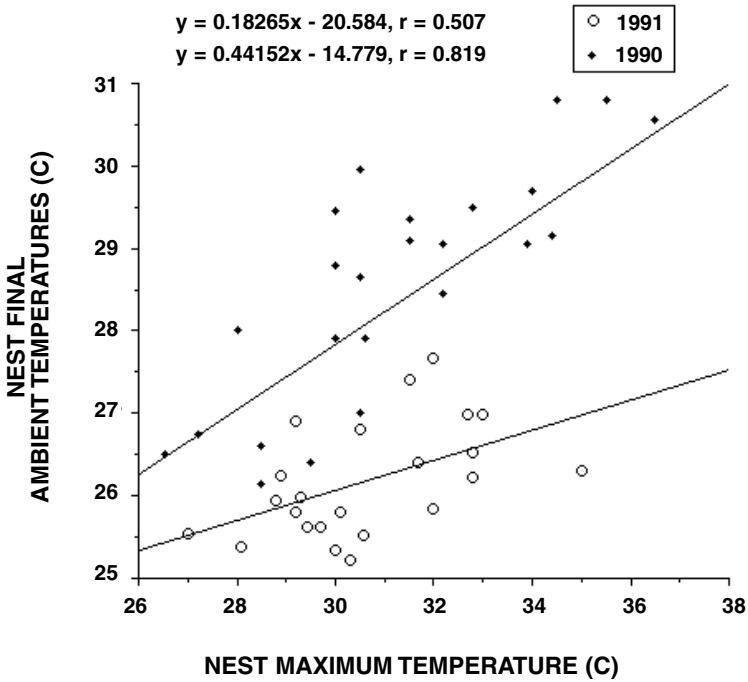

Fig. 7. Soil temperatures in or closely adjacent to the sidewalls of nests of alligator snapping turtles. The August ambient temperatures have tended to be warmer in nests with high maximum temperatures than in cooler nests. The association was much stronger in 1990 than in 1991. A non-linear association according to a second order polynomial improves the 1991 correlation by only 3%, and the 1990 correlation by less than 0.5%.

Sex Ratios and Temperature.—When the 4 measured temperatures are averaged to provide a single index of temperature for each nest, the resultant indices are significantly correlated ($r = 0.738$, $p < 0.01$, on arcsin-transformed data) with the sex ratios of the samples from the various nests (Fig. 8). In both years, male-biased sex ratios are associated with cool nests and female-biased sex ratios with warm nests. The correlation is much stronger for 1990 ($r = 0.867$, $p < 0.01$) than for 1991($r = 0.514$, $p < 0.05$). In 1990, many nests were in highly exposed situations, several others were deeply shaded, and few were only lightly shaded (or with the day being evenly divided between being exposed or shaded). In 1991, most of the nests were shaded to varying degrees. In August 1990 we took soil temperature profiles (from the surface down to 40 cm) at 2 very shady sites. In 1991, we transplanted a nest to 1 of these sites and obtained a 78% hatch consisting of 15 males and 6 females (71.4% male). As

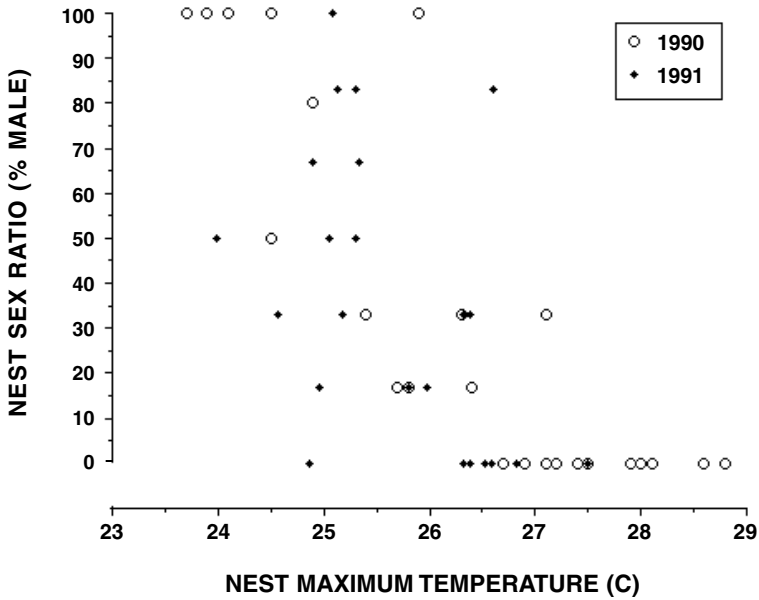

Fig. 8. Hatchling sex ratios in nests of alligator snapping turtles. Nest sex ratio is estimated from a random sample of 6 hatchlings. The temperature index is the average of nest maximum, minimum, and starting ambient and final ambient temperatures as recorded in or closely adjacent to the sidewalls of the egg chamber.

the maximum temperature in this nest reached only 25.8°C, it is possible that this nest was so cool that cool females (Ewert and Nelson 1991; also, see below) developed (perhaps in 1-2 other nests, too). This would, of course, confound any linear association between sex ratio and temperature.

As the mid-range temperatures [(maximum + minimum)/2] averaged nearly the same in 1991 (26.5°C) as in 1990 (26.2°C), we examined the association between these indices and nest sex ratio (Fig. 9). A warm pivotal temperature (midpoint between warm female-biased and cooler male-biased temperatures) of 25.9°C is defined by the fitted line, and 4 nests with balanced sex ratios have mid-range temperatures of 24.3, 24.5, 25.5, and 25.9°C. These indices are lower than the laboratory estimate of 27.2°C (see below) and they may underestimate the actual average trends in daily temperatures (Fig. 5). Because, however, short exposures to warm temperatures in fluctuating thermal patterns, such as those in nests, disproportionately influence sex determination in snapping turtles, the computed average fluctuating temperature should be lower than the laboratory constant temperature (Yntema 1976, Georges 1989, and see below).

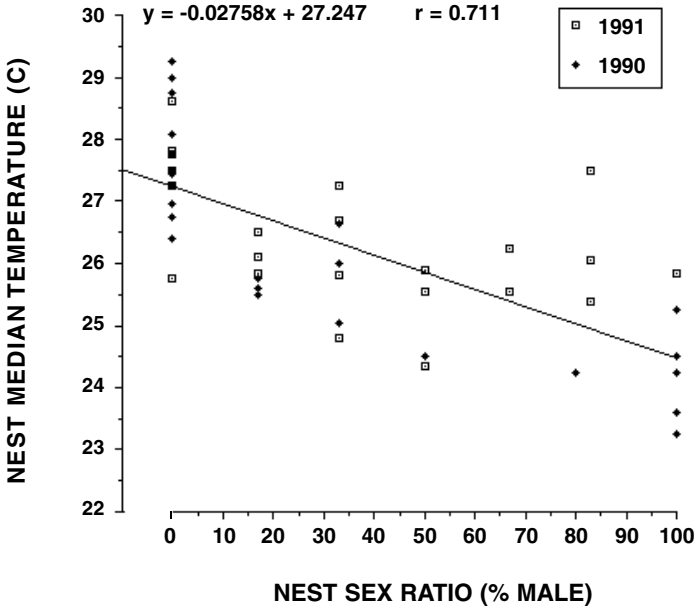

Fig. 9. Hatchling sex ratios in nests of alligator snapping turtles. Nest sex ratio is estimated from a random sample of 6 hatchlings. The median temperature is the simple average of nest maximum and minimum temperatures as recorded closely adjacent to the sidewalls of the egg chamber. A warm pivotal temperature (gives a 1:1 sex ratio when female-biased > male-biased temperatures) is suggested at ca. 25.9°C, which is cooler than predicted from laboratory data. The index temperatures probably are biased toward being cooler than the functional temperatures that determine sex because both the seasonal cycle (actual time spent above a given temperature) and developmental rate (amount of development completed per unit time) are weighted toward the nest maximum.

Sex Ratio and Habitat.—In both 1991 and 1990, nests yielding female-biased sex ratios prevailed on the spoil mounds (Table 5). Nests in other habitats produced varied sex ratios, but with balanced representation from all-female to all-male extremes. In general, nests on the mounds were less intensively shaded than the sometimes completely shaded nests on natural or just slightly altered levees. Nests on sandbars were extensively exposed. Thus, the greater mix of degrees of shading in the "other" category of habitat fostered a balanced mix of often extreme sex ratios that, as a blend, approximated sex ratio parity.

Sex Ratio and Annual Recruitment.—If all protected nests with diagnosed hatchlings are assigned equal weighting, without regard to clutch size or relative hatching success, the combined sex ratio is 34.8% male for the

Table 5. Sex ratios (% male) in alligator snapping turtle nests according to habitat. The category "other" includes sandbars, levees with spoils, and natural levees.

Year & Habitat	Nests Weighted Equally		Nests Weighted by Hatching Success	
	No. of Nests	Sex Ratio	No. of Hatchlings	Sex Ratio
1991 Mounds	16	32	339	28
1990 Mounds	13	20	318	23
Mounds[a]	29	27	651	26
1991 Other	7	43	135	48
1990 Other	11	47	254	43
Other[a]	18	45	389	45
Sandbars[a]	6	5	122	8
Levees with Spoils[a]	10	65	221	55
Natural Levees[a]	2	65	46	68

[a] Total for both years of study (1990 and 1991).

23 protected nests in 1991, and 32.5% male for the 24 nests protected in 1990. If weighting is adjusted for the productivity of individual nests, the sex ratio for 1991 falls to 33.2% male and the sex ratio for 1990 remains 32.5% male.

We considered a hypothetical case in which all nests contribute to annual recruitment (i.e., all contain fully fertile clutches that escape predation and suffocation) and were assigned equal weighting. We apportioned these nests among 4 categories according to shading (open-nearly open, partly open, mostly shaded, deeply shaded) and used the known sample sex ratios from the protected nests to assign 2 sex ratios (1 each for 1991 and for 1990) to the remaining (depredated and unprotected) nests. Accordingly, the combined sex ratio for 64 nests in 1991 is 35.8% male, and for 41 nests in 1990 is 31.6% male.

Sex Ratio and Viability.—We have estimated the viability associated with 3 broad groupings of sex ratios: strongly female-biased, strongly male-biased, and balanced to weakly biased (Table 6). We eliminated the infertile eggs from these estimates (fairly precisely for 1991, approximately for 1990; see Table 4 and text) because these eggs cannot be affected by nest environments. Several nests in each category had complete survival. On average, however, the highest viability is associated with intermediate sex ratios and the lowest with female-biased sex ratios. Several nests in obviously female-biased environments either failed completely or fared less well than those making greater proportions of males elsewhere. Thus, nearly half of the nests with strongly female-biased sex ratios (13 of 27 nests, Table 6) had viabilities of 70% or less, whereas only 40% of the strongly male-biased nests and none of

Table 6. Mean viability in nests (% fertile eggs hatching per nest) according to nest sex ratios (% male).

Period (No. of Nests)	Strongly Female-biased (0, 17% male)	Parity & Weakly Biased (33, 50, 67% male)	Strongly Male-biased (80, 83, 100% male)
1991 (24)	77.8 (14)	89.2 (4)	88.2 (6)
1990 (26)	57.0 (13)	94.7 (9)	67.3 (4)
Total (50)	67.8 (27)	93.0 (13)	79.8 (10)
% viability not exceeding (Total for 50 nests)	60.0 (9) 70.0 (13)	60.0 (0) 70.0 (0)	60.0 (2) 70.0 (4)

the intermediate nests did this poorly. Possibly the greatest rates of mortality will be associated with making the favored sex in unbalanced sex ratios (Frank and Swingland 1988). Although we have a trend in this direction, alternatively, the most favorable conditions for development may coincide with parity in sex ratio.

Laboratory Work

Temperature and Incubation Period.—As temperature is the primary factor affecting the length of incubation (Packard and Packard 1988, Etchberger et al. 1992), the results of laboratory incubation at constant temperatures should function as a reference for interpretation of field results. The rate of incubation (Fig. 10; here, the inverse of total duration) increases with temperature, but exponentially, such that rates of change decline across warm temperatures. The range of constant temperatures that sustain development on a continuous basis is much narrower than the range that is tolerated for a few hours or days. Thus, whereas 20.5-21.5°C may be tolerated for several days during early development and may even be beneficial (Yntema 1968, Ewert 1985), alligator snapping turtle embryos will die if they cannot become warmer as they reach more advanced stages of development. The warmest tolerated constant temperature appears to be just a little greater than 30°C, as the incidences of deformity and mortality have already begun to increase at 30°C. However, our records of nest temperature suggest that even 36°C can be tolerated briefly.

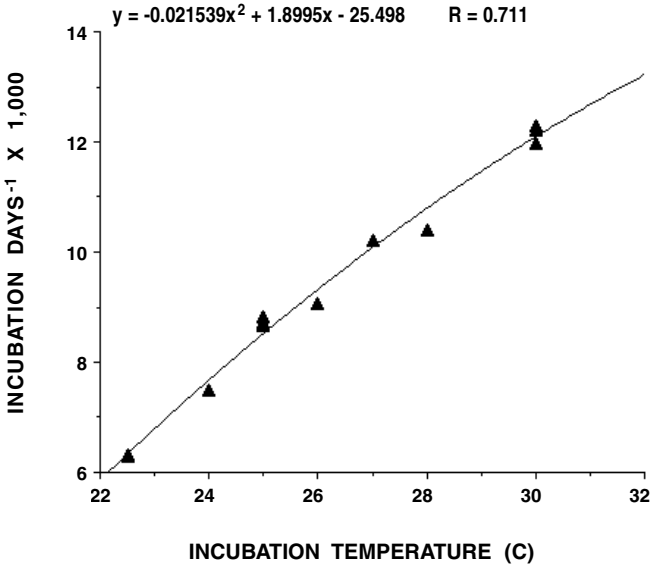

Fig. 10. Average embryonic developmental rate in alligator snapping turtles as a function of temperature. The slight upward curvature in the association occurs partly because very early embryonic development (ca. 5-7% of the total incubation period) in several series of eggs occurred at cool field temperatures prior to transfer to constant temperatures, and partly because late development (20-25% of the incubation period) is less sensitive to temperature than early development (see Ewert 1985).

Temperature-dependent Sex Determination at Constant Temperatures.—Although warm (29-30°C) incubation temperatures yield exclusively females in the alligator snapping turtle, all other temperatures allow both sexes to develop (Fig. 11). However, most hatchlings from 25, 26, and 27°C are male. Thus it becomes possible to achieve sex ratio parity (1 male to 1 female) by adding females from warm (28-30°C) incubations to a much larger group of mixed sexes from mild (25-27°C) incubations. Alternatively, an addition of hatchlings (mostly females) from cool temperatures to the mild group will also give sex ratio parity. Hypothetically, samples from incubation at just 24.5°C or 27.2°C, known as pivotal temperatures (Mrosovsky and Pieau 1991), will have 1:1 sex ratios.

Incubation at Multiple vs. Single Constant Temperatures.—It is possible that incubation over a given series of constant temperatures or a range of fluctuating temperatures will give a different result from constant incubation at any 1 of these temperatures. Some of our samples from field nests suggest that some clutches consist entirely of males (Fig. 8), whereas laboratory

incubations at constant temperatures averaged, at most, 2.2 males per female (Fig. 11). The same enigma has been observed in the Australian freshwater crocodile (*Crocodylus johnstoni*) (Webb et al. 1987), which shows strongly male-biased sex ratios in some natural nests but not in others and never at constant laboratory temperatures. However, laboratory incubations in which eggs start at a cool temperature and finish at a warmer 1 have yielded appreciably higher proportions of males (Webb et al. 1987). In natural nests, the crocodilian eggs, like alligator snapping turtle eggs, begin incubation at cool temperatures and experience progressively warmer ones later. Hence, in 1991 we applied step-shifts in constant temperature from a moderately cool temperature (24°C), through a cool male-forming temperature (25°C), to a warmer male-forming temperature (27°C).

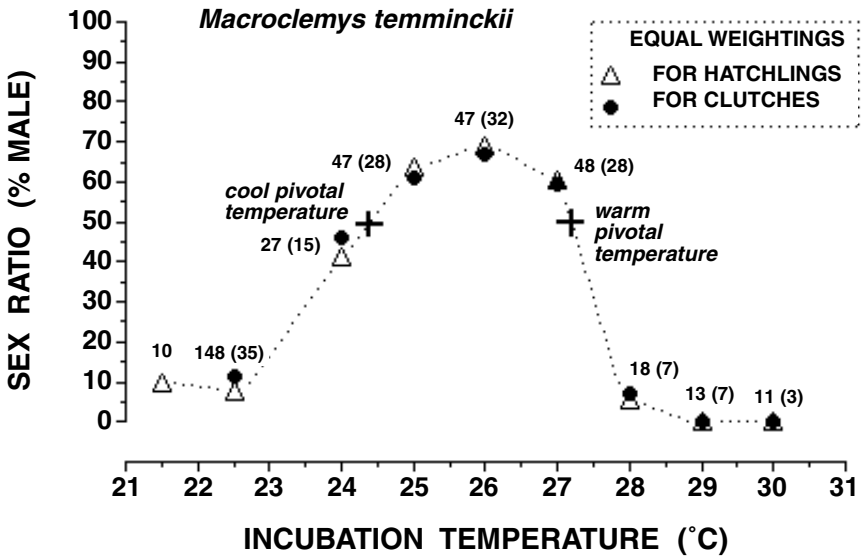

Fig. 11. Hatchling sex ratios [% male = 100 x male/ (female + male)] in alligator snapping turtles as a function of various incubation temperatures. Sample sizes (no. of hatchlings diagnosed, with no. of clutches providing hatchlings in parentheses) are listed for each tested temperature. The lines connecting plotted points do not represent actual measurements, but rather, suggest hypothetical clarity to the pattern of response. "Pivotal temperatures" that hypothetically give 50% of each sex are 24.6°C and 27.2°C.

Our series of step shifts yielded a sex ratio of 70.4% male (50 males: 21 females), whereas 25°C gave 61.8% male (21 males: 13 females), 26°C gave 69.1% male (23 males: 10 females, 1 intersex), and 27°C gave 55.8% male (19 males: 15 females). The temperature of 24°C was assumed to give female-biased sex ratios on the basis of data from 1990 and was not rigorously retested; a small sample in 1991 gave 1 male and 5 females. Hence, although the step series of shifts did give a greater male bias than that from any 1 of its component temperatures, the increase was only modest and scarcely greater than the greatest male-bias at a constant temperature (i.e., 26°C), which was closely bracketed by the shifts. Thus, the above regime of changing incubation temperature does not support the hypothesis that varying temperatures have effects that cannot be explained with constant temperatures.

Aside from the test series, we carried 1 entire clutch (38 eggs in 2 boxes) through the step shifts. The hatch was 36 males: 1 female (97.2% male); the 38th egg was damaged. Hence, laboratory incubation can produce a strongly male-biased sex ratio in at least an occasional clutch. This may provide partial explanation for the all male, 6-hatchling samples from some nests.

Temperature Response Polymorphisms.—We considered an alternative explanation for why some clutches might be providing exclusively males when the response of the overall population is at most 2.2 males per female. All of the embryos in some clutches might respond to the most potent of male-making temperatures by becoming males, whereas some embryos in other clutches might be destined to become female at most of these same temperatures. The data collected for testing the effects of step increases in temperature are also suitable to check for heterogeneous responses among clutches, an indication of polymorphism. In particular, each clutch was represented at 25, 26, and 27°C, or across the "male hump" (Fig. 11). The test for heterogeneity across the hump was not significant ($Chi^2 = 33.6$, 25 df, $p > 0.1$). However, we found that among clutches, the frequency of males across the hump was related to the frequency of males made by the step shifts. Specifically, 7 clutches (each represented by 3 eggs) gave 3 males from constant temperatures plus 3 males from step shifts; 16 clutches gave at least 1 female from a constant temperature and 1 female from the step shift, and only 2 clutches gave 3 males in 1 category but at least 1 female in the other. Hence, as a generality, if 25, 26, and 27°C made only males from a given clutch, then the step treatment made only males, too ($Chi^2 = 14.2$, 1 df, $p < 0.001$). Building from this observation, we combined the results of the step shifts with those from the constant temperatures and found highly significant

heterogeneity ($Chi^2 = 54.9$, 25 df, $p < 0.001$; or in a select, balanced group with complete survival, $Chi^2 = 47.2$, 20 df, $p < 0.001$).

In 1990 we examined hatchlings from incubations at 22.5°C for the presence of a temperature response polymorphism. Our justification was that preliminary work on incubation in 1986 had yielded only males (2 from 22.5°C, 1 as an advanced embryo from 21.5°C) from 1 clutch but only females (16 at 22.5°C, 9 as advanced embryos from 21.5°C) from 2 other clutches. However, among 130 hatchlings in 1990 from 22.5°C, only 10 were males, and these were distributed nearly randomly among 7 clutches. Unlike the male-producing clutch in 1986, all clutches with males also contained 2 or more females. There was a weak association between males and the samples with completely successful hatching. However, the association weakened further when correction was made for the disproportionately large number of turtles in those samples with complete hatching.

DISCUSSION

Survey

Nests of the alligator snapping turtle were widely distributed throughout the study area except for the uppermost section. As 1991 provided the highest count of any year, it appears that the local population cannot be declining, despite concerns about populations in other places (Pritchard 1989). The local population appears to be stable or increasing slightly. Dissections of adult females from Louisiana indicate that none ovulate more than 1 clutch per year and that a few may skip a year (Dobie 1971). The brief nesting season along the Apalachicola River indicates that this condition also occurs in western Florida. Projecting from this information and the possibility that 1 female split a clutch between 2 nests, the local population contained at least 62 adult females in 1991. More likely, given continued use of known nesting sites downstream that were not censused in 1991 (assume 7 females based on the 1990 data), a few peripheral nesters (assume 10 females, as along Saul Creek Road), and a modest 25% skipping nesting in 1991 (see Frazer et al. 1991), there are at least 100 adult females living between the Brickyard area and the bay. At the same sex ratio as in hatchlings, in which females exceed males by 2:1, at least 150 adult alligator snapping turtles live in the area. We lack any knowledge of the numbers of yearlings or older subadults. The population might seem a little sparse at roughly 1.2 adults per km^2 of floodplain (calculated from H. Leitman 1984), but it equates to 18.4 adults per km^2 of open water, or perhaps 6 adults per km^2 of open water plus low and almost continuously flooded floodplain forest. This population density seems reasonable for a specialized predator such as the alligator snapping turtle. This species does seem to be more abundant here than the common snapping turtle. Comparisons with other species are more difficult as all make small, obscure nests, many of which fall prey to fish crows (*Corvus ossifragus*) and disappear without a trace.

Life History Factors

Mean clutch size and its variance have remained stable throughout 2 decades of observation. Although both larger and smaller clutches (from 10-61 eggs) are known from the Gulf Coast states (Pritchard 1989), the mid-range remains the same as the median (35 eggs), and the mean (35.1 eggs) for the Apalachicola sample. Clutch size along the Apalachicola River clearly averages larger than in populations sampled across Louisiana about 3 decades ago (Dobie 1971), where the species has been more intensively harvested (Pritchard 1989). A smaller average clutch size in Louisiana may result from selective removal of most of the larger, older females. Indeed, females encountered along the Apalachicola are very large relative to those sampled in

Louisiana by Dobie (1971). Still, occasional females in Louisiana do become very large (Pritchard 1989), perhaps in local areas of low hunting pressure.

Published reports that detail egg viability within turtle nests (Table 2) are available for a few species, including sea turtles (Whitmore and Dutton 1985). Typically, several eggs fail to advance beyond early stages, but more than half of the eggs hatch. Total or nearly total infertility of entire large clutches is more unusual and could be cause for concern. Since 1986, 3 of 73 clutches (4%) of alligator snapping turtles from along Apalachicola River have thus failed. This could be natural, or this might mean that the population has a shortage of males. Some hunting has probably occurred along the Apalachicola River (Pritchard 1989) and may have continued until recently (Paul Moler, pers. commun.). Males, because of their large size, have greater market value than females; they can also be removed from the population and leave less evidence of their absence. Overall, the species is so secretive that only depredated nests (indicating the presence of females) are noticed. However, a single male can fertilize several females; hence, populations with female-biased sex ratios can be productive. Nonetheless, at some level of reduction, males can be assumed to lack sufficient sperm for the excess of females, or local blocks of habitat may simply lack males.

Significance of Temperature-dependent Sex Determination

We recorded strongly female-biased sex ratios from nests in 1990 and 1991. However, we cannot be sure that these represent a typical annual trend, nor can we be certain that we examined a representative sample of nesting habitats. Still, empirical data already show that female-biased hatchling sex ratios predominate among reptiles with temperature-dependent sex determination, and that male-biased hatchling sex ratios are rare (Bull and Charnov 1988, Ewert and Nelson 1991). By contrast, in most amniote vertebrates, sex ratios at birth are closer to parity. Many of the field studies on temperature-dependent sex determination have involved man-made nesting substrates that are more open than local natural features. These man-made sites may provide focal points of warm conditions in an otherwise cooler environment. Whereas successful hatching of the nest transplanted by us to the "coolest available" location suggests that all local substrates are sufficiently warm for development of alligator snapping turtles, physiological constraints on development may still favor warm conditions for producing females. These conditions could be so rare and thus hard to find naturally that nesting turtles have evolved an innate search image for seeking such places before giving up to nest elsewhere. Man's creation of many open places may thus have made the searching unnaturally easy.

Although we began this project with the expectation that there would be strong temperature response polymorphisms among clutches, we initially looked for them under the wrong conditions. Such conditions would have required more extreme differences among individuals than those that we found, because we had assumed that a greater range of temperatures would express the polymorphism (i.e., from 22.5-27°C instead of 25-27°C). However, identification of the lesser polymorphic condition should still enhance the capacity for future sex ratio adjustment (Conover and Van Voorhees 1990), because the necessary genetic variability can be assumed to be present. Further, it is being expressed over a range of temperatures that all embryos must experience, at least during the early weeks of development.

The pattern of sex ratios across an array of constant temperatures (Fig. 11) suggests superficially that males are harder to produce than females. No single temperature yields all males or even nearly all males, whereas both extremes of temperature (ca. 22.5°C, > 29°C) yield only, to nearly exclusively, females. However, the temperature range that gives a bias toward males occupies an appreciable portion of the safest range for embryonic development (25-27°C within 24-29°C) and is a commonly expressed range in field nests with partial shading. Nearly all of the nests that contained only females were located in unnaturally open (man-made) situations. If nests that contained 1 or more males is considered as being "normal," the overall sex ratios would have been 51% male for 16 nests in 1991, and 60% male for 13 nests in 1990, which are less deviant from parity than the sex ratios for all nests. One can speculate that with greater shading and cooler summers (often functions of cloud cover as well as vegetation) greater male biases would occur. This would be a good prediction based on the strong association between cool temperatures and male-biased sex ratios in the data from 1990. However, the much weaker trend from the 1991 data, together with the result from the cool, experimental nest (71.4% male), suggest that the feminizing process at cool temperatures (Fig. 11) can be expressed and might impose an upper limit on male bias. Perhaps, as in the step shift experiment, this ceiling would be about 70% male.

In the consideration of a low upper limit to male sex ratios and the low proportions of males that some individual clutches gave from the step shift experiment (and associated constant temperatures), it is tempting to speculate on a novel twist to temperature-dependent sex determination. Whereas some embryos may be genetically programmed to become males or females over an appropriate range of incubation temperatures, other embryos might become males only under extremely constrained incubation temperatures, and still others might not become male at any temperature. This last group of embryos, thus, would have temperature-independent sex determination, as in most vertebrates. However, it is a special group as it contains only females.

Unfortunately, demonstration of such a group becomes difficult because any single embryo cannot be tested at all temperatures throughout the temperature sensitive period of development, when temperature is actually determining sex (Yntema 1976).

Significance of the Spoil Mounds

It should be evident throughout this report that the spoil mounds are just 1 form of man-made modification to the natural habitat. The man-made beaches, sandbars and smaller patches of coarse, sandy spoil along the levees are other forms. From a perspective of having increased the amount of nesting habitat along the levees, these new areas have benefited turtles. They so completely dominate the higher portions of levees that completely natural high levees have become scarce. In addition to being high and dry, the spoil areas appear to offer easy substrate for digging as compared with the generally forested high banks, such as near the Ft. Gadsden State Historical Site. Roots tend to be fewer than in natural levees and the coarse spoil sands offer easier digging than the hard silt and clay of natural levees or high banks. The few low areas along sandbars may be deceptive in wet years and result in drownings of nests. However, this fate is a risk on all sandbars, whether made from dredged spoil or from naturally transported sand.

By acting as unnatural attractants for nesting, spoil mounds may become focal points for predation (Eichholz et al. 1979). Our study was not designed to evaluate this point, and our only quantative observation was small and inconclusive. It does appear that the spoil mounds have allowed armadillos (*Dasypus novemcinctus*) to become permanent residents along the levees since 1981. However, we lack any evidence that armadillos are preying on alligator snapping turtle eggs or on the eggs of other turtles. Tracks suggest that armadillos are oblivious to turtles. As some of the alligator snapping turtle nests have been made at the far inland sides of mounds, more than 200 m from the river, finding these would appear to require predators to adopt a relatively complex search plan for working mounds as opposed to working the narrowly linear natural levees.

The spoil mounds and sandbars probably have changed turtle populations in 2 ways. First, they have increased the proportions of females in the annual recruitment of alligator snapping turtles and probably some of the other species as well. For the short term, and without disproportionately high nest predation, this should have given a boost to all turtle populations with temperature-dependent sex determination. In the long term, as in a few generations (at ca. 15 years each in alligator snapping turtles, c.f. Dobie 1971), the female bias could become a little harmful if various species have temperature response polymorphisms as in alligator snapping turtles.

According to the Fisherian hypothesis (Bull 1983), parents that tend to produce the greatest proportions of males in suitable warm environments will come to dominate populations. Subsequently, as natural revegetation covers the mounds and sandbars and renders them more shady, populations will become male-biased for a while, and annual recruitment will fall as fewer females mature to lay eggs. In more time, this perturbation should dampen, and thermal relationships will approach pre-development associations.

The second change applies to species that seem relatively specialized toward using the mounds and sandbars; the spiny softshell is the most obvious example. The seemingly small local population may be derived from a few individuals that have recently dispersed down the river and found suitable habitat along the man-made sandbars. As the sandbars become overgrown, spiny softshells may become locally extinct for lack of nesting habitat. The species should persist up the river, however, where sandbars are a natural feature. Barbour's map turtles seem to be more common along the sandy sections of the mainstem than in the more natural side channels. Original populations may have been smaller than they are today. Hence, Barbour's map turtles may also decline locally as the sandbars, beaches, and mounds become fully revegetated. Although they have temperature-dependent sex determination, its expression probably follows that of other map turtle species in producing only males at mild to cool temperatures (Ewert and Nelson 1991), such as in the thermal regimes along forested levees.

MANAGEMENT RECOMMENDATIONS

Alligator Snapping Turtle Populations

Nesting frequency and clutch size suggest that the population has remained stable during 16 years of observation. Direct observation in the early 1980s indicated that the population included large, old adults. We have no reason to believe that the present population lacks them. As our observations in 1991 suggest the presence of small, probably young adults, the overall population appears to have a mixed age structure indicative of a healthy population. Although we estimate a population density of 6 adults per km^2 of normally available habitat, our estimate is very speculative and difficult to interpret in terms of carrying capacity. Our only cause for concern has been our finding of low fertility in 3 nests, which could indicate a shortage of males. The latter may be attributed to the female-biased sex ratio in annual recruitment of hatchlings, or perhaps to some illegal hunting. In general, however, the population seems to be healthy. Thus, we feel that perpetuation of present regulatory statutes (which limit turtle hunters to a possession of 1) and environmental conditions are satisfactory for the next several years.

Beyond the immediate future, ecological succession on the spoil mounds and sandbars could reduce productivity of alligator snapping turtles.

Future of the Dredged Spoil Mounds, Sandbars, and Beaches

There are 9 large and discretely separated floodplain disposal sites (2 are closely spaced groups of 4 sites each to give a total of 15 mounds) involved in our study. Six of these sites were surveyed for vegetation in 1978 (Eichholz et al. 1979). Although vegetation analyses were not part of our study, we roughly estimate that voluntary succession has covered more than half of the areas shown as barren in 1978 and only $^1/_5$ to $^1/_4$ of the mound surface areas remain barren or just thinly shaded near ground level. In another 10 years of natural succession, the mounds may be nearly completely wooded. At this time, sex ratios of the annual recruitment of alligator snapping turtles should have returned to parity or may have become slightly male-biased. Alternatively, nesting females may gradually cease using the mounds, although common snapping turtles will likely continue to seek them. For enhancement of turtle populations, maintenance of some open area on the mounds would be beneficial to the several species of turtles that use them. However, as this option is less natural than a second option for fostering beaches and sandbars, perhaps the second option deserves more serious attention.

Aerial photographs taken in 1977 show exposed deposits of nearly virgin dredged spoil when these features should nearly have covered their maximum area (Fig. 1). Today, from the Brickyard area to the confluence with the Jackson River, 9 partially within bank, partially onshore disposal areas remain as beaches or as mostly open sandbars with a river frontage of tall herbs and shrubs. Shoreline lengths of these 9 areas as measured on the 1977 aerial photographs collectively equal 5% of the shoreline from the Brickyard area to the confluence with the Jackson River, or 9% of the shoreline along the reach bordering Forbes Island (including both sides of the mainstem). The 8 largest of these areas had open beach frontages of 0.35-0.45 km each. Today, while perhaps $^2/_3$ of the open beach frontage remains, the face has retreated and the treeline has advanced until just narrow bands of sand remain.

As the mounds become overgrown, alligator snapping turtles may nest on beaches more often than at present. Maintaining open space on existing beaches should sustain Barbour's map turtles and spiny softshells, both of which are more dependent on open areas. Also, adding sand to increase the heights of the lower beaches by 1-2 m would lessen instances of nests drowning. At present, weekend boaters also picnic on the beaches and tend to trample (and occasionally to trash) some portions favored by turtles. However, most boaters seem to restrict themselves to areas with barren shorelines. Thus, a thin barrier of woody or herbaceous shoreline vegetation should enhance stretches of beach for wildlife.

Although it is beyond this study to detail how current practices of dredging might be modified to maintain the disappearing beaches, 2 suggestions seem appropriate. First, from the perspective of nesting in turtles, placement of spoil on the beaches should not occur during the spring or summer. Early fall (or winter) placement would allow nests of incubating eggs from the current season to hatch. Summer placement of spoil is likely to smother developing embryos. Second, and perhaps more important, several years should lapse between successive additions to any given beach. Thus, if for instance, spoil were deposited every 7 years, any loss of annual recruitment in 1 year, as by smothering under spoil deposited during the summer, should be more than offset by 6 years of barren sand and early vegetational succession on an appropriately contoured beach.

Additional Study

The present study leaves many areas of uncertainty regarding population dynamics of alligator snapping turtles and suggests other work that could benefit local populations of other turtles. More work is needed on the sex ratios of hatchling alligator snapping turtles that form the annual recruitment.

As the soils temperature data from the Quincy Agricultural Experiment Station suggest that 1991 and 1990 were similar years but were quite different from 3 years during the late 1970s, perhaps the sex ratios determined during 1991 and 1990 are not truly representative. With our present knowledge we cannot project how these different years might affect sex ratios. Hence, we need data on sex ratios from years with a wider variety of weather conditions.

Another unsolved issue concerns the extent to which alligator snapping turtles that nest along the mainstem represent the entire local population. Are there appreciable numbers of females that seek high ground near backwaters, such as the 1 that nested along Saul Creek Road? One way to approach this issue is with radio telemetry to determine the extent and evenness of dispersal of post-nesting females from along the mainstem. As this work could interfere with normal nesting activity, the project would have to proceed with caution. However, even if females are temporarily prevented from nesting while we equip them with transmitters, they should still nest within the next few days, as most other species of turtles respond in this manner.

In addition to capturing and marking nesting females, some general trapping of backwaters is appropriate. This procedure is about the only available way to determine the general distribution of males in relation to the question of adequate numbers to fertilize the female subpopulation.

With 8 species of turtles proven to be nesting along the river, plus 2 other species (*Pseudemys concinna, Sternotherus odoratus*) observed locally in the river, another (*Kinosternon subrubrum*) seen on the floodplain, another (*Deirochelys reticularia*) seen close by, and still another (*Malaclemys terrapin*) probably living in the bay, the lower Apalachicola River supports the richest community of turtles in Florida, North America, and perhaps the Western Hemisphere. The Barbour's map turtle and the alligator snapping turtle are Species of Special Concern and, along with the Gulf Coast box turtle and loggerhead musk turtle, receive protection through regulated taking. As all of these species have temperature-dependent sex determination, procedures such as those applied to the alligator snapping turtle could yield interesting information about each of them, especially when sampled from the same local community of turtles. In contrast to alligator snapping turtles, procedural drawbacks do include the longer nesting seasons of most of the species and the much greater difficulty in finding their small hidden nests.

ADDENDUM

We discovered after completion of this report that the nesting season is sometimes prolonged beyond 11 May, the estimated latest date for nesting that we have given in this report. In 1993, a very cool, dry year, nesting continued sporadically through 18 May. This observation has not affected the census data and other findings of this report.

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