THE NATURAL HISTORY OF A NORTHERN TURTLE, CHRYSEMYS PICTA BELLII (GRAY).

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ABSTRACT

Comparisons of life history patterns within a widely distributed species can reveal the ecological factors that control abundance and distribution. The turtle is an example of a long-lived, iteroparous organism that experiences delayed maturity and heavy mortality at early life stages. In this 2-year mark-recapture study, I estimated individual growth, reproductive success, and age-specific survivorship of the western painted turtle near the northern limit of its range.

In comparison with southern populations, growth rates were lower and individuals attained larger sizes. The slower growth rate delayed sexual maturity in northern females. Males matured earlier than females. Females produced larger but fewer clutches when compared with most other parts of the geographical range. In general, females did not produce clutches every year. Reproductive potential for this population, near the northern limit of the range, was therefore reduced.

Age-specific survivorship in this population was fairly stable after the turtles left the nest. There were more females than males in the population and recruitment was low in all but one of the six lakes within the study area. Levels of predation on nests were very high during years of high reproductive activity. Predation on adults was also higher in such years; most of those taken were probably nesting females.

Level of blood lactate in overwintering turtles was measured as a potential factor limiting northern distribution. Lactate concentrations rose 3 to 24 times normoxic levels after 3 months of ice cover. This was less than levels reported for animals in laboratory simulations of hypoxic hibernation. As the turtles were found on the lake bottom rather than buried in the mud, it is likely that this species overwinters under less hypoxic conditions than previously supposed. Most hatchlings remained in the nest over the winter. While this is a successful behavior in other parts of the geographical range, most hatchlings in this population failed to survive. Distributional limits may therefore be set by hatchling rather than adult overwintering survival. There was indirect evidence that some hatchlings emerged in the fall.

When compared with southern populations, this northern population showed the following responses to climate: slower growth, reduced annual reproductive potential, and high overwintering mortality of hatchlings. However, it appears that overwintering in adults is less an obstacle than previously thought.

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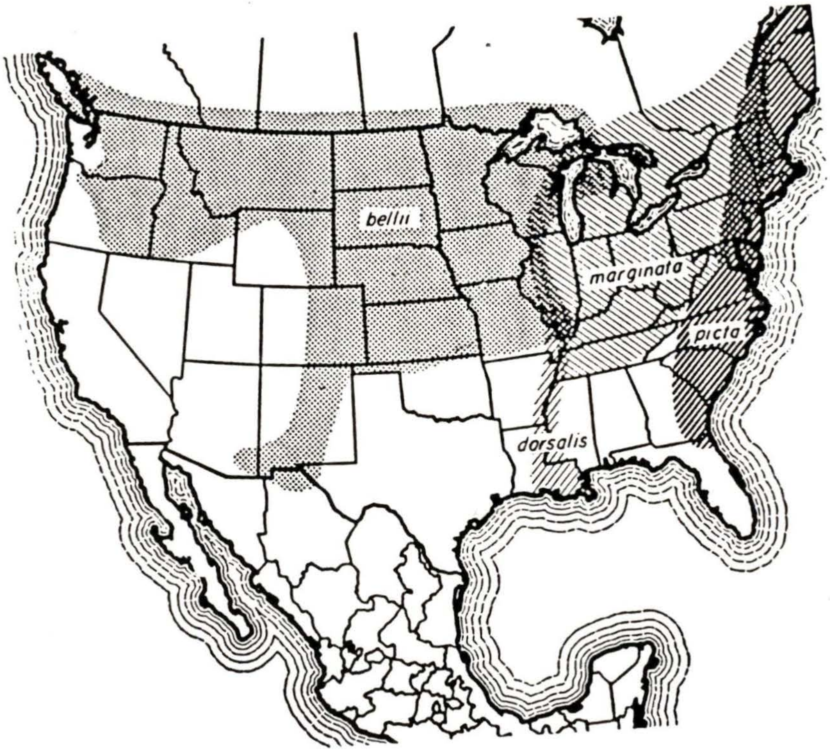
INTRODUCTION

Increasing latitude is associated with decreasing annual temperature and photoperiod. These environmental factors affect the physiology and ecology of an organism by decreasing length of growing season, limiting food resources, restricting reproductive periods, and increasing overwinter mortality. A species represents a limited set of capabilities of response to environmental variation. Comparisons of northern and southern populations within species may therefore allow definition of the domain of possible responses, separate from phylogenetic effects.

The most widespread and abundant of North American turtles, the painted turtle (*Chrysemys picta*, Figure 1), holds considerable promise for the investigation of reactions of ectotherms to varying environments. Northern individuals in this species tend to: (1) attain larger sizes, (2) grow faster, (3) be more carnivorous, (4) mature later, and (5) produce larger and fewer clutches per year (MacCulloch and Secoy 1983). These characteristics may have important implications for population dynamics and life history evolution.

One of the possible factors limiting the northern distribution of an ectotherm is overwintering survival. Northern turtles are assumed to hibernate under severely hypoxic conditions buried in the mud at the bottom of ice-covered lakes (Ernst and Barbour 1972, Gregory 1982). These conditions demand reliance on anaerobic metabolism, which results in lactate acidosis. Physiological responses to cold hypoxia have been documented in the laboratory (Jackson and Ultsch, 1982; Ultsch and

Figure 1. Distribution of the subspecies of *Chrysemys picta*. from Carr 1952.


bellii
marginata
picta
dorsalis

Jackson, 1982a,b; Ultsch *et al.* 1985; Gatten, 1987; and Jackson, 1987) and show that turtles are unequaled among vertebrates in their ability to tolerate extreme hypoxic acidosis. The values attained in the laboratory are evidently near the tolerance limit for turtles; therefore, turtle distribution may be limited by low availability of oxygen due to persistence of ice cover. However, the existence of such physiological obstacles to overwintering survival has not been established in the wild. In addition, hatchlings are reported to overwinter in the nest at northern latitudes (Cagle 1950, Bleakney 1963, Gibbons and Nelson 1978, Ewert 1979, Christens and Bider 1987). Overwintering mortality of hatchlings in the nest due to freezing is therefore also a possible limiting factor.

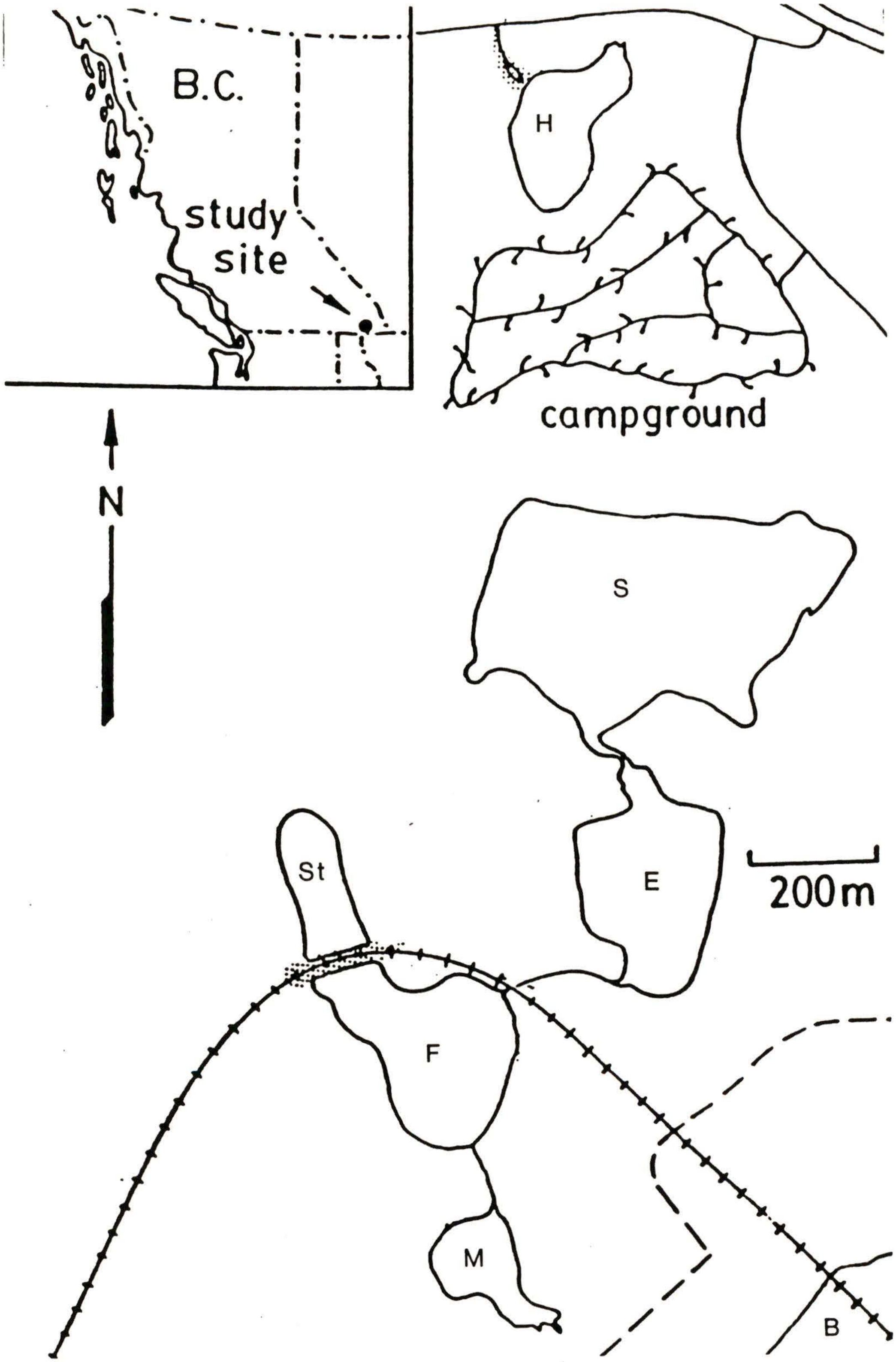
The major objectives of this study were: (1) to document major features of the life history and ecology of a northern population of the painted turtle in southeastern British Columbia, (2) to compare those features with southern populations, and (3) to describe overwintering behavior of turtles and determine lactate levels in the wild for comparison with published data from laboratory simulations of hibernation. A large number of animals in the population had previously been marked (Macartney and Gregory 1985), providing an opportunity to obtain more long-term data on survivorship and growth.

METHODS

Study Site

The study site consisted of six kettle lakes in Kikomun Creek Provincial Park in southeastern British Columbia (Figure 2), located in the Rocky Mountain Trench (lat. 49^{o} 15’, long. 115^{o} 15’, elevation 760 m). Mean daily temperatures for 1941 - 1970 are - 5 to - 10^{o}C in January and 18^{o}C to 20^{o}C in July (Farley 1979). Annual precipitation is 30 to 40 cm with 10 to 13 days of measurable precipitation in January and 3 to 5 days in July (ibid.). The lakes are all spring-fed, the water level depending on a nearby dam on Elk River. During the summer, there is much human activity in the campground and around the beaches. Hidden Lake (depth 7 m) is separated from the rest of the lakes by the campground. Surveyor’s is a deep lake ($>$10 m) with two beaches and heavy recreational use. Engineer’s is shallower (2 m) and is readily accessible by canoe. A channel about 1 m deep connects Surveyor’s and Engineer’s Lakes in times of high water. The remaining three lakes are less easily accessible and rarely visited by the public. Shallow, partially overgrown channels connect Engineer’s and Fisher Lakes (depth 2 m) and Fisher and Muskrat Lakes (depth 1.5 m). Fisher and Stink Lakes (depth 1.5 m) were once continuous but have since been separated by a now disused railway grade. There is a water-filled conduit that allows turtle movement between the two lakes. A stream flows southwest from Stink Lake to a reservoir on a ranch within the park boundaries.

Figure 2. Map of study site. The lakes are Hidden Lake (H), Surveyor's Lake (S), Engineer's Lake (E), Stink Lake (St), Fisher Lake (F), Muskrat Lake (M), and Baynes Lake (B - outside the park). There is an abandoned railway grade running between Stink and Fisher Lakes; a conduit joins the two lakes.


B.C.
study site
campground
H
S
E
St
F
M
B
N
200m

The lakes all have soft mud bottoms partly or mostly covered by Stonewort (*Chara* sp.). The mud can be penetrated easily by hand to about 0.7 m. The shallow littoral zone round the lake perimeter is primarily composed of Spike Rush (*Eleocharis* sp.) and Cattail (*Typha latifolia*).

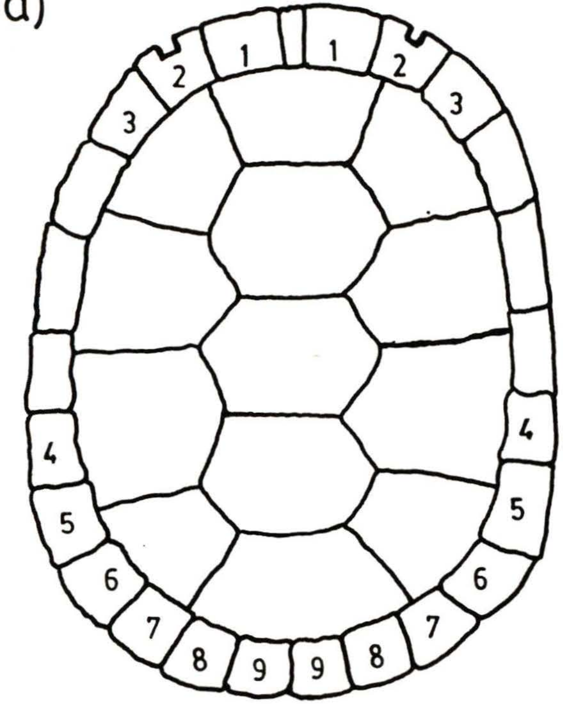
General Sampling and Testing Procedures

Turtles were captured during the summers of 1987 (May 9 to September 9) and 1988 (April 26 to September 29). At the beginning of each day of sampling, usually around 1000 h Mountain Daylight Time (MDT), I recorded water temperature (depth 30 cm) and shaded air temperature at water level. I visited lakes on most days that weather permitted. In 1987, each lake was visited in turn during four sampling periods of approximately 1 month each. This was done to detect differences in timing of reproductive events among the lakes. Lakes were visited in two rounds of sampling during 1988. Clear days were preferable as overcast skies made seeing the turtles underwater difficult. I captured turtles from a canoe using a long-handled dip net or by snorkeling.

I marked individuals by filing notches in marginal scutes (Figure 3) following the existing code (Macartney and Gregory 1985) which was based on Cagle's (1939) method. At the time of capture, I recorded individual mark, sex, plastron length, and length of annuli on pectoral and abdominal laminae (Figure 4). Sex was determined by secondary sexual characteristics (foreclaw length and length and thickness of tail, Figure 5). Animals smaller than the smallest identifiable male were classified as juveniles; males are smaller than females (Carr 1952). Plastron length is the straight line length of the lower shell along the midline (Peters 1964) and is the common

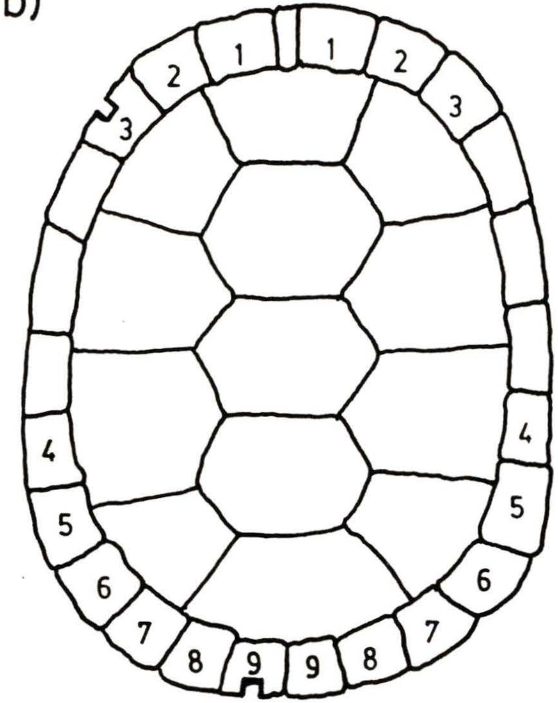
Figure 3. The carapace of a painted turtle showing marking scheme (from Macartney and Gregory 1985).

a)



2-2

b)



9,3-0

Figure 4. Body measurements taken from turtles at each capture. (a) plastron length (PL) (b) length of right pectoral lamina (RPL) showing annuli (annulus present at hatching = 0 and annuli formed during subsequent years). Plastral laminae shown are: gular (g), humeral (h), pectoral (p), abdominal (ab), femoral (f), and anal (an). From Macartney and Gregory (1985).

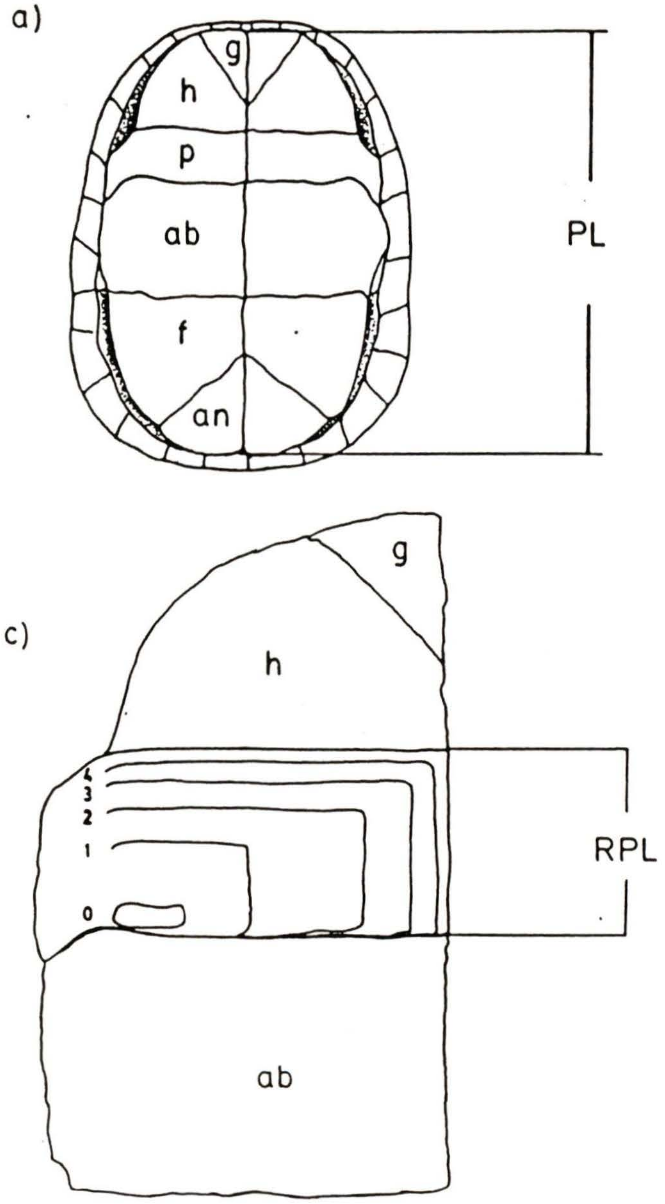
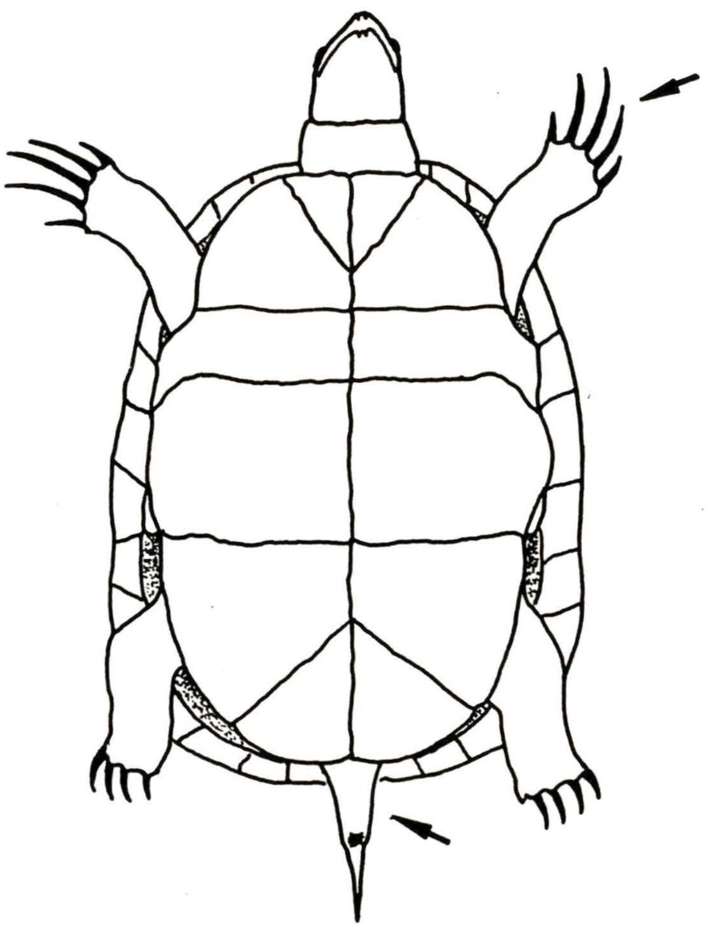
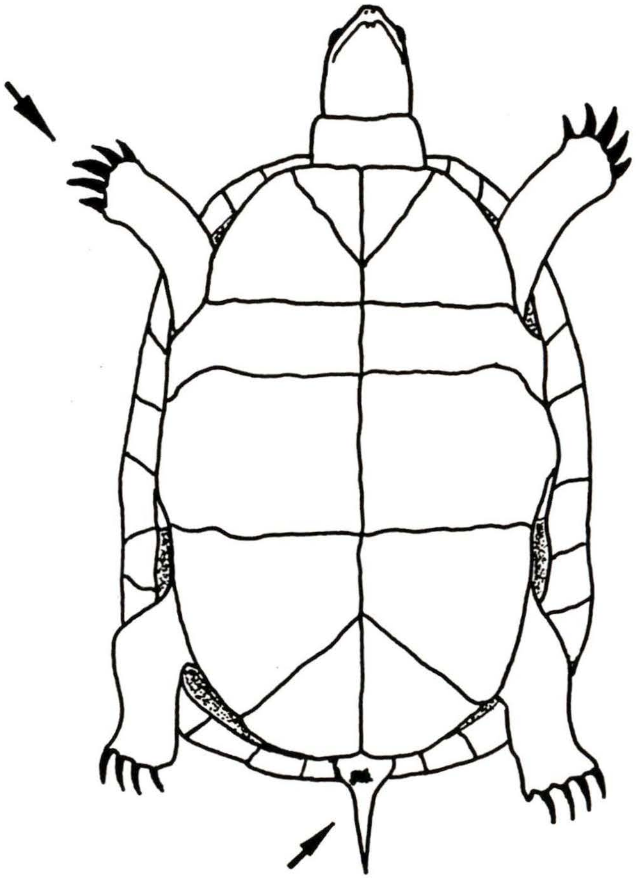

a)
g
h
p
ab
f
an
PL
c)
g
h
4
3
2
1
0
RPL
ab

Figure 5. Secondary sexual characteristics of male and female painted turtles. Males have longer foreclaws and cloaca is located beyond the lower margin of the plastron. The tail in the male is longer and the base of the tail, where the penis is located, is thicker.



MALE



FEMALE

measure of size in pond turtles (Cagle 1950, Cagle 1954, Gibbons 1967, Gibbons 1968a, Bayless 1973, Wilbur 1975a, Whillans and Crossman 1977, Gibbons *et al.* 1981, Hart 1982). Pectoral and abdominal laminae lengths were the maximum distance measured at the midline of the plastron. Annuli were measured at the midline from the posterior edge of the plate to the corner of the annulus.

At the time of measuring, I sprayed a spot of paint on the carapace to avoid repeatedly capturing the same individuals during a short time period. The paint wore off within 2 weeks or with ecdysis.

In all statistical tests (described below), differences were considered to be significant at $a = 0.05$.

Population composition

I determined sex composition separately for each lake. Except between Engineer's and Surveyor's Lakes, interlake movements were few; animals were assigned to the lake of original capture. Engineer's and Surveyor's Lakes were combined because park visitors frequently caught turtles in Engineer's Lake and released them in Surveyor's Lake. Deviations in sex ratio from 1:1 in each lake and all lakes combined were tested by chi-square goodness-of-fit test. Differences in size between sexes and among lakes were tested by 2-way analysis of variance (ANOVA).

Survivorship

I calculated minimum 2-year survivorship for males, females, and juveniles as the proportion of animals marked in 1985 that were recaptured in 1987 or 1988. Survivorship is therefore a minimum value as it indicates the last capture of an individual and not its death. A contingency table for number of recaptured and not recaptured individuals was used to test for differences between sexes.

I determined minimum survivorship by size class for females and juveniles. Animals were assigned to age groups using the growth curve of length on age (see below) and the plastron length in 1985. As juveniles included males and females, I assumed that male and female survivorship was similar at this stage. Because juveniles had already been included in estimates of female survivorship, male survivorship was not calculated. One-year survivorship estimates (s_x) were calculated as the square root of 2-year survivorship estimates. This was based on the assumption that survivorship was similar for the 2 years between sampling. Rate of mortality (q_x) was calculated as $1 - s_x$. Mortality rate (q_x) was used to calculate the number of individuals that would be alive at the beginning of each yearly interval starting with 1000 individuals at time zero (l_x). Differences in minimum survivorship for each age class were compared graphically by semi-log plot.

Survivorship of turtles was grouped for the three lakes with heavier human use (Hidden, Surveyor's and Engineer's Lakes) and the three lakes that were less often visited (Stink, Fisher's, and Muskrat Lakes). This was done to try to detect effects of human interference. A contingency table was used to compare minimum survivorship between these two groups. A Yates correction for continuity was used to correct for 1 degree of freedom.

I collected carcasses and shells of dead turtles and determined sex where possible. Any dead turtles were saved and were deposited in the collection of the University of Victoria. In 1987, I checked nests for frequency and type of predation. Several nests were excavated the following spring to determine overwintering survivorship of hatchlings. Apparently dead hatchlings from nests were left at room temperature for 24 hours to be certain that they would not revive.

Growth

I used average air temperature data (Environment Canada) for nearby Elko, B.C. (lat. 49^{o} 17', long. 115^{o} 7', elevation 940 m) combined with reported threshold temperatures of activity (10^{o}C) and growth for this species (Cagle 1954, Sexton 1959, Musacchia and Grundhauser 1962, Brattstrom 1965, Ernst 1971c, 1972) to estimate length of growing season.

Growth curve for age-length data

I determined growth from increase in plastron length. Yearly growth interval data were calculated separately for males and females. Data from 1987 and 1988 were combined with plastron lengths measured in 1985 (Macartney and Gregory 1985) to give three different intervals of growth: 1985 to 1987, 1985 to 1988, and 1987 to 1988. The models used to estimate growth parameters from length interval data (see below) require constant time intervals. To reduce differences in length of actual growth intervals, I used intervals of $365x$ +/- 30 days, where x is an integer representing number of years. Negative values of growth (usually less than 3 mm) were included because I assumed that measurements would err equally in either direction.

Walford plots (Walford 1946) were used to determine parameters of the von Bertalanffy growth model. Size at the end of the growth interval (l_{t+d}) was regressed on size at the beginning of the interval (l_t):

$$l_{t+d} = \mathtt{L_{inf}}(1 - k) + kl_t$$

The slope of the regression is k where $k = -e^{-K}$ (Ricker 1975) where K is the Brody growth coefficient. The intercept is $\mathtt{L_{inf}}(1 - k)$, where $\mathtt{L_{inf}}$ is asymptotic length or the length at which the regression line intercepts a line of 45^{o} form the origin ($l_t = l_{t+d}$). The use of the von Bertalanffy growth model was supported by the high correlation coefficients of the Walford regressions and the clear linearity of scatter plots.

The Brody growth coefficient measures the exponential rate of approach to asymptotic size. This is apparent from the rearrangement of the von Bertalanffy model:

$$l_t = \mathtt{L_{inf}}(1\text{-}e^{-K(t\text{-}to)})$$

to

$$\mathtt{L_{inf}} - l_t = ce^{-Kt}$$

where c is a constant. K is the exponential rate at which the difference between the asymptotic size and actual size ($\mathtt{L_{inf}} - l_t$) decreases (Ricker 1975). K is not expressed in units of length and time and is, therefore, not a true growth rate (ibid.).

Male and female regressions were compared by analysis of covariance (ANCOVA) for each time interval. I also used a repeated measures multivariate ANCOVA (Wilkinson 1986) to test differences between males and females that were captured in 1985 and recaptured both in 1987 and 1988. The dependent variables were plastron length in 1987 and 1988 with plastron length in 1985 as the covariate.

To estimate parameters of the von Bertalanffy model, data for the three intervals (1, 2, and 3 years) combined were used in a nonlinear regression model (Statgraphics 1986). By using all growth intervals, average growth rate over different growing seasons could be determined. The formula used was (Fabens 1965):

$$l_{t+d} = \mathtt{L}_{\mathtt{inf}} - (\mathtt{L}_{\mathtt{inf}} - l_t)e^{-Kd}$$

Growth curve for known-age animals

I could determine the age of some individuals by counting annuli on the right pectoral lamina. The age of an animal with several detectable annuli could be decided only if the innermost annulus was formed in the first, second, or (rarely) the third year. The large variation in length of annuli observed in animals of known-age indicated that counting from later annuli would give unreliable estimates of age. For this reason, I was reluctant to follow Sexton (1959) and use the average length of annuli observed in known-age animals to estimate the age of individuals with missing annuli.

If the age at first capture was known, I could include individuals that had lost annuli by adding the number of years since the first capture. Examination of recaptured individuals indicated that most animals added an annulus between the end of June and the beginning of July. The exceptions were smaller individuals which showed growth by the beginning of June. Therefore, an animal captured in the spring and recaptured during the spring of the following year would show one additional annulus. An animal captured during the late summer and recaptured the following spring would show no additional annulus. An animal captured in the spring and recaptured the following year in the late summer would show two additional annuli. By considering the time of capture, I could often decide the age by counting back from the number of annuli at recapture. To account for growth between deposition of annuli, turtles that had grown since the previous capture but had not yet added an annulus were accorded an additional half year.

These known-age animals were used to construct a growth curve. A nonlinear regression model (Statgraphics 1986) was used to estimate parameters of the von Bertalanffy growth model:

$$l_t = L_{inf}(1-e^{-K(t-to)})$$

where l_t is length, L_{inf} is asymptotic length, t is age, and t_o is a hypothetical age at which the length of the animal is zero (Ricker 1975). Because t_o in this context is biologically meaningless and was not required to compare growth curves, this was not attempted.

Reproduction

I used secondary sexual characteristics as indicators of sexual maturity in male painted turtles (Moll 1973, Hart 1982, MacCulloch and Secoy 1983). The size of sexual maturity in females was determined by the smallest gravid female (Moll 1973, Hart 1982). Palpation forward of the hind legs was used to determine the presence of oviducal eggs. X-ray photography (Gibbons and Greene 1979) revealed the number of eggs.

The records of capture of gravid and non-gravid females captured during the reproductive season were followed for 1985, 1987, and 1988. A reproductive season was defined as that time during which gravid females were present in the population. Individual records for females that were gravid in 1985 were compared with recapture records from 1987 and 1988. The same was done for 1987 and 1988.

The number of oviducal eggs was regressed on plastron length to determine if reproductive potential changed with size. In 1988, I marked X-rayed turtles with a numbered label on the carapace. I hoped to find a nesting individual that had been X-rayed to compare number of oviducal eggs to actual clutch size.

During the nesting season, I visited the lakes to search for nesting turtles. If a nesting female was found, I marked the location with spray paint. The next day, I checked to see if the nest had been completed. Completed nests were impossible to detect unless I had observed the female in the process of nesting and had marked the location. Nesting attempts were often abandoned and could be easily recognized by the round hole that remained. I marked the completed nests with buried coins so that I could locate the nest later with a metal detector. The nests were checked daily for predation.

In 1987, I unearthed two nests, counted the eggs, and measured egg length and width. In 1988, I excavated most nests and measured and counted the eggs. Depth of the top and bottom of excavated nests was recorded. Correlation analysis was done on egg length, egg width, and clutch size. Variation in egg length and width was compared among nests by ANOVA.

In the nests that I had excavated, I placed an observation port made of a short length of plastic tubing from the soil surface to the topmost eggs in the nest. I could then measure temperature using a digital thermometer with remote probe. Using a fibre optics scope or by eye, I could also observe the topmost eggs and determine time of hatching. I protected these nests from predation by covering the site with chicken wire nailed into the ground. I left some nests untouched to add to 1987 data on predation rate and to detect any influence my disturbance of the nest may have had on survivorship. Three nests in spring of 1988 and eight nests in spring of 1989 were excavated to determine overwintering survival and hatching success.

I took 24-hour temperature profiles using a probe placed in the ground at a depth of 8 cm and a maximum-minimum thermometer placed unshaded on the surface. I took temperature readings at 400 MDT and every 2 hours from 800 h MDT to 2400 h MDT over one 3-day period (starting August 27, 1988). I chose 8 cm soil depth as it was the average depth of the middle of a turtle nest. This gave me an indication of extremes and variation of temperature to which eggs are subject in the nest. Using a maximum-minimum thermometer allowed me to be sure that periodic measurements included maxima and minima for the day. Maximum-minimum thermometers were placed in an actual nest from which the eggs had been removed (1987-1988) and at 8 cm depth beside nests (1988-1989) to suggest extremes of temperature from egg deposition to emergence of hatchlings the following spring.

Hibernation

In September 1987, I fitted two male (plastron lengths: 155 mm, 161 mm) and two female turtles (plastron lengths: 171 mm, 174 mm) from Fisher Lake with radio transmitters (Lotek Engineering Model FRT-8) to enable me to locate them during the winter. Fisher Lake was chosen as it is shallow (2 m) and the signal frequencies required shallow water for precise location. One of the females was equipped with a temperature-sensitive transmitter. In 1988, I fitted two males (plastron lengths: 165 mm, 173 mm) and two females (plastron lengths: 174 mm, 176 mm) from Hidden Lake with radio transmitters (one temperature-sensitive on a male). I chose Hidden Lake for the second winter because turtles may have chosen different hibernacula in a lake with deeper water (7 m). The transmitters weighed 40 gm and were roughly cylindrical (length 5.5 cm, diameter 1.5 cm) with a 29 cm whip antenna. They were shaped to fit against the left rear edge of the carapace with the antenna trailing. The transmitter was attached by nylon ties passed through two holes drilled in the margin of the shell.

In July 1987, eight turtles had been captured by dip net for the determination of summer plasma lactate levels. The radio-tagged turtles were first sampled a few days after release in September. Turtles were located on three separate visits (November 22, January 2, February 17) to the site during the winter of 1987 - 1988. I made two visits (December 28, March 25) in the winter of 1988 - 1989. On each occasion, a hole was cut in the ice and the turtles captured by hand. In January 1988, turtles could be seen through the ice, sitting on the bottom. On the other occasions, I could locate the turtles by feel or by immersing my head to see under the ice using a diving mask. Blood samples (see below) were taken from each radio-tagged turtle and any other turtles that were captured serendipitously. Post-winter samples were taken from turtles tagged in 1987 at the end of April 1988.

I measured water temperature (using both a mercury thermometer and readings from the single temperature-sensitive transmitter), ice thickness, water depth below the ice, and distance from shore of each capture location. In 1989, I determined dissolved oxygen levels with a YSI oxygen meter (model 57). Readings were taken at the site of capture and at two arbitrarily chosen locations near the deepest parts of the lake. In addition, I made searches under the ice using SCUBA.

Cardiac puncture (Stevens and Creekmore 1983) was used to take blood samples. The blood sample (0.2 cc) was immediately injected into 0.4 cc of cold 8% perchloric acid and kept on ice. The period between capture and deproteinization by perchloric acid was about 40 seconds. The samples were placed in a freezer within an hour. They were stored for about a week before being analyzed. Plasma lactate levels were determined by an enzymatic test (Sigma no. q826-UV) and absorption was measured on a narrow-bandwidth spectrophotometer (Pye Unicam SP8-400 at 0.5nm bandwidth). Plasma lactate levels were compared among sample times using ANOVA. Differences among means were tested by Tukey's HSD procedure.

RESULTS

The beginning of the annual activity cycle was not observed for this population. Turtles were active when I arrived in the field (May 9, 1987 and April 26, 1988). Amount of pond vegetation and insect activity appeared to decline after July. Mean monthly air temperatures from May to September for Elko, B.C. (Environment Canada 1982) exceeded the reported threshold temperature for activity (10^{O}C, Figure 6). Shaded air temperatures ranged from 14 to 28^{O}C at around 1000 h MDT, the beginning of the sampling day (Figure 7). Water temperatures ranged from 16 to 24^{O}C (Figure 8) and were 16^{O}C (depth 30 cm) at the beginning and end of the field season (May 9 and September 17, 1987). Turtles were still active at these times. There were fewer active animals after the end of August although water temperatures did not noticeably decline.

Population Composition

There were more females captured than males in all lakes except Hidden, where numbers were similar (Figure 9). Data from Muskrat Lake were not included in the analysis as this lake was visited only twice in 1987 and once in 1988. I found a total of only 30 turtles in Muskrat Lake. Sex ratios were significantly different in Surveyor's and Engineer's Lakes ($p = 0.01$) and for all lakes combined ($p = 0.02$). More juveniles were captured in Hidden Lake than in any of the other lakes. I found only five juveniles, including one hatchling, in Engineer's and Surveyor's Lakes. Hatchlings and small juveniles were generally more difficult to find and catch. They were found in the reeds rather than in the open pond or on basking logs.

Figure 6. Air temperatures for Elko, B.C. (Environment Canada). Temperatures are monthly means for 1959 to 1980. The reported threshold temperature for activity in painted turtles (10^{o}C) is indicated.

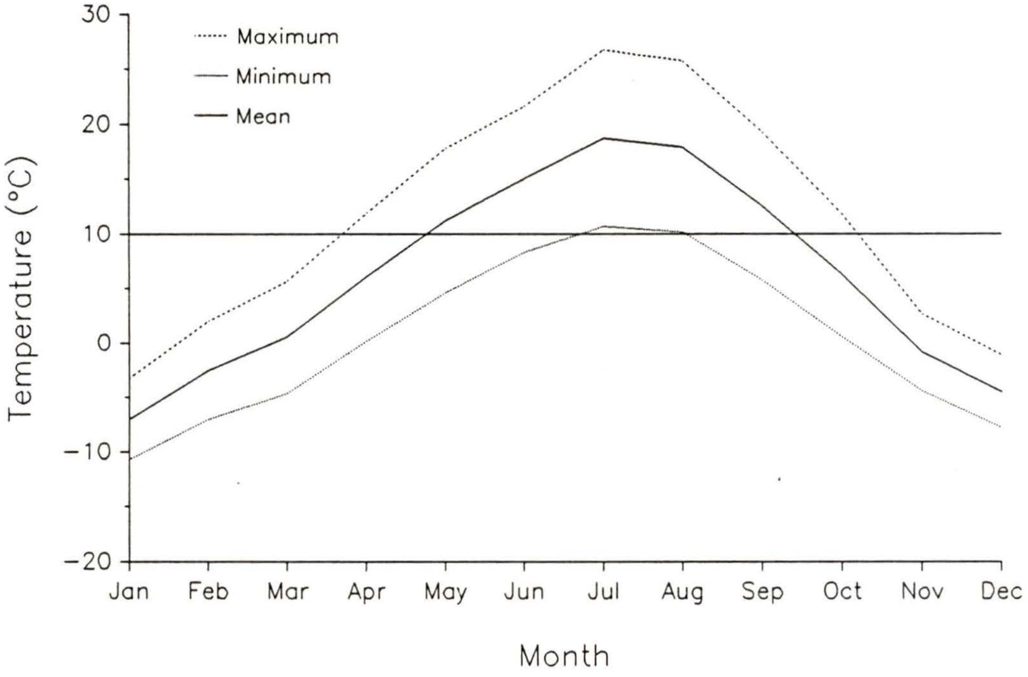

Maximum
Minimum
Mean
Temperature (°C)
30
20
10
0
-10
-20
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Month

Figure 7. Air temperatures at the beginning of sampling days. Sampling generally started around 1000 h MDT.

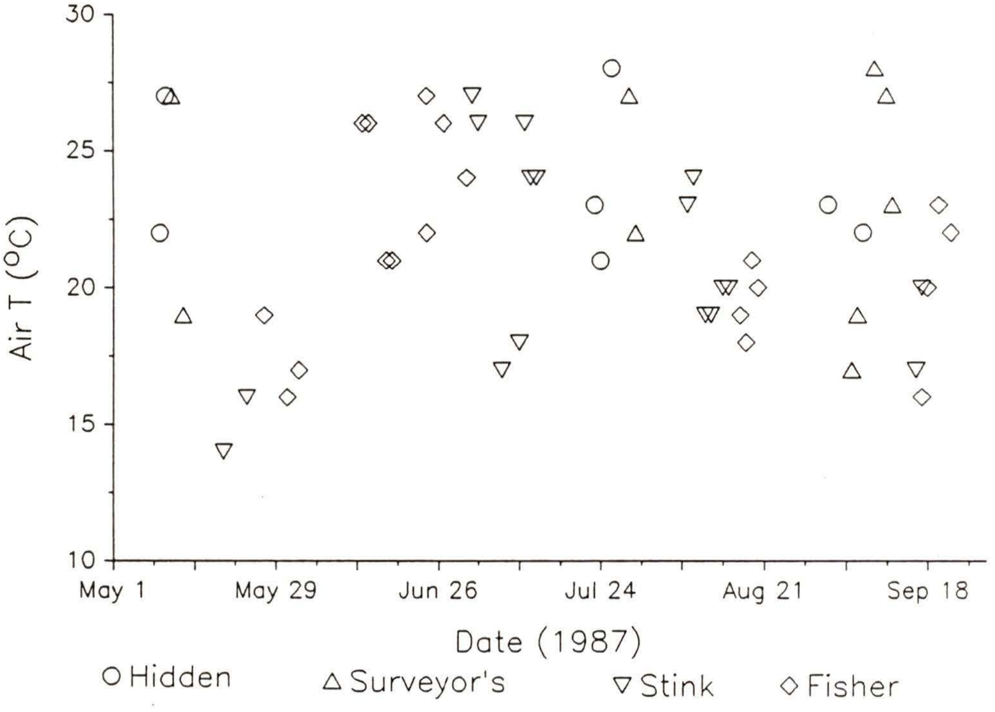

30
25
20
15
10
Air T (^{o}C)
May 1
May 29
Jun 26
Jul 24
Aug 21
Sep 18
Date (1987)
○ Hidden
△ Surveyor's
▽ Stink
◇ Fisher

Figure 8. Water temperatures (depth 30 cm) at the beginning of days of sampling (around 1000 h MDT).

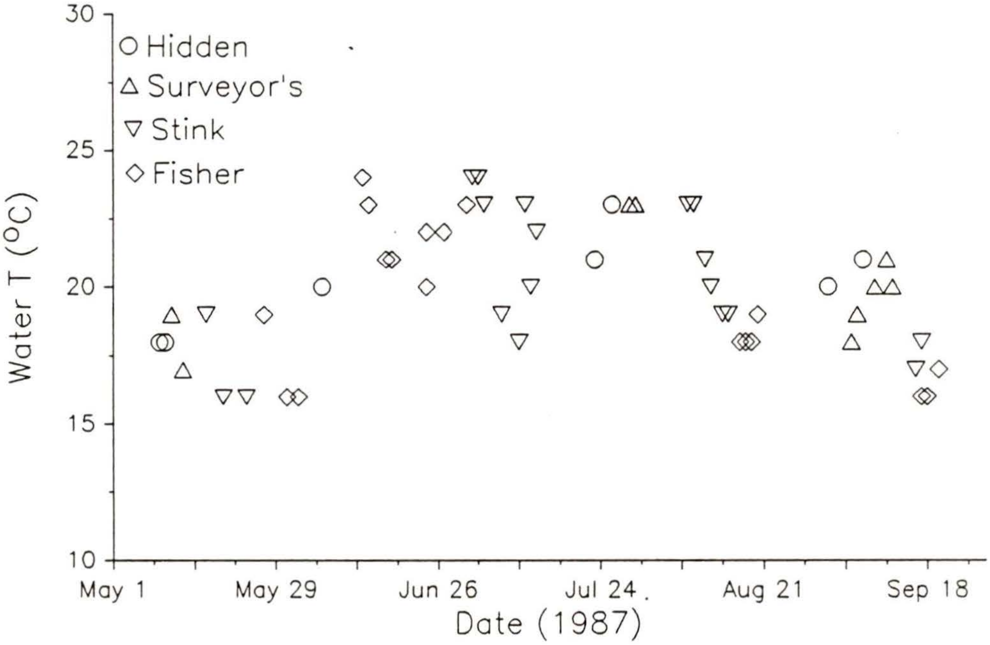
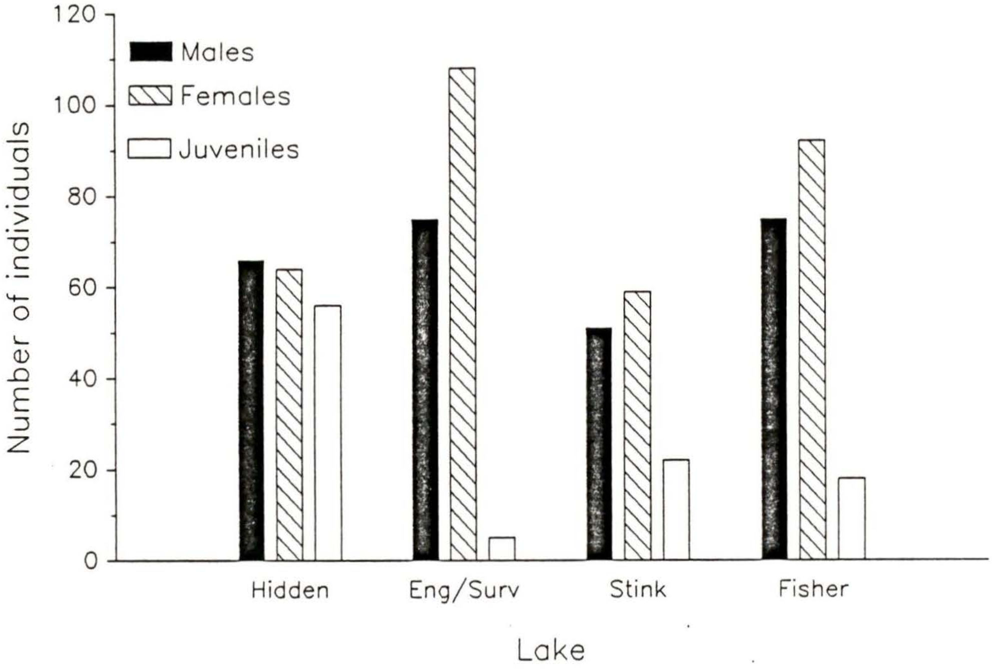

○ Hidden
△ Surveyor's
▽ Stink
◇ Fisher
Water T (°C)
30
25
20
15
10
May 1
May 29
Jun 26
Jul 24
Aug 21
Sep 18
Date (1987)

Figure 9. Number of individual males, females, and juveniles captured in 1987 and 1988 combined. Animals were counted only once. Juveniles were all individuals under 90 mm plastron length. Data from Surveyor's Lake and Engineer's Lake were combined. Sex ratio in Surveyor's/Engineer's Lakes was significantly different from 1:1.



Number of individuals
0
20
40
60
80
100
120
Males
Females
Juveniles
Hidden
Eng/Surv
Stink
Fisher
Lake

The frequency distribution of female plastron lengths was dominated by larger animals (Figure 10). An unbalanced ANOVA design (STATGRAPHICS 1986) was used to adjust for unequal but proportional sub-class sizes. Analysis of variance indicated that females were, on average, larger than males ($p < 0.001$). Size differed among lakes ($p = 0.01$). There was no significant interaction between sex and lake ($p = 0.91$). The animals in Hidden Lake were, on average, the largest (Figure 11).

Survivorship

Minimum survivorship (recaptures/marked) were: males 0.74 (228/309), females 0.64 (269/418), and juveniles 0.62 (58/93). Minimum survivorship over 2 years was different between males and females (chi-square = 75.47, df = 2, $p < 0.001$).

Minimum survivorship for Hidden, Surveyor's and Engineer's Lakes combined was 0.70 (284 of 403). Survivorship for Stink, Fisher, and Muskrat Lakes combined was 0.64 (265 of 417). Minimum survivorship over the 2 years was different between these two location categories (chi-square = 4.13, df = 1, $p = 0.04$ with Yates correction for continuity).

Minimum rates of survival within age groups (Figure 12) showed little change as indicated by the straight line relationship on semi-log plot. Maximum longevity would be approximately thirty years.

Figure 10. Frequency of males, females, and juveniles plastron lengths for animals captured in 1987 and 1988. Animals were counted only once. The mean of female plastron lengths was 153.3 mm (SD = 21.61, range = 91 to 200 mm). The mean of male plastron lengths was 138.5 mm (SD = 18.87, range = 90 to 187 mm).

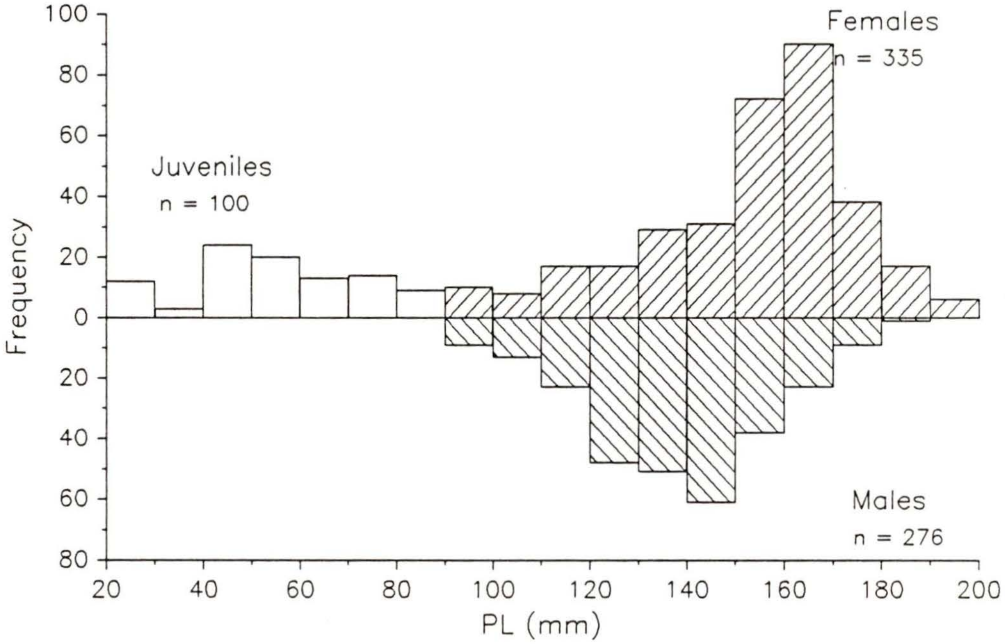
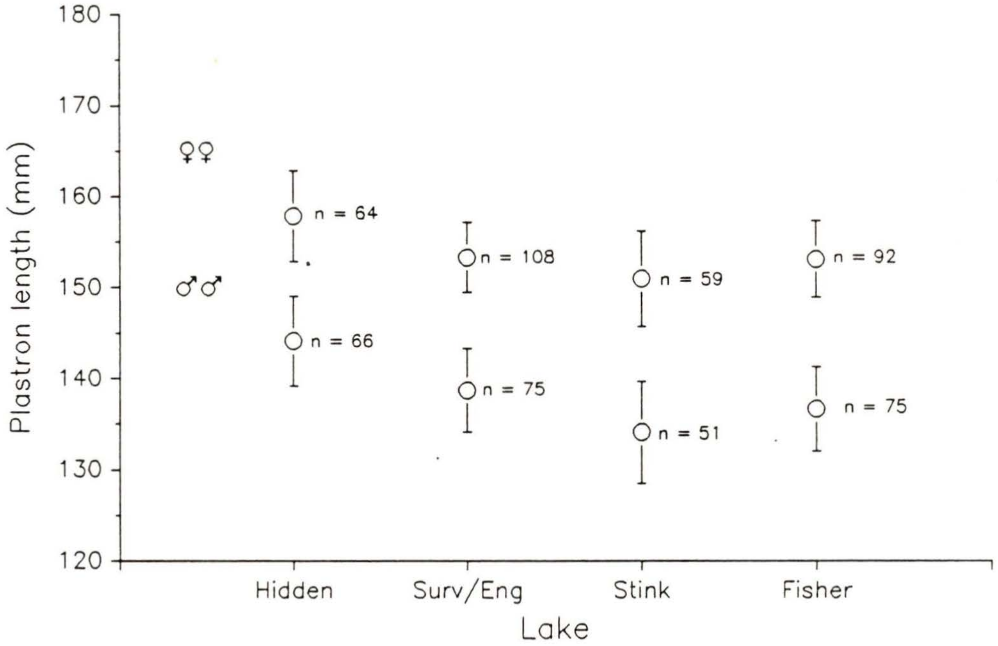

Females
n = 335
Juveniles
n = 100
Males
n = 276
Frequency
100
80
60
40
20
0
20
40
60
80
20
40
60
80
100
120
140
160
180
200
PL (mm)

Figure 11. Mean plastron lengths of males and females in each lake. Data from Surveyor's and Engineer's Lakes were combined due to transfer of turtles by park visitors. Vertical bars are 95% confidence limits.


Plastron length (mm)
180
170
160
150
140
130
120
♀♀
♂♂
n = 64
n = 66
n = 108
n = 75
n = 59
n = 51
n = 92
n = 75
Hidden
Surv/Eng
Stink
Fisher
Lake

In 1987, I observed 14 completed nestings. Of these, only four (29%) survived past the beginning of July. These four were located near Hidden Lake in areas of comparatively heavy use by campers; one was found within the campground. This human activity at Hidden Lake might have discouraged more timid predators such as coyotes (*Canis latrans*), a potential predator on nests. In contrast to Stink and Fisher Lakes, I did not see coyotes near Hidden Lake. I found 19 destroyed nests that I had not observed under construction. From the proportion of the population that was gravid (see below), nesting activity was much reduced in 1988. Although I observed 13 nestings in 1988, I found only four destroyed nests. The total of observed nestings plus other destroyed nests was 33 in 1987, and 17 in 1988.

I could recognize two types of egg predation: eggs were either slit the length of the shell or had one end opened. I found egg shells that had been opened at one end near the entrance to a Columbia Ground Squirrel (*Spermophilus columbianus*) burrow. I found eggs similarly opened around a turtle nest that was destroyed during the day, suggesting that squirrels were probably diurnal predators on turtle nests. This assumes that only squirrels opened eggs this way. I found no clue about which animals were responsible for slitting open the eggs. I found egg shells in a coyote scat and incompletely-digested whole eggs along with turtle leg bones in bear (*Ursus americanus*) scat. The latter suggests that a gravid female had been eaten.

On April 30 1988, three nests from 1987 were excavated. Of 25 eggs, 6 had not developed and 19 eggs had hatched (Table 1). Of these 19 hatchlings, only one was still alive in the nest. On March 26 1989, eight nests from 1988 were excavated. Of 63 eggs, 34 had developed to the hatchling stage. All were dead. The number of eggs or hatchlings recorded at nesting agreed with the number of eggs examined in

Figure 12. Minimum survivorship for juveniles and females marked in 1985. Survivorship was grouped by age class. Age was estimated from plastron length using the growth curve derived from age-length data (see Figure 14). Maximum longevity is approximately 30 years.

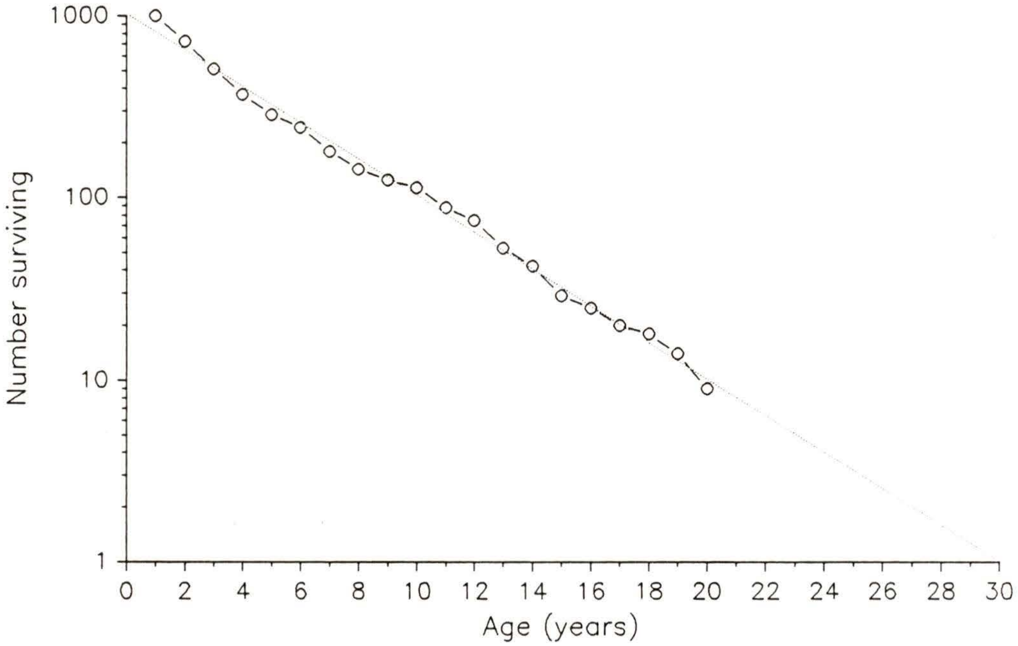

1000
100
10
1
Number surviving
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
Age (years)

Table 1. History of nests followed over the winters of 1987-1988 and 1988-1989. Only one hatchling was found alive in the spring.

Nest #	Clutch size	Undeveloped	Hatched
1987-1988			
# 3	not excavated	1	3
# 4	11	5	6
# 9	not excavated		10 (1 alive)
1988-1989			
# 1	11	2	2
# 3	8	7	1
# 5	9	2	6
# 6	13		5[1]
# 7	9	3	3
# 8	12	1	11
# 16	not excavated	9	
# 17	not excavated	5	6

[1] Only 5 hatchlings could be removed because the ground was frozen.

the spring in most cases. Three nests had fewer eggs and hatchlings. On September 9, 1988, I found a dead hatchling at the ground above a nest. Because the ground was slightly disturbed around the observation port, I suspected that it may have emerged from that nest.

A maximum-minimum thermometer that had been placed in a previously excavated nest showed a minimum of - 6^{o}C. In 1988 - 1989, a maximum-minimum thermometer placed at 8 cm depth beside a nest indicated a minimum of - 5^{o}C.

Turtles were found in different stages of development ranging from having absorbed the yolk sac but still surrounded by the shell to being completely free. In two of the nests, hatchlings were seen to orient themselves facing upwards.

In 1987, I found 19 turtle shells of which all but three were found around Stink, Fisher and Muskrat Lakes. From the condition of the shells, all the turtles had been killed that year. I found the crushed remains of three others that had likely been killed in previous years. Only two turtle carcasses were found in 1988, a juvenile and a gravid female that had been run over within the campground. Two disarticulated turtle shells were found in Fisher Lake and one in Hidden Lake. These turtle shells bore no signs of predation and may have died over the winter.

Six of the 19 turtle shells were marked and the sex could therefore be determined. All were females. The rest of the shells either were not marked or, more often, were in pieces making it impossible to read the mark, if present.

By examining the turtle shells, I could distinguish two types of predation. Turtles were either found with the head, and/or several of the limbs and viscera removed or with a large part of the carapace and the viscera removed. I found seven of the first type and twelve of the second.

Growth

The largest male captured was 190 mm plastron length; however, most individuals did not exceed 180 mm plastron length. The largest female was 219 mm. The largest animals of either sex showed little increase in size from 1985 to 1988 (Table 2).

Growth of smaller animals was included in the Walford plots of larger time intervals because the sex of individuals that were immature at first capture could usually be determined at recapture (Table 2). Juveniles were included only in the 1-year interval data because within other intervals most animals had matured or were not recaptured. The data used in the age-length estimation of the von Bertalanffy model were for smaller animals than the length interval model (Table 3). This was a consequence of being unable to decide with certainty the age of older animals because annuli disappeared with age.

The linearity of the Walford regressions (Figure 13) indicated that the von Bertalanffy growth model was plausible. For each interval, the Brody growth coefficient ($K = -\ln$ of slope) was higher in males than females and the mean asymptotic size was smaller (Table 4). The Walford regression of 1-year interval data for immature animals showed the smallest value of asymptotic length and largest K. In tests of difference between male and female regressions for each time

Table 2. Summary statistics for length interval data used in Walford plots. All plastron lengths (PL) are in mm.

	N	Minimum	Maximum	Mean	S.D.
one-year interval (1987 - 1988)					
Males					
PL1	83	95	173	143.2	16.12
Pl2		95	174	143.2	15.32
Females					
PL1	155	75	199	154.4	27.10
PL2		89	200	157.5	24.10
Juveniles					
PL1	10	48	75	63.3	10.67
PL2		68	87	79.3	7.13
two-year interval (1985 - 1987)					
Males					
PL1	187	51	186	134.7	24.18
PL2		94	187	140.6	19.85
Females					
Pl1	198	51	189	139.8	33.06
PL2		91	189	149.8	24.97
three-year interval (1985 - 1988)					
Males					
PL1	66	48	188	135.1	26.31
PL2		95	190	141.4	20.76
Females					
PL1	100	48	190	134.7	34.09
PL2		100	193	149.0	22.57

Table 3. Summary statistics for length interval and age-length data used to estimate parameters of the von Bertalanffy growth model. Statistics are for plastron length at original capture. For length interval data, the number of observations per time interval are shown in parentheses (n1 = 1 year etc.). All plastron lengths (PL) are expressed in mm.

	N	Minimum	Maximum	Mean	S.D.
Length interval data:					
Male PL	510 (141,248,121)	48	188	134.3	24.06
Female PL	663 (216,256,191)	25	199	142.6	32.92
Age-length data:					
Male PL	84	86	148	110.7	13.75
age (yr)	2.5	13.5	6.1	2.2	
Female PL	187	74	159	116.2	18.14
age (yr)	2	12.5	5.4	2.1	

Figure 13. Walford plots of male (solid line) and female (dotted line) length increment data. All slopes, constants, and coefficients of determination are significant ($p < 0.001$).

A. 1987 to 1988

Males: $PL2 = 8.5 + 0.95PL1$ (r^2 0.99, $n = 83$)

Females: $PL2 = 20.9 + 0.89PL1$ (r^2 0.99, $n = 155$)

B. 1985 to 1987

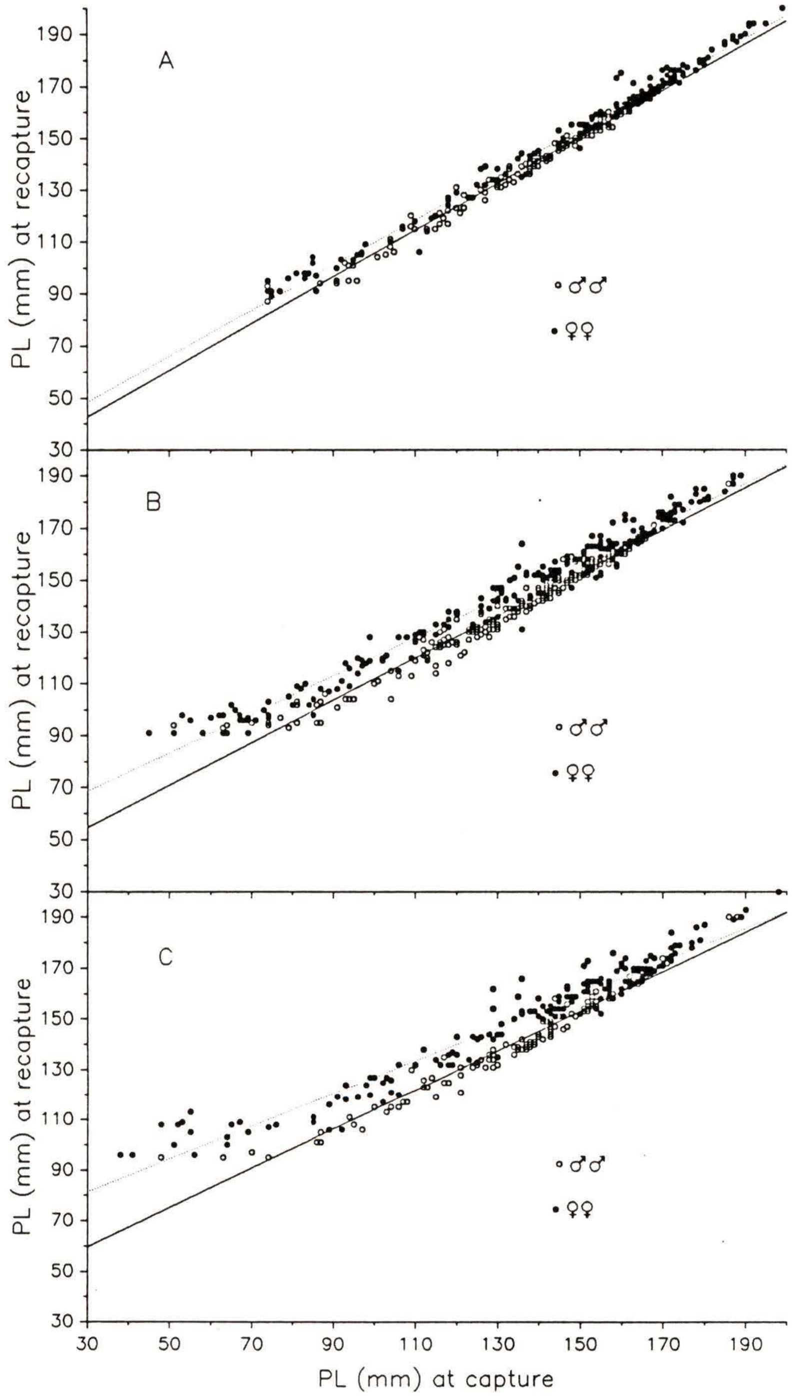
Males: $PL2 = 32.4 + 0.80PL1$ (r^2 0.96, $n = 187$)

Females: $PL2 = 45.7 + 0.75PL1$ (r^2 0.97, $n = 198$)

C. 1985 to 1988

Males: $PL2 = 37.1 + 0.77PL1$ (r^2 0.94, $n = 66$)

Females: $PL2 = 63.3 + 0.64PL1$ (r^2 0.92, $n = 100$)


A
B
C
PL (mm) at recapture
PL (mm) at capture
30
50
70
90
110
130
150
170
190
○ ♂♂
● ♀♀

interval, slopes were significantly different ($p < 0.001$). The differences between adjusted means were therefore not tested (Snedecor and Cochran 1967). A repeated measures multivariate ANCOVA for animals caught in 1985 and recaptured both in 1987 and 1988 ($n = 23$ males, 17 females) indicated no significant difference between slopes ($p = 0.49$) and a difference between adjusted means ($p = 0.002$).

Larger asymptotic length and smaller K for females relative to males were also estimated from the combined length interval form of the von Bertalanffy growth model (Table 4).

The estimates for mean asymptotic lengths were similar for length interval and age-length data (Table 4). The pattern of growth appeared to fit the model derived from age-length data (Figure 14).

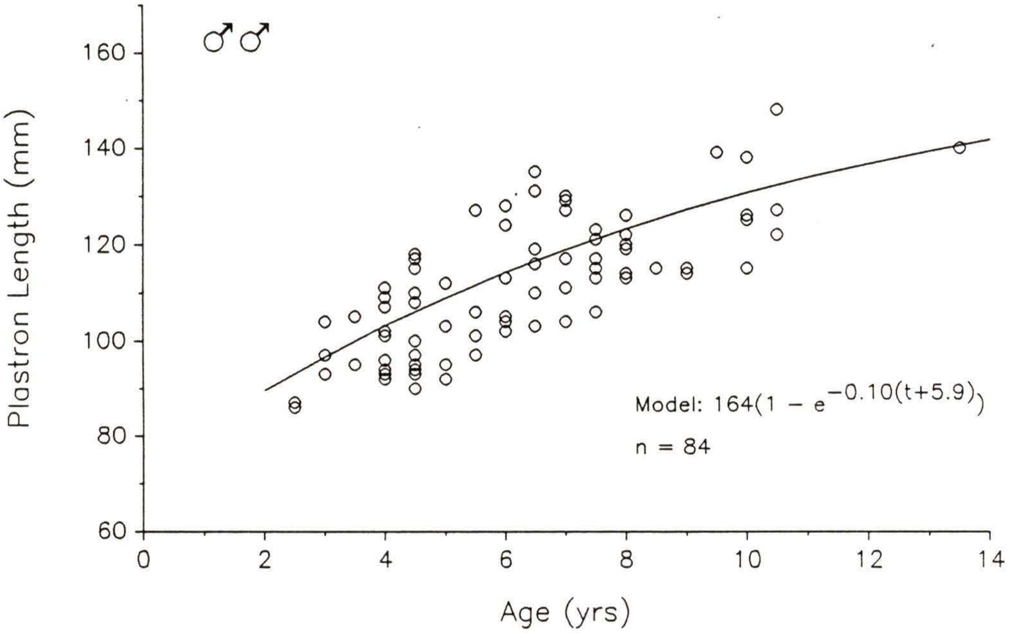
Reproduction

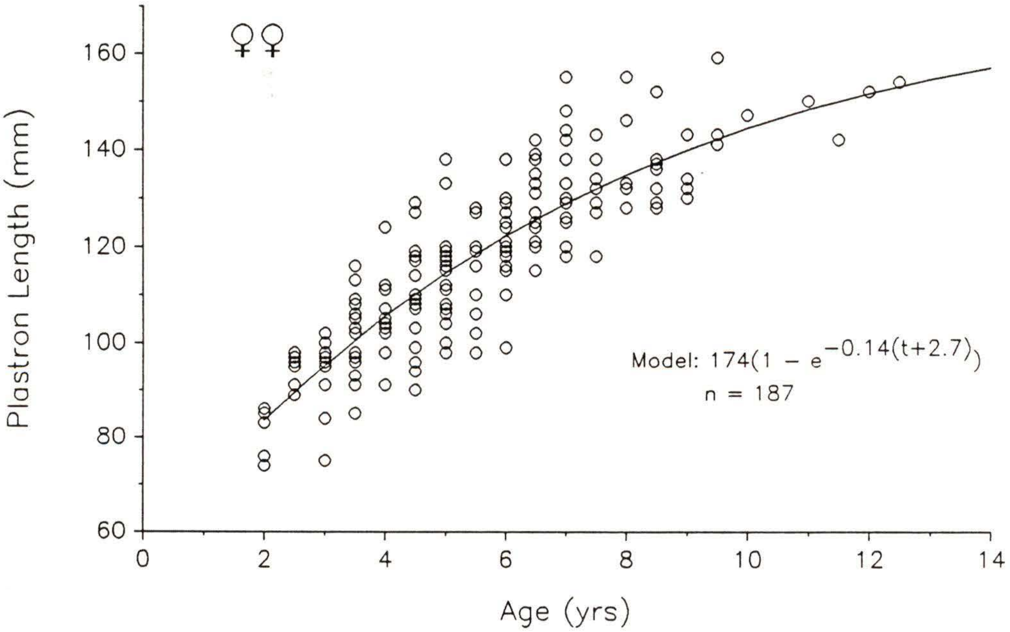
The smallest animal with secondary male sexual characteristics was 86 mm plastron length. Commonly, male characteristics were present by 90 mm plastron length; smaller animals were classified as juveniles. The correlation between the appearance of secondary sexual characteristics in the male and sexual functioning was not established because mating was not observed. However, on several occasions during September, males could be seen approaching females. Males would follow females and, facing them, extend their forelegs while vibrating their foreclaws near the head of the female. This presumed courtship behaviour was similar to that reported for *Pseudemys* and *Chrysemys* (Carr 1952).

Table 4. Estimates for parameters of the von Bertalanffy growth model. The formulas used were:
(1) Walford plots:
$l_{t+d} = L_{inf}(1 - k) + kl_t$
(2) for length-interval data,
$l_{t+d} = L_{inf} - (L_{inf} - l_t)e^{-Kd}$
where L_{inf} is asymptotic length, K (-ln k) is the Brody growth coefficient, l_t is length at capture, l_{t+d} is length at recapture and d is interval between captures in years,
(3) for age-length data,
$l_t = L_{inf}(1-e^{-K(t-to)})$
where t is age and t_o is the hypothetical age when the length is zero. S.E. is standard error.

	L_{inf} (S.E.)	K (S.E.)	r^2
(1) Walford plots:			
1987 to 1988 (1-year equation)			
Males	163.4	0.05	0.99
Females	181.6	0.12	0.99
Juveniles	108.7	0.43	0.94
1985 to 1987 (2-year equation)			
Males	164.2	0.22	0.96
Females	179.3	0.29	0.97
1985 to 1988 (3-year equation)			
Males	162.8	0.26	0.94
Females	173.9	0.45	0.92
(2) Length interval data (all intervals combined):			
Males	162.7 (1.42)	0.10 (0.004)	0.97
Females	175.4 (1.22)	0.16 (0.005)	0.95
(3) Age-length data:			
Males	164.1 (39.20)	0.10 (0.08)	0.57
Females	173.8 (13.16)	0.14 (0.03)	0.77

Figure 14. Age-length data for males (n = 86) and females (n = 74). The von Bertalanffy models derived from non-linear regression of age-length data are shown.


♂♂
Plastron Length (mm)
60
80
100
120
140
160
0
2
4
6
8
10
12
14
Age (yrs)
Model: $164(1 - e^{-0.10(t+5.9)})$
n = 84


♀♀
Plastron Length (mm)
60
80
100
120
140
160
0
2
4
6
8
10
12
14
Age (yrs)
Model: $174(1 - e^{-0.14(t+2.7)})$
n = 187

I could detect oviducal eggs by palpating at the beginning of the field season but detection was often ambiguous. Later in the season, after the oviducal eggs were calcified, the presence of eggs in gravid females became unmistakable. Oviducal eggs were not apparent in X-ray photographs until after the eggs became calcified. At the beginning of May, 10 of 14 females showed no eggs on the X-ray photographs although I could detect oviducal eggs by palpating. Two of these were later recaptured, X-ray photographed, and found to be gravid. Of 146 gravid females, the smallest was 151 mm. This was used as the lower size limit of sexual maturity in this population. Gravid females were found at the beginning of each field season (May 9, 1987 and May 8, 1988).

It was not possible to decide if a female was non-gravid in a given year because females were not always captured during the reproductive season. In addition, some females captured during the nesting season would certainly have already produced a clutch that year. The numbers of females that laid eggs in consequent years are therefore underestimates. There were no known instances of females producing more than one clutch a year. Only one individual was found to be gravid throughout the summer; it had only one hind limb and so probably was unable to construct a nest.

Recapture rates were low for 1987 to 1988; however, some females reproduced in consecutive years (Figure 15). Eighty percent of gravid females captured both in 1985 and 1987 were gravid (Figure 16). Eleven percent of gravid females that were captured in 1985 and recaptured in 1988 were again gravid; all nine individuals that were non-gravid in 1985 and recaptured in 1988 were non-gravid (Figure 17). The number of gravid females may be an underestimate as some individuals may have already laid eggs when captured . There were more gravid

Figure 15. Capture history of gravid and non-gravid females captured both in 1987 and 1988. Non-gravid females were individuals of reproductive size captured within the time that gravid females were present in the population.

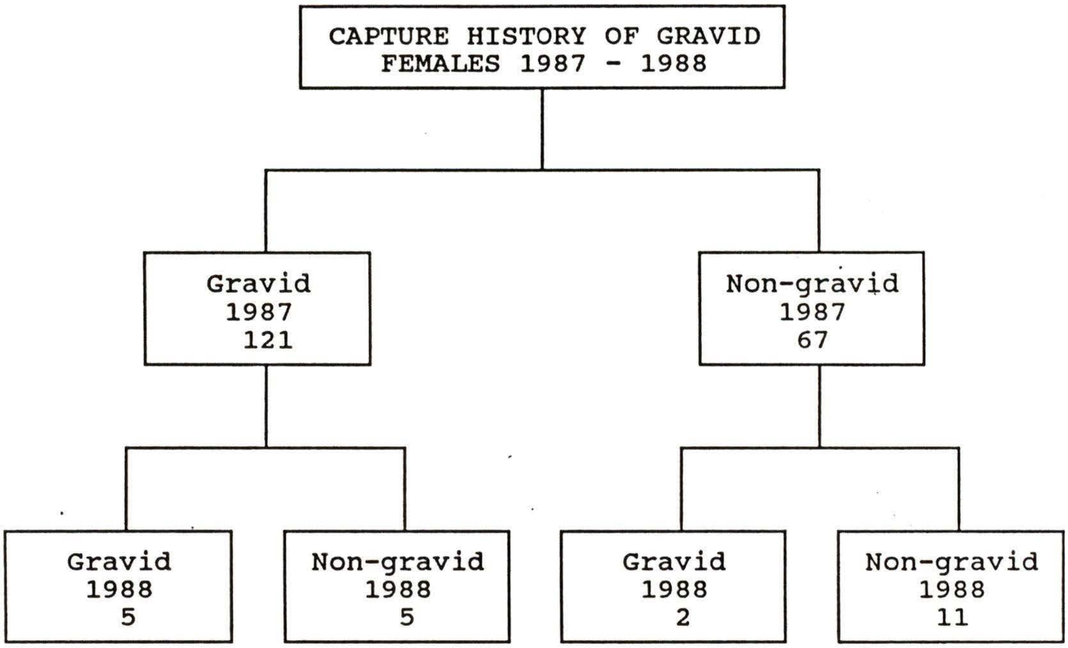

CAPTURE HISTORY OF GRAVID FEMALES 1987 - 1988
Gravid 1987 121
Non-gravid 1987 67
Gravid 1988 5
Non-gravid 1988 5
Gravid 1988 2
Non-gravid 1988 11

Figure 16. Capture history of gravid and non-gravid females captured in 1985 and recaptured both in 1987 and 1988 (i.e. only females captured during the reproductive season in every year). Non-gravid females were individuals of reproductive size captured within the time that gravid females were present in the population.

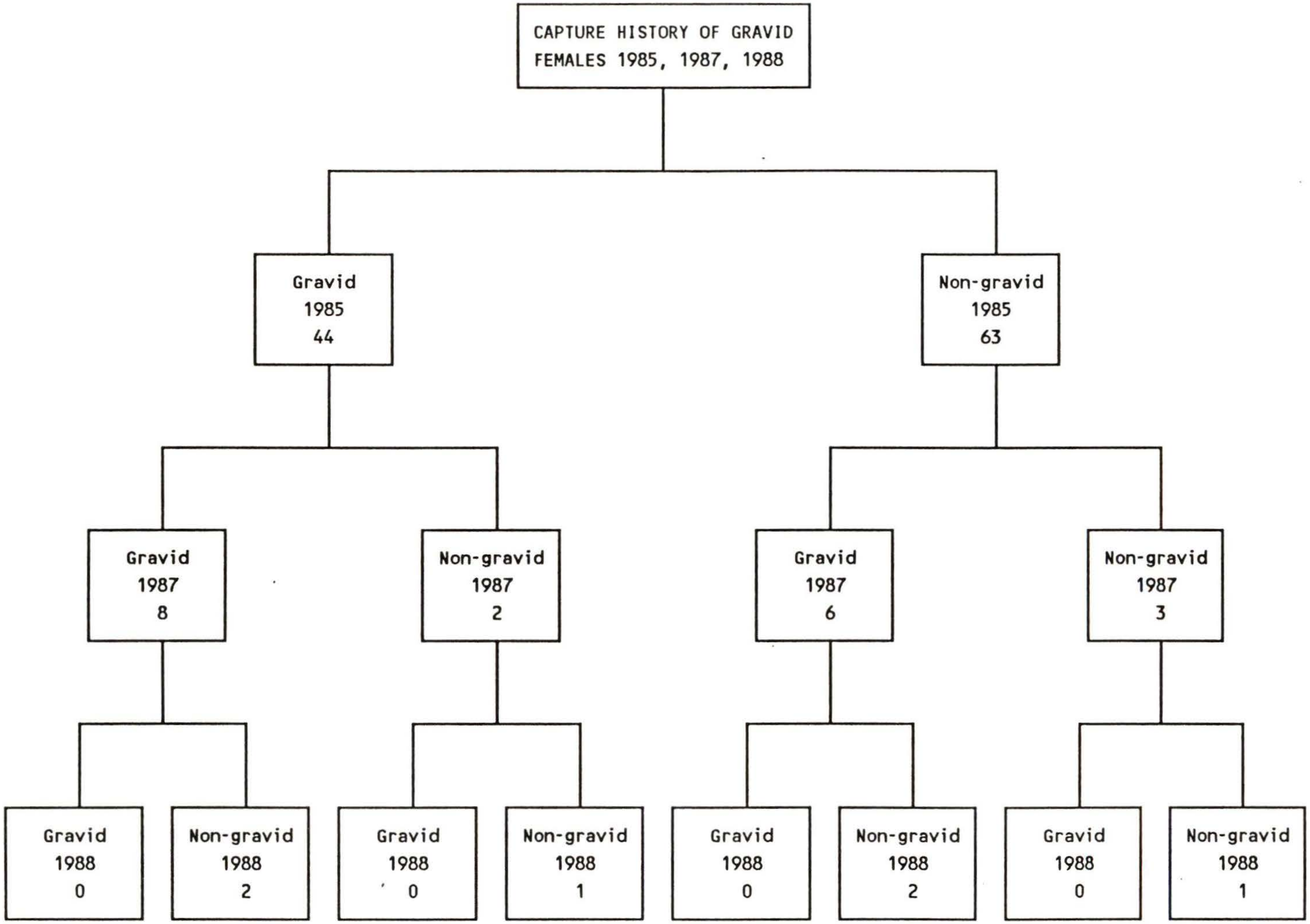
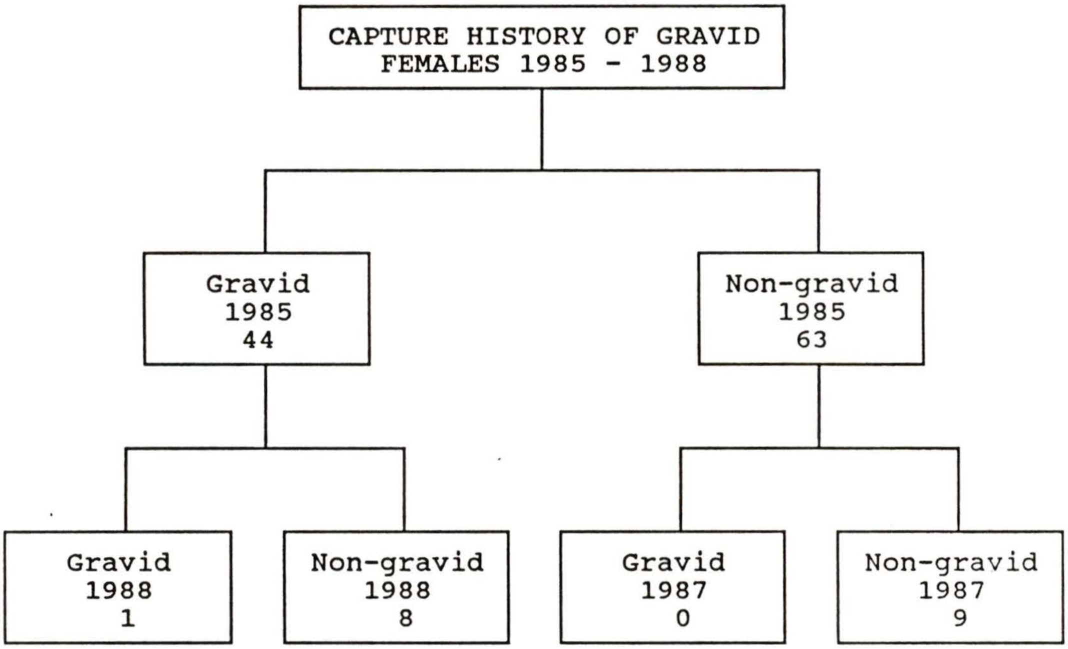

CAPTURE HISTORY OF GRAVID FEMALES 1985, 1987, 1988
Gravid 1985 44
Non-gravid 1985 63
Gravid 1987 8
Non-gravid 1987 2
Gravid 1987 6
Non-gravid 1987 3
Gravid 1988 0
Non-gravid 1988 2
Gravid 1988 0
Non-gravid 1988 1
Gravid 1988 0
Non-gravid 1988 2
Gravid 1988 0
Non-gravid 1988 1

Figure 17. Capture history of gravid and non-gravid females captured in 1985 and 1988. Non-gravid females were individuals of reproductive size captured within the time that gravid females were present in the population.


CAPTURE HISTORY OF GRAVID FEMALES 1985 - 1988
Gravid 1985 44
Non-gravid 1985 63
Gravid 1988 1
Non-gravid 1988 8
Gravid 1987 0
Non-gravid 1987 9

females (n = 121) and a higher proportion (55%) in 1987 compared with 1988 (n = 25, 29%, Figure 18).

Nesting was observed from June 3 to June 26, 1987 and from June 4 to June 18, 1988. This may be a slight underestimate of duration of nesting because I found gravid females until July 4, 1987 and until June 23, 1988. I found that females became decreasingly susceptible to disturbance as nest construction proceeded. Females that had just started nesting often abandoned their attempt when I arrived but individuals that had already started to lay eggs remained on the nest. They reacted to disturbance by retracting their limbs and head. The females mainly constructed nests on the northern (south-facing) and eastern sides of the lakes (Figure 19). The exception to this was near Hidden Lake where a westward-facing parking lot attracted nesting females. Mean distance from surface to top of the nests was 4.5 cm (n = 6, SD = 0.66, range = 4.5 - 6.0 cm). Mean depth of bottom of the nest was 10.9 cm (n = 6, SD = 0.66, range = 10.5 - 12.0 cm). Temperatures were less variable at 8 cm depth compared with unshaded temperatures at the surface (Figure 20). At the surface, maxima were around 1500 h MDT and minima were around 0600 h MDT. At 8 cm soil depth, maxima were around 1800 h MDT and minima were around 1100 h MDT. Temperatures at the surface ranged from 8.0°C to 44.0°C, and at 8 cm deep from 20.0°C to 32.5°C. The highest temperature taken from an actual nest was 30.5°C. A maximum-minimum thermometer placed in a nest from which the eggs had previously been removed indicated a maximum annual temperature of 29°C.

Most of the nests were close to Hidden, Stink, and Fisher Lakes except for two destroyed nests found near Muskrat Lake. I never found nests near Surveyor's or Engineer's Lakes. This was consistent with finding only one hatchling in these

Figure 18. Proportion of captured females that were gravid. Some of the females captured after nesting began (beginning of June) may have already laid eggs. These figures may therefore be an underestimate.

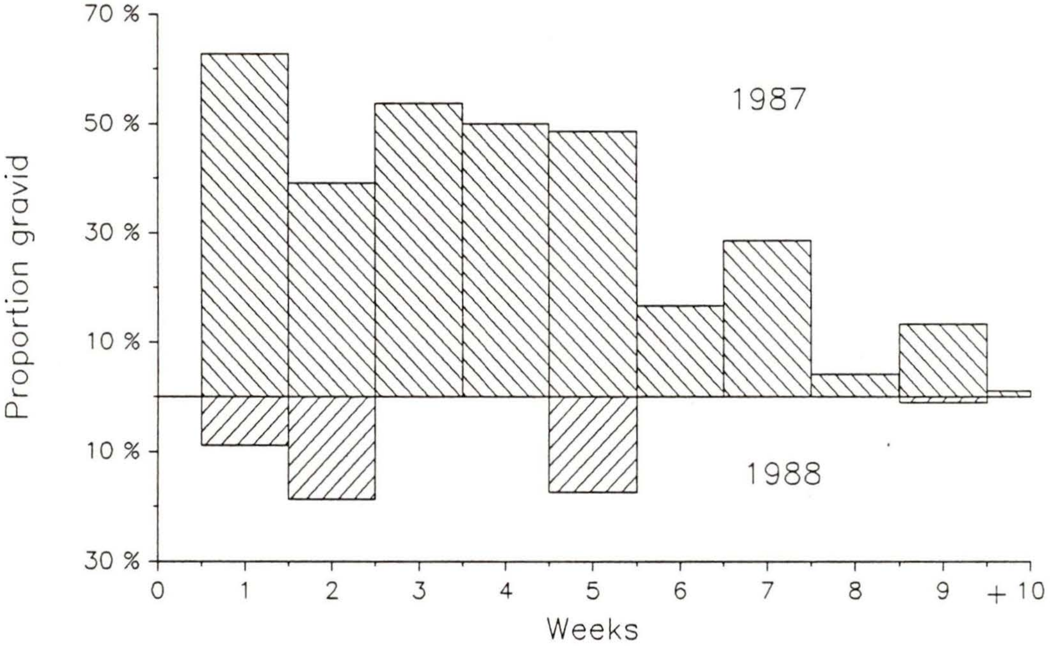

70 %
50 %
30 %
10 %
10 %
30 %
Proportion gravid
1987
1988
0
1
2
3
4
5
6
7
8
9
+ 10
Weeks

Figure 19. The lakes of Kikomun Creek Provincial Park showing nesting sites. Sites tended to be located on the north or northeastern slopes on the sides of Lakes. An exception to this is the parking lot in the northwestern side of Hidden Lake.

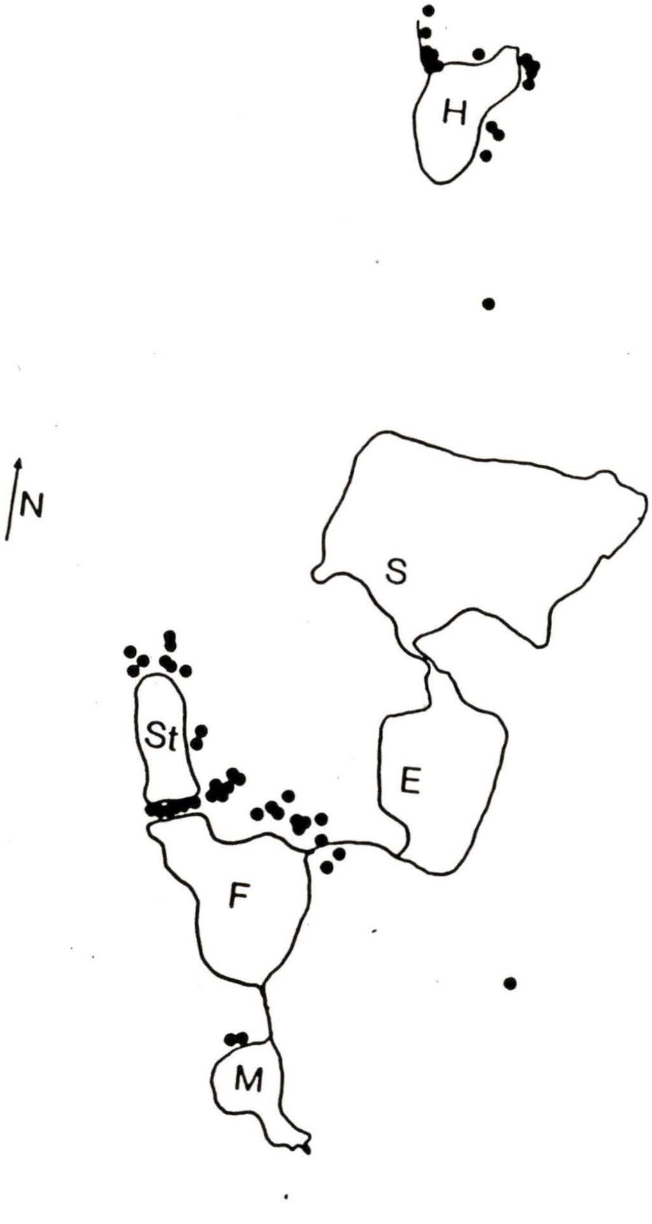
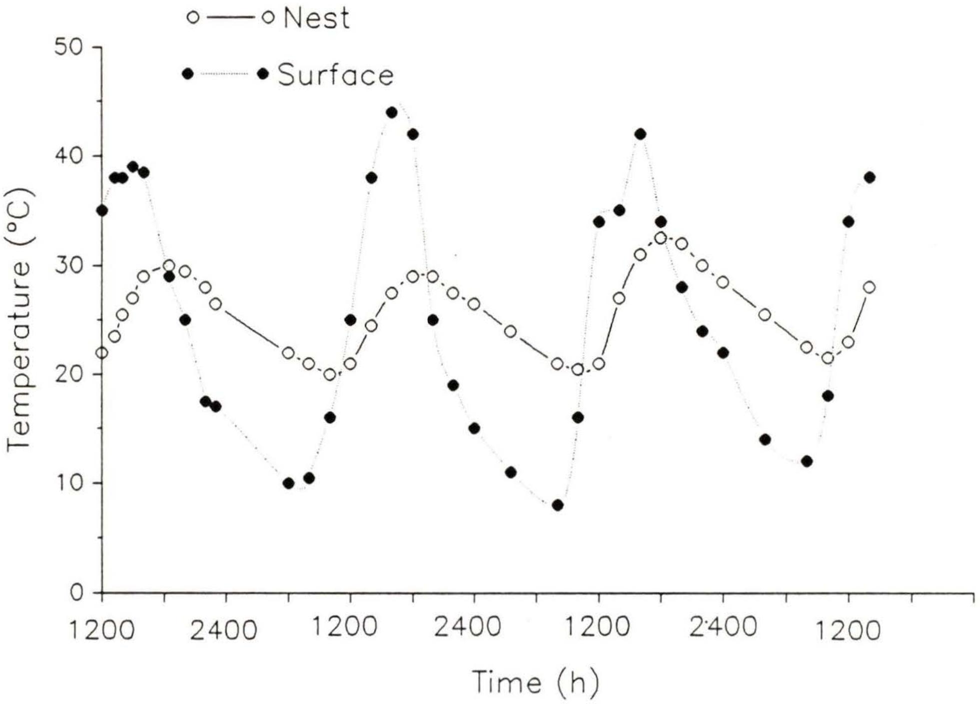

H
N
S
St
E
F
M

Figure 20. Temperature profiles at the surface and a probe placed in the ground at 8 cm depth. This depth was the mean of the mid-depth of nests. Data were gathered starting August 27, 1988. Time is Mountain Daylight Time (MDT).


Nest
Surface
Temperature (°C)
0
10
20
30
40
50
1200
2400
1200
2400
1200
2400
1200
Time (h)

lakes. However, there were two reports by campers of turtles nesting in the sand beach by Surveyor's Lake. Surveyor's and Engineer's Lakes have no open, southern-facing areas except Surveyor's beach. There is, however, an open slope on the eastern side of Engineer's Lake which appears to be suitable but was never used. On several occasions, gravid females from Engineer's Lake were found near a road 200 m from the lake. Gravid females (n = 46, in 1987) from Surveyor's Lake and Engineer's Lake may therefore nest farther afield.

There was a significant correlation ($r = 0.66$, $n = 39$, $p < 0.001$) between size (plastron length) and number of oviducal eggs (Figure 21). It was not possible to measure the eggs from the X-ray photographs because the orientation of the eggs would have affected the measurements. There was no evidence of senility or cessation of egg production in larger (older) animals. Several gravid females were quite old judging from wear on their shells. In 1988, I found one nesting individual that previously had been X-ray photographed. She laid 10 eggs compared with the 11 that were apparent in the photograph. Because I often found eggs on the bottom of the lakes, it is likely that not all oviducal eggs are deposited in nests.

I excavated two nests in 1987 and eleven nests in 1988. Clutch size varied from 6 to 17 (mean 11.1, S.D. 2.93). Eggs were oval (n = 137, mean length = 31.6 mm, SD = 1.95, range 26.8 - 38.8 mm; mean width = 20.4 mm, SD = 0.69, range 19.2 - 23.3 mm). Width and length were positively correlated ($r = 0.398$, Figure 22). Length and width of eggs were negatively correlated with clutch size ($r = -0.176$ and $r = -0.259$, respectively, Figure 23). These correlations were significant but slight. Egg length and width varied significantly among clutches ($p < 0.001$, means of egg lengths within clutches: 29.6 - 35.4 mm; means of egg widths within clutches: 19.7 - 21.3 mm).

Figure 21. Relationship of size (plastron length) to number of oviducal eggs ($r = 0.66$, $n = 39$, $p < 0.001$). Number of eggs was determined by X-ray photography.

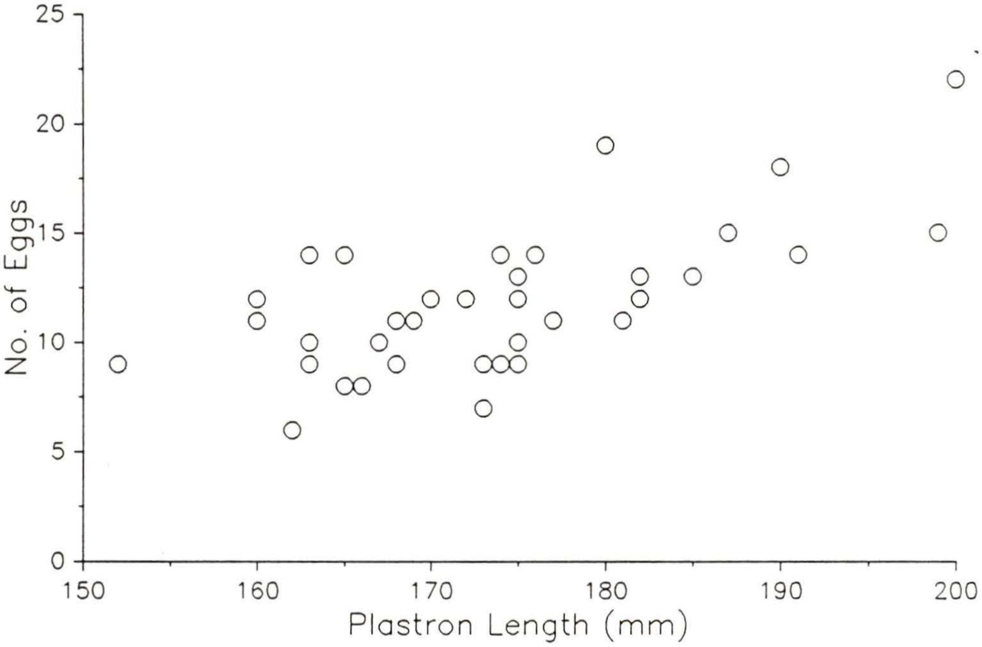

No. of Eggs
0
5
10
15
20
25
150
160
170
180
190
200
Plastron Length (mm)

Figure 22. Correlation between length and width of eggs in nest ($r^2 = 0.15$, $n = 136$, $p < 0.001$).

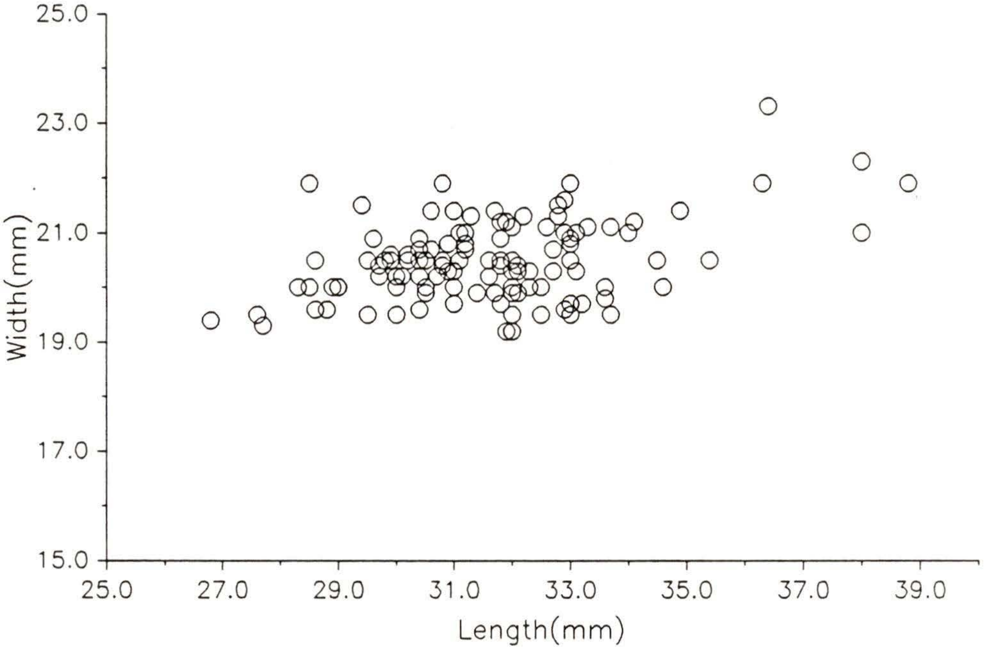
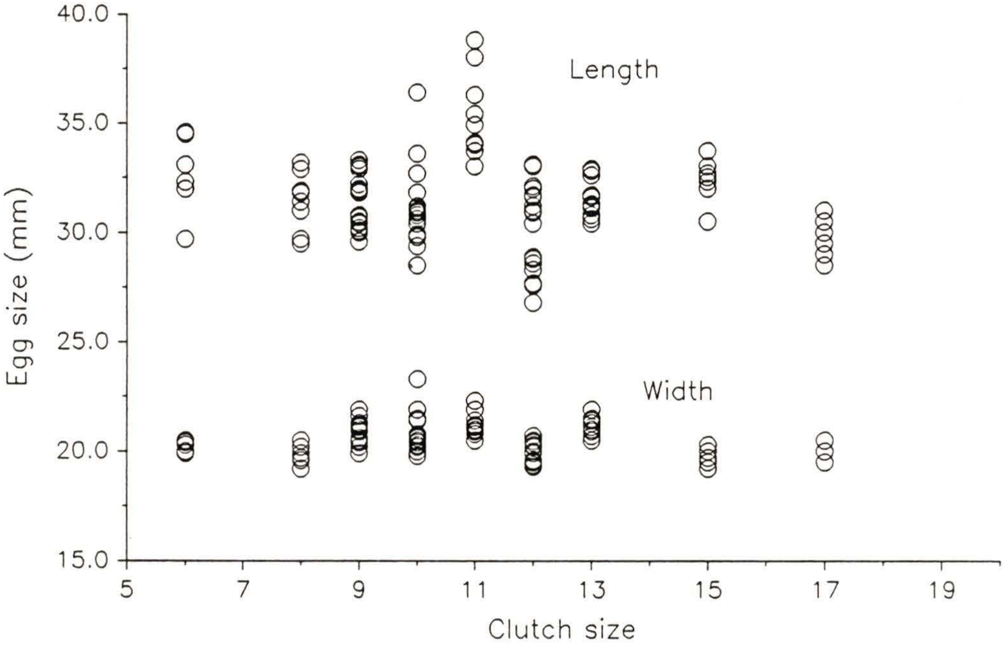

25.0
23.0
21.0
19.0
17.0
15.0
Width(mm)
25.0
27.0
29.0
31.0
33.0
35.0
37.0
39.0
Length(mm)

Figure 23. Relationship of egg length and egg width with clutch size. Number of nests excavated was 13. The correlations were small (length with clutch size: $r = -0.18$, $n = 136$; width with clutch size: $r = -0.26$, $n = 136$)


40.0
35.0
30.0
25.0
20.0
15.0
Egg size (mm)
Length
Width
5
7
9
11
13
15
17
19
Clutch size

Hibernation

In all cases, I found hibernating turtles close to shore on top of the mud bottom. On eleven occasions, I found untagged turtles nearby, also exposed. The transmitters did not noticeably restrict the movement of the turtles. One of the turtles moved 100 m from Fisher Lake to the adjacent Stink Lake between September and November 1987. The following spring, one of the tagged turtles moved from Fisher Lake to Surveyor's Lake within 1 month, a straight-line distance of about 700 m. The radio-tagged turtles moved little (maximum 3 m) during the 3 months of winter observation but although lethargic, were quite capable of movement. On several occasions the animals moved during capture attempts. During three dives using SCUBA, no animals were found near the middle of the lake. During a dive in November 1987, one turtle was found close to shore, on the lake bottom. Sporadic probing in the mud near the shore and near the middle of the lake did not produce any buried turtles. It became increasingly difficult to approach the shore with SCUBA as the ice thickness increased. Oxygen levels were low (3.0 - 3.8 ppm) towards the middle of the lake (depth 12 m). Dissolved oxygen at sites used by turtles ranged from 8.6 to 9.4 ppm at the end of December 1988 and 5.5 to 6.2 ppm at the end of March 1989 (Table 5).

I discovered an intermittent light leak in the lid of the spectrophotometer in the spring of 1989. Because I was unsure of the when the problem began, I discarded all previous lactate values. Samples taken in the winter of 1988 - 1989 were sent to another laboratory (University of British Columbia). Only these values for September, 1988 and December, 1988 are reported here. The values for March 1989

Table 5. Environmental measurements for locations of overwintering turtles. Temperature data are from temperature-sensitive transmitter and thermometer. Water depth is depth below the ice.

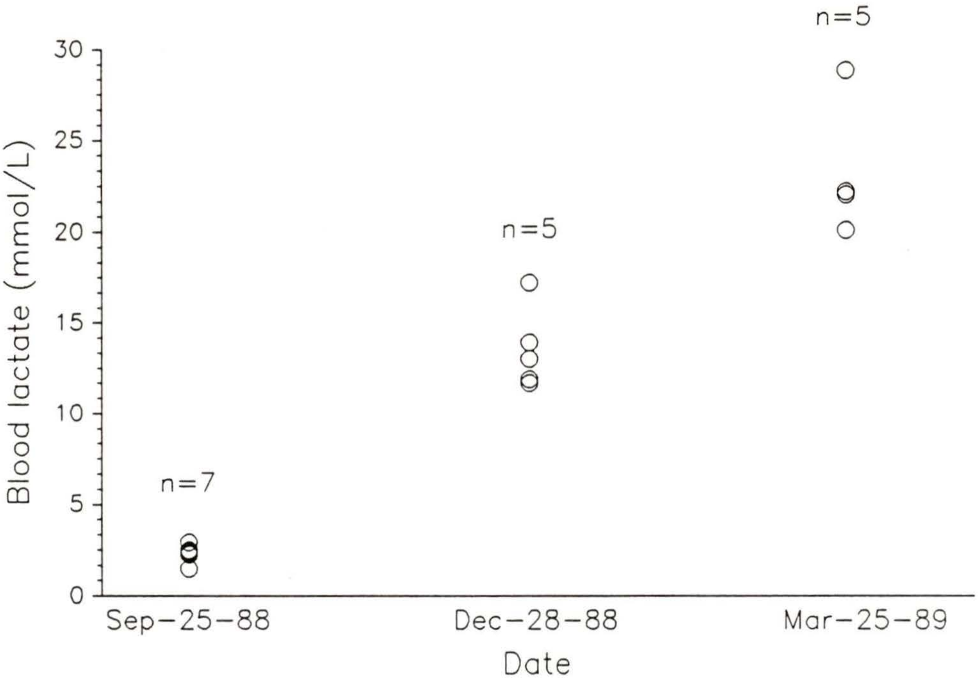
Date	Water Temp. (^oC)	Ice Thickness (cm)	Water depth (cm)	Distance to shore (m)	O_2 level (ppm)
Sep-29-87	15-17	---	---	---	
Nov-21-87	1-3	3	33-54	1.5-2.7	
Jan-02-88	1-3	20	30-60	1-3	
Feb-18-88	2	29-38	0[1]-50	0.6[1]-6.5	
Apr-26-88	14	---	10-100	0.5-10.0	
Sep-25-88	13	---	---	---	
Dec-28-88	3	12	85	3-6.5	8.6-9.4
Mar-25-89	3.5	40-55	40-45	2-6	5.5-6.2

[1] dead turtle

were used as it was possible to properly seal the spectrophotometer if one were aware of the problem. There were significant differences ($p < 0.001$) among lactate levels taken in September 25, 1988 ($n = 7$, mean = 2.41 mmol/L, SD = 0.07), December 28, 1988 ($n = 5$, mean = 13.55 mmol/L, SD = 2.25) and March 25, 1989 ($n = 5$, mean = 23.05 mmol/L, SD = 3.35). Mean lactate levels at each date differed significantly from the preceding date ($p < 0.05$, Figure 24).

In February 1988, I found one of the turtles, frozen in a spot where ice cover reached the bottom of the lake. Whether this death resulted from disturbance due to handling earlier in winter is not known. I found no other frozen turtles, but they would have been difficult to locate without a radio. I could not receive a signal from the temperature-sensitive transmitter after September 1988. After surveying the other lakes and areas between the lakes, I assumed that this was due to transmitter failure rather than the animal having moved out of range.

Figure 24. Lactate levels for winter of 1988 - 1989. Of four turtles with radio transmitters, one was not located in September and another was never found after September.


Blood lactate (mmol/L)
0
5
10
15
20
25
30
n=7
n=5
n=5
Sep-25-88
Dec-28-88
Mar-25-89
Date

DISCUSSION

Population Composition

From observations of nesting locations and success, the observed differences in number of juveniles among lakes is due to differences in recruitment. The significant deviations from unity in sex ratios were in Surveyor's and Engineer's Lakes and in all lakes combined. Populations in other parts of the range of this subspecies have similar numbers of males and females (Christiansen and Moll 1973, MacCulloch and Secoy 1983). Sex ratios approaching 1:1 have been reported for other subspecies of *C. picta* (Cagle 1954, Gibbons 1968a, Ernst 1971b). Bayless (1975) reported more males than females in *C. p. picta* in New York.

The reason for the larger proportion of females in this population is unknown. There is a temperature component to sex determination in these turtles (Bull and Vogt 1981, Vogt and Bull 1982, Gutzke and Paukstis 1984, Paukstis *et al.* 1984, Schwarzkopf and Brooks 1987), which may influence sex ratios in different locations. Sampling bias may also affect these results (Ream and Ream 1966). These biases are related to sex differences in basking patterns (affecting catches in basking traps) and wariness of older individuals. There was less sampling bias of this kind in this study because turtles were taken primarily by dip net. Males and females appeared to have an equal probability of capture because they were equally visible.

Another explanation may be that using the maturity criterion of youngest animal displaying male sex characteristics excludes males that matured after that size. This overestimation of numbers of females has been a difficulty in other studies of turtles (see Gibbons 1970). However, there were no instances of a turtle over 90 mm being classified as a female due to absence of male secondary characteristics and then being classified as a male upon recapture.

Survivorship

This population showed no overall increase or decrease in minimum age-specific survivorship from young to old animals. Because only 2-year survivorship data were available I had to make the assumption that survivorship was similar for each of those 2 years. This survivorship curve is similar to a diagonal curve (Pearl 1930), implying a constant mortality rate for all age groups . This pattern of survivorship agrees with other findings for *C. picta* (Wilbur 1975b) and the related species *Pseudemys scripta* (Gibbons and Semlitsch 1982). However, Gibbons (1968) found that survivorship decreased after the juvenile stage.

All the marked turtle shells that I found were females. There are few aquatic predators and few carcasses were found in the water. Muskrats occur in Fisher Lake and Hidden Lake and are potential predators of turtles in the water (Cagle 1950). The few carcasses found in lakes may have been a result of winterkill rather than predation. Turtles in this area would be most vulnerable to predation on land. Possible land predators in the park include badgers, coyotes, and ravens. The importance of land predators has been reported in other studies (Cagle 1950, Wilbur 1975b). The animal that was able to bite out most of the carapace may have been a bear. There were no similar carcasses found in 1985 or 1988. I found indications (scats, footprints) of bears around Stink and Fisher Lakes in 1987. The vulnerability of nesting females is emphasized by the presence of whole turtle eggs and leg bones in a bear scat.

In 1985, more than half (10 of 17) of the turtle carcasses that could be identified to sex were males (Macartney and Gregory 1985). However, most of the predation (15 of a total of 18 carcasses) that year took place along the channel between Engineer's and Surveyor's Lakes. This channel had dried in 1985 so that animals travelling between the two lakes would be more vulnerable. The remaining three carcasses found in 1985 were females that were gravid when marked. Only one carcass found in 1988 was a result of predation; this lower predation rate could be a result of decreased nesting activity. In addition, there was no sign of bears in the park in 1988.

Growth

Maximum plastron lengths (males = 190 mm, females = 219 mm) approach the maximum lengths reported for this species (in Saskatchewan: males = 208 mm, females = 243 mm, MacCulloch and Secoy 1983).

Yearly growth of turtles is depends on length of growing season. This in turn may be limited by availability of food, environmental temperature, or some intrinsic cycle separate from temperature (Evans and Hegre 1940). Shorter growing seasons due to lower temperatures may therefore partially influence growth in northern ectotherms.

Records for 1951 to 1980 (Environment Canada 1982) indicate that mean monthly air temperatures exceeded 10^{0}C from May to September. Other studies have measured threshold temperatures for activity in this species. Minimum voluntary temperature was 8°C (Brattstrom 1965) and temperatures lower than 8 - 10°C induced torpor (Musacchia and Grundhauser 1962). Sexton (1959) stated that *C. p. marginata* migrated from a pond (overwintering site) to adjacent swamps (summer range) when water temperatures exceeded 8°C. Others (Cagle 1954, Ernst 1971b) found that the threshold for activity of *C. p. marginata* was a water temperature of 10°C. Ernst (1972) found that these turtles were active when air temperatures exceeded 10°C even when water temperatures were lower. Similar threshold water temperatures were found for *C. p. bellii* in southern Saskatchewan (MacCulloch and Secoy 1983). These temperatures correspond to late March in Michigan (Sexton 1959) and late April near the northern range limit (MacCulloch and Secoy 1983; this study).

Feeding has been observed when water temperature exceeds about 15°C (Sexton 1959, 1965; MacCulloch and Secoy 1983) or 18°C (Ernst and Ernst 1972), and approaches 20°C (Ernst 1971b). Animals in this study were active and feeding at water temperatures of 15°C at the beginning of May. The optimum temperature, presumably when fastest growth will occur, is from 20 - 25°C (Cagle 1954). If purely temperature dependent, the length of season when activity and feeding are possible would therefore be reduced at higher latitudes. Basking would increase period of growth by increasing body temperature and digestive rate (Parmenter 1980).

The shift from a carnivorous to a herbivorous diet with increasing age in painted turtles has been suggested to be partly responsible for decreased growth in adults (Gibbons 1967, Knight and Gibbons 1968a, Gibbons and Tinkle 1969, Quinn and Christiansen 1972). In a study of adult and juvenile growth in three populations of *C. picta* in Michigan, a more carnivorous diet was shown to contribute to accelerated growth rate (Gibbons 1967). These observations on differing growth in different age classes and populations have been used to suggest that a more carnivorous diet may be responsible for accelerated growth among populations of northern turtles (MacCulloch and Secoy 1983). There may be a tendency to a more carnivorous diet in northern populations of painted turtles (MacCulloch and Secoy 1983) but differences are obscured by variations in age structure and available food. More important, it has not been established that northern populations experience accelerated growth. The exception seems to be Saskatchewan where males were determined to be 115 and 129 mm plastron length at 3 and 4 years old respectively (MacCulloch and Secoy 1983). This compares to plastron lengths of 88 mm at 3 years in New Mexico and 96 mm at 4 years in Wisconsin (Christiansen and Moll 1973).

The models described here growth parameters of only mature individuals. One-year interval Walford plots of juveniles indicated quite different growth patterns. In my study, the larger values of the Brody growth coefficient (K) for females compared with males suggest a more rapid decrease in amount of growth theoretically remaining to the animal. In conjunction with a larger asymptotic size for females, this implies a faster growth rate. Regression lines for females lie above those of males; therefore, the differences in slopes (e^{-K}) of Walford regressions imply differences in growth between sexes. These differences decrease as the animals get larger. Differences in adjusted means would have implied differences in growth rate at all size classes. The results of the repeated measures ANCOVA indicated a significant difference between male and female growth rate. However, the smaller sample size of the repeated measures test may have resulted in similarities between slopes of male and female regressions.

A shorter growing season at higher latitudes may have the effect of lowering annual amount of growth. Unfortunately, there are few studies that allow direct comparison of growth between northern and southern populations. The studies of *C. picta* in which growth was measured include those of Gibbons (1967, 1968), Wilbur (1975), Hart (1982), and MacCulloch and Secoy (1983). Of these, only Hart (1982) used a growth model that allows direct comparisons with my study.

Gibbons (1967) used linear regressions of length on age for mature males and juveniles to compare the differences in growth among three populations of *C. picta* in southwestern Michigan. Gibbons (1968) again used a linear model to predict growth from 5 yrs to 50 yrs for this species in Michigan. Wilbur (1975) used a logarithmic model to describe age-length relationships in young (9 to 10 yrs) *C. picta* in Michigan. He suggested that growth after 10 years was linear with time and that there was no evidence for asymptotic growth. While asymptotic growth is a questionable concept (Knight 1968), the largest individuals in this study showed no discernible growth during the 3 years of sampling. MacCulloch and Secoy (1983) described growth by both length increase within arbitrary size classes and age-length data. The absence of a model in their study makes comparisons difficult. Both MacCulloch and Secoy (1983) and Wilbur (1975) used existing annuli to infer plastron length of an individual in previous years. This is based on a study by Sergeev (1937; cited by Cagle, 1954) which suggests that the ratio of plastron length to annulus remains constant throughout the life of the animal. This constant relationship of annulus length to plastron length is questionable. In age-length studies of turtle growth, this method increases the already present bias towards individuals with more complete annuli.

Hart (1982) used Walford regressions to compare growth of females from Louisiana and Manitoba. The Walford regressions for females were:

$l_{t+1} = 3.16 + 0.75l_t$ (Louisiana, n = 10) and

$l_{t+1} = 2.85 + 0.84l_t$ (Manitoba, n = 10)

(reported incorrectly as $l_{t+1} = 31.6 - 0.75l_t$ and $l_{t+1} = 28.5 - 0.84l_t$). L_{inf} is equal to 12.6 cm for Louisiana and 17.8 cm for Manitoba. The larger value for K (-ln of slope) for females is related to both a smaller mean asymptotic size and slower growth. This compares to values of $L_{inf} = 18.2$ cm and $K = 0.89$ for the 1 year data in this study. Using this model, the females in my study population had the lowest annual growth and the largest mean asymptotic size of the three locations.

Slower growth can delay sexual maturity, if maturity is size dependent (see following). The age of sexual maturity is an important life history characteristic affecting rate of population increase (Cole 1954).

Reproduction

The smallest male showing secondary sexual characteristics was 86 mm plastron length and 3.5 yrs old. The sex of most animals was apparent by the time the animal was 90 mm plastron length or about 4 years old. The smallest gravid female collected was just over 150 mm plastron length. From the growth curve, a female this size is estimated to be 7 to 8 years old.

Males in this population mature earlier than females. This assumes that the appearance of secondary sexual characteristics in males indicates functional sexual maturity. This is the case with *C. picta* in Michigan (Gibbons 1968b), although Ernst

(1971) found that males (*C. picta* in Pennsylvania) first mated the year following development of secondary sexual characteristics. Allowing for sexual function a year after external signs of maturity, the males in this study mature 2 to 3 years before females.

In two populations of *Pseudemys scripta*, the population with the faster growing individuals contained mature males that were younger and mature females that were larger (Gibbons *et al.* 1981). Therefore, males reached maturity at fixed size and females reached maturity at fixed age. This supposes no advantage to large size in males, in contrast to females. The possible advantages of increased size at maturity for males include preference by potential mates or defense of territory. There is no evidence that these behaviors exist in P. scripta. Advantages of increased size for females include increased fecundity. However, these benefits might be offset by decreasing lifetime reproductive output with increasing age of maturity. The primary cost of delayed maturity to the individual may be risk of predation before reproductive potential is fulfilled.

A similar phenomenon may occur in *Chrysemys picta bellii*. Turtles of the genera *Chrysemys* and *Pseudemys* are so closely related that they are often combined generically (Carr 1952). Differing growth rates at differing latitudes may result in patterns of sexual maturity similar to those observed by Gibbons *et al.* (1980). However, the size of maturity in males is variable (Table 6). Except for my study population, males mature at larger sizes farther north. The few records of age at maturity for females suggest that northern individuals are older at maturity compared with southern populations. Because larger individuals produce more eggs, this pattern of female sexual maturity may compensate for fewer clutches per year due to shorter reproductive seasons (Moll 1973). There are no data for true warm

Table 6. Sizes of sexually mature individuals of western painted turtle, *Chrysemys picta bellii*. Footnotes indicate reference and criteria for sexual maturity.

Location (lat.)	Sex	N	PL (mm)	Age (yrs)
New Mexico	M	55	88	3[1]
(35°N)	F	54	132	5-6
Iowa	F	40	136[2]	
Wisconsin	M	32	96	4[3]
(46°N)	F	23	136	7-8
Minnesota	M	12	83[4]	
	F	33	123	
Minnesota	M	32	98[5]	
	F	22	110	
Manitoba	M	12	100[6]	
(50°N)	F	10	168	
Saskatchewan (50°N)	M	12,64	115,129	3,4[7]
B. C.	M	646	90	4
(49°N)	F	146	151	7-8[8]

[1] Christiansen and Moll 1973
M - presence of sperm in epididymes
F - presence of enlarged yolked ovarian follicles, eggs, or corpora lutea.

[2] Quinn and Christiansen 1972: dissection

[3] Christiansen and Moll 1973; Moll 1973
preserved specimens (see above)
live specimens: M - secondary sex characteristics
F - palpation of oviducal eggs or nesting.

[4] Legler 1954: M - secondary sex characteristics
F - dissection.

[5] Ernst and Ernst 1972. not stated.

[6] Hart 1982: M - dissection or secondary sex characteristics, F - enlarged ovarian follicles

[7] MacCulloch and Secoy 1983
smallest male exhibiting secondary sex characteristics.

[8] MacCartney and Gregory 1985, this study:
M - secondary sex characteristics
F - palpation of oviducal eggs

climate populations. Although New Mexico is near the southern limit of the range of this subspecies, growth could be retarded by lower temperatures at higher altitude (New Mexico 1050 - 1200 m; Wisconsin 320 m; Christiansen and Moll 1973).

Size and age at maturity are important life history attributes which may be subject to selective pressure (Cole 1954). From the population standpoint, delayed maturity results in decrease in intrinsic rate of population increase r (ibid.). The equation (Figure 25)

$$1 = e^{-r} + be^{-ra} - be^{-r(n+a)}$$

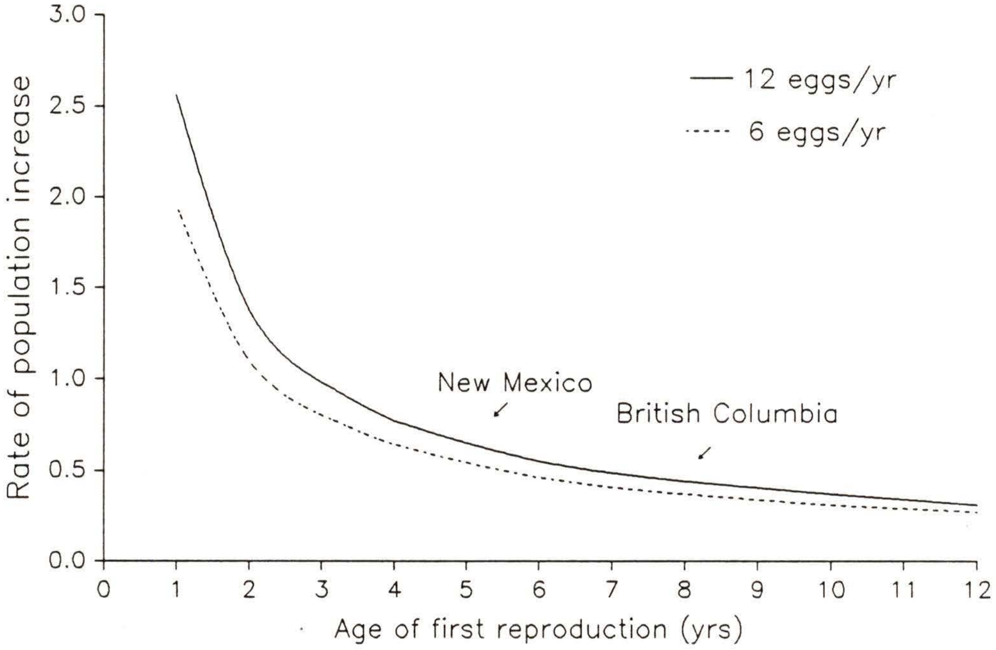
was solved for r where b is the mean clutch size, a is the age of first reproduction, and n is the reproductive lifetime (Cole 1954). This equation represents a simple form of population growth with exponential increase, perfect survivorship, and overlapping generations. The reproductive lifetime was set to 25 years; individual *C. picta* may reach 40 years of age (Gibbons 1968a, Wilbur 1975a). After 8 years, the advantage in reducing age of sexual maturity is slight. There would have to be twice the annual individual reproductive output in a population of animals that matured at 8 years (e.g. British Columbia) to equal the potential population increase of a population in which individuals matured at 5 or 6 years (e.g. New Mexico). The potential for expanding into new locations and recovering from environmental disturbances is obviously reduced in northern populations.

Turtles in this population are probably capable of producing eggs throughout their lifetime. Older individuals may therefore have greater fecundity because number of oviducal eggs increases with size. This agrees with data from Ernst (1971) and Tinkle *et al.* (1981) for *C. p. marginata* in Michigan. However, in the latter study, only 9% to 13% of variation in clutch size was explained by plastron length

Figure 25. The effect of delayed maturity and reproductive effort on intrinsic rate of population increase *r*. The equation

$$1 = e^{-r} + be^{-ra} - be^{-r(n+a)}$$

was solved for *r* where *b* is the mean clutch size, *a* is the age of first reproduction, and *n* is the reproductive lifetime (Cole 1954). The reproductive lifetime (*n*) was set at 25 years. The ages of maturity at New Mexico and British Columbia are indicated.


Rate of population increase
3.0
2.5
2.0
1.5
1.0
0.5
0.0
0
1
2
3
4
5
6
7
8
9
10
11
12
Age of first reproduction (yrs)
12 eggs/yr
6 eggs/yr
New Mexico
British Columbia

compared with 44% in this study. Others (Cagle 1954, Gibbons and Tinkle 1969) have found no correlation between clutch size and body size.

In this study, the female that had 22 oviducal eggs approached the maximum (clutch size = 23) reported for the species (in Saskatchewan, MacCulloch and Secoy 1983). There is a trend among northern populations to lay more eggs while producing fewer clutches (Moll 1973, Christiansen and Moll 1973, MacCulloch and Secoy 1983). Information on latitudinal variation in clutch size and yearly frequency of oviposition is summarized in Table 7. Anomalies such as New Mexico may be due to altitudinal effects (Christiansen and Moll 1973). The increasing clutch size with decreasing yearly frequency of clutches at increased latitude may result in little overall difference in total production of eggs (Moll 1973).

The trends shown here may be confounded by differences among subspecies, which vary in size. Although at a similar latitude to this study, *Chrysemys picta marginata* are smaller (approximate maximum plastron length 170 mm, Carr 1952) and mature at a smaller size (carapace length 104 mm, Schwarzkopf and Brooks 1985). *C. p. marginata* in Ontario produces smaller clutches (mean 7 - 8) and occasionally (13% of females) produce two clutches per year (Schwarzkopf and Brooks 1985). In my study population, the proportion of gravid females was greatly reduced in 1988 compared with the previous year, suggesting that not all females reproduce every year. Once every second or third year may be a better estimate of average reproductive potential. Because more turtles in Ontario produce clutches at least once a year (43 - 73%, Schwarzkopf and Brooks 1985), the overall reproductive effort may therefore be similar.

Table 7. Clutch sizes of painted turtles at various locations. Observations in order of decreasing latitude.

Location	Clutch size (mean)	Number of Clutches	Subspecies, Reference
Saskatchewan	17-23	1	*C. p. bellii*[1]
British Columbia	6-20	1	*C. p. bellii*[2]
	7-18	1	*C. p. bellii*[3]
	9-22	1	*C. p. bellii*[4]
Ontario	6-9		*C. p. marginata*[5]
	(7-8)	1-2	*C. p. marginata*[6]
Wisconsin	3-16(10.7)	1-2	*C. p. bellii*[7]
	7-15(10.2)		*C. p. bellii*[8]
Michigan	6-7	2	*C. picta*[9]
	(6.5)		*C. picta*[10]
S.Michigan	3-10(7.55)	rarely twice	*C. picta*[11]
Pennsylvania	4-6(4.73)		*C. picta*[12]
Illinois	6-17(8.7)	2-3	*C. p. bellii* x *marginata*[7]
Virginia	1-7(4.23)	1-2	*C. p. picta*[13]
Tennessee	3-9(4.8)	2-5	*C. p. dorsalis* x *marginata*[7]
New Mexico	5-15(9)	1-2	*C. p. bellii*[14]
Louisiana	1-6(4.1)	2-5	*C. p. dorsalis*[7]

---

[1] MacCulloch and Secoy 1983

[2] Holland 1937

[3] Macartney and Gregory 1985

[4] This study

[5] Whillans and Crossman 1977

[6] Schwarzkopf,Brooks 1986

[7] Moll 1973

[8] Christiansen,Moll 1973

[9] Wilbur 1975b

[10] Gibbons 1968b

[11] Tinkle *et al.* 1981

[12] Ernst 1971a

[13] Mitchell 1985

[14] Christiansen,Moll 1973

The latitudinal trends in reproductive effort are a product of at least 2 factors: (1) size of the animal, which generally increases with latitude within subspecies and varies among subspecies, and (2) length of reproductive season which decreases with increasing latitude. Painted turtles probably produce as many clutches as can develop in the reproductive season (Moll 1973).There were significant differences in egg length and egg width among clutches. This variation was only slightly ($r^2 = 0.15$) attributable to differences in clutch size. For five nests sampled in Saskatchewan (MacCulloch and Secoy 1983), egg length decreased and egg diameter was unchanged with increasing clutch size. Clutch sizes (17 - 23) and egg length (30.0 to 37.5mm) were larger than those in this study. Egg widths were similar (18.2 to 22.9mm). For *C. picta marginata*, egg size was correlated positively with body size (Congdon and Tinkle 1982, Schwarzkopf and Brooks 1986). Schwarzkopf and Brooks (1986) reported no significant correlation between egg size and clutch size although clutch size was correlated positively with body size. The small amount of variation in egg size accounted for by clutch size in my study population indicates that some other factor must account for most of the variation in egg size. Schwarzkopf and Brooks (1986) found that, for sequential measurements of individuals, clutch size did not vary among years; there was a slight variation in egg size. This suggests that some quality that varies among years (e.g. length of growing season, food availability) may affect egg size in their study population. This is the opposite of patterns predicted by optimal egg size theory (Smith and Fretwell 1974, Brockelman 1975). According to this model, parental investment in the form of increased lipid stores within the egg should reach an optimum level where increased offspring survivorship is balanced by decreased parental fitness. The variation in egg size would become small and clutch size would vary in response to environmental changes.

Congdon *et al.* (1982) suggest that evidence for optimization includes little variation among individuals and no correlation of egg size with body size. While there seem to be different patterns of variation, by these criteria, egg size may not be optimized within populations of freshwater turtles (Congdon and Tinkle 1982, Congdon *et al.* 1982, Congdon and Gibbons 1983, 1985, Schwarzkopf and Brooks 1986, this study). Brockelman's (1975) model is based on competition among young, which may not apply to this population. There seem to be ample quantities of insect larvae to serve as food for young turtles. High mortality among eggs and hatchlings due to predation and overwintering mortality respectively may favor increased clutch size. Egg size in northern populations may be the minimum that allows sufficient lipid stores for the hatchlings to develop successfully and overwinter.

Observations on distribution of nesting areas agree with the 1985 survey (Macartney and Gregory 1985). Nest sites appeared to be chosen for maximum solar exposure, on northeast slopes surrounding the lakes. Fluctuations in temperature (range 20^oC to 30^oC) were modified by depth of soil. Nest temperature is important in these animals because incubation temperature determines sex (Bull and Vogt 1981, Vogt and Bull 1982, Gutzke and Paukstis 1984, Paukstis *et al.* 1984, Schwarzkopf and Brooks 1987). Eggs incubated at 22^oC produce a mixture of males and females, at 27^oC eggs produce males, and at 32^oC produce females (Gutzke and Paukstis 1984). Schwarzkopf and Brooks (1987) found that the distribution of nest sites on northeast slopes resulted in maximum temperature rather than sex selection. Sex ratios were correlated with nest temperatures but nests containing females occurred over the entire range of nest temperatures (expressed as accumulated heat units). The temperature profile presented in this study was limited to a few consecutive days. More data are needed for nests and eggs within nests to establish patterns of nest site selection and sex determination.

Hibernation

Previous laboratory studies (Gatten 1981, 1987; Jackson and Ultsch 1982; Ultsch and Jackson 1982a,b; Herbert and Jackson 1985a,b; Ultsch *et al.* 1987; Jackson 1987) have involved the investigation of plasma lactate increase under simulated hibernation conditions. Gatten (1981) found body lactate levels of 62 mmol/L (558 mg%) in a turtle after 67 days in an outdoor tank at 0 - 8^{o}C (mean 3.7^{o}C). Ultsch and Jackson (1982a) found that lactate levels increased to approximately 90 mmol/L in painted turtles after 90 days at 3^{o}C under severely hypoxic conditions compared to 30 - 85 mmol/L in oxygenated water. In contrast, the range of lactate levels among the turtles in this study was 20 - 29 mmol/L after more than 90 days under ice cover.

Ultsch and Jackson (1982b), Ultsch *et al.*(1985), Gatten (1987), and Penney (1987) have discussed costs and benefits of overwintering in the water column as opposed to burying in the mud. Possible advantages of burial in the mud include avoidance of predators (e.g. raccoons) in the spring when turtles are still cold and sluggish. There is also an aerobic fungus that attacks laboratory turtles at low temperature in oxygenated water (Ultsch *et al.* 1985). However, I have never seen this fungus (probably *Achlya*) in my study population. Overwintering with access to dissolved oxygen has obvious advantages for alleviation of lactate acidosis by extrapulmonary respiration (Herbert and Jackson 1985b). Oxygen levels taken by oxygen meter in December 1988 were 8.6 ppm and 9.4 ppm at locations where turtles were found (Table 5). This contrasted with readings taken at the middle of the lake (12 m) where oxygen levels were 3.8 and 3.0 ppm. Higher oxygen levels near the shore may explain a preference for those sites in spite of the greater danger of freezing. The level of oxygen used in laboratory simulations of oxygenated conditions by Ultsch and Jackson (1982b) was 9.4 ppm. I suggest therefore that the high availability of oxygen in the lake is likely responsible for the low blood lactate levels found in this study. Further work is needed to explain the disparity in levels between laboratory and field values under apparently similar conditions.

Because I did not find any of the radio-tagged turtles buried in the mud, at least some turtles must overwinter in the comparatively oxygen-rich water column. This is likely not an artifact of the tagging procedure because I found other untagged turtles nearby. This contrasts with the frequently-made statement that aquatic turtles overwinter buried in the mud (cf. Ernst and Barbour 1972, Gregory 1982). On the other hand, there have been many observations of painted turtles swimming under the ice (e.g. Carr 1952, Sexton 1959, and Gibbons 1967). Furthermore, because turtles in the laboratory have been shown to tolerate much higher plasma lactate levels than observed here, I suggest that acidosis is not the major factor limiting the northern distribution of painted turtles.

By contrast, I found only one living hatchling in the nests examined in the spring. The supercooling limit for a closely related species, *Pseudemys scripta*, is - 5^{o}C (Lowe *et al.* 1971). *C. p. marginata* hatchlings can survive 24 hr of - 4^{o}C but fail to survive - 10.9^{o}C (Storey *et al.* 1988). Winter temperatures of nests in Michigan reached -3.3^{o}C with 0% to 80% winterkill which was negatively correlated with snow cover (Breitenbach *et al.* 1984). Winter temperatures of two nests in Ontario reached - 8^{o}C; all hatchlings survived (Storey *et al.* 1988). These temperatures are lower than those observed in my study population (- 5 and - 6^{o}C). The high winterkill in my study population may be due to differences in freeze tolerance between the two subspecies. The low amount of snowfall (109 cm, Environment Canada 1982) in Kikomun Creek Provincial Park would certainly contribute to overwintering mortality. More information is needed on the effect of duration of subfreezing temperature on hatchling survival.

Hatchling *C. picta* generally overwinter in the nest (Hartweg 1944, 1946, Sexton 1957, Williams 1957, Woolverton 1961,1963, Bleakney 1963, Wilbur 1975a,b, Tinkle *et al.* 1981, Christens and Bider 1987), although there are reports of fall emergence (Ernst 1971b, Pennsylvania). Other species emerge from the nest in the spring in northern regions (*Emydoidea blandingii*: Congdon *et al.* 1983, *Chelydra serpentina*: Congdon *et al.* 1987). Advantages of spring emergence may be more food and fewer predators (Wilbur 1975a,b; Gibbons and Nelson 1978), plus avoidance of energy expenditure and shelter-seeking in the fall. Cessation of winter cold may be the cue to begin emergence from the nest (Gibbons and Nelson 1978). Although cold conditions have been suggested as an explanation of spring rather than fall emergence (Sexton 1957, Ernst and Barbour 1972), indirect evidence suggests delayed emergence in this species as far south as Louisiana (Cagle 1954).

In two of the nests, hatchlings were seen to orient themselves facing upwards as reported by Breitenbach *et al.* (1984). This may be the last step before emerging from the nest. In my study population some hatchlings may have emerged from the nest in the fall. The nest that had evidence of fall emergence was the first one observed the previous nesting season. Therefore, the individuals that do not emerge and are subject to freezing may have developed later. Since spring emergence is the general pattern for this species, most turtles at the northern limit of the range may be exhibiting specific behaviour that is ill-suited to these conditions. It is likely that the northern limit of painted turtle distribution could be set by heavy overwintering mortality of hatchlings.

Conclusions

Growth rates for this population are lower, probably in response to a shorter growing season. This has resulted in delayed sexual maturity for females, the consequences of which are a potential reduction in the rate of population increase. Females apparently produce clutches at a rate of less than one a year, less than recorded for any other population. Larger clutches are produced, probably as a result of larger body size.

Survivorship after the animal leaves the nest is relatively constant with age. The nesting females are most vulnerable as there are more land predators. Adults hibernate at the bottom of ice-covered lakes, a refuge from freezing. The turtles in this population hibernate unburied and not in the anoxic environment under the mud. Overwintering survivorship of hatchlings in the nest is very low, probably because of extended periods of freezing in the soil. Successfully overwintering hatchlings possibly leave the nest in the fall. Distributional limits may therefore be set by overwintering survival of hatchlings rather than adults.

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