NESTING ECOLOGY AND HATCHING SUCCESS OF THE WOOD TURTLE, *GLYPTEMYS INSCULPTA*, IN QUÉBEC

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Abstract.—The nesting ecology of Wood Turtles (*Glyptemys insculpta*) was studied in Québec, Canada during 1996 and 1997. Females made long-distance migrations to nesting grounds, where they staged for up to nine days before nesting. Fifty-five percent of the estimated female population was observed at this staging area. Wood Turtles exhibited strong nest site fidelity, with 95% of females observed to nest in two consecutive years returning to the same nest site. Nesting occurred for approximately two weeks during mid-June. Turtles were observed nesting during all daylight hours, with morning and evening peaks in activity. Clutch size was positively correlated to female size with larger females having larger clutches. Mean clutch sizes were significantly different between years. Nest success was 74% in 1996 and 65% in 1997. Nests constructed during the first half of the nesting season had significantly greater success, suggesting that northern Wood Turtle populations may be delimited by insufficient degree days for the completion of incubation. Staging, nest-site fidelity, and a short nesting season make them vulnerable to anthropogenic disturbances.

Key Words.—conservation, *Glyptemys insculpta*, movement, nesting, recruitment, reproduction, survivorship, Wood Turtle

INTRODUCTION

Wood Turtle (*Glyptemys insculpta*) populations occupy a disjunct range throughout the northeastern United States and southeastern Canada (Ernst et al. 1994). Recent studies have demonstrated that Wood Turtle populations are undergoing significant declines (e.g., Garber and Burger 1995; Daigle and Jutras 2005; Saumure et al. 2007). Agricultural and recreational activities, poaching, shooting, as well as habitat destruction and fragmentation have been implicated as factors contributing to the decline of the species (e.g., Harding 1991; Garber and Burger 1995; Ernst 2001; Saumure et al. 2007).

Wood turtles are a long-lived species with delayed sexual maturity and relatively limited reproductive output (Brooks et al. 1992; Ernst et al. 1994; Walde et al. 2003), factors that will hinder recovery efforts. Sexual maturity is reached from 12 - 18 years of age at the northern limits of their range (Brooks et al. 1992, Saumure and Bider 1998; Walde et al. 2003). Although individual clutch sizes may vary from 5 - 18 eggs, clutch sizes typically average 8 - 11 eggs (e.g., Harding and Bloomer 1979; Farrell and Graham 1991; Ross et al. 1991). As a result of nest predation rates exceeding 80%, few data exist on natural nest success and recruitment (Harding and Bloomer 1979; Brooks et al. 1992). However, recruitment rates of 74 - 77% have been documented for eggs raised in incubators or nests protected by nest covers (Farrell and Graham 1991; Tuttle and Carroll 1997). Moreover, few studies have investigated the spatio-temporal aspects of nesting migrations (Arvisais et al. 2002) or nest-site fidelity. Efforts to protect this imperiled species are hindered by our lack of knowledge concerning its reproductive ecology (Bury 2006; McCallum and McCallum 2006).

Although the Wood Turtle has been protected throughout most of its range for many years (Levell 2000), it was only recently assigned the legal status of vulnerable in Québec (*Gazette Officielle du Québec* 2005). Although several studies have investigated the population ecology of Wood Turtles in Québec, none have focused on nesting ecology (Saumure and Bider 1998; Arvisais et al. 2002; Walde et al. 2003; Daigle and Jutras 2005; Saumure et al. 2007). The goal of our study was to document the nesting ecology of a large *G. insculpta* population at the northern limit of the species' range. Specific objectives were to describe: (1) the movements of females to nesting areas; (2) nesting activities and chronology; (3) clutch size and frequency in relation to body size; (4) nest-site fidelity; (5) nest success; and (6) recruitment.

MATERIALS AND METHODS

Study site.—The present study began in May of 1996 and continued until December of 1997 along a river in the *Municipalité Régionale de Comté Le centre de la Mauricie*, Québec, Canada. The exact location of the

population is not revealed due to the potential threat of collection for the pet trade (e.g., Garber and Burger 1995; Niederberger and Seidel 1999). Although detailed descriptions of the research site have been published elsewhere (Arvisais et al. 2002, 2004; Walde et al. 2003), these papers do not adequately describe the nesting area. The nesting area was an old, yet operational, gravel pit. Nesting was confined to a portion of the gravel pit that has remained essentially undisturbed by mining activities for > 50 years. The substrate in the pit was comprised of a fine-medium gravel and sand. Very little vegetation was present, except around the perimeter of the gravel pit itself. The nesting site was approximately 1.5 ha and located from 10 - 100 meters of the river. Three infrequently used access roads crossed the gravel pit.

Techniques.—During May of 1996 - 97, intensive searches of the entire study area were undertaken to locate as many *G. insculpta* as possible. Each subject was marked, measured, weighed, aged, and sexed as described in Walde et al. (2003). In addition, radio transmitters were attached to 16 adult female *G. insculpta* in May 1996 (Arvisais et al. 2002) to document nesting sites as well as movement patterns to nesting grounds. In 1996, turtles were not relocated frequently enough for movement patterns to be described accurately; therefore, telemetry data reported for pre- and post-nesting movements are for the 1997 field season only. Turtles were located daily from 26 May until the end of June. Locations were recorded with a Trimble GeoExplorer I (Trimble Navigation Ltd., Sunnyvale, California, USA) Global Positioning System (see Arvisais et al. 2002) and plotted on a topographic map to obtain information on female nesting migrations.

Nesting.—The nesting area was observed daily from 26 May until 1 July 1996 - 97 for signs of nesting activity and/or the presence of turtles. Observations at the nesting area were made using binoculars and/or spotting scopes. As female turtles in a pre-nesting state are known to be sensitive to visual or auditory disturbances (e.g., Kaufmann 1992; Horne et al. 2003), care was taken to remain silent and hidden behind a blind. Once females began to arrive at the nesting site, they were watched carefully for signs of nesting. A constant watch was kept from approximately 05:00 to 21:00. Typically, turtles that remained in the gravel pit after sunset were nesting; in which case, observations continued until the turtle retreated. The date, time and general location of gravel pit entry and exit points were recorded for each turtle. Each time a turtle was observed in the gravel pit it was termed a "visit"; a visit represented one bout of activity in the gravel pit. If a turtle exited and returned to the gravel pit within 60 minutes it was considered a single visit. The first day that a female was seen attempting to nest was

recorded as the initiation of the nesting season and the last observed nest excavation marked the end of the season, as per Congdon et al. (1983). Once a subject was deemed to be making a true nest, constant watch was initiated to determine the time when the first egg was laid. As turtles were no longer visibly disturbed once egg-laying had begun, subjects were approached so the number of eggs could be counted, provided no other turtles were in the gravel pit or within sight of the laying female. If direct approach was not possible, observers tried to position themselves so that the number of eggs laid could be ascertained directly or indirectly, i.e., head retractions (Harding and Bloomer 1979). The time when the nest was covered completely and the female began to move away from the site was recorded as the completion of nesting. At this point, an observer approached the turtle to confirm its identification and notes were taken on behavior of the turtle and direction of retreat. The exact location of the nest in relation to three numbered stakes (triangulated) was measured. The nest itself was staked with a metal spike and numbered tag, placed 1m north of the nest. If the turtle had not been identified previously, it was marked and all aforementioned data were recorded. For each year, we divided the nesting season in half and nests constructed during the first half were categorized as early nests, while those in the latter period were deemed late nests. The data from the two years were pooled to assess whether early nesters had greater nest success than those nesting in the late category.

Nest monitoring and hatching.—Nests were visited two to three times a week throughout the summer to obtain information on predation, natural, and unnatural disturbances. In mid-August, nests were visited daily to determine when hatching began. Hatchling emergence was characterized by a hole in the substrate approximately 3 - 4 cm in diameter. Upon observing the first of such holes, 1 m^2 covers were placed over all remaining nests to restrain the hatchlings when they emerged. These wooden frames measured 2.5 cm by 10 cm and 1 m per side and were covered with 1.27 cm hardware cloth. These covers were partially buried in the ground to prevent hatchling escape. Moreover, fern fronds were placed on top of the cover, in the northeast corner, to provide some shade for newly emerged hatchlings. The nests were then checked two to eight times per day for the emergence of hatchlings and the date(s) of emergence were recorded. The number of eggs and hatching success were calculated by adding together the number of young that emerged from the nest, plus, the number of unhatched and/or rotten eggs in the nest cavity. The number of eggs that hatched was compared with the number of eggshell fragments and the appearance of these shell membranes. Eggshell membranes from which hatchlings emerged were white, soft, and leathery compared to those of eggs that had

rotted, which were brownish, hard, and brittle (pers. obs.). Undeveloped eggs were defined as eggs enclosing a dead embryonic turtle; whereas, infertile eggs did not contain an embryo. If no hatchlings emerged from a given nest, the number of eggs was determined by a direct count following excavation. If a single hatchling emerged, the nest was considered successful. When no hatchlings emerged, nest failure was evaluated based on characteristics of the destroyed nest, the appearance of the eggs, and/or shell fragments. In 1996, nests from which no hatchlings emerged were left undisturbed to be excavated in the spring to assess if hatchlings spent the winter in the nest cavity. In 1997, all nests were dug up during the second week of November to determine if hatchlings entered the winter months alive in the nest cavity.

Terminology.—For the purpose of clarity the following terminology is used. Nesting refers solely to the act of nesting, i.e., excavating a nest, laying eggs, and covering it up. Nest success is the relationship between the number of nests from which at least one hatchling emerged and the total number of nests constructed. Hatchling recruitment is the number of hatchlings that emerge from nests. Recruitment success is the percentage of hatchling recruits compared with the total number of eggs known to have been laid in the nest site.

Although nest-site philopatry was first defined as the mechanism by which "females come back to the same area where they hatched to lay their own eggs." (Reinhold 1998), it was subsequently redefined as the "return of females to the same geographic location, irrespective of whether this nest site is their natal site" (Valenzuela and Janzen 2001). Due to the long and somewhat ambiguous history of the word "philopatry" in the literature (e.g., Mayr 1963; Greenwood 1980; Waser and Jones 1983), we follow Rowe et al. (2005) in using "nest-site fidelity" to represent what Valenzuela and Janzen (2001) termed nest-site philopatry.

Statistical analysis.—To obtain information on the number of females in the population, estimates of mature turtles (>180 mm) were calculated using the M_t model (Rivest and Lévesque 2001). Differences between means were tested for using the Student's t-test. Contingency tables for analysis of nest success as a product of nesting time were analyzed with the adjusted G-tests of independence (G_{adj}) using William's correction (Sokal and Rohlf 1995). Correlations among populations were analyzed using linear regressions in SigmaPlot 8.02 statistical software (SPSS Inc. 2002). Statistical significance was accepted at $P < 0.05$.

RESULTS

Population size.—The calculated population estimate and corresponding 95% Confidence Interval for sexually mature individuals in the population during 1997 was 231 (152 - 309). This corresponds to an estimated sexually mature female population of 114 (75 - 153) turtles. Fifty-two individual females (46% of estimated female population) were observed in the nesting area. An additional 11 gravid female turtles were observed on the staging ground adjacent to the nesting area but not observed to nest. Thus, 63 female *G. insculpta* were observed in the vicinity of the nesting area, which represents 55% of the estimated female population.

Movement patterns.—Seven of the 15 turtles followed by radio-telemetry were observed to nest in the nesting area and two others were suspected of nesting therein or close by. These latter turtles were included in analyses of movement to the nesting area because movement patterns put them in the general area of the gravel pit. The remaining six turtles were not observed nesting but some ($n = 4$) were gravid and telemetry data suggest that these turtles nested in other areas. Data on a single turtle are not included because of transmitter failure.

Movement to the nesting area were along waterways for all turtles observed ($n = 9$); therefore, distances reported are not straight-line distances. Two general movement patterns to the nesting area were observed. The first movement pattern was a relatively slow migration over more than 14 days ($n = 3$), which began shortly after emergence from hibernation. The second pattern was a quick migration ($n = 6$), whereby the turtles stayed relatively close to where they hibernated and on approximately 10 June (three days before nesting season began) moved directly to the nesting area over two to seven days. There was no significant difference between the slow and fast groups for mean distance traveled to the nesting area, 2240 ± 1041 m and 2113 ± 1360 m, respectively. The mean distance traveled by all turtles to the nesting site was 2156 ± 1196 m ($n = 9$, range = 840 - 3740 m). Two turtles had exceptionally long movements during one day: one was observed to move 2940 m and the other 2400 m, both of these against the current.

Staging and timing of nesting.—We observed 29 and 33 females digging nests in 1996 and 1997, respectively. The nesting periods lasted from 9 - 21 June, 1996 (13 days) and 13 - 28 June, 1997 (16 days) (Fig. 1). In 1996, a straggler nested on 1 July but was deemed an outlier because of abnormal behavior and movements for weeks prior to nesting. During 1996, one turtle was observed

A

B
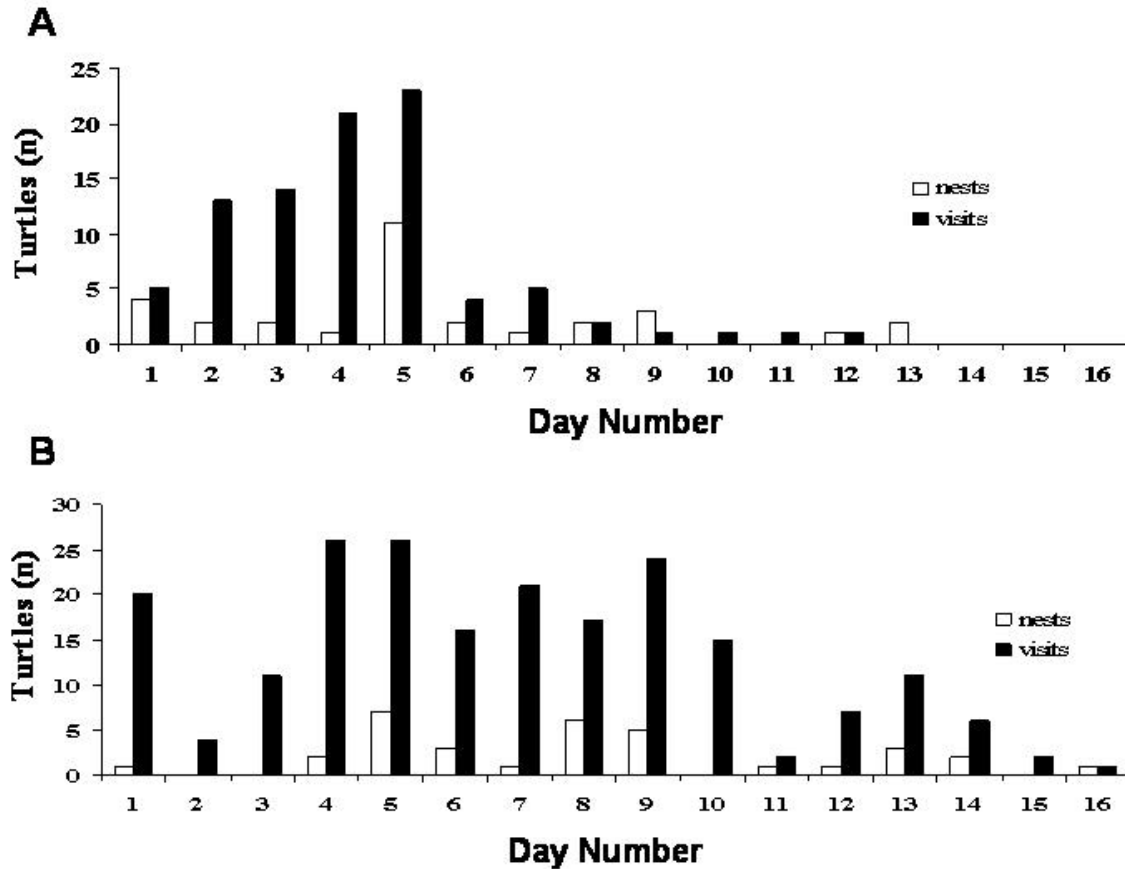
FIGURE 1. Number of *Glyptemys insculpta* that nested and visited nesting area in relation to the first day a nest was made in a) 1996 (first day of nesting was 9 June), and b) 1997 (first day of nesting was 13 June).

visiting the nesting area on 7 June and nine on 9 June, which was the day the first nest was completed. Seventy-six percent ($n = 93$) of all visits to the nesting area occurred from 10 - 14 June 1996. During the same five day period, 66% of the known nests were constructed (Fig. 1A). On 13 June, a heavy midday rain stimulated nesting activity and 34 turtles were identified in the nesting area with 38% ($n = 11$) of all nests being constructed. The remaining 9 nests were constructed over the following week and fewer turtles visited the area during this period. The last nest, as well as visit, was on 21 June, the end of the nesting period for 1996. In 1997, the first turtle arrived at the nesting area on 10 June, and the following day another was seen. From 12 - 15 June visits were more numerous. The first nest was constructed on 13 June. From 16 to 21 June, there were 130 visits, which accounts for 58% of all the visits to the gravel pit during the nesting period. From 16 - 21 June, 24 out of the total 33 nests were constructed (73%) (Fig. 1B). The remaining eight nests were completed during the following week, from 22 to 28 June.

Many turtles were captured for the first time at the nesting area in 1996; therefore, the number of visits and activities may not be accurate for that year because some of the turtles were not identified or captured on their first visit to avoid disturbing other turtles. In 1997, 224 visits to the nesting area represented more than 375 hr of activity. From this, the mean time spent for all visits, for both nesters and non-nesters was 103 min. The mean number of days nesting turtles were observed at the nesting area from first sighting until nesting was completed was 3.3 days, with a range of 1 - 9 days.

For turtles that were observed to nest in the 1997 season, the average time spent at the nesting area that did not result in a nest was 121 min ($n = 71$). During visits that resulted in nest completion, the mean time spent at the gravel pit was 232 min ($n = 24$). The mean nesting time (digging, laying, and covering the nest) of these turtles was 131 min and ranged between 86 and 202 min. On average, a female spent 101 min to choose the nest site location on the day she actually nested. Upon covering a nest, the turtle left the nesting site immediately, typically retreating to the river.

Excavations of nests were started at almost all hours during daylight, albeit with a predominantly bimodal distribution of nesting activity (Fig. 2). In the morning,
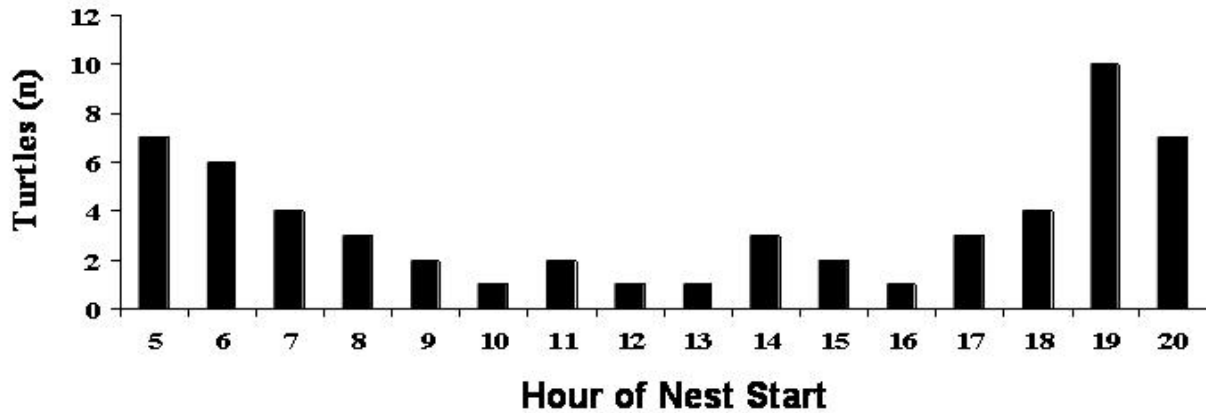
FIGURE 2. Time of day at which *Glyptemys insculpta* started nest building and number of turtles for each hourly category in 1996 and 1997 (n = 57).

38.5% (*n* = 22) of nests were started between 05:00 and 09:00. Forty-four percent of nests (*n* = 25) were started in the evening between 16:00 and 21:00 with most, 37% (*n* = 21) from 18:00 to 21:00. The remaining 17.5% (*n* = 10) of nests were started at various times during midday.

During the time that the nine radio-tracked turtles were in the vicinity of the nesting area, they were regularly observed in the adjacent staging ground. This area consisted of a 200 m length of river and flood plain plus a bog-like habitat centered on the nesting area. This staging area was utilized by 80% of the nesting females during both years of the study. During the study, 63 females (55% of population) were documented within the staging area and/or at the nest site. While staging, turtles tended to use natural habitats that were unaltered by human disturbances. Approximately 20 m of the waterfront within the staging area had been cleared of alder (*Alnus rugosa*) thickets (beside a cottage) and was devoid of turtles, while 28 females were observed in the adjacent alder thicket areas where the vegetation was undisturbed.

Nest-site fidelity and reproductive output.—Of the 44 turtles that visited the nesting area in 1997, 30 had visited in 1996. Thus, a minimum of 68% were likely gravid in two consecutive years. Of the 33 that nested in 1997, 64% (*n* = 21) were known to have nested in the nesting area in 1996. One turtle that nested at this area in 1996 nested 200 meters upstream in 1997. Therefore, of the turtles that nested in two consecutive years, 95% (*n* = 21) returned to the same nest site. Of the turtles that returned to nest, 43% (*n* = 9) nested within 10 m of their nest from the previous year.

The mean carapace length (CL) and plastron length (PL) of nesting turtles in 1996 and 1997 were not significantly different from female turtles not observed to nest in the population (Table 1). Nesting turtles, however, had significantly more annuli than non-nesting turtles (Table 1). Turtles that nested in both years were significantly larger for mean CL and PL than those that nested in only one year, but the mean number of annuli was similar (Table 2). There was a significant positive correlation between number of eggs and female CL, PL, and mass (Table 3).

Mean clutch size was significantly different between 1996 (9.4 ± 2.4 eggs, range = 5 - 13, *n* = 27) and 1997 (10.6 ± 2.1, range = 5 - 15, *n* = 30; *t* = -2.045). In 1997, one nest containing 20 eggs was excluded from calculations as it was deemed an outlier. Nest success was 74% in 1996, and 65% for the 1997 season. Nests constructed during the first half of the nesting period had significantly greater nest success than those constructed during the latter half (G_{adj} = 7.984) with 31 of 40 nests (77.5%) constructed during the first half of the 1996 and 1997 nesting season being successful; whereas only 9 of 22 (40.9%) constructed during the second half were successful. The number of hatchling recruits in 1996 was 148 (total eggs = 253) and in 1997 was 175 (total eggs = 337). Thus, recruitment success for 1996 and 1997 were 59 and 52%, respectively. Twelve infertile eggs were observed; eight in 1996 and four in 1997.

Incubation period.—Hatching dates were 17 August - 7 October in 1996 and 19 August - 5 October in 1997 (Fig.

TABLE 1. Morphometrics of nesting and non-nesting *Glyptemys insculpta* observed in 1996 and 1997.

	Number	Carapace Length	Plastron Length	No. of Annuli
Nesting Females	39	201 ± 10 (181-224)	193 ± 9 (177-214)	22 ± 3* (15-30)
Non-nesting Females	42	201 ± 12 (185-225)	193 ± 12 (170-214)	19 ± 4 (13-33)

Note: Values are given as the mean ± standard deviation (range).
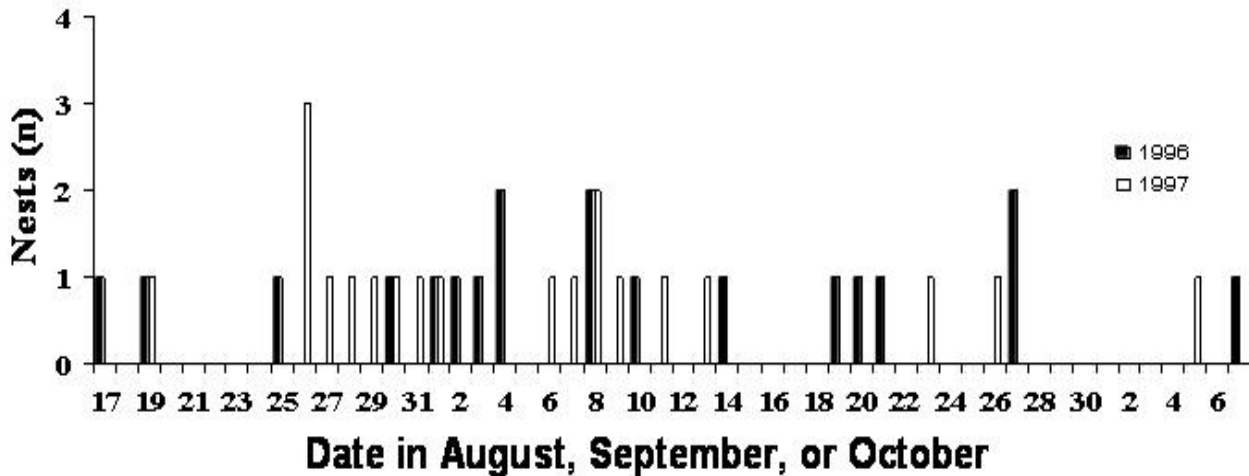*Difference between groups is significant, *t* = 3.00, *p* < 0.01

FIGURE 3. Dates and numbers of nests of *Glyptemys insculpta* hatching per day in 1996 and 1997.

3). The average incubation period was 86.8 ± 12.4 days (range = 65 - 116, *n* = 19) in 1996 and 77.5 ± 9.4 days (range = 60 - 99, *n* = 20) in 1997. The incubation periods were significantly different between years ($t = 2.37$, *df* = 37, *P* = 0.023).

Mortality.—Of the six nests left to overwinter in 1996, two had a total of 10 dead hatchlings in them in the spring. In 1997, 11 nests were excavated in mid-November. Only one nest had a living hatchling and it had a large yolk sac, this turtle was reburied in the nest and was found dead two weeks later. All other failed nests in both years had eggs that had not completed development, rotting eggs, and/or eggs associated with insects. No mammalian predation of nests at the nesting area occurred during the study. Raccoons (*Procyon lotor*), red fox (*Vulpes fulva*), skunks (*Mephitis mephitis*), as well as feral and domestic cats (*Felis domestica*), and dogs (*Canis familiaris*) were observed within the nesting area.

DISCUSSION

Timing of nesting.—Most studies of *G. insculpta* populations have observed nesting activities around mid-June (e.g., Farrell and Graham 1991; Brooks et al. 1992; Kaufmann 1992). Recent studies, however, have documented nesting as early as late May (Foscarini 1994; Smith 2002). The difference in dates for the onset of nesting is likely a combination of annual weather patterns but one cannot ignore the possibility of turtles nesting earlier due to global climate change. Interestingly, the onset of nesting in *G. insculpta* shows little latitudinal variance. *Glyptemys insculpta* may be selecting the optimal thermo-period for incubation, i.e., July and

August. Moreover, a reduced incubation period may decrease the probability of egg predation.

We observed a bimodal daily nesting period, with most nests constructed in early morning or mid to late evening (Fig. 2). Although morning nesting has been reported in the literature, it has been considered an aberrant behavior (Pallas 1960; Farrell and Graham 1991; Harding and Bloomer 1979). Our study corroborates previous observations that nesting is stimulated by periods of rain (Pallas 1960; Harding and Bloomer 1979). Future studies must elucidate if environmental extremes, substrate quality, or predator drive timing are causing site selection for nesting.

Movement patterns.—Turtles moved up to 3700 m to the nesting site despite occurrence of many potential, less distant nesting sites. Female *G. insculpta* can travel long distances to nest (Harding 1991; Quinn and Tate 1991; Saumure 2004). Although lengthy nesting migrations appear widespread in freshwater turtles (e.g., Plummer and Schirer 1975; Obbard and Brooks 1980; Morreale et al. 1984), most studies suggest a paucity of suitable nesting sites to account for the behavior. Our observations of females by-passing nesting areas used by other *G. insculpta* suggest a more complex explanation. Porter (1972) suggested that communal egg-laying probably occurs because a particular area is especially favorable for egg deposition and development. Thus, females may select ideal nesting sites with optimal physical conditions (Congdon et al. 1983; Morreale et al. 1984, Wilson 1998).

Staging.—Turtles staged in the vicinity of the nesting site for several days prior to actually nesting. Similar observations of staging have been documented for Slider

TABLE 2. Morphometrics of *Glyptemys insculpta* observed to nest in only one year or two consecutive years, 1996 and 1997. Values are given as the mean ± standard deviation (range).

	Number	Carapace Length (mm)	Plastron Length (mm)	No. of Annuli
1 Year	12	194 ± 10 (181–209)	188 ± 8 (177–200)	21 ± 4 (16–25)
2 Years	23	204 ± 10* (188–224)	195 ± 9** (182–214)	22 ± 4 (15–30)

* Differences between categories is significant, $t = 2.87$, $p < 0.01$.
** Differences between categories is significant, $t = 2.32$, $p < 0.01$.

(*Trachemys scripta*) and Blanding's Turtles (Cagle 1950; Congdon et al. 1983). Since staging *G. insculpta* tended to use unaltered habitats, they are at least partially sensitive to exogenous disturbances. This presents us with an interesting dichotomy, as anthropogenic clearings are clearly used as nesting sites. Given that the staging area represents only 0.2% of the area known to be occupied by this population, poaching or additional development therein could be catastrophic.

Nest site fidelity.—Our observations of nest site fidelity support previous accounts in Michigan (Harding 1991). Nest site fidelity may reflect a shortage of nest areas (Loncke and Obbard 1977), female selection of the best nest sites (Porter 1972; Congdon et al. 1983; Morreale et al. 1984), or innate return of females to natal nesting areas (Carr 1967).

The nesting area located in the gravel pit has changed little in at least 50 years. Local landowners confirmed that Wood Turtles have been nesting in this area throughout this duration. Regardless of whether turtles are returning to natal nesting areas, nest site fidelity in *G. insculpta* suggests that conservation efforts should include the identification and protection of nesting areas.

Reproductive Output.—We observed significant positive correlations between clutch size and CL, PL, and body mass (Table 3). Similarly, an Ontario study found that *G. insculpta* CL was positively correlated with clutch size (Brooks et al. 1992). Thus, within a population, larger Wood Turtles have larger clutches of eggs. Moreover, turtles that nested in both years of our study were significantly larger than turtles observed to nest only in one year (Table 2). Larger turtles may have increased fecundity because they can reproduce more frequently. Since *G. insculpta* are larger in this population than those seen further south (Daigle 1997; Walde et al. 2003), a greater proportion of females may be capable of annual reproduction.

Mean clutch sizes differed significantly between 1996 and 1997. The mean clutch size during our two-year study lies within the range of those reported from seven other populations (Table 4). Since northern populations of wood turtles are larger than those occurring further south (Daigle 1997; Walde et al. 2003), it was predicted that northern populations would also have larger clutches.

Clutch size was not significantly correlated to increase in CL when compared among populations ($r = 0.52$, $P = 0.183$). However, although this is not statistically significant, the proportion of variance in clutch size explained by body size between populations is similar to that observed within our study (see Table 3). Therefore, it is likely that this non-significant result is due to a low sample size (Cohen 1992). Data from additional study locations as well as implementation of long-term studies that account for annual variability in clutch size could provide conclusive explanations for the above observations (Bury 2006; Fitch 2006).

Predation.—Mammalian predators can destroy > 80% of *G. insculpta* nests (e.g., Harding and Bloomer 1979; Brooks et al. 1992). Surprisingly, no mammalian predation of eggs was observed during this study despite the presence of many potential nest predators. Whether mammalian predators were naïve at exploiting this food resource (Doody et al. 2003) is subject for speculation.

Incubation period.—Although the average incubation period in our study (Fig. 3) was similar to those in New Hampshire (mean = 76 days, range = 66-82; Tuttle and Carroll 1997), the range was greater for our population. Cagle (1950) documented that cooler incubation temperatures result in a greater range of hatching dates. Increased incubation periods at northern latitudes may result in lower recruitment, as insufficient time / degree-days for development may be a limiting factor (Cagle 1954; Christiansen and Moll 1973; Compton 1999). Our observations of higher nest success for nests that were constructed during the first half of the nesting season would support these conclusions.

Nest and recruitment success.—Despite the absence of mammalian predation at our study site, nest success was lower than expected. Recruitment success rates of 74 - 77% have been previously recorded for *G. insculpta* although incubation conditions varied. These past studies have reported on nests under nest protectors (Tuttle and Carroll 1997), *ex situ* (Farrell and Graham 1991) and Smith (2002), excavated nests as soon as hatchlings began to emerge to prevent depredation by dipterans. The lower recruitment success observed at our northern population

TABLE 3. Linear regressions (*r*) for comparisons of carapace lengths, plastron lengths, and mass with clutch size among 53 *Glyptemys insculpta* nests for which measurements of the female were known. All comparisons represent significant differences ($p < 0.01$).

	Year	Carapace Length	Plastron Length	Body Mass
Clutch Size	1996	0.53	0.50	0.58
	1997	0.51	0.55	0.60
	Years Combined	0.50	0.49	0.55

may have been due to predation by insects (Walde 1998).

In addition, lower recruitment success may have resulted from insufficient time and degree days to complete incubation (Obbard and Brooks 1981; Brooks et al. 1991, 1992). This hypothesis was modeled by Compton (1999) and is supported by our observation of higher nest success for those nests laid earlier in the season.

TABLE 4. Comparisons of clutch size and mean carapace length of female *Glyptemys insculpta* among eight disparate populations. Latitudes are estimated from locations provided in the sources.

	Carapace Length (mm)	Clutch Size			
		n	Mean	Range	Source
Ontario (45°N)	203	21	8.8	3 - 13	Brooks et al., 1992
Québec (46°N)	201	56	10.2	5 - 20	Present study
Wisconsin (44°N)	187	11	11.0	--	Ross et al. 1991
Michigan (46°N)	182	--	10.4	5 - 18	Harding and Bloomer 1979
Ontario (43°N)	181	26	8.0	5 - 11	Foscarini 1994
New Hampshire (43°N)	172	9	7.8	6 - 9	Tuttle and Carroll 1997
New Jersey (41°N)	171	21	8.5	5 - 11	Farrell and Graham 1991
New Jersey (41°N)	165	--	8.0	5 - 11	Harding and Bloomer 1979

Despite its survival advantage for some species (Carr 1952), our lack of evidence of overwintering hatchling *G. insculpta* is in line with most other studies (Harding and Bloomer 1979; Brooks et al. 1992; Ernst et al. 1994; Buech et al. 2004). Only one unconfirmed report of a *G. insculpta* hatchling successfully overwintering in the nest is known (Parren and Rice 2004). The inability of hatchling *G. insculpta* to over-winter in the nest probably limits the northern distribution of the species.

Conclusion and Suggestions.—Our study provides much insight into the nesting ecology of *G. insculpta*. A short nesting season, nest-site fidelity, and staging behavior render the species vulnerable to disturbances and/or poaching. Within a single week, > 50% of the female population at our site was present within a 200 m staging ground and the nesting site. An additional reason for protecting nesting sites is that female Wood Turtles are extremely sensitive to disturbance prior to the initiation of laying. Anthropogenic disturbances at nesting sites could cause *G. insculpta* to delay nesting and/or nest in less favorable habitats. Such a delay and/or movement may reduce nest survivorship, as nests constructed earlier in the nesting season had higher success rates. Additional investigation into the nesting ecology of the wood turtle, as well as how anthropogenic disturbances could influence nesting activity is warranted.

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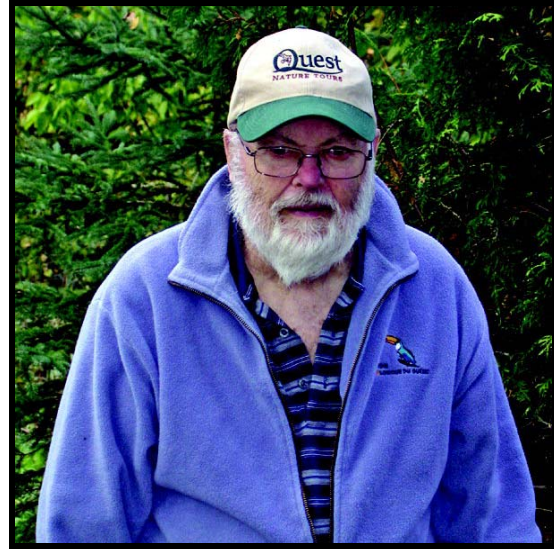
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