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ECOLOGY OF THE WOOD TURTLE,
Clemmys insculpta, QUÉBEC, CANADA

by

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A thesis submitted to the
Faculty of Graduate Studies and Research
in partial fulfillment of the requirements for the degree of
Master of Science

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ABSTRACT

The most northeasterly population of wood turtles (*Clemmys insculpta*) was studied during 1996 and 1997 in Québec, Canada. A total of 188 turtles (55 males, 83 females, and 50 immatures) was captured, measured and marked for future identification. The adult sex ratio was not significantly different from 1:1. Males were significantly larger than females for measures of carapace length, 214.5 and 201 mm, respectively. Wood turtles from northern populations are larger than those from southern regions. The population density was estimated to be 0.44 turtles/hectare. Courtship occurred in the spring but was more common in the fall. Nesting occurred in mid-June with nesting activity taking place at all times of the day but more frequently in early morning and evening. Females migrated over 3 km to a nesting area and exhibited nest fidelity. Sixty-six percent of turtles nested in 2 consecutive yr and these females were significantly larger than turtles that nested in only 1 yr of the study. There was no mammalian predation but, some arthropods were suspected of being predators. Mean clutch size was 10.1 (range=5-20) eggs. Comparisons with other populations of *C. insculpta* are also made.

RÉSUMÉ

La population de tortue des bois (*Clemmys insculpta*) occupant la localité la plus au nord-est connue fut sous étude en 1996 et 1997 au Québec, Canada. Au total, 188 tortues (55 mâles, 83 femelles et 50 immatures) furent capturées, mesurées et marquées pour identification future. Le sex ratio des adultes fut déterminé comme n'étant pas significativement différent de 1:1. Avec une longueur de carapace de 214.5 et 201.0 millimètres respectivement, les mâles furent déterminés comme étant significativement plus gros que les femelles. Les tortues des bois en provenance de populations plus nordiques sont plus grosses que celles en provenance de populations plus au sud. La densité de population fut estimée à 0.44 tortue par hectare. Bien que les activités de reproduction eurent lieu au printemps, elles furent plus communes à l'automne. La période de nidification fut concentrée à la mi-juin. L'activité de nidification fut observée à tout moment de la journée, bien que plus plus fréquemment tôt le matin et en soirée. Les femelles effectuèrent des migrations dépassant 3 kilomètres vers un site de nidification et démontèrent une fidélité au site. Soixante-six pourcent (66%) des tortues nidifièrent à chacune des deux années consécutives. Ces femelles démontrèrent une taille significativement supérieure à celle des tortues n'ayant nidifié que dans une seule année de l'étude. Aucune prédation par mammifères ne fut observée, mais certains arthropodes furent soupçonnés. Le nombre moyen d'oeufs par ponte fut de 10.1 (variant de 5 á 20) oeufs. Des comparaisons avec d'autres populations de *C. insculpta* furent aussi effectuées.

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ACKNOWLEDGMENTS

This thesis is dedicated to two naturalists and good friends who took the time to show me and educate me about Natural History and Conservation. Thanks Mary Gartshore and Peter Carson. I would also like to thank my thesis committee members, Drs. J. Roger Bider and Rodger Titman, for their support and assistance throughout this project. A special thank-you is extended to all those who made this project a reality by assisting in the field, notably; Marie-Hélene Garneau, Linda Paetow, Nicole Alfers, J.F. Dufour, Marcella Trembley, Alexandre Henri, Denis Masse, Jean-Claude Bourgeois, Jacques Jutras, Claude Daigle, Daniel Dolan, and Yves Robitaille. This project was greatly aided by Raymond Saumure and David Rodrigue who were always willing to answer all my questions, listen to my theories, provide papers and equipment and, still remain my friends. Thanks.

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PREFACE

This thesis was written in manuscript form. It is made up of two sections. The first and second sections are manuscripts prepared for submission to the journal entitled: Chelonian Conservation and Biology. Both manuscripts consist of an introduction, materials and methods, results, discussion, and literature cited sections. A series of Tables and Figures complete each manuscript. It was considered by the thesis committee members that because the manuscripts submitted are on many aspects of the ecology of a species at the northern limit of its range, they provide a thorough review of the literature relevant to the topics investigated in this study. Therefore, no separate section is submitted to review the literature as it was considered to be redundant in this case. This thesis format is in accordance with the Guidelines for Thesis Preparation by the Faculty of Graduate Studies and research of McGill University which states:

> "Candidates have the option of including, as part of the thesis, the text of one or more papers submitted or to be submitted for publication, or the clearly-duplicated text of one or more published papers. These texts must be bound as an integral part of the thesis.
>
> If this option is chosen, connecting texts that provide logical bridges between the different papers are mandatory. The thesis must be written in such a way that it is more than a mere collection of manuscripts; in other words, results of a series of papers must be integrated.
>
> The thesis must still conform to all other requirements of the "Guidelines for Thesis Preparation". The thesis must include: A Table of Contents, an abstract in English and French, an introduction which clearly states the rationale and

> objectives of the study, a review of the literature, a final conclusion and summary, and a thorough bibliography or reference list.
>
> Additional material must be provided where appropriate (e.g. in appendices) and in sufficient detail to allow a clear and precise judgment to be made of the importance and originality of the research reported in the thesis.
>
> In the case of manuscripts co-authored by the candidate and others, the candidate is required to make an explicit statement in the thesis as to who contributed to such work and to what extent. Supervisors must attest to the accuracy of such statements at the doctoral oral defense. Since the task of the examiners is made more difficult in these cases, it is in the candidate's interest to make perfectly clear the responsibilities of all the authors of the co-authored papers."

As previously stated, the manuscript will be submitted to the journal Chelonian Conservation and Biology for publication. The papers will be co-authored by the candidate, the thesis supervisors, Drs. J.R. Bider and R. Titman, and consultants Jean-Claude Bourgeois, Claude Daigle, Jacques Jutras, and Denis Masse. Dr. J.R. Bider initiated the research and coordinated the project in collaboration with the consultants. The above mentioned consultants working for the Québec Ministère de l'Environnement et de la Faune and Parks Canada conducted most of the field work pertaining to radio telemetry data and organized the annual population surveys and collection and marking of turtles outside the nesting areas. The collection of all other data and the writing of scientific papers was the sole responsibility of the candidate.

I. ECOLOGY OF THE WOOD TURTLE, *Clemmys insculpta*, AT THE NORTHERN LIMIT OF ITS RANGE, QUÉBEC, CANADA

*Manuscript for submission to the journal Chelonian Conservation and Biology

INTRODUCTION

The wood turtle, *Clemmys insculpta*, ranges throughout Northeastern United States and Southeastern Canada, from Ontario east to Nova Scotia (Ernst *et al.*, 1994). Wood turtle populations are scattered and disjunct throughout their distribution with little hope of interpopulation exchange or recolonization into areas from where they have been extirpated (Harding & Bloomer, 1979; Brooks, 1994). In Québec, wood turtles are considered to be widespread but uncommon in the southern part of the province, yet only four watersheds with populations have been identified to date (Beaulieu, 1992; Bider and Matte, 1996; Daigle, 1997)

In 1992, *Clemmys insculpta* was listed in Appendix II of the Convention on the International Trade of Endangered Species of Flora and Fauna (CITES) (Buhlmann, 1992, 1993). Currently, the wood turtle is listed as threatened, endangered, or protected by law in most of the U.S. states that it occupies (Klemens, 1992; Buhlmann, 1993; Harding, 1991). In Québec, the wood turtle was included on a list of species which were susceptible to being declared vulnerable or threatened (Beaulieu, 1992). In Canada, this species has been assigned the status of 'vulnerable' by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) (Litzgus & Brooks, 1996; Green, 1996).

Recent studies have shown that many wood turtle populations have lately undergone significant declines (Harding & Bloomer, 1979; Garber, 1989; Harding, 1990; Beaulieu, 1992; Ernst *et al.*, 1994; Gilhen *et al.*, 1994; Garber & Burger, 1995; Bider & Matte, 1996). It has been suggested by some of these authors that collection for the pet trade is the single greatest cause for "population crashes", with habitat loss and fragmentation contributing significantly. One of these studies concluded that human recreational activities caused a decline in two populations to the point of local extinction (Garber & Burger, 1995).

There have been numerous studies conducted on wood turtles which have examined specific aspects of their habitat requirements or behaviours such as home range, daily activities, mating frequencies and reproduction, dominance and habitat use (Powell, 1967; Carroll & Ehrenfeld, 1978; Ernst, 1986; Lovich *et al.*, 1990; Brewster & Brewster, 1991; Ross *et al.*, 1991; Quinn & Tate, 1991; Brooks *et al.*, 1992; Kaufmann, 1992a, 1995). Unfortunately, there are very few published studies which report the general ecology of this species. The most complete and often cited studies of ecology and life histories are those of Harding and Bloomer (1979) in Michigan and New Jersey, and Farrell and Graham (1991) in New Jersey.

In general, researchers have concluded that more detailed studies of wood turtle life histories must be conducted (Harding & Bloomer, 1979; Farrell & Graham, 1991; Ross *et al.*, 1991; Brooks *et al.*, 1992; Litzgus & Brooks, 1996; Saumure, 1997). In the management recommendations section of the COSEWIC report it is recommended that studies of Canadian wood turtle populations be started, continued and/or expanded (Litzgus & Brooks, 1996). Our objectives in this study were to gather information on morphometrics, density, daily and annual activity, feeding, mating, predation, and parasites from a population at the northern limit of the wood turtles' range in Québec, Canada. These findings were then to be compared with previously published data. Information about wood turtle ecology from its northern limits may be important in the planning and application of conservation and management strategies.

MATERIALS AND METHODS

Turtles were captured and marked from May to October of 1996 and 1997 along a 7.05 km section of a meandering river and the surrounding habitats in Municipalité Régionale de Compté (MRC) Le centre de la Mauricie, Québec, Canada. Some of the tributary creeks and gravel roads in the general area were also surveyed. The total area over which turtles were captured was 538 ha. The exact location of the population will not be revealed due to the threat of collection by humans for the pet trade (Litzgus & Brooks, 1996; Garber & Burger, 1995) .

The geology of the area is that of an esker (Allard, 1978); gravel and sand with exposed granitic outcrops. The river is between 5 and 10 m in width, with an average depth of approximately 1-2 m depending on the season and rainfall patterns. The river bottom is sandy with pebbly deposits and the flood plain is predominantly alder (*Alnus rugosa*) thicket, with several ox-bow lakes and beaver ponds. Vegetation beyond the flood plain is at the border of the boreal/Great Lakes St. Lawrence Lowland forest (Farrar, 1995) with white spruce (*Picea glauca*), white birch (*Betula papyrifera*), and trembling aspen (*Populus tremuloides*) being dominant tree species with some maple species (*Acer* spp.) also present. Wild strawberry (*Fragaria virginiana*), May flower (*Maiathemum canadense*) and starflower (*Trientalis borealis*) are all common flowering plants in the herbaceous layer. The number of frost free days (FFD) at this area was 100 (Wilson, 1971). Most of the land in the study area is privately owned and has little to no development on it at present, although there has been some logging and aggregate mining in the past and the number of summer homes in the area is increasing.

During May of 1996 and 1997, an intense search of the study area was undertaken to locate and mark as many wood turtles as possible. This was accomplished by canoeing and walking along the river and hand capturing or dip-netting the turtles. For each new turtle captured several measurements were recorded; date, time, location, weather, and temperature. Dominant vegetation surrounding the turtle's location was recorded at all levels, i.e. dominant trees, shrubs and herbaceous plants. The straight line carapace (CL) and plastron lengths (PL) were measured using large vernier calipers (forester type, ± 1 mm, Haglof, Sweden) and the turtle was weighed using a spring scale (Pesola, ± 50g or ± 10g, Switzerland). Adult turtles were sexed using characteristics of minimum length of carapace and the presence or absence of male secondary sexual characteristics, males exhibiting plastron concavity and a longer, thicker preanal tail (Wright, 1918; Harding & Bloomer, 1979; Lovich *et al.*, 1990; Brooks *et al.*, 1992; Kaufmann, 1992a, 1992b). Turtles of undetermined sex and below a minimum size were considered to be immature (min. size to be determined during study).

Age was determined by counting growth annuli which is considered a reliable estimator of age until approximately 15-20 years after which time growth is very slow and it is difficult to discern separate annuli (Harding & Bloomer, 1979; Harding, 1985; Lovich *et al.*, 1990). For a turtle whose growth annuli numbered greater than 20 we continued to count all visible annuli as it was considered to be unlikely that more than one growth annulus was deposited per year at this northern location with its short growing season. Data were taken on limb and tail loss, presence/absence of parasites and shell abnormalities. Posterior carapace marginal scutes were marked for later individual identification (Cagle, 1939), using a 6 mm rat-tail file that made permanent U-shaped notches, with a numbering system similar to one described by Froese and Burghardt (1975). After the data collection was complete, turtles were returned to the point of capture. This marking period continued from early May until late October in both years of the study.

Radio transmitters (Holohil AI-2m(4) with 2 year batteries) were installed in May of 1996 and as many as 20 turtles were monitored daily and later in the season, weekly, into the late fall of 1997 and, monthly after hibernation had begun. Radio transmitters were encased in a piece of brass pipe with a 30 cm whip antenna. Transmitters were attached to the turtles by drilling 2 holes in the marginal carapace scutes and screw bolting it on. Transmitters were attached well off center near the posterior on males and centered at the front on females (this does not prevent males from mounting females).

Statistical analysis

Results from telemetry and surveys indicated that the population being studied was isolated with no chance of immigration or emigration and therefore is considered to be a closed population and therefore the Lincoln-Peterson method was used. The Jolly-Seber population estimator is considered to be best method for estimates for open populations and therefore could not be used (Lindeman, 1990; Pollock *et al.*, 1990).

Differences between sexual and morphometric parameters were tested for using the Student's *t*-test and χ^2 (Zar, 1996). Correlations among populations were analysed using Table Curve 2D. Statistical significance was accepted at $p<0.05$.

RESULTS

A total of 188 wood turtles was captured and marked during 1996 and 1997. Using the Lincoln-Peterson index, the size of the population was estimated at 238 turtles (95 % confidence limits 191-285). The estimated density based on this calculation is 0.44 turtles / ha.

The smallest male to show secondary sexual characteristics and the smallest gravid female were considered to be the minimum size, for males and females respectively, at which sexual distinction was possible. The smallest male had a CL of 170 mm and a PL of 160 mm (Fig.1.1). It also had the fewest number of annuli, 11 (Fig. 1.2). The smallest male observed in courting or mating activities had a CL of 205 mm and a PL of 183 mm with 15 annuli visible. The smallest female observed in these activities had a CL 188 mm and a PL of 182 mm with 14 annuli. The smallest gravid female had a CL of 181 mm and a PL of 177 mm with a minimum annulus count of 20. This same female was also the smallest female observed nesting during the study. The female turtle with the fewest annuli (14) that was known to be gravid or nest had a CL and PL of 203 and 194.5 mm respectively.

Males were significantly larger than females for measurements of mean CL and weight but not for PL (Table 1.1.). The mean number of annuli for males and females were not significantly different ($p>0.05$) (Table 1.1.). One female turtle had 33 countable annuli. By counting the number of large annuli on turtles that have both large and small annuli it was found that an average of 16 -17 large annuli were present. Age frequency distribution is represented in Figure 1.2.

The sex ratio of all turtles captured was 1 : 1.51, males to females (55 males: 83 females) which is significantly different from one to one ($\chi^2=5.7$, $p<0.05$). This, however, represents a biased sample as many females were first captured at nesting areas. The removal of these females gives a 1.0 : 0.98, male to female adult sex ratio (55 males : 54 females) which is not significantly different from 1 : 1 ($p>0.05$). A total of 50 (31.4 %) immature turtles was captured during the study (Fig.1.1, Fig.1.2). The results of spring surveys in May (1996 and 1997) revealed a ratio of adult to immature captures of approximately 4 : 1. A less intense survey in the fall of 1997 revealed a 2 : 1 adult to immature capture ratio, which is significantly different from the spring survey ($\chi^2=4.34$, $p<0.05$).

Seasonal Activity

The monthly activity patterns, based on captures/recaptures and following individuals with radio transmitters, demonstrated that from late October or early November turtles began hibernating. Hibernating turtles were always located in a river usually in less than 100 cm of water. Turtles were observed to hibernate under cutaway banks, under wood debris, and in muskrat burrows. The majority of turtles did not move much, if at all, during the hibernating months but one turtle was observed to move 40 m. In early May, turtles emerged from hibernation and began basking on the river banks, and usually returned to the river at night. Turtles were observed to bask at air temperatures greater than 9 °C. During the first half of June, turtles were observed basking usually within 10 m of water and female turtles were observed to nest during this same month. Of all turtles captured and recaptured, 82 % were caught in May and June. Very few turtles were captured during July and August when turtles were observed to be semi-terrestrial, often walking large distances from the rivers. In September turtles returned to the rivers and were often seen basking nearby. By late October, turtles were preparing to hibernate.

Dietary Habits

Feeding was observed several times during the active months, except October. Turtles were seen eating numerous different species of plants; both leaves and fruits of strawberries (*Fragaria* sp.) and birch leaves (*Betula papyrifera*) being common. One turtle was observed snipping fern stems at the base and then eating the tip of the frond. *Boletus* and *Amanita*, two genera of mushrooms, were consumed on several occasions. Invertebrates eaten included slugs, worms and millipedes. Also, turtles were seen fighting over and eating numerous items of carrion, including mice, toads, and fish. On three separate occasions turtles were observed with feathers in their mouths.

Mating

Courting and mating activities were observed from May until November. Over the two year study, 35 courting or mating events were observed with 77 % (n=27) occurring in the fall, and 49 % (n=17) in October alone. Mating/courting behaviour was usually observed in the water, but twice males were observed mounted on females on land. In both terrestrial mountings the tails/cloacas were not observed to be in contact. Mating activities appeared to be more frequent during midday with most observations occurring between 11h00 and 13h00. The mean age of courting males and females was not significantly different but males were significantly larger than females who were observed in mating activities (Table 1.2.). In all but 4 of the observations the male was larger than the female (CL measurements). Males observed in mating activities were not significantly larger (CL) or older (annuli count) than the mean of all males in the population ($p>0.05$). Females involved in these activities were significantly larger (CL) than all females in the population ($t=3.31$, $p<0.001$) but were not older (annuli count) ($t=0.645$, $p>0.05$). Females and males were observed in mating activities more than once in a season and with more than one partner. Turtles were seen mating with the same partner during both years of the study. One male was observed coupled with 5 different females.

Injuries, predation, and parasites

During the study, 65 (34.6%) turtles were observed to have scars from injuries or mutilations that were not congenital. Of the 188 turtles caught, 46 (28 females, 12 males, and 6 immature) had a part of their tail missing. There was no significant difference between the number of males and females with tail injuries (χ^2=2.55, $p>0.05$), but there was a significant difference between adult and immature turtles (χ^2= 7.71, $p<0.01$). Eighteen (9.6%) turtles had at least one limb amputated, with or without a tail injury and 6 (3.2%) had 2 limbs amputated. There were no significant differences between sexes (χ^2=0.05, $p>0.05$) or between adults and immatures (χ^2=3.70, $p>0.05$) for leg amputations. No dead turtles were found during the study. Animals seen in the study area which could have caused these mutilations in acts of attempted predation include red fox (*Vulpes fulva*), muskrat (*Ondatra zibethica*), otter (*Lutra canadensis*), skunk (*Mephitis mephitis*), raccoon (*Procyon lotor*), feral and domestic cats (*Felis domestica*) and dogs (*Canis familiaris*), or any other opportunistic predator.

Leeches (*Placobdella* sp.) were observed attached to all parts of turtles but were most common on skin in the limb sockets. Leeches were observed on turtles in May, June, September, and October. Seventy percent of all observations of leeches were in May.

DISCUSSION

Our estimate of 238 turtles indicates that wood turtles are capable of sustaining a relatively large population at the northern limit of their range. This is the largest known population in Québec and the second largest recorded in Canada. Recruitment appears to be good, with immature turtles comprising 31 % of all turtles captured (Fig.1.2). Other studies have found immatures/juveniles to make up much less of the population: 8.5 % in Wisconsin (Ross *et al.*, 1991), 12 % in the Algonquin Park region, Ontario (Brooks *et al.*, 1992), and 18.8 % for the Maitland river in Ontario (Foscarini, 1994). Sixty-six percent of a New Jersey population comprised immatures (Farrell & Graham, 1991), the only study that reports a higher percentage of immatures. Spring and fall surveys of our population produced significantly different ratios of adult to immature turtles captured. This could indicate that there are seasonal differences in activities or habitat use between adult and immature turtles, which may be influencing the percentage of immature turtles captured.

Due to a short growing season it was assumed that not more than one growth annulus would be deposited per year and therefore act as a reliable estimator of age, at least until maturity, when growth slows considerably and growth annuli are sometimes too small to distinguish as separate (Harding & Bloomer, 1979; Harding, 1985; Lovich *et al.*, 1990). We found that on average 16-17 large growth annuli were formed before growth slowed considerably but, often found it easy to continue to count many smaller annuli. Also, due to differing growth rates between individuals it was sometimes possible to count over 20 large annuli and on one individual 26 large annuli were present, as well as small ones. A recent study of wood turtles from a population in southern Québec confirmed, based on multiple recaptures, that only one annulus per year was produced (Saumure, 1997). Saumure (1997) concluded that growth annuli were a reliable estimator of age at least until 26 years (annuli), the oldest turtle in that population. He made dental stone casts of the right pleural scute (Zangerl, 1969; Galbraith & Brooks, 1987) and counted the number of annuli from these. If counts of annuli are a reliable estimator of age our observation of a female with 33 annuli would equal the oldest wild specimen observed by Ross *et al.* (1991) in Wisconsin. However, we felt our counts of annuli are at best minima because annuli were often too small and/or too worn to count. Captive wood turtles have been known to live as long as 58 years (Oliver, 1955).

Until recently, little data have been made available regarding wood turtles from different study sites but, in the last ten years a sufficient number of studies has been published to permit comparisons among populations. The suggestion that average CL from northern populations of wood turtles are larger and that they mature later and at a larger size than do southern populations was first proposed by Brooks *et al.* (1992). A more recent study (Daigle, 1997) confirmed that there was a strong negative correlation between number of FFD and mean size at maturity for wood turtles. We have reproduced the table from Daigle (1997) and added our data to it, as well as data from Foscarini (1994), Tuttle and Carroll (1997), and Saumure (1997) (Table 1.3.). The addition of the data from these four populations should allow for further conclusions to be drawn about interpopulation variability. When the mean CL for males and females was compared (separately) to the number of FFD, a strong negative correlation was obtained (males r=0.918, p<0.01; females r=0.889, p<0.01). Thus, we can conclude that wood turtles are larger (CL) as FFD decrease across the species' geographic range.

In an attempt to quantify whether turtles were maturing later and at a larger size in northern populations, males and females were compared separately for mean number of annuli, the minimum age at maturity, and minimum CL at maturity with the number of FFD for all populations that data was available (Table 1.3). There were no strong correlations for any of these variables, however, there was a correlation between number of FFD and minimum size at maturity for females (min. CL at first nesting) (r=0.735, $p<0.05$). It is possible that one of the reasons no correlation was found between most of these variables was because of the differences among studies to assign males and females to categories of adult, mature, or sexually mature. Until some form of standardization or consensus on what traits and characteristics for wood turtles will be used to assign turtles to specific categories any relationships among these features will be unclear. The one variable that was similar among studies, minimum CL at first nesting, did show a correlation with FFD.

The minimum size (CL) at which male secondary sexual characteristics can be detected was used as the cutoff point for distinguishing males and because female wood turtles essentially retain external characteristics similar to an immature, we used a minimum size (CL) of a female observed to be gravid or nest as the distinguishing size for a female. Males in our population began to display plastron concavity and widening of the head at a CL of 170 mm and an annulus count of 11, while the smallest female confirmed breeding (observed nesting) had a CL of 181 mm and 20 annuli (Fig. 1.1, Fig. 1.2). Table 1.3 shows the minimum CL and minimum age at which several studies assigned a sexual status to turtles. While there is a wide range of variation in the minimum age at maturity, 7 - 8 annuli for males and females in New Jersey (Harding and Bloomer, 1979) and 11 annuli for males, 14 for females in this study, there appears to be a general trend that male secondary sexual characteristics are apparent at fewer annuli than females. This can be attributed to the fact that the only way to confirm that a turtle is a female is to observe her to be gravid or nesting, while a male can be distinguished by secondary sexual characteristics. It is possible that these secondary sexual characteristics begin to be displayed while a turtle is in its adolescent years, a couple of years prior to sexual maturity and therefore biasing samples towards younger males. In our study, the number of annuli present on the youngest male observed mating was 15, while the youngest female observed nesting had 14 annuli. Since most mating occurs in the fall (after the year's growth) and nesting occurs in the spring (before the year's growth) it is apparent that both females and males in our northern population are sexually mature at a minimum of 15 years.

Differing growth rates between individuals complicates the use of a minimum age at which to assign a sexual status, as not necessarily all turtles will be sexually mature at the same age. The range of CLs for turtles with 15 annuli was 170 - 242 mm, a difference of 72 mm. The small turtle (CL = 170 mm) was recorded as an immature and the large turtle (CL = 242 mm) was distinctly male (Fig.1.1). Due to this large difference in size observed at any given age, we used a minimum size based on CL to assign turtles' sexual status. It has been found that for many species of turtles that a critical size is the determining factor at which maturity is attained, not a minimum age (Cagle, 1948; Gibbons, 1968; Congdon *et al.*, 1983; Ross, 1989) but, for some other species it is thought to be correlated with age (Tinkle, 1961; Graham & Doyle, 1977). Table 1.3 illustrates that the minimum age at which maturity was assigned varied greatly among populations but, the general size (CL) appears to be similar for most studies, approximately 160 to 180 mm. There is, however, a tendency towards a larger minimum size at maturity at more northerly locations. This could suggest that a larger body size is necessary at northern locations for sufficient reserves to be accumulated so an individual can survive hibernation and reproduce without threatening their well-being by depleting energy reserves, as has been suggested by other researchers (Galbraith *et al.*, 1989; Millar & Hickling, 1990; Brooks *et al.*, 1992).

Sex and immature to adult ratios

Published sex ratios for other wood turtle populations have ranged from 1 : 1.9 to 1 : 0.8, males to females respectively (Farrell & Graham, 1991; Ross *et al.*, 1991). Since wood turtles do not have temperature dependent sex determination (Bull *et al.*, 1985), their sex ratios are not subject to environmental conditions and therefore no sexual biases should be expected over the species' range. Our study found that the sex ratio did not differ significantly from 1 : 1, which is similar to most other studies (Harding & Bloomer (Michigan), 1979; Harding, 1985; Farrell & Graham, 1991; Ross *et al.* (BR site), 1991; Kaufmann, 1992a; Daigle, 1997; Tuttle & Carroll, 1997; Saumure, 1997). The large number of studies that support the 1 : 1 sex ratio suggests that the few studies that display ratios that are significantly different from 1 : 1 (Harding & Bloomer (New Jersey), 1979; Ross *et al.* (WR), 1991; Foscarini, 1994) are the result(s) of either: biased sampling techniques (as was observed in our study when several females were captured at a communal nesting area, the removal of which gave a 1:1 ratio), environmental factors that may be unequally removing one sex from the population (e.g. females being killed on road edges while possibly searching for a nest site), or the use of inappropriate size/age classes to distinguish males from females as immature turtles often resemble females, or a combination of the above (Ream & Ream, 1966; Gibbons, 1970; Stickel, 1978; Harding & Bloomer, 1979; Litzgus & Brooks, 1996). While we did observe an even male to female sex ratio over the course of the entire study, the significantly different results of adult to immature captures from spring and fall surveys, 4 : 1 and 2 : 1, respectively, suggest that sampling biases which are not obvious can occur.

Dietary habits

Observations of feeding habits during this study support the claim that wood turtles are opportunistic omnivores (Harding & Bloomer, 1979). Three feeding observations were of particular interest. First, a turtle cut down large fern fronds by biting through the stem and then was observed to eat only the fresh growing tips. This complex feeding strategy may indicate a high level of intelligence, previously noted for this species (Tinkelplaugh, 1932). A second interesting feeding observation involved the consumption of birds. A study that examined stomach contents of wood turtles found bird remains in 8 % of samples (Surface, 1908). Harding and Bloomer (1979), also document the eating of eggs or young of birds. Observations in our study also indicated the consumption of bird parts. Whether the birds were captured alive, or were the product of scavenging carrion, is unknown. Other studies have documented the consumption of carrion of fish and birds (Surface, 1908; Harding & Bloomer, 1979; Farrell & Graham, 1991). We also observed carrion of toads and mice being eaten. Studies of wood turtles in Michigan (Harding & Bloomer, 1979) documented the eating of newborn mice. It could be that wood turtles are more carnivorous than previously suspected. In captivity wood turtles will eat many meaty items (Harding & Bloomer, 1979; Merrit, 1980). In fact, some populations of the wood turtle have developed an apparently successful method of obtaining proteins, a feeding strategy known as 'stomping', which is used to lure and capture earthworms (Kaufmann, 1986; Kaufmann *et al.*, 1989). Turtles in our population were not observed to use this feeding strategy. During our study, up to four turtles were observed fighting over a piece of carrion, suggesting that meat is a favoured food. Since wood turtles at the northern limit of their range are larger than those from the south and their annual period of activity is shorter, it is possible that northern turtles need to consume more protein containing material. It has been suggested that growth in some turtles is limited by the relative amount of proteinaceous material in their diet (Gibbons, 1967; Zug, 1993) and that larger body sizes can result from increased carnivory (MacCulloch & Secoy, 1983).

We found that the density of wood turtles in our study area was approximately 0.44 turtles per hectare (tu/ha). Our density is slightly higher than that for turtles from a population in northern Ontario, 0.24 tu/ha (Brooks *et al.*, 1992), a site where the number of FFD is lower than ours (Table 1.4). Densities of wood turtles from southern locations with more FFD are greater, for example, 2.6 tu/ha for a New Hampshire population (Tuttle & Carroll, 1997) and 10.7 tu/ha for a population in New Jersey (Farrell & Graham, 1991). The density of turtles is strongly positively correlated with the number of FFD (r=0.958, $p<0.01$). It is possible that because northern turtles are larger they require a greater area without intrapopulation competition in which to forage to obtain the necessary resources and build sufficient fat reserves to survive the longer winters. It could also be that the general trend of decreasing biodiversity and primary productivity associated with shorter growing seasons may be limiting the numbers and/or the variety of food available to northern turtles (Fleming, 1973; Teeri & Stowe, 1976; Heywood, 1978; Currie & Paquin, 1987; Crane & Lidgard, 1989; Cox & Moore, 1995). This could be forcing turtles to utilize a larger area and/or necessitating less competition for resources within an area so that dietary requirements can be met. Food availability has been suspected of limiting the density of other turtles (Ross, 1989). These latter concepts support our suggestions that some food types are limited and may help to explain the aggressive encounters we observed over food.

Activity

In no part of this species' range is it known to be active year round. Seasonally, turtles began to hibernate in October or November and subsequently emerged in the spring, April and May, as has been observed for other populations (Harding & Bloomer, 1979; Ernst, 1986; Farrell & Graham, 1991; Kaufmann, 1992a; Foscarini, 1994). Differences can be accounted for by variation between the onset of winter and start of spring over the geographic range of the species. While Pope (1939) stated that hibernation may occur on land this has not been documented by any of the more recent studies. However, Harding and Bloomer (1979) reported an observation of a mud covered wood turtle emerging from between tree roots above the water line, but they did not know if this was a hibernation site. If wood turtles do hibernate on land it is undoubtedly a rare and unusual event. Hibernation sites are reported only in aquatic habitats, usually in a river, with turtles resting on the bottom, tucked under the banks, in beaver ponds, or resting in muskrat or beaver channels, sites that are similar to those used by other populations (Harding & Bloomer, 1979; Ernst, 1986; Brooks & Brown, 1991; Farrell & Graham, 1991; Foscarini, 1994). A possible explanation for turtles being larger as the number of FFD decreases is that larger body size may allow for larger energy reserves which may reduce metabolic costs (Galbraith *et al.*, 1989; Graham & Forsberg, 1991; Brooks *et al.*, 1992). It may be that in a northern population where the turtles must hibernate for longer periods larger energy reserves are necessary for overwinter survival. Associated with hibernation is lactate buildup which is a result of anaerobic respiration. It is possible that the increase in size produces a dilution effect to counteract the sometimes lethal lactate buildup, however, it has been observed that some turtles can survive longer winters simply by increasing their ability to dispose of lactates (Ultsch *et al.*, 1985).

Of the turtles caught during this study, 82 % were captured during May and June while basking close to the river or at nesting areas. This high rate of capture was attributed mainly to the tendency for turtles in our population to remain close to the river at this time of year, where they seek refuge from cold weather. Similar results have been obtained for other populations (Harding & Bloomer, 1979; Ernst, 1986; Farrell & Graham, 1991). Also, it was relatively easy to see turtles at this time of year since plants had not yet leafed out.

In a population of turtles from a southern location the lowest temperatures at which males and females basked were 14 and 16.8 °C, respectively (Ernst, 1986), but during our study basking was observed at temperatures of 9 °C with many observations falling below the minima reported by Ernst (1986). As basking is considered important for a turtle to increase its body temperature (Boyer, 1965), it is possible that wood turtles at the northern limits of their range have adapted to initiating basking at lower temperatures. During July and August, wood turtles were rarely observed since they were dispersed throughout the study area and not concentrated at rivers or nesting areas. Also, dense vegetation may have hindered detection. Similar results were obtained by Farrell and Graham (1991) with only 9 % of all captures occurring during the period June to September. In September and October wood turtles returned to the rivers, as described elsewhere (Harding & Bloomer, 1979; Ernst, 1986; Farrell & Graham, 1991). During the fall, prior to hibernating, turtles were observed close to the river and spent nights submerged in the water.

Mating

Most of our observations of courting behaviours were in the spring and fall when turtles were congregated in aquatic habitats, supporting the bimodal pattern of courting behaviour observed by others (Carroll & Ehrenfeld, 1978; Harding & Bloomer, 1979; Farrell & Graham, 1991; Kaufmann, 1992a; Foscarini, 1994). Although, courting and mating can occur during any month that turtles are active, it is more frequently observed in spring and fall. This may be the result of hormonal fluctuation (Licht, 1982) or it may simply be because males and females are congregated in aquatic habitats during these periods (Harding & Bloomer, 1979). In an Ontario population, 50 % of courting behaviour occurred during the month of May and there was at least one observation per month from June to September, but very little observation was conducted during September and October thus, the frequency of fall matings may have been overlooked (telemetry surveys were conducted every three to four weeks) (Foscarini, 1994). In our study, 50 % of the courting activities were observed during October alone, and 70 % occurred during the fall. If anything, this was an underestimate of the fall importance for mating, as we also spent less time in the field during the autumn months. Similar results showing an increase in mating behaviour in the fall were reported by Harding (1990). Carroll and Ehrenfeld (1978) observed that mating behaviours peaked in the spring, with a second mating period occurring in September and October. They also reported that mating attempts in the fall were longer than those of the springs. Further support of the importance of the fall mating period is provided by Kaufmann (1992a), who also found that fall mountings were of a longer duration than spring mountings and that significantly more fall mating attempts resulted in insemination. The suggestion that the increase in mating behaviour in fall was a result of hormonal fluctuations was confirmed by Licht (1982) who reported that testosterone production and spermatogenesis peak during late summer and fall. In Nova Scotia, Powell (1967) found that female turtles in summer and fall have mature follicles, which are then stored over winter, and ovulated in the spring. If the fall is in fact the primary mating period for this species, females must be capable of storing sperm to fertilize eggs the following spring, as has been suggested by another study (Kaufmann, 1992a). The storage of viable sperm for over one year has been documented for many other species of North American turtles (Smith, 1956; Berry & Shine, 1980; Gist & Jones, 1987), but has not been shown for wood turtles. While we have no evidence that our population has longer mating attempts in the fall or that there is a greater frequency of sperm transfer during this period, the fact that 70 % of mating attempts observed occurred in the fall may indicate that it is more important. At our northern location there is little post-hibernation time (2-3 weeks) in the spring before it is necessary for female turtles to ovulate their mature follicles, in preparation for oviposition by mid-June. If the spring was the period that was important for sperm transfer, we should have observed numerous matings in the spring, but did not.

Our observations that mating occurred most often between 1100 and 1300h differ from those reported in other studies. Farrell and Graham (1991) report that mating was commonly observed in the early morning, while others (Harding & Bloomer, 1979) report that it is most often observed in late afternoon. It is possible that our population was mating during the midday period because this is the time at which the turtle has had sufficient time to emerge from the water and bask to increase its body temperature. Turtles, being ectotherms, are typically temperature sensitive related to their activity and turtles that are larger, as our study population was, may require more basking time to reach temperatures that are ideal for normal activity

(Boyer, 1965; Cloudsey-Thompson, 1971; Hutchison, 1979; Huey, 1982). A more southern location will be warmer earlier and later during the day, and also reach a higher day time temperature, compared to a more northern location (United States Environmental Data Service, 1968; Canada Department of Transport, 1970). In a controlled experiment, wood turtles maintained at a higher temperature have several activity periods during the day, while those kept at a lower temperature have only one activity period centered around midday (Graham & Dadah-Tosti, 1981). The observations of our population having its mating behaviour centered around midday may be explained by these results. This could also explain why mating behaviour in southern populations occurs during the early morning and evening, times at which turtles were more active (Harding & Bloomer, 1979; Farrell & Graham, 1991).

Mating behaviours of the wood turtle are almost always aquatic (present study; Ratner & Anderson, 1978; Harding & Bloomer, 1979; Harding, 1990; Farrell & Graham, 1991; Kaufmann, 1992a). During this study, mountings were observed on land twice. The behaviours surrounding these events were unknown. The lack of contact between the tails in both of these occurrences suggests that copulation was unsuccessful. Others have observed mating of the wood turtle on land (Ratner & Anderson, 1978; Harding & Bloomer, 1979; Kaufmann, 1992a), but Harding and Bloomer (1979) found that terrestrial copulation is rare. Kaufmann (1992a) observed 15 terrestrial mating sequences and observed no copulatory ties. It seems that although mating behaviour is occasionally observed on land its role is not significant in the copulatory behaviour of the wood turtle. Aquatic copulatory behavior appears to be much more common and results in insemination (Kaufmann, 1992a).

Injuries, Predation, and Parasites

Commonly reported injuries to wood turtles include tail loss, partial or complete amputation of limb(s), shell damage, and death (Farrell & Graham, 1991; Brooks *et al.*, 1992; Kaufmann, 1992a; Foscarini, 1994; Gilhen *et al.*, 1994, Saumure, 1997). Tail loss was the most common and the percent tail loss (24.5 %) in our population is within the range reported by other studies. Reported tail loss ranges from 59 % in Ontario (Foscarini, 1994) to 16.8 % in New Jersey (Farrell & Graham, 1991). While in our study there was no difference for the rates of tail amputation between sexes, adults suffered significantly greater tail loss than immatures. It is possible that immature turtles lacking a completely ossified shell (Zug, 1991) are more often killed during an attack, therefore reducing their numbers in samples (Wilbur, 1975; Bury, 1979). It is also possible that tail damage is not solely the result of predation but may also be the result of aggressive adult turtle encounters. Immature turtles not being as involved in aggressive encounters for dominance and mate selection would therefore be less subject to this form of injury. Tail injuries are known to be caused by conspecifics in captivity (Bell, 1972). During this study, aggressive encounters in which tail biting occurred were observed between males and males, females and males (pre-copulatory), and females and females. Tail biting by turtles of the genus *Clemmys* is known to occur during agonistic encounters and prolonged tail biting is considered to be a highly aggressive act (Ernst, 1967; Kaufmann, 1992a), but it is not clear if any permanent damage is incurred. During this study, bleeding was observed on two occasions after a tail had been bitten, once in a male-male encounter and the other in a female-female. The first author, having being bitten by a female wood turtle can attest to the strength of a wood turtle's bite. The bite on a finger removed a large chunk of skin, leaving a deep wound. It is possible that such an attack to a tail could sever the caudal veins, causing a part of the tail to atrophy.

The results obtained for limb amputation (9.6 %), are similar to those obtained by others: 9.6 %, Harding & Bloomer, 1979; 8.6 %, Farrell & Graham, 1991; 12.9 %, Foscarini, 1994. The percentage having two limbs amputated (3.2 %) is similar to that reported by Harding and Bloomer (1979). Several studies report that it is not uncommon to find turtles with one or two limbs chewed off by a predator such as a raccoon (Harding & Bloomer, 1979; Harding, 1985; Farrell & Graham, 1991) or otter (Gilhen *et al.*, 1994), but in the latter study it is not clear whether they observed this mutilation directly. A study in southern Québec (Saumure, 1997) reported a much higher rate of limb amputation, 32.3 %, and a double amputation rate of 13 % . Saumure (1997) believed that a few very efficient predators, or the relative abundance/density of the predatory species was the reason for high rates of limb amputation but did not have any evidence to support this.

The effects of limb amputations on turtles are unknown. During this study female turtles, despite missing one and/or two limbs, were observed traveling to a nesting area and nesting, and one turtle that was missing two front limbs nested in both years of the study. Rear limb amputations were uncommon, but some females were observed at nesting sites constructing nests using only one rear leg. These observations are similar to those of Harding (1985), suggesting that turtles are capable of living normal lives, even with the loss of limbs, provided sufficient mobility is maintained. However, Harding (1985) did notice there were significantly less injured turtles recaptured during his study, suggesting that longterm survival may be compromised.

The seasonal occurrence of leeches on wood turtles has been well documented (Koffler *et al.*, 1978; Harding & Bloomer, 1979; Farrell & Graham, 1991; Foscarini, 1994; Saumure & Bider, 1996). We found no turtles with leeches during summer months and believe that this is because turtles are primarily terrestrial at this time, as has been suggested by others. While some studies report leeches on wood turtles in all months (Harding & Bloomer (Michigan), 1979; Foscarini, 1994), their presence is highest in the spring. These observations are from populations in the western part of the species' range, which are more aquatic than eastern populations (Harding & Bloomer 1979).

CONCLUSION

In conclusion, the ecological data presented on wood turtles from the northern limit of their range have enabled comparisons to be made across the species' range. Increasing size is correlated with decreasing FFDs. Seasonal and daily activity patterns, food preference and density are all ecological traits that are to some degree affected by increased size.

Clemmys insculpta is reported to be disappearing or in decline over most of its range (Merrit, 1980; Garber, 1989; Farrell & Graham, 1991; Harding, 1991; Brooks & Foscarini, 1992; Brooks *et al.*, 1992; Kaufmann, 1992a; Brooks, 1994; Ernst *et al.*, 1994; Gilhen *et al.*, 1994; Garber & Burger, 1995). The previous authors have suggested that: increased predation on any or all life stages (egg, immature, adult), habitat destruction and alteration, fragmentation of the species' range by development, and collection for the pet trade (considered the largest threat) are factors causing the decline. The population examined in this study is relatively concentrated especially during spring and the fall, making it vulnerable to exploitation for the pet trade, as well as to other above mentioned causes. The data and comparisons presented provide an indepth understanding of wood turtle ecology and ecological requirements and will be useful in the planning and implementation of conservation and management strategies. Recent action by federal authorities to list *Clemmys insculpta* as 'vulnerable' in Canada (Litzgus & Brooks, 1996; Green, 1996) is a positive step but, until the species is protected in all regions of its distribution, it will likely continue to decline.

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Table 1.1. Body measurements of wood turtles from a population in Municipalité Régionale de Compté Le Centre de la Mauricie, Québec, 1996 - 1997.

Sex	n	Carapace length (mm)	Plastron length (mm)	Mass (g)	Age estimate (# of annuli)
Male	55	214.51 ± 4.21*	191.54 ± 11.40	1173 ± 252**	19.7 ± 4.2
Female[a]	83	201.07 ± 10.88	192.69 ± 10.33	1083 ± 168	20.4 ± 4.1
Immature	50	129.56 ± 39.73	122.27 ± 38.74	375 ± 188	7.7 ± 3.9

Note: Values are given as mean ± standard deviation.

[a] all females measured during the study were included

* Significant differences between sexes , $t = 1.936$, $df = 136$, $p < 0.05$.

** Significant differences between sexes , $t = 2.49$, $df = 136$, $p < 0.01$.

Table 1.2. Size (carapace length) and age (# of annuli) of wood turtles observed in courting or mating activities during 1996 - 1997, from a population in Municipalité Régionale de Compté Le Centre de la Mauricie, Québec.

Sex	**n**	**Carapace length (mm)**	**Age estimate (# of annuli)**
Male	30	219.8 ± 11.1*	19.8 ± 3.7
Female	33	208.5 ± 10.6	19.9 ± 2.5

Note: Values are given as mean ± standard deviation.

* Significant differences between sexes , $t = 4.06$, $df = 61$, $p < 0.001$.

Table 1.3. Comparisons of frost free days (FFD) with carapace length, age, minimum age and size at maturity of adult wood turtles among 11 locations.

		MALES				FEMALES				
			Carapace length	Number of annuli			Carapace length	Number of annuli		
Location	FFD[a]	N	Mean (range)	Mean	Min	N	Mean (range)	Mean	Min	Source
ON (45 °N)	90	21	219 (199-244)	21.6	17	57	202 (185-225)	24.6	18	Brooks *et al.* 1997
QC (46°N)	100	55	215 (170-242)	19.7	11	83	201 (181-225)	20.4	14	Present study
QC (45.5°N)	113	9	216 (176-?)	16.8	10	10	201 (195-?)	16.8	15	Saumure 1997
QC (45°N)	120	19	195 (176-211)	--	--	23	182 (167-209)	--	--	Daigle 1997
WS (44°N)	140	28	201 (--)	--	--	48	187 (--)	--	--	Ross *et al.* 1991
MI (46°N)	140	86	200 (169-228)	21.5	12	10 5	182 (158-218)	20.2	15	Harding & Bloomer 1979
ON (43°N)	150	83	198 (173-?)	21.1	12	13 6	181 (158-?)	20.5	10	Foscarini 1994
NH (43°N)	150	17	182 (--)	--	--	29	172 (--)	--	--	Tuttle & Carroll 1997
VA (39°N)	190	11	196 (--)	--	5	14	183 (--)	--	--	Lovich *et al.* 1990
NJ (41°N)	210	311	178 (160-206)	--	7-8	46 4	165 (160-188)	--	7-8	Harding & Bloomer 1979
NJ (41°N)	210	69	177 (161-201)	--	14	49	171 (158-200)	--	14	Farrell & Graham 1991

ON-Ontario, QC-Quebec, WS-Wisconsin, MI-Michigan, NH-New Hampshire, VA-Virginia, NJ-New Jersey

Note: Approximate latitudes are estimated from locations provided in the sources.

[a] Mean number frost-free days (U.S. Department of Commerce, Environmental Data Service (1968) and Wilson (1971)).

Table 1.4. Comparison of frost free days (FFD) and wood turtle density (# of turtles/hectare) among six locations.

	FFD[a]	turtles/ hectare	Source
Ontario (45°N)	90	0.24	Brooks *et al.* 1992
Québec (46°N)	100	0.44	Present study
Michigan (46°N)	140	2.5	Harding and Bloomer 1979
New Hampshire (43°N)	150	2.6	Tuttle and Carroll 1997
New Jersey (41°N)	210	10.7	Farrell and Graham 1991
New Jersey (41°N)	210	12.5	Harding and Bloomer 1979

Note: Approximate latitudes are estimated from locations provided in the sources.

[a] Mean number frost-free days (U.S. Department of Commerce, Environmental Data Service (1968) and Wilson (1971)).

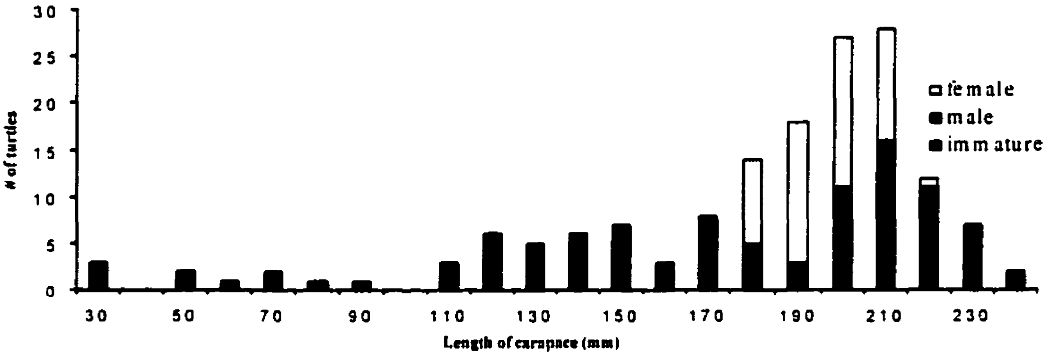

Figure 1.1. Population size structure (length of carapace in mm) of 156 wood turtles captured from Municipalité Régionale de Compté Le centre de la Mauricie, Québec, Canada in 1996 and 1997. Turtles captured by biased sampling techniques (e.g. at nesting areas) have not been included.

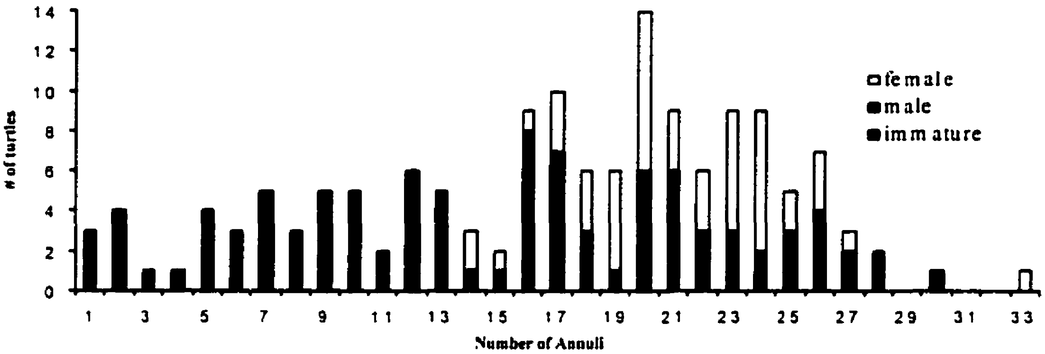

Figure 1.2. Population age structure (number of annuli) of 153 wood turtles captured from Municipalité Régionale de Compté Le centre de la Mauricie, Québec, Canada in 1996 and 1997. Turtles captured by biased sampling techniques (e.g. at nesting areas) have not been included.

CONNECTING TEXT

While collecting data on the ecology of the wood turtle, detailed accounts of the nesting ecology and hatching success of the species were made. Relatively little is known on this subject and a large amount of data was gathered. Therefore, it is presented as a separate manuscript.

II. NESTING ECOLOGY AND HATCHING SUCCESS OF THE WOOD TURTLE, *Clemmys insculpta*

*Manuscript for submission to the journal Chelonian Conservation and Biology

INTRODUCTION

Many aspects of the wood turtle's (*Clemmys insculpta*) biology have been reported upon but, very little is known about the nesting ecology of this species. This may be because most data on nesting activity have been obtained indirectly in the course of working on other aspects of turtle behavior. The information obtained on nesting wood turtles has typically included small sample sizes (usually less than 10) or the specimens were kept in captivity, and/or the eggs were incubated under laboratory or semi-natural conditions (e.g., Gammons, 1871; Pallas, 1960; Bleakney, 1963; Powell, 1967; Combs, 1971; Ratner & Anderson, 1978; Harding & Bloomer, 1979; Graham & Forsberg, 1986; Farrell & Graham, 1991; Quinn & Tate, 1991; Ross *et al.*, 1991; Brooks *et al.*, 1992; Brooks & Foscarini, 1992; Kaufmann, 1992a). In the few studies that examined nesting activity in the field, little additional data (e.g. incubation period, date of emergence) were obtained due to nest predation rates of 70 - 100 percent, or the removal of eggs for incubation under laboratory conditions (Harding & Bloomer, 1979; Farrell & Graham, 1991; Brooks *et al.*, 1992).

Nest predation is considered a major factor reducing egg survivorship in all freshwater turtles (Bleakney, 1963; Plummer, 1976; Tinkle *et al.*, 1981; Congdon *et al.*, 1983; Brooks *et al.*, 1992; Buech & Connors, 1992). It is widely accepted that freshwater turtles have a type III survivorship curve which is characterized by high mortality of eggs and hatchling stages and low mortality of adults (Gibbons, 1968; Harding & Bloomer, 1979; Congdon *et al.*, 1983; Harding, 1990; Farrell & Graham, 1991; Ross *et al.*, 1991; Garber & Burger, 1995). The occurrence of predation on freshwater turtle nests, over the entire incubation period, has been documented in only a few studies. Some of the most thorough studies include those of Congdon *et al.* (1983) on Blanding's turtle (*Emydoidea blandingii*), Christens and Bider (1987) and

Tinkle *et al.* (1981) on the painted turtle (*Chrysemys picta marginata*) and Burger (1977) on the diamondback terrapin (*Malaclemys terrapin*). Similar studies have not been conducted for the wood turtle. In general, researchers have concluded that more detailed studies of wood turtle life histories must be conducted (Harding & Bloomer, 1979; Farrell & Graham, 1991; Ross *et al.*, 1991; Brooks *et al.*, 1992; Litzgus & Brooks, 1996).

The objectives of this study were to describe movement patterns of females to nesting areas, nesting activities, time of nesting (month, day, and time of day), clutch size, clutch frequency, nest site fidelity, predation, hatch dates, nest success and recruitment rates. This represents the first published intensive study of the nesting ecology of the wood turtle. This information will promote the development and implementation of conservation and management strategies.

MATERIALS AND METHODS

A comprehensive study of wood turtle nesting ecology began in May of 1996 and continued until December, 1997, on a river in the Municipalité Régionale de Compté (MRC) Le centre de la Mauricie, Québec, Canada. The exact location of the population is not revealed due to the threat of collection for the pet trade (Litzgus & Brooks, 1996; Garber & Burger, 1995).

The geology of the area is that of an esker (Allard, 1978); with gravel and sand deposits that have been mined, resulting in many open pits in the region. The river is generally slow moving and meandering, between 5 and 10 m wide, 1-2 m deep, and has a sandy bottom with rocky outcrops. The flood plain is characterized by alder (*Alnus rugosa*) thicket with several ox-bow lakes and beaver ponds. Most of the land in the study area is privately owned and has little to no development on it at present, although there has been some logging in the past, as well as open-pit mining of gravel.

To obtain information on the number of females in the population and their general movement patterns, turtles were captured and marked from May to October of 1996 and 1997. During May of both years, an intense search of the study area was undertaken to find and mark as many wood turtles as possible. For each new turtle captured several measurements were recorded; date, time, location, weather, and temperature. Also, the straight line carapace (CL) and plastron lengths (PL) were measured using large vernier calipers (forester type, ±1 mm, Haglof, Sweden) and the turtle was weighed using a pipe scale (Pesola, ± 50g or ± 10g, Switzerland). Adult turtles were sexed using characteristics of minimum length of carapace and the presence or absence of male secondary sexual characteristics; males exhibit plastron concavity and a longer, thicker preanal tail (Wright, 1918; Harding & Bloomer, 1979; Lovich *et al.*, 1990; Brooks *et al.*, 1992; Kaufmann, 1992a, 1992b).

Age was determined by counting growth annuli, which is considered a reliable estimator of age until approximately 15-20 yr, after which time growth is very slow and it is difficult to discern separate annuli (Harding & Bloomer, 1979; Harding, 1985; Lovich *et al.*, 1990). For a turtle whose growth annuli numbered greater than 20 we continued to count all visible annuli, as it was considered to be unlikely that more than one growth annulus was deposited per year at this northern location with its short growing season. Data were taken on limb and tail loss, presence/absence of parasites and shell abnormalities. Females were palpated for the presence of eggs in the oviducts. This was accomplished by inserting the index fingers into the rear limb sockets and rotating the fingers, if eggs were present small circular lumps could be felt. Carapace marginal scutes were marked for later individual identification (Cagle, 1939), using a 6 mm rat-tail file that made permanent U-shaped notches, with a numbering system similar to one described by Froese and Burghardt (1975). After the data collection was complete, turtles were returned to the point of capture.

A known nesting area for wood turtles in this region is in an old gravel pit. The substrate in the pit is comprised of a fine-medium gravel and sand. There is very little vegetation present except around the edges. The general area that was observed for nesting was approximately 1.5 ha. Three access roads cross the gravel pit.

In mid-May of 1996, radio transmitters (Holohil AI-2M(4) with 2 yr batteries) were attached to 16 adult female turtles. In 1996, turtles were located once per week. In 1997, these turtles were located daily from 26 May until the end of June and their locations were plotted on a topographic map in order to obtain information on female movement to and from nest areas. This also enabled researchers to detect the location of previously unknown nesting areas.

From 26 May until 1 July , in 1996 and 1997, the main nesting area (gravel pit) and the surrounding areas were observed on a daily basis for the presence of female turtles and signs of nesting activity. Once females began to arrive at the nesting area a constant watch was kept during all daylight hours. If any turtles remained in the gravel pit after sunset it was usually because they were nesting and observations therefore continued after dark until the turtle finished and had retreated. For each turtle, the date, time and general location were recorded at first entry into the gravel pit and also when it left the area. In addition to this main nesting area other gravel/sand pits, dirt roads, high sandy river banks and tributary creeks were periodically surveyed for evidence of nesting activity.

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 (Congdon *et al.*, 1983). All observations at the nesting area were made from a blind using binoculars and/or spotting telescopes. Females in a pre-nesting state were extremely sensitive to any sounds or movements (this study; Wever & Vernon, 1956; Kaufmann, 1992a) in the gravel pit and observers took care to remain silent and out of view. Females were carefully watched for any sign of nesting. Notes on behaviors were recorded with the time at which they occurred: flicking sand over shell, 'smelling' the soil, starting of digging, and false nest start and end. When it was determined that a turtle was making a true nest, constant watch was initiated in order to determine the time when the first egg was laid. At this point, if no other turtles were in the gravel pit or within sight of the laying female, she was approached so the number of eggs could be counted. When a turtle laid an egg, it retracted its head (Harding & Bloomer, 1979). If direct approach was not possible, observers tried to position themselves so that the number of eggs laid could be obtained directly or indirectly.

Each time an egg was laid, the same head retraction behavior was repeated as for the first one. Once a turtle had started to lay, she continued until finished and was not scared off by noise or movement. The time at which the turtle began to cover the nest was recorded as the time at which egg laying was completed. Finally, the time when the nest was totally covered and the female began to move away from the site was recorded as the time the nest was completed. 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 3 numbered stakes (triangulated) was measured and the nest was staked with a metal spike and numbered tag. If the turtle had not previously been identified, it was marked and all relevant data, as described above, were taken.

At the first signs of hatchlings emerging from a nest, characterized by a hole in the substrate approximately 3-4 cm in diameter, 1 m^2 nest covers were placed over nests to restrain the hatchlings when they emerged. These were frames constructed of wood measuring 1 inch (2.5 cm) by 4 inch (10 cm) and 1 m per side and then covered with wire grating with 1.27 cm galvanized mesh. These covers were partially buried in the ground to prevent hatchling escape. The nests were then checked every day for the emergence of hatchlings. The date(s) of emergence was recorded, all young were measured (CL, carapace width (CW), and PL) using vernier calipers (±0.05 mm), weighed (standard electronic laboratory scale, ± 0.005) and then notched on marginal scutes with toe nail clippers for identification as young from specific nests. The number of eggs and hatching success were calculated, adding 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 confirmed at this time by the number of egg shell fragments and the appearance of these shell membranes. Egg shell membranes from which hatchlings emerge are usually white, soft, and leathery compared to those of eggs that have rotted which are usually brownish, hard, and brittle (personal observation). Undeveloped eggs had an embryonic turtle that had died at some stage of development and infertile eggs did not contain an embryo. If a nest had no hatchlings emerge the number of eggs was determined simply by counting them. If a single hatchling emerged the nest was considered successful. When no hatchlings emerged, the reason for the nest failure was evaluated from characteristics of the destroyed nest or the appearance of the shell fragments. In 1996, nests from which no hatchlings emerged were left undisturbed to be excavated in the spring. 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.

For the purpose of clarity the following terminology is used. Nesting refers only to the act of nesting, i.e. excavating a nest and laying eggs. 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 a nest. Recruitment success is the percentage of hatchling recruits compared with the total number of eggs laid.

Statistical analysis

Differences between means were tested for using the Student's *t*-test (Zar, 1996). Correlations among populations were analysed using Table Curve 2D. Statistical significance was accepted at $p<0.05$.

RESULTS

Female turtles congregated in large numbers primarily at a nesting area in an old sand/gravel pit adjacent to the river. Other secondary nesting areas included naturally eroding river valley slopes (sandy), dirt/sandy roads, sand points in the river, and a small sand pit. No large congregations of turtles were observed at these secondary areas. Unless specifically stated data reported are from the main nesting area.

Telemetry data are reported for female turtle movement pre- and post-nesting for the 1997 field season only. Data from both years were similar, but in 1997, turtles were located more frequently than in 1996. Seven of the 15 turtles followed were observed to nest in the main nesting area and 2 others were suspected of nesting there, but were not observed to do so (these latter turtles were included in movement to the main nesting area analysis). The remaining 6 turtles were not observed to nest but some (n=4) were gravid. These turtles were suspected of nesting in other areas.

All turtles moved to the main nesting area along waterways, therefore, distances reported are not straight line distances. The direction of movement (against or with the current) did not seem to be significant (data not shown). Two general movement patterns to the main nesting area were observed; the first was a relatively slow migration over more than 14 days, which began shortly after turtles emerged from hibernation (n=3), and the second was a fast migration whereby the turtles stayed relatively close to where they hibernated and on approximately 10 June (3 days before nesting season began) moved directly to the main nesting area over a 2-7 day period (n=6). There was no significant difference between the slow and fast group for mean distance traveled to the main nesting sight, 2240 ± 1041 m and 2113 ± 1360 m, respectively ($p>0.05$). The mean distance traveled by all turtles to the main nesting area was 2156 ± 1196 m (n=9, range=840-3740 m). Two turtles moved great distances during one day; one traveled 2940 m and the other 2400 m, both of these against the current.

In 1996, 29 females were observed to construct nests and in 1997, 33. The nesting period lasted 13 days in 1996, 9-21 June, and 16 days in 1997, 13-28 June (Fig. 2.1). In 1996, 1 turtle nested on 1 July, a late nester for that year

During the 1996 season, 1 turtle was observed visiting the main nesting area on 7 June, and 9 on 9 June which was the day of the first nest. Between the 10-14 June, 76 % (n=93) of all visits to the nesting area (during the nesting period) occurred. During the same 5 day period 64 % of the known nests were constructed (Fig. 2.1a). On 13 June, a heavy midday rain stimulated nesting activities and 34 turtles were identified in the nesting area when 39 % (n=11) of all nests were constructed. The remaining 9 nests were constructed over the following week and fewer turtles visited the area during this period. The last nest (and visit) was on 21 June, the end of the nesting period. One other turtle visited the nest area and constructed a nest on 1 July, and was considered to be an outlier.

In 1997, the first turtle arrived at the main nesting area on 10 June, and the following day another 1 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 accounted for 58 % of all the visits to the gravel pit during the nesting period. Within this period, 16-21 June, 24 of the 33 nests were constructed (73 %) (Fig.2.1b). The remaining 8 nests were made over the following week, 22 to 28 June.

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 which 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 nesting time (digging, laying, and covering the nest) of 24 turtles varied between 86 and 202 min, with a mean of 131. Therefore, on the day of nesting, a female spent on average 101 min before beginning to excavate a nest.

Excavation of nests was started at almost all hours during daylight but never before 0500 or after 2100h, with almost equal numbers of nests being started in the morning and evening (Fig. 2). In the morning, 38.5 % (n=22) of nests were started between 0500 and 0900h. Forty-four % of nests (n=25) were started in the evening between 1600 and 2100h with most, 37 % (n=21) from 1800 to 2100h. The remaining 17.5 % (n=10) of nests were started at various times during the midday. In both years nesting was stimulated by rainfall.

During the nesting period of 1997, 44 female turtles visited the main nest area and of these, 33 were observed nesting. Of the 44 turtles that visited the main nesting area, 30 were identified as having visited in 1996. Thus, 68 % were believed to be gravid in two consecutive years. Of the 33 that nested in 1997, 64 % (n=21) were known to have nested at the main nest area in 1996. One turtle that nested at this area in 1996 nested at a secondary area in 1997. Of the turtles that returned to nest, 43 % (n=9) nested within 10 m of their nest from the previous year.

During the time that the 9 radio tagged turtles were within the general area of the main nesting area, but not necessarily at the nest area, they were regularly observed in the adjacent habitat. This area was considered to be a staging grounds and consisted of a length of river and flood plain approximately 200 m long, plus a boggy habitat, all centered around the main nest area. Thirty-six female turtles were observed at the staging grounds in 1996 and 41 were seen using these areas in 1997. All were palpated and believed to be gravid. Of the 39 turtles identified at the nesting area in 1996, 31 (79 %) had been at the staging grounds, while in 1997, of the 44 turtles documented at the nest area, 35 (80 %) had been observed at these staging areas. In the two years of the study, 63 females were identified at the staging areas and/or at the nest area. Turtles tended to use natural habitats that were unaltered by human disturbance while on the staging grounds.

The mean CL and PL of nesting turtles in 1996 and 1997 were not significantly different from female turtles not observed to nest in the population ($p>0.05$) (Table 2.1) but, nesting turtles had significantly more annuli than non-nesting female turtles. 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 age was similar (Table 2.2). There was no correlation between CL, PL, or age with clutch size (Table 2.3).

No mammalian predation of nests at the main nesting area occurred during the study. Raccoons (*Procyon lotor*), red foxes (*Vulpes fulva*), skunks (*Mephitis mephitis*), as well as feral and domestic cats (*Felis domestica*) and dogs (*Canis familiaris*) were observed at the nesting area. One nest in each year had a large concentration of ants (sp. unknown) associated with them, and both of these nests failed to produce any young. Almost 50 % (n=15) of nests in 1997 had fly larvae (sp. unknown) associated with them.

Hatching dates were 17 August - 7 October in 1996, and 19 August - 5 October in 1997 (Fig. 3). The average incubation period was 87 ± 12 days (range = 65-116, n=19) in 1996 and 77.5 ± 9 days (range = 60-99, n=20) in 1997. The incubation periods were significantly different between years (t=2.589, p<0.05).

Mean clutch sizes were significantly different between 1996 (9.4 ± 2.4 eggs, range = 5-13, n=27) and 1997 (10.9 ± 2.7, range = 5-20, n=31) (t=2.24, p<0.05). Nest success was 76 % in 1996, and 61 % for the 1997 season. The number of hatchling recruits in 1996 was 158 (total eggs = 253) and in 1997 was 175 (total eggs = 338), and the recruitment success was 62 and 52 %, respectively. Twelve infertile eggs were observed, 8 in 1996 and 4 in 1997.

Hatchling measurements are presented in Table 2.4. Approximately 8 % (n=12) of hatchlings had deformities in the form of extra or fewer marginal scutes or extra median carapace scutes.

Of the 6 nests left to overwinter in 1996, two had hatchlings (# of hatchlings=10) in them in the spring but all were dead. In 1997, 11 nests were excavated in mid-November to establish whether any hatchlings actually enter the winter season in the nest alive. Only one nest had one live hatchling in it and it had a large yolk sac still present, this turtle was reburied in the nest and was found dead 2 weeks later. All other failed nests in both years had eggs that had not completed development, rotting eggs, and/or eggs with fly larvae associated with them.

Detailed Description of Nesting Behaviour

This account is based on average times involved for more than 50 complete and many partial nestings. Turtles were, on average, present at the nesting area for 3.3 days before they began excavating their nests. This part of the nesting sequence is included in the description. Evening nesting at 1930h was chosen to illustrate a typical nesting sequence, as many nests were excavated in the evening and many started at around this time.

Day 1 - The turtle was observed at the nesting area in the evening, generally having entered the nesting area from the cover of vegetation. The turtle was usually wet, having just left the river or occasionally, another body of water. Within minutes it flipped sand over its carapace, and the sand stuck to the wet areas, partially concealing the turtle. It moved farther into the nesting area, where the substrate was relatively flat and composed of sand and gravel with very little vegetation. The turtle walked around, frequently stopping and touching its head to the ground and pushing its face through the sand, as if to smell the soil. Usually the turtle continued walking, but on several of these stops it raised its posterior slightly and with its head still fully extended, began to move the sand with its front legs, alternating each one in a sweeping arc from beside its head to beside its body, often flicking sand onto its carapace with this motion. This activity created a small depression (4-7 cm deep) that the turtle continued to smell. After this, one of two things happened, either the turtle walked away or, it then moved forward and rested in the depression. Once in the depression, the turtle remained fairly still from 1-10 min, occasionally flicking or smelling the sand. The turtle then raised itself on its front legs and began digging with its hind legs. Often it abandoned these starts. On several occasions, what we considered to be completed egg chambers were abandoned, and further inspection revealed that there was a large rock in the chamber. This walking, smelling, flicking, and digging lasted up to 8 hours, but averaged 120 minutes. The turtle then left the nesting area, returning to the river.

Day 2 - The turtle was observed in the morning, between 0500 - 1000h, and again in the evening, between 1600 - 2200h. During these visits it remained for approximately 2 hr. The same behaviour was exhibited as on Day 1.

Very few sightings at the nesting area occurred during the middle of the day. During this time turtles were observed basking or in the shade of a shrub, usually close to the river.

Day 3 - The same turtle was observed at the nesting area in the morning (between 0500-1000h) and remained for about 2 hrs, and exhibited similar behaviour as performed over the past 2 days, then left the area before midday.

It returned to the nesting area in the evening. What follows is a detailed account of a wood turtle nesting.

1730h It arrived at the nesting area and proceeded much as on day 1. For approximately 120 minutes the turtle walked around sniffing and occasionally beginning to dig.

1900h Sniffing the sand.

1901h Sniffing and pushing sand, it then raised its posterior carapace and began to push sand around with its forelegs in arcs from its head to the side of its body, while it continued to sniff the sand. Occasionally, it raised its head to look around.

1903h It moved forward and rested its body in the small depression made by scraping away the sand. It remained in this form for a few minutes, occasionally sniffing the sand, scraping with its forelegs, and flicking sand.

1910h It raised itself up on its forelegs and began to dig with its hindlegs. From this time on the front legs did not move, thereby acting as supports but also aiding to fix the nest chamber in one place and ensuring that the eggs were deposited into the hole. The nest chamber was constructed by scraping the walls and floor several times on the opposite side of the cavity with the claws and then lifting out the loosened clump of wet sand by using the palm and inside of its leg as a scoop. Small piles were formed on each side of the hole. The digging of the hole was accomplished by alternating (always) between each of the hind legs. Each time a leg was inserted or withdrawn from the hole the turtle raised its posterior carapace. This process was continued until a smooth urn shaped nest chamber was formed that was approximately 10-12 cm deep. The diameter of the nest chamber was larger than the opening through which it was dug.

2020h The turtle stopped digging and placed both hind feet on each side of the hole. It remained like this for a couple of minutes.

2023h It extended its head and then quickly retracted it, and the first egg simultaneously appeared and dropped into the nest chamber. Immediately after the egg dropped it lifted itself up (thereby raising its posterior carapace) and inserted a hind leg into the nest cavity (lowering its posterior carapace). The claws were curled up and the egg was manipulated around in the cavity using the knuckles. It then removed its leg from the chamber and inserted the other hindleg, alternating between legs it continued to manipulate the egg in the chamber with its knuckles. Approximately 1.5 min later the second egg was laid with the same retraction of the head. The manipulation of this egg and all remaining ones was done in the same manner as the first. Eventually, the 10 oval eggs were packed into the nest chamber tightly, with no apparent order to their positioning (horizontal, vertical, etc.) with the top egg approximately 5-7 cm below the surface.

2039h The turtle began to pull sand into the nest with its hindlegs with alternating scraping motions. After a couple of scrapes from each foot the turtle began to pack the nest by folding the claws out of the way so that it was kneading the soil with its knuckles, and with its hindlegs fully extended and its plastron well above the ground it rocked in an alternating fashion, putting the weight on one foot then the next. It then resumed its scraping with one leg then the other and rocked and kneaded this into place. This process continued until the hole was filled to level with the ground, but the turtle continued to scrape and knead, often trying to pull sand in from out of its reach. Sometimes while the turtle was doing this it got displaced from the actual nest but continued to scrape and knead as if it were on the nest.

2128h The nest was completed and the turtle began to walk back towards the water.

2140h The turtle moved down the slope and into the river.

DISCUSSION

Time of nesting

The discovery of this relatively large population of wood turtles that nests communally has provided much insight into their nesting ecology, a subject on which very little information has been published. Turtles nested during mid to late June in both years. The beginning of the nesting period was later in 1997 than in 1996 probably due to the cold and late spring. Most studies of wood turtle populations that have observed nesting activities state that it occurs around mid-June (Ratner & Anderson, 1978; Harding & Bloomer, 1979; Harding, 1990; Foscarini, 1994; Farrell & Graham, 1991; Brooks *et al.*, 1992; Kaufmann, 1992a; Graham & Forsberg, 1986; Pallas, 1960; Powell, 1967; Tuttle & Carroll, 1997) but, nesting has been observed as early as late May (Foscarini, 1994) and as late as early July (Powell, 1967, Ratner & Anderson, 1978; Harding & Bloomer, 1979) in some years. The difference in dates for the starting of the nesting period is probably a combination of differences between yearly weather patterns (as was observed in this study) and to a lesser degree geographic location. It was expected that populations from southern locations would begin to nest earlier than northern populations because warm spring weather occurs much earlier in the southern part of the wood turtles' range than at the northern limits (Canada Department of Transport, 1970; United States Environmental Data Service, 1968) as has been observed for other species of turtles (Obbard & Brooks, 1987). This was not observed, and it appears that there is almost no latitudinal variation in the initiation date of nesting as most populations of wood turtles appear to nest around the same date. This could be because turtles are selecting the time of year at which their eggs would have to spend the minimum amount of time in the ground for incubation, thereby using the hottest months, July and August, for incubation. By minimizing the amount of time the eggs are in the ground the risk of predation may be decreased.

The fact that most previous studies report nesting activity for a 1 -2 week period (Powell, 1967; Ratner & Anderson, 1978; Harding, 1990; Brooks *et al.*, 1992; Kaufmann, 1992a; Foscarini, 1994; Tuttle & Carroll, 1997) would support the observations and conclusions of this study that nesting of the wood turtle occurs during a very short time period and that it has a distinct peak. In both years, nesting and turtle visits to the nesting area peaked over a 5 day period that started 4 days after the first nest was constructed (Fig.2.1). Turtles in a captive population were observed to nest from 31 May to 10 July (Farrell & Graham, 1991), showing a marked difference in the length of the nesting period from wild populations. thereby demonstrating the need for data from studies of wild populations.

The time of day when wood turtles nested during this study was different from almost all other published reports. Nesting was observed to be divided evenly between the early morning and mid to late evening (Fig. 2.2). Morning nesting has only been reported twice and both of these observations were during studies in captivity, which was considered to be the cause of the morning nesting (Pallas, 1960; Farrell & Graham, 1991). Morning nesting was considered an unusual event in Michigan and New Jersey (Harding & Bloomer, 1979) and most nesting of the wood turtle has been observed in the evening (Ratner & Anderson, 1978; Combs, 1971; Brooks *et al.*, 1992; Harding, 1990). It is possible that females are simply using a time of day that is not too hot (or sunny) as they are in an exposed situation for up to 4 hours and once started there is no hope of moving to thermoregulate. Turtles have been shown to avoid direct sunlight or only remain exposed for a short time when the air temperature is high (Ernst, 1972). Nesting in this study was stimulated by rain and similar behaviour was observed by Pallas (1960) but, Harding and Bloomer (1979) believe this to be unusual for this species. It could be that the nesting substrate is loosened by rain or that a turtle may better be able to select an optimal nest site, e.g. one that is not flooded, has sufficient drainage and moisture retention, heat retention, and/or some other important characteristic.

Movement Patterns

The use of telemetry equipment supplied information on the movement of female wood turtles to the main nesting area. Observations of turtles moving up to 3700 m to the nesting area were surprising, as many nesting areas exist within the studied area. During studies of home range and activity patterns of the wood turtle, others have noticed that females sometimes travel long distances to nesting areas (Harding, 1990; Quinn & Tate, 1991). Long distance movements to nesting areas has been recorded for other species of turtles e.g. soft shell turtles (*Trionyx muticus*), Blanding's turtles, snapping turtles (*Chelydra serpentina*), and slider turtles (*Pseudemys scripta* (*troostii*)) (Cagle, 1950; Plummer & Schirer, 1975; Obbard & Brooks, 1980; Congdon *et al.*, 1983; Morreale *et al.*, 1984). It appears that long distance movements to suitable nesting areas is not uncommon among freshwater turtles, however, most studies have concluded that this is probably because suitable nesting areas are not available or are limited. Our observations of females passing by nesting areas that were used by other wood turtles suggests that some other mechanism is involved. It is possible that females are selecting the best nesting site with optimal physical conditions, not simply any site (Congdon *et al.*, 1983; Morreale *et al.*, 1984). Porter (1972) suggested that communal egg-laying probably occurred because a particular area is especially favorable for egg deposition and development. Also, it could be that they are returning to their place of birth.

During a home range experiment, Carroll & Ehrenfeld (1978) concluded that wood turtles were capable of homing for distances up to only 2 km but, from our observations, turtles are capable of homing over greater distances and similar results have been obtained in other studies (Harding & Bloomer, 1979; Quinn & Tate, 1991). A study in Ontario suspected that wood turtles may be migratory based on the movement patterns of one female turtle (Quinn & Tate, 1991). The female movement patterns we observed were similar to migration patterns. Migration can be defined as a spatial and temporal movement that is repeated in space and time. Using the above definition of migration, wood turtles are migratory, as has been observed for snapping turtles based on movement patterns associated with their nesting (Obbard & Brooks, 1980).

Nest site fidelity

Wood turtles also exhibited nest site fidelity. Of the turtles that nested in the first year, 67 % returned the following year and nested. Only one turtle that used the main area in 1996 was observed to use an alternate area in 1997. Of the turtles that did not return to nest it was not known whether they were gravid, and none of them were observed on alternate nesting sites. Only one other study indicates that wood turtles may show nest site fidelity (Harding, 1990), although some other studies suggest that the same turtles were sometimes observed at the same nesting area (Harding & Bloomer, 1979; Quinn & Tate, 1991, Foscarini, 1994). Thus, fidelity to a nesting site occurs in at least some wood turtle populations. Diamond back Terrapins, snapping turtles, Blanding's turtles, and painted turtles show nest site fidelity (Burger, 1977;

Obbard & Brooks, 1977, Congdon *et al.*, 1983; Christens & Bider, 1987). Obbard and Brooks (1977) suggested that this could indicate a shortage of nest areas but, this may involve selection of the best nesting habitat available (this study, Porter, 1972; Congdon *et al.*, 1983; Morreale *et al.*, 1984). Since wood turtles and other turtle species exhibit nest site fidelity, conservation of these species should involve identification and protection of nesting areas.

Reproductive output

A minimum of 65-70 % of the female population was gravid per year. This is high compared to other freshwater turtles: 48 % of Blanding's turtles (Congdon *et al.*, 1983), 57 % of ornate box turtles (*Terrapin ornata*) (Doroff & Keith, 1990), and 70 % of painted turtles (Moll, 1973; Tinkle *et al.*, 1981).

If a female turtle's reproductive output is limited by the amount of energy it can contribute to nesting activities without jeopardizing overall survival (Lindsey, 1966; Galbraith *et al.*, 1989; Brooks *et al.*, 1992) a larger turtle should be capable of greater reproductive output. Studies on other species of turtles have found that a correlation exists between size of a turtle (CL) and the number of eggs laid, with larger turtles producing larger clutches (Cagle, 1944, 1950; Einem, 1956; Tinkle, 1961; Powell, 1967; Tinkle *et al.*, 1981; Gibbons *et al.*, 1982; Congdon *et al.*, 1983; Congdon & Gibbons, 1985; Graham & Forsberg, 1986; MacCulloch & Weller, 1988; Galbraith *et al.*, 1989, Congdon & van Loben Sels, 1991; Rowe, 1992). It has been suggested that females optimise energy use and larger turtles a lot more energy to reproduction, resulting in increased clutch size. However, this trend has not been observed in all species of turtles (Cagle, 1954; Gibbons & Tinkle, 1969; Ernst, 1971; Tinkle *et al.*, 1981, Congdon & Gibbons, 1985). No significant correlation between

CL, PL, or age (# of annuli) with clutch size was observed during this study (Table 2.3). There was a positive but insignificant relationship between both CL and PL with clutch size. These results are different from an Ontario study that found carapace length to be significantly positively correlated with clutch size for wood turtles (Brooks *et al.*, 1992). It is possible that the relationship between CL and clutch size was obscured in the current study because of the significantly different mean clutch sizes observed among years and the large differences between years for an individual's clutch size. However, this seems unlikely since a large sample size was obtained and all body sizes were represented in the sample.

Since wood turtles increase in size (CL) at locations with decreasing numbers of frost free days (Daigle, 1997; see section 1 of thesis), it may be that there is a concurrent trend producing more eggs per clutch with increase in size (Ross *et al.*, 1991). In Table 2.5, we summarize published data from 9 locations. Clutch size does not increase with increased size (CL) when compared among populations ($r= 0.53$, $p>0.05$), contrary to what was expected. This suggests that there is no increased fecundity in the form of larger clutches for larger wood turtles. However, turtles which nested in both years of this study were significantly larger than turtles that were only observed to nest in one year (Table 2.2). Therefore, increased fecundity may in fact be gained by larger turtles. In general, since turtles are larger in this population compared to populations from more southern localities (see section 1 of thesis), a greater proportion may have the necessary reserves to reproduce yearly. This factor would have to be weighed against the increased amount of reserves required by turtles that hibernate longer in regions of longer winters, which could be decreasing overall reproductive potential as body reserves may be depleted. However, before any conclusions can be made regarding increased fecundity for larger females, long-term studies that account for variability among years with large sample sizes are necessary.

Nesting Behaviour

Our description of nesting behaviour is similar to that of Harding and Bloomer's (1979) but some key things are different. One of the most important observations is that turtles were observed to stage in the area around the nesting site for an average of 3 days before actually nesting, and some individuals for as many as 9 days. During this period they made several visits into the nesting area apparently looking for appropriate nesting sites and/or conditions and making numerous trial holes. Similar observations of staging were obtained for slider and Blanding's turtles (Cagle, 1950; Congdon *et al.*, 1983). Description of the nesting behaviours was similar to previous reports (Harding & Bloomer, 1979; Pallas, 1960; Combs, 1971) but some differences were apparent. Observation of sand sniffing has been reported for many species of turtles but it is not known what role it plays. It has been suggested that it is thermosensory and/or chemosensory in function (Stoneburger & Richardson, 1981; Linck *et al.*, 1989). In all of our observations the turtle excavated a body pit with her front legs and entered it before beginning to dig the nest chamber with her hind feet. Similar behaviour was observed for turtles nesting on soft substrates but not on hard substrates in New Jersey (Farrell & Graham, 1991). No other studies report the use of body pits. Both Pallas (1960) and Harding and Bloomer (1979) observed the head to be retracted and the posterior carapace to be raised as each egg was laid. We observed only retracting of the head as each egg was laid and the carapace was raised shortly after so that a foot could be inserted into the nest cavity to manipulate the egg in the chamber. This is important when attempting to count the number of eggs laid because each time a turtle removes or inserts a foot into the hole the posterior carapace is raised and then lowered. Only the sudden retraction of the head provides an accurate indication (from a distance) of the number of eggs laid, as has been observed for Blanding's turtles (Linck *et al.*, 1989).

Staging

While staging turtles spent a lot of their time basking, presumably to increase their body temperature and thus speed up or aid the development of eggs. Staging turtles tended to use natural habitats that were unaltered by humans. An area inside the staging area had been cleared of an alder thicket (beside a cottage) and no turtles were observed in this clearing, while 28 females were observed in the adjacent areas where the vegetation had been unaltered. Furthermore, several immature turtles were identified in this same area of natural vegetation and it was the only place that after-hatch-year turtles (age class one) were observed. This suggests that wood turtles are sensitive to unnatural habitats on their staging grounds, even though they are using human made clearings for actual nesting sites. Sixty-three different female turtles used the staging grounds and/or nesting area during the two years of the study, which accounts for 76 % of the female turtles observed during the study (n=83). Since the staging area and primary nesting area is a small area, development or poaching could potentially have catastrophic effects on this population.

Clutch size

The largest clutch for a wood turtle, 20 eggs, was recorded. Gammons (1871) reported 18 but, Carr (1952) rejected this account claiming it to be some sort of hallucination because of the many odd behaviours described. The largest accepted clutch size for a wood turtle was 18 eggs, in a Michigan population, but none of the eggs proved to be fertile (Harding, 1977). Harding (1977) questioned whether a relationship existed between egg fertility and clutch size. We have no data to suggest that there is such a relationship but, all 20 of the eggs in the large clutch were fertile; 17 hatchlings emerged from the nest, and the other three died from unknown causes late in the incubation period. Overall, very few eggs were found to be infertile (n=12, 0.02%) during this study and there were many large clutches (13-15 eggs).

Predation

No mammalian predation of nests was observed at the main nesting area during both years of the study. Typically, mammalian predation destroys up to 100 % of wood turtle nests (Ratner & Anderson, 1978; Harding & Bloomer, 1979; Harding, 1990; Brooks *et al.*, 1992; Buech & Connors, 1992; Tuttle & Carroll, 1997). It is not known why nests at the main nesting area were not depredated since some nests at other sites were. It has been suggested that turtle nest predation increases near ecological edges (Temple, 1987). As all nests were within 25 m of an edge we should have expected predation, but there was none. It may be that predators have not yet learned where this food resource is or how to obtain it. Snow's (1982) observation of a single skunk moving between two nesting areas separated by almost 2 km and preying on nests supports the theory of a predator having to learn where and when to look for food. Raccoons, red foxes, skunks, as well as feral and domestic cats and dogs, all species commonly associated with turtle nest predation, were observed at the nesting area.

Even though no mammalian predation was observed, arthropods seemed to be playing a role as predators of wood turtle eggs. Ants were suspected of causing the failure of one nest in each year of the study. Ants have been recorded to prey upon eggs of box turtles (*Terrapin carolina carolina*) (Ewing, 1933), snapping turtles (Hammer, 1969), diamond back terrapins (Burger, 1977), as well as other species of turtles. Also, a large number of nests were preyed upon by fly larvae. The mechanism of this predation is not yet fully understood. It is possible that fly larvae were scavenging embryos that died during their development, and if this is the case, it is not predation but, fly larvae may potentially have been the cause of death. Almost 50 % of all nests had fly larvae associated with them but not all eggs in a nest were infected, therefore it is possible for some hatchlings to emerge from infested nests. Fly larvae have been identified as infesting other turtle eggs (Muller, 1921; Acuña-Mesén & Hanson, 1990) and it is believed that the flies act as predators not scavengers (Iverson & Perry, 1994). Flies may play a significant role as an inconspicuous predator of turtle eggs across North America.

Incubation period

The dates of hatching, mid-August to early October, were similar in both years of the study even though the nesting season started slightly later in 1997 (Fig. 3). The average incubation period was significantly different in both years, 87 and 77.5 days for 1996 and 1997 respectively. Wood turtle eggs gathered during the course of other studies and incubated under artificial or semi-natural conditions hatched between 47-71 days, most around 60 days (Ratner & Anderson, 1978; Harding & Bloomer, 1979; Brewster & Brewster, 1991; Farrell & Graham, 1991; Harding, 1990). Incubation periods in our study are similar to those of a recent study in New Hampshire where the incubation period averaged 76 days with a range of 66-82 (n=8) (Tuttle & Carroll, 1997). The average time taken for incubation is similar for both populations although the range is greater in our population. A study of diamond back terrapins (*Malaclemys centrata*), found that eggs incubated under controlled conditions at 29.5 °C and 26 °C hatched at essentially the same time and concluded that development did not fluctuate with the temperatures examined (Cunningham, 1939). Clutches of the slider turtle incubated at 30 °C hatched between 68-70 days, and at 24 °C hatched between 61-79 days. The time required for hatching was approximately the same although the range was greater at cooler temperatures (Cagle, 1950). This is essentially the difference observed between our population and Tuttle & Carroll's (1997) New Hampshire population. An increased range over which eggs hatch could have an effect on the hatching success, especially in northern populations, as some eggs may not have enough time or degree days to complete incubation (Cagle, 1954; Christiansen & Moll, 1973).

Hatchling success

Hatchling wood turtles are a uniform light brown (head, legs and shell) and almost circular (Table 2.4) with a tail almost as long as the CL (see also Harding & Bloomer, 1979). They lack the orange and black coloration of the adults. The size of hatchlings was similar to that previously described by Harding and Bloomer (1979) and Tuttle and Carroll (1997). Cohort hatchlings almost always emerged from a nest on the same day. This may be an adaptive strategy to avoid predation, as has been suggested for other species of turtles (Congdon *et al.*, 1983; Christens & Bider, 1987). The first hatchling out creates an opening through which nest odors may escape thereby possibly attracting predators to what remains in the nest. Nest success of 76 and 61 % in 1996 and 1997 respectively, was lower than expected. The resulting hatchling success was 62 and 52 % for 1996 and 1997, respectively. Eggs incubated under laboratory conditions had a hatching success of 74 % but, 12 % of eggs were infertile which is higher than we observed (Farrell & Graham, 1991). Hatchling success of 77 % has been reported for wood turtles in New Hampshire for nests protected from predators (Tuttle & Carroll, 1997), which is higher than in our population. The lower than expected nest and hatching success may have been due to insufficient time and degree days to complete incubation and/or predation by fly larvae. Since turtle eggs are dependent on environmental conditions such as temperature and rainfall to meet incubation requirements, differences in yearly climatic factors could also have a significant influence on hatching success (Moll, 1979). It has been suggested that hatchling recruitment in wood and snapping turtles in northern-eastern Ontario is decreased because embryos do not have sufficient time to complete incubation in some years (Obbard & Brooks, 1981; Brooks *et al.*, 1991; Brooks *et al.*, 1992). Since our study is at the northern limits of the wood turtles' range it is likely that some nests do not complete incubation simply because of insufficient time and degree days.

In northern portions of a species' range, overwintering in the nest by hatchling turtles may be an adaptation for survival (Carr, 1952). No evidence of hatchlings overwintering in the nest was observed during this study. In nests that were left to overwinter (1996) only two nests had hatchling turtles in them and all were dead. All other nests had whole eggs that had not completed embryogenesis or had rotting eggs with fly larvae associated. In 1997, we determined that live hatchlings were present in a nest at the beginning of winter but were soon found dead, probably because of the extreme cold and lack of any insulating snow layer. In no part of this species range have hatchlings been observed to successfully overwinter in the nest (Harding & Bloomer, 1979; Harding, 1990; Brooks *et al.*, 1992; Ernst *et al.*, 1994), although none of these studies state whether this was tested or how they came to this conclusion. Our observation of turtles hatching and being found dead in the nest in the spring corresponds to the observations of Obbard and Brooks (1981) for snapping turtles in a northern region. Unsuccessful overwintering in the nest has been observed for many species of turtles in northern regions of their distribution (Breckenridge, 1960; Hammer, 1970; Obbard & Brooks, 1981; this study), suggesting that this strategy is not utilized by all species. The shortened growing season for northern populations, coupled with unsuccessful overwintering in the nest, are probably factors limiting the northern distribution of wood turtles and possibly other species of turtles.

Conclusion

In summary, knowledge has been contributed to wood turtle nesting ecology, a subject on which little information had previously been available. Some turtles migrated over 3 km to a nesting area. Female turtles 'visited' the nest area for over 3 days before nesting and during this time utilized a 'staging area.' While on the staging area, turtles used natural areas primarily (unaltered by humans). Turtles congregated at a 'preferred' nesting area and nesting was relatively synchronous.

These aspects have important conservation and protection implications because they demonstate that a relatively small area is utilized by a large proportion of the turtles within a population for a limited period of time. These characteristics render this species vulnerable to habitat alteration and destruction, development, and/or poaching. Guidelines for conservation of the wood turtle throughout its range will be facilitated by the contribution of this nesting and nest site data to already existing knowledge.

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Table 2.1. Body measurements of female wood turtles observed to nest and those not observed to nest during 1996 and 1997.

	Number	Carapace length (mm)	Plastron length (mm)	# 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, $t=3.00$, $p<0.01$.

Table 2.2. Body measurements of female wood turtles observed to nest in only 1 year and 2 consecutive years, 1996 and 1997.

	Number	Carapace length (mm)	Plastron length (mm)	# 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

Note: Values are given as the mean ± standard deviation (range).
* Differences between categories is significant, $t=2.87$, $p<0.01$.
** Differences between categories is significant, $t=2.32$, $p<0.01$.

Table 2.3. Pearson correlation coefficients (*r*) for comparisons of carapace lengths, plastron lengths, and number of annuli with clutch size among 56 wood turtle nests for which measurements of the female were known.

	Carapace length	Plastron length	# of annuli
Clutch size	0.50	0.56	0.06

Note: All comparisons indicate no significant difference ($p>0.05$).

Table 2.4. Body measurements of hatchling wood turtles from 1997.

	N	Carapace length (mm)	Carapace (mm)	Plastron length (mm)	Weight (g)
hatchling	144	33.6 ± 0.15 (29.4-37.5)	31.7 ± 0.17 (25.2-34.6)	28.5 ± 0.15 (24.4-32.3	7.4 ± 0.91 (4.9-9.3)

Note: Values are given as the mean ± standard deviation (range).

Table 2.5. Comparisons of clutch size and mean carapace length of female wood turtles among nine locations.

	Carapace length (mm)	Clutch size			Source
		n	Mean	Range	
Algonquin Park, Madawaska (45°N)	203	21	8.8	3-13	Brooks *et al.* 1992
Quebec (46°N)	201	56	10.2	5-20	Present study
Wisconsin (44°N)	187	11	11.0	--	Ross *et al.* 1991
Virginia (39°N)	186	10	9.9	--	J.F. McBreen *
Michigan (46°N)	182	--	10.4	5-18	Harding & Bloomer 1979
Ontario (43°N)	181	26	8.0	5-11	Foscarini 1994
New Hampshire (43°N)	172	9	7.8	6-9	Tuttle & Carroll 1997
New Jersey (41°N)	171	21	8.5	5-11	Farrell & Graham 1991
New Jersey (41°N)	165	--	8.0	5-11	Harding & Bloomer 1979

Note: Approximate latitudes are estimated from locations provided in the sources.

* Personal communication in Ross *et al.*, 1991.

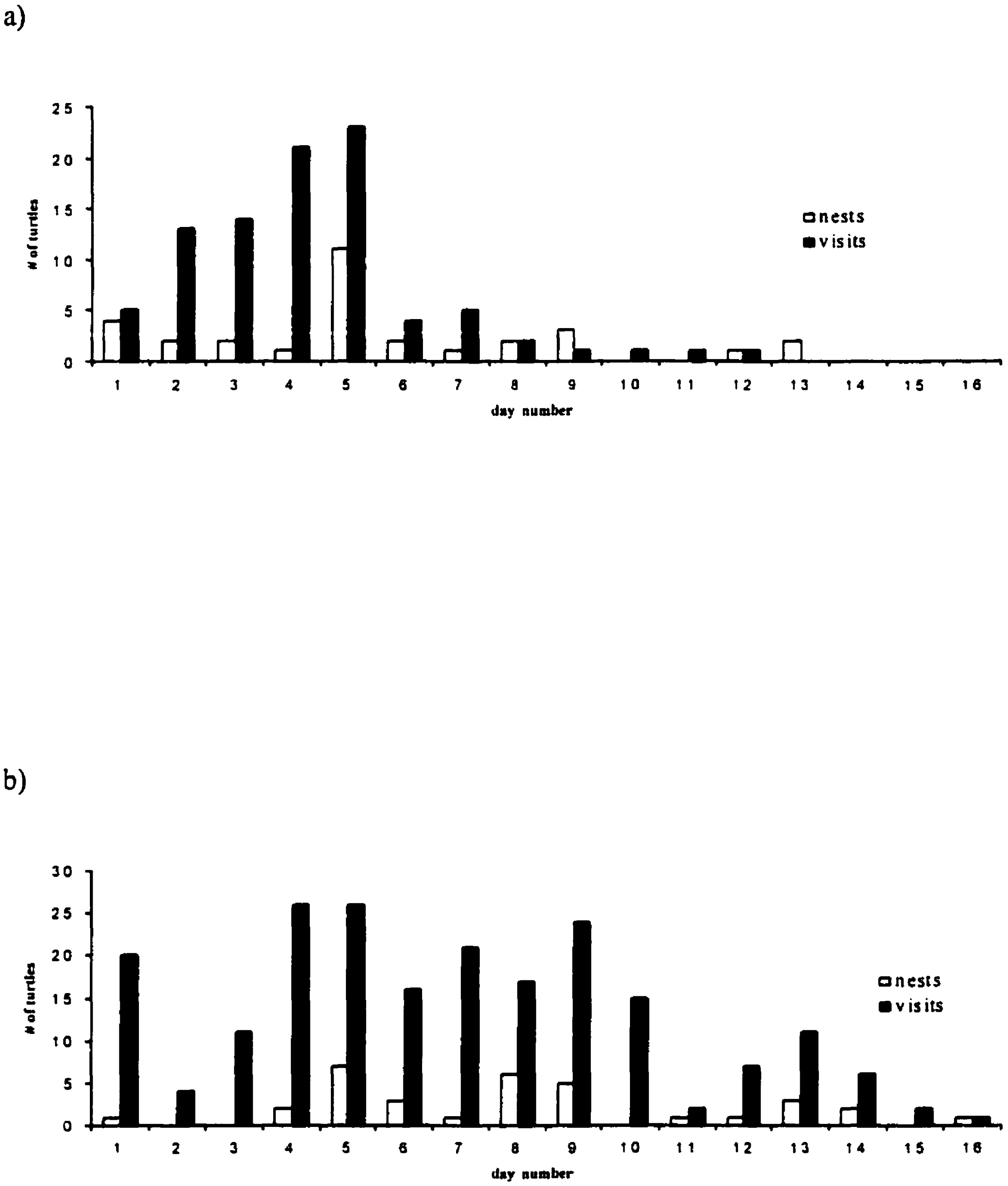

Figure 2.1. Number of wood turtles that nested and visited the primary nesting area in relation to the first day a nest was made a) 1996, and b) 1997.

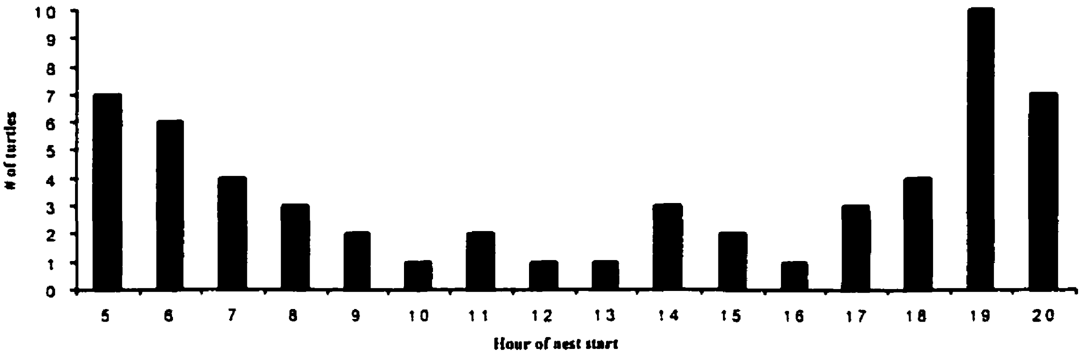

Figure 2.2. Time of day at which turtles started nest building at the primary nesting area and number of turtles for each hourly category in 1996 and 1997 (n=57).

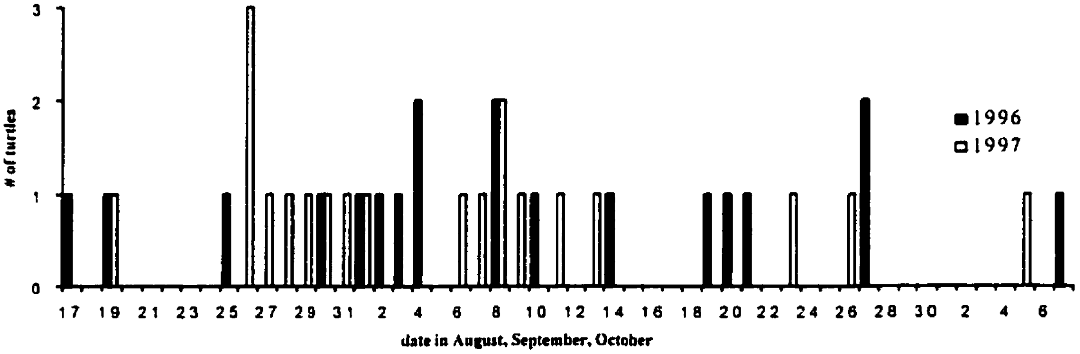

Figure 2.3. Dates and numbers of nests hatching per day in 1996 and 1997 at primary nesting area.