To the Graduate Council:

I am submitting herewith a dissertation written by Joseph C. Mitchell entitled "Population Ecology and Demography of the Freshwater Turtles Chrysemys picta and Sternotherus odoratus." I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology.

Arthur C. Echternacht, Major Professor

We have read this dissertation
and recommend its acceptance:

Accepted for the Council:

Vice Chancellor
Graduate Studies and Research

POPULATION ECOLOGY AND DEMOGRAPHY OF THE FRESHWATER TURTLES *CHRYSEMYS PICTA* AND *STERNOTHERUS ODORATUS*

A Dissertation

Presented for the

Doctor of Philosophy

Degree

The University of Tennessee, Knoxville

Joseph Calvin Mitchell

August 1982

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1979, granted permission to study turtles in Laurel Lake. Mr. E. C. Robins, Jr. granted permission to collect turtles in Grassy Swamp Lake. The Virginia Commission of Game and Inland Fisheries granted trapping permits.

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ABSTRACT

Records of over 6000 captures of about 1950 individual turtles were analyzed to determine ecological and demographic characteristics of syntopic populations of the freshwater turtles Chrysemys picta (Emydidae) and Sternotherus odoratus (Kinosternidae). Populations of these turtles were studied over a three year period in an urban lake near Richmond, Virginia, U.S.A. Monthly samples from a nearby lake provided information on reproductive cycles and their variations between species and years.

Male reproductive cycles were synchronous between species and years except for onset of spermatogenesis; S. odoratus began about one month later than C. picta. Peak spermiogenesis was in August, as were maximum testis weights. Female cycles were generally concordant but S. odoratus were ovigerous about three weeks longer than C. picta. Both species exhibited size specific fecundity and produced multiple clutches. Age specific fecundity was demonstrated by S. odoratus. Mean clutch size was 4.2 for C. picta and 3.1 for S. odoratus. There was little variation between years. Female minimum age at maturity at this site was six years for C. picta and four years for S. odoratus. Males matured in their third and second years, respectively.

Chrysemys picta exhibited age and sex specific differences in growth rates, but male and female S. odoratus grew at almost identical rates. Most individuals of both species grew significantly less during drought years. Delayed emergence from the nest was documented for this area for C. picta, but results suggest most S. odoratus emerge the year of egg deposition. Population sizes were estimated to be 517 for C.

picta and 534 for S. odoratus. Both populations appear to be growing. Sex ratios were not significantly different from unity. Female C. picta at this site mature at age eight years and males at age four, whereas female S. odoratus mature at age four and males at two years of age. The differences in age at maturity between sites is discussed from the standpoint of life history evolution. Survivorship during the study period was high for all sex and age groups, except for juvenile C. picta. The population ecology and life histories of these species are compared and discussed in relation to urban environments.

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CHAPTER 1

INTRODUCTION

Recent interest in the evolution of life histories (Williams, 1966; Pianka, 1970, 1972; Stearns, 1976, 1977, 1980) has illustrated the need for comparative demographic information on a variety of species. This information is used to support or refute theoretical projections of whether clusters of life history strategies exist (Pianka, 1970) or occur along a continuum of strategies (Stearns, 1976). Life history traits, such as clutch size and frequency, age at first reproduction and age-specific survivorship, are presumably controlled by natural selection and adjustments to local environments should, therefore, result in geographic variation in these traits.

Investigations of reptilian life histories from a demographic viewpoint were pioneered by the works of Blair (1960) and Tinkle (1967). Subsequent development of our understanding of reptile life histories was based on both intraspecific and interspecific studies of lizard demography (Tinkle, et al., 1970; Turner, et al., 1970; Tinkle and Ballinger, 1972; Ballinger, 1973, 1980; Vinegar, 1975; Iverson, 1980; Dunham, 1981; and others). A framework upon which life history studies of freshwater turtles can be based was established by the investigations of Cagle (1937, 1939, 1942, 1944, 1950, 1954), Sexton (1959a, b) and Tinkle (1958a, b, 1961). Studies of freshwater turtle demography have, however, lagged behind those of lizards. Only one life table has been published for freshwater turtles and is on a population of Chrysemys picta in southeastern Michigan (Wilbur, 1975b; Tinkle, et al., 1981). Clearly, a seroius gap in the development of our knowledge of life

histories of freshwater turtles is the lack of comparative demographic data.

Variation in parameters of freshwater turtle populations has been documented by several investigators both between species (Cagle, 1942, 1948; Mahmoud, 1969; Gibbons, 1970a; Vogt, 1980) and among populations of the same species (Cagle, 1954; Tinkle, 1961; Gibbons and Tinkle, 1969; Moll and Legler, 1971; Gibbons, et al., 1979, 1981). Gibbons (1967) and Quinn and Christiansen (1972) demonstrated differences in growth rates among populations of Chrysemys picta and attributed them to differences in habitat quality and substrate types, respectively. Moll (1973) and Christiansen and Moll (1973) showed that reproductive characteristics of C. picta varied latitudinally, as did Tinkle (1961) for Sternotherus odoratus. Information on some demographic parameters, such as age at first reproduction, clutch size and clutch frequency, have been published by Moll and Legler (1971), Gibbons (1968c, 1969), Gibbons and Coker (1977), Ernst (1971c), Iverson (1977, 1978, 1979a, b), Cox and Marion (1978) and others. Gibbons and his co-workers (1979, 1981) are involved in long-term studies of the life history of Chrysemys (=Pseudemys) scripta in southeastern North America. The late D. W. Tinkle and his students, notably J. D. Congdon (1981), have continued the long-term study of a Michigan population of C. picta. Though not exhaustive, these studies demonstrate adaptations to local environments and suggest complex geographic variation in life history characteristics.

Many freshwater turtle populations exist in aquatic systems which are under varying degrees of pressure from man's activities (Gibbons,

1970b; Christy, et al., 1974; Moll, 1973, 1980) and many of these are in areas of urban development. Populations in urban areas would be expected to exhibit variation in population and demographic characteristics when compared to populations inhabiting relatively undisturbed systems (e.g., preserves: Sexton, 1959b; Wilbur, 1975b; government protected areas: Gibbons, et al., 1981). This paper reports a study of the population ecology and demography of two species of freshwater turtles, Chrysemys picta (Emydidae) and Sternotherus odoratus (Kinosternidae), which inhabit urban lakes in Virginia (U.S.A.). The results are based on an intensive three year investigation involving over 6000 captures of 1943 individual turtles. There were three objectives, 1) to obtain as much ecological information as possible on these two species in this geographic region, 2) to obtain population ecology and demographic data to compare these characteristics with those of other populations and 3) to compare the life histories of these two syntopic species. The results of this study are presented here under three chapter headings: reproduction, growth, and ecology and demography. A summary is included which provides an overview of the life histories of C. picta and S. odoratus.

Data on populations inhabiting two Virginia lakes were obtained during this investigation. Laurel Lake was utilized for an intensive mark-recapture study and Grassy Swamp Lake for reproductive samples. Figure 1 illustrates the relative locations of these study sites. These lakes occur in an area of Virginia characterized by mild winters and warm humid summers. Turtles have been found every month of the year except January. Details of the climate of the area are provided in Appendix A.

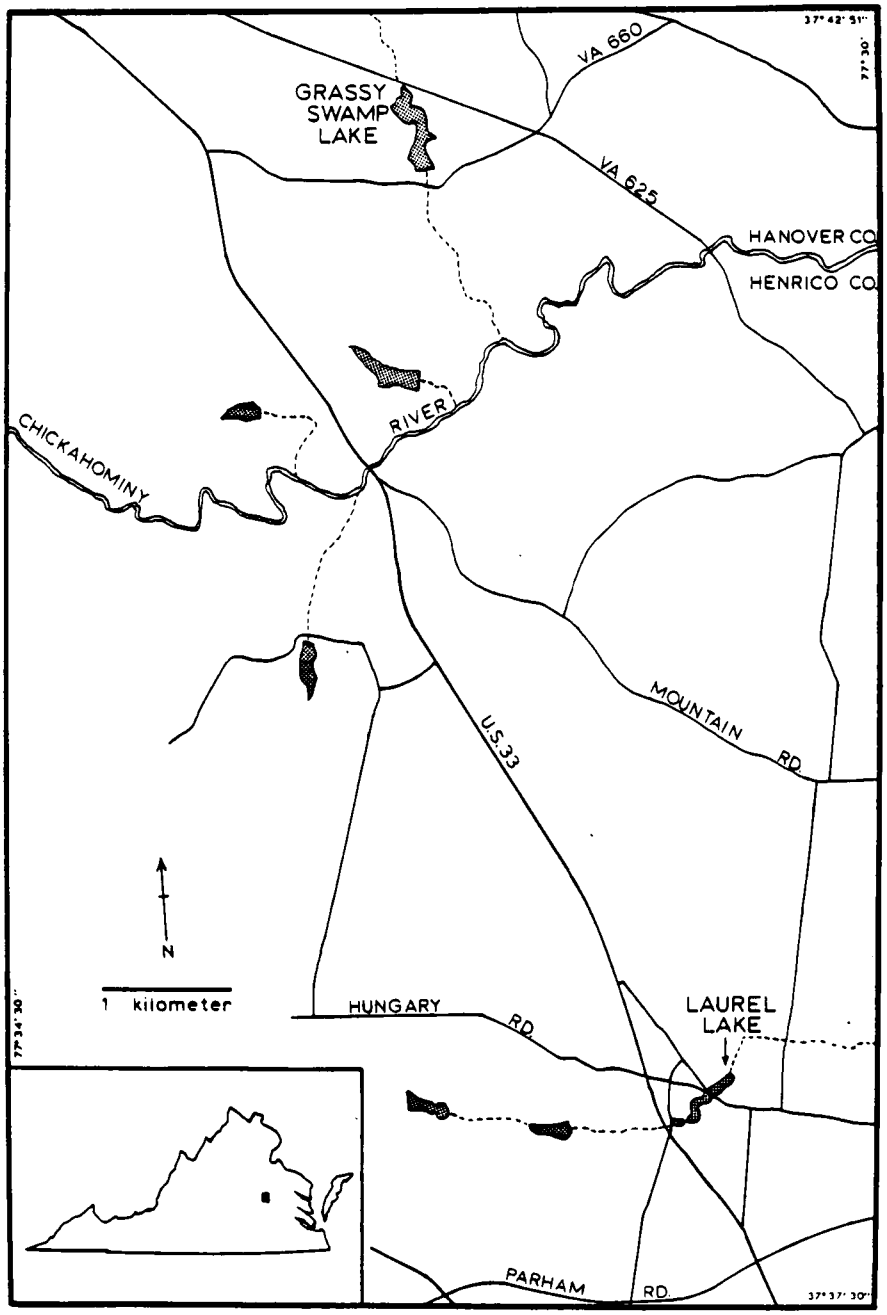

Figure 1. Relative locations of Grassy Swamp Lake and Laurel Lake study sites. Solid lines indicate major roads in the area and stippled areas are lakes. The insert shows the study area relative to the state of Virginia.

Chrysemys picta picta, the eastern painted turtle, is an abundant, medium size basking turtle inhabiting a variety of aquatic habitats in the eastern and northern United States (Ernst and Barbour, 1972; Conant, 1975). This species mates in spring and the one to ten eggs are laid in a terrestrial nest in late spring and early summer. Except for the studies of Emlen (1969) and Bury, et al. (1979), behavior has been little studied. Its population ecology has been the subject of several investigations (Sexton, 1959b; Ream and Ream, 1966; Gibbons, 1968b,c; Ernst, 1971c, 1974, Bayless, 1975). Gibbons (1967, 1968b), Ernst (1971b) and Wilbur (1975a) studied growth, Sexton (1959b), Emlen, (1969) and Ernst (1970) studied movements and information on carapacial algae and parasites is provided by Gibbons (1968a), Ernst (1971d) and MacCulloch (1981). Reproduction has been widely considered (e.g., Gibbons, 1968c; Ernst, 1971a, Moll, 1973; Callard, et al., 1978).

The stinkpot, Sternotherus odoratus, is a locally abundant, inconspicuous turtle inhabiting a variety of habitats in eastern North America (Ernst and Barbour, 1972; Conant, 1975). This species is seen only occasionally out of water; it spends most of its time on the bottom. Mating occurs in early spring and one to seven eggs are laid in a variety of terrestrial sites in late spring and early summer. Mahmoud (1967) described courtship behavior but other aspects of stinkpot behavior have not been addressed. It has been the subject of few population studies (Cagle, 1942; Wade and Gifford, 1965; Mahmoud, 1969; Tinkle, 1961). Movements have been studied by Ernst and Barbour (1972) and Mahmoud (1969) published analyses of growth. Reproduction is the most studied aspect of S. odoratus biology (Risley, 1933, 1938;

Cagle, 1937; Edgren, 1942, 1949, 1956, 1960; Tinkle, 1961; Gibbons, 1970c; Iverson, 1977).

Both of these species offer excellent opportunities to study population ecology and demography. They are abundant, are captured with a variety of methods and inhabit aquatic systems which provide definitive population boundaries. They can be marked with a unique number which, for all but the youngest turtles, is retained for life (Sexton, 1959a) and age and growth rates can be inferred from measurements of annuli deposited on the scutes of the shell (Sexton, 1959a; Wilbur, 1975a; Risley, 1933; Mahmoud, 1969). These species are well known taxonomically and a considerable base of natural history information is available for each.

CHAPTER II

REPRODUCTION

Introduction

Reproduction is the most commonly studied aspect of the biology of freshwater turtles. Some information is available on most North American species (Ernst and Barbour, 1972; Moll, 1979). Reports vary from brief notes (Nichols, 1933, 1947; Edgren, 1949, 1956, 1960; Adler, 1961; Gibbons, 1970c; Sanderson, 1970) to quantification of reproductive cycles (e.g., Atland, 1951; Legler, 1960; Moll and Legler, 1971; Christiansen and Dunham, 1972). These studies demonstrate considerable inter- and, in some species, intraspecific variation in reproductive parameters.

Of the reproduction studies on the North American freshwater turtle fauna, Chrysemys picta has received the most attention. Seasonal macroscopic changes of testes were first described by Gibbons (1968c) who demonstrated the relationship between testis weights and body size. Ernst (1971a) described the spermatogenic cycles for a Pennsylvania population and Moll (1973) and Christiansen and Moll (1973) showed that spermatogenic cycles of western and midwestern C. picta varied latitudinally. Respectively more studies have been done on female reproduction. Seasonal macroscopic changes have been described for ten populations (Powell, 1967; Gibbons, 1968c; Ernst, 1971a; Moll, 1973; Christiansen and Moll, 1973; Callard, et al., 1978). Cagle (1954) was the first to demonstrate wide geographic variation in clutch size and size at maturity. More recently, Gibbons

and Tinkle (1969) demonstrated that clutch size varied significantly among three southern Michigan populations. Information on various aspects of female reproduction, including clutch size, nesting, eggs, incubation time and neonates, is found in Cagle (1937, 1954), Legler (1954), Gemmell (1970) and Ernst (1971c).

Sternotherus odoratus reproduction has received considerably less attention. Risley (1933, 1938) pioneered the study of reptilian spermatogenic cycles with his studies of this species. Mahmoud and Klicka (1972) demonstrated gross seasonal changes in testis weights in Arkansas and Oklahoma samples. Spaet (1973) described seasonal changes in tubular and interstitial areas of S. odoratus testes. Recently, McPherson and Marion (1981a) described the male cycles of an Alabama population and presented a standardized classification of spermatogenic stages. Seasonal changes in the female reproductive cycle have been examined by Risley (1933), Mahmoud and Klicka (1972) and McPherson and Marion (1981b). Tinkle (1961) described geographic variation in various aspects of female reproduction from museum specimens, particularly clutch size, clutch frequency and age at maturity. Gibbons (1970c) and Iverson (1977) presented information on clutch size, number of clutches per year and egg data for Florida populations. Information on various aspects of stinkpot reproduction, including clutch size, egg size, nests, incubation time and neonates have been published by Risley (1933), Cagle, (1937), Edgren (1942, 1949, 1956, 1960) and Ewert (1979). Generalized temperate zone reproductive cycles of male and female freshwater turtles were reviewed by Moll (1979) who used C. picta and S. odoratus in his examples.

In the studies noted above it is clear that considerable geographic variation exists in reproductive parameters among populations of Chrysemys picta and Sternotherus odoratus. It is necessary, therefore, to understand the timing and variations of reproductive cycles of local populations on order to evaluate their life histories. This chapter presents a detailed description of the male and female cycles of these two species in Virginia. The objectives were 1) to quantify the seasonal macroscopic and microscopic changes in the testes in males, 2) to quantify the characteristics of the female reproductive cycles and 3) to evaluate some of the factors that contribute to their variation.

Materials and Methods

Samples of male and female Chrysemys picta and Sternotherus odoratus were captured monthly during 1980 and 1981 from Grassy Swamp Lake, Hanover County, Virginia, U.S.A. Grassy Swamp Lake is an approximately four hectare, shallow, apparently eutrophic, impoundment located 13 kilometers northwest of Richmond, Virginia at an elevation of 67 meters above mean sea level. Most of the northern end of the lake is less than two meters in depth and supports dense growths of Nuphar luteum Sibthorp and Smith and Nymphea odorata Aiton. The watershed consists primarily of stands of Quercus alba L. and Acer rubrum L. and is in an area of housing development. The southern section is traversed by a power line and the lake is open to fishing and boating, Community associates are Chelydra serpentina, Kinosternon subrubrum, Pseudemys rubriventris and the introduced Pseudemys scripta elegans.

Most turtles were captured in funnel traps (Iverson, 1979) baited with sardines and set around the lake margin, particularly in the northern section. Several individuals were caught by hand while wading. All specimens from Grassy Swamp Lake were fixed and stored in 10% formaldehyde, usually within three hours of capture, none later than six hours. Before fixing, most turtles were measured to the nearest millimeter along the midline of the carapace and/or plastron and weighed to the nearest gram. Later, the left testis of all males was removed, weighed to the nearest milligram on an electronic balance and stored in a vial. These testes were prepared for routine histological examination, sectioned at six microns and stained with Harris' hematoxylin and eosin; a second was stained with Berg's stain for spermatozoa (Berg, 1958). Testicular sections were staged by using the classification developed for freshwater turtles by McPherson and Marion (1981a); their terminology is used herein. Seminiferous tube diameters and epithelial cell heights were determined by taking the average of ten measurements (in microns) of circular tubules and their epithelia. Epididymes were qualitatively noted as enlarged or small. Presence of sperm was determined by staining a small section of epididymus with toluidine blue, squashing it on a slide and examining it for few or abundant spermatozoa. A male was considered mature if it had an advanced stage of spermatogenesis recorded for it.

Female reproductive tracts were removed after dissection of the plastron and measurements were taken to the nearest millimeter of enlarged follicles and shelled eggs. The number of follicles, eggs

and corpora lutea were recorded and the ovaries, without oviductal eggs, were weighed to the nearest gram. Due to slight differences in follicle sizes between species, follicles were assigned to the following classification scheme: C. picta: Class I - less than 6 mm in diameter, Class II - 6-11 mm and Class III - greater than 11 mm; S. odoratus: Class I - less than 5 mm, Class II - 5-9 mm and Class III III - greater than 9 mm. Class I follicles were numerous throughout the year and were not counted. Before ovulation of the first clutch, there were usually two distinct sets of follicles present, corresponding to Classes II and III. Following ovulation there was a distinct set of corpora lutea. These regressed in size during the postovulatory period. If a second clutch was produced, another, larger set could be distinguished from the first. Evidence of multiple clutches was based solely on this criterion. Oviductal eggs were weighed separately to the nearest 0.1 gram. Where possible the age of an individual was noted by counts of growth annuli (see Chapter III). Criteria for maturity were vitellogenic follicles (Class II in autumn or Class III), oviductal eggs or corpora lutea in females.

Following prepreservation dissection from ovigerous females, several clutches of eggs were incubated in moist vermiculite at room temperature (approximately 27±3 C). Incubation times were noted from day of dissection to pipping and are assumed to approximate natural incubation periods. Hatchlings were measured and weighed as above and usually released after processing.

Statistical computations throughout this study follow Zar (1974) and most were performed on the University of Richmond's VAX computer

using Statistical Package for the Social Sciences (SPSS) programs (Nie, et al., 1975). Minimal statistical significance was set at P=0.05. All specimens and histological slides are to be deposited in the National Museum of Natural History.

Results

Reproduction in Male Chrysemys picta

Body size and age at maturity. The 171 adult male C. picta examined for reproduction averaged 111.7±13.2 mm (77.4-136.5) in carapace length (CL) and 103.1±11.9 mm (72.0-124.4) in plastron length (PL). Two three-year old males (77.0 and 80.1 mm PL) collected in September 1980 contained mature spermatozoa in the tubular lumen (stages 6 and 7, respectively; see below). All four-year old males, ranging in size from 72 mm PL (caught in April 1981) to 85.9 mm PL (76.7-85.9, N=10, all caught in July or later in the growing season) were sexually mature. Their spermatogenic stages were concordant with stages registered for older males collected at similar times. Since sexual maturity is achieved in the third year, males have mature spermatozoa in the epididymes for use in their first mating in the spring of their fourth year.

Testicular weight cycle. An analysis of covariance (ANCOVA) was used to test the hypothesis that monthly variation in testis weight was not significantly affected by plastron length, a measure of body size. The design included raw testis weight as the dependent variable, month of collection as the independent variable and plastron length as

the covariate. A scatterplot of testis weight with plastron length indicated a linear relationship. A priori tests of normality and homogeneity of variances were not performed as indicated by Zar (1974), who stated that ANCOVA is sufficiently robust to preclude them. Results of the ANCOVA indicated that monthly testis weight variation was significantly affected by body size ($F=73.70$, 1, 170 d. f., $P<0.001$). To make unbiased comparisons between monthly samples, raw testis weights were adjusted by the equation $\hat{Y}_i = Y_i - X_i - \hat{X}_j(\beta xy)$, where $\hat{Y}_i$ is the adjusted testis weight, Y_i is the raw testis weight, X_i is the plastron length at capture, $\hat{X}_j$ is the mean plastron length of the total sample and β_{xy} is the regression coefficient of testis weight versus plastron length (Steel and Torrie, 1960). Adjusted testis weights exhibited minimal values in May, an increase June through July, peak values in August and September and regression October through April (Figure 2). August and September adjusted weights were concordant with maximum spermatogenesis (see below).

A multiple ANCOVA was performed to determine if adjusted testis weights (dependent variable) differed significantly between months (1980 and 1981 samples combined) and years (independent variables). Plastron length was included as the covariate. The classical design of the ANCOVA (Nie, et al., 1975) was used, wherein testis weights are adjusted for the covariate before tests are performed with the independent variables. The results indicated a significant effect on adjusted testis weight due to month ($F=54.8$, 7, 170 d. f., $P<0.001$). and an insignificant effect due to year ($F=0.004$, 1, 170 d. f., $P=0.947$). Since combined monthly sample variances of adjusted testis weights were

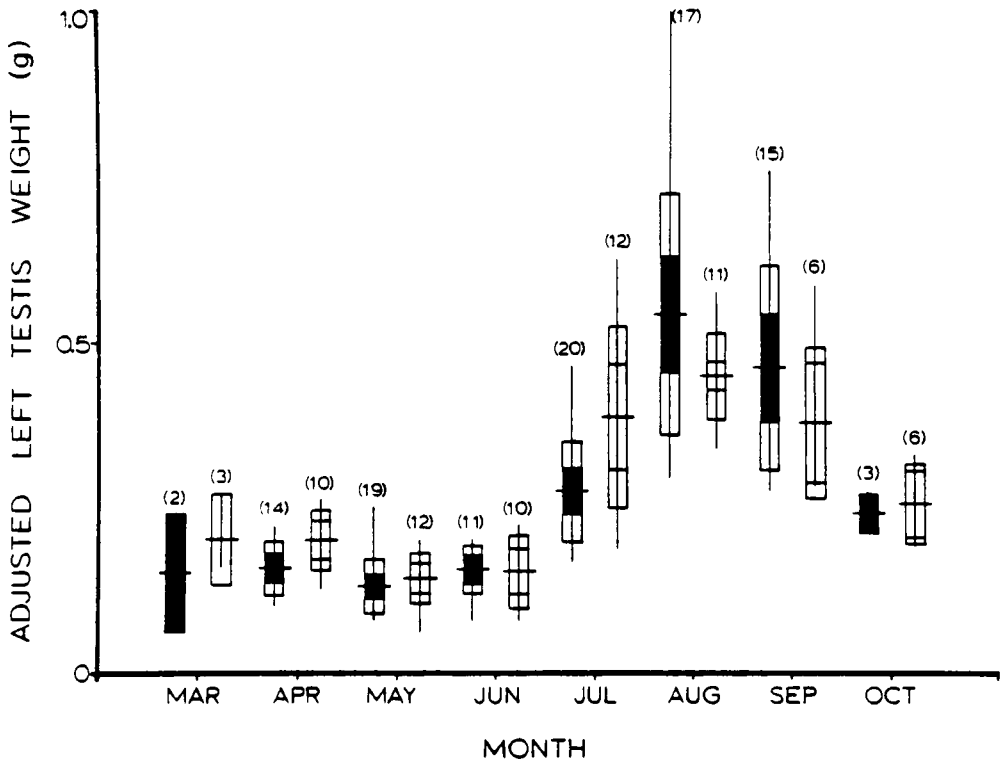

Figure 2. Seasonal variation in adjusted left testis weights for Chrysemys picta. Closed rectangles respresent 1980 and open rectangles 1981. The mean is the horizontal line, outer rectangle one standard deviation, inner rectangle two standard errors and vertical line the range.

heterogeneous (Bartlett's test, B=13.04, P<0.001), they were transformed to their logarithms (B=0.723, P=0.653) and subjected to a one-way analysis of variance (hereafter ANOVA). This test also showed a significant month effect (F=65.1, 7, 170 d. f., P<0.001). Tukey's Honestly Significant Difference (HSD) test on log-transformed adjusted testis weights (mean range = -0.310 to -0.883) showed that August and September samples differed significantly (P<0.05) from July and October samples, while both these groups were significantly different from samples taken in April through June. October and March samples were not significantly different.

Spermatogenesis. Examination of testicular histosections revealed that spermatogenesis in C. picta began in April with appearance of primary spermatocytes (stage 2). Cellular debris (dead cells from previous cycles) was found in most specimens and a few spermatozoa were found in their lumen. Spermatogonia were abundant and outnumbered Sertoli cells. Table 1 illustrates the seasonal distribution of this and other stages for 1980 and 1981. Meiotic divisions producing secondary spermatocytes and a few undifferentiated spermatids (stage 3) began in late-May (1981) or early-June (1980). Cellular debris was reduced and epididymes of some turtles contained reduced numbers of spermatozoa. By mid- to late-June spermatids were differentiating (stage 4) and many individuals in mid-July contained abundant spermatids and mature spermatozoa (stage 5). Tubule diameters and epithelial heights increased during this period (Figure 3). Stage 6 represents peak spermiogenesis and spermiation, all individuals collected in mid-August were in this stage. Tubule diameters and epithelial heights

Table 1. Seasonal changes in the spermatogenic cycle of *Chrysemys picta*. Numbers refer to number of turtles.

	Spermatogenic Stages							
	1	2	3	4	5	6	7	8
1980								
Mar	2							
Apr	1	13						
May		19						
Jun		1	6	2				
Jul				8	10			
Aug					5	12		
Sep						12	3	
Oct							2	1
1981								
Mar	1							
Apr	7	3						
May		9	3					
Jun			8	1				
Jul				4	8			
Aug					4	7		
Sep						4	2	
Oct							6	

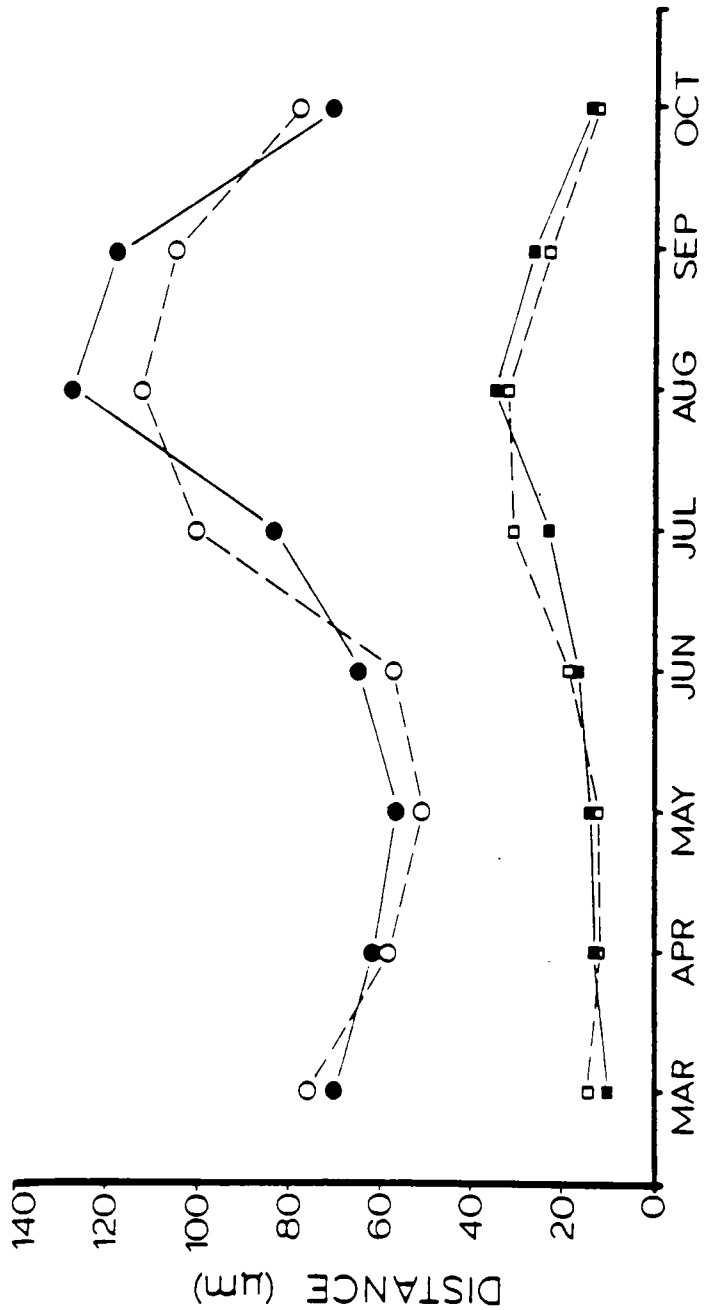

Figure 3. Seasonal changes in mean diameter of seminiferous tubules and height of the tubular epithelium (lower lines) for Chrysemys picta. Closed circles and boxes represent 1980 and open circles and boxes 1981. Sample sizes as in Figure 2.

reached maximal sizes (Figure 3) this month. Spermatozoa accumulated in the lumen and migrated to the epididymes. Males exhibiting stage 6 were collected into September but, by the middle of the month, some turtles showed a significant reduction in number of spermatids (stage 7) and in tubule diameter and epithelial height (Figure 3). October tubules were small and were characterized by an increase of Sertoli cells in the basement of the epithelium and a few germinal spermatozoa (stage 8). Tubule diameters and epithelial heights continued to decrease through the winter months and reached minimal size by April of the following year (Figure 3). Cellular debris accumulated during this time, Sertoli cells outnumbered spermatogonia and spermatozoa were often found in the lumen (stage 1). Photomicrographs illustrating these stages for this species are in Ernst (1971a), Moll (1973, 1979) and Christiansen and Moll (1973). Statistics in Table 2 describe the variation in seminiferous tubule diameters and epithelial heights by stage.

Components of variation in the male cycle. Forward, stepwise, multiple linear regression was used to gain an insight into the factors that contribute to the variation in the male reproductive cycle. Testis weight was selected as the dependent variable, since it is commonly used to quantify reptilian testicular cycles (e.g., Licht and Gorman, 1970; White and Murphy, 1973; van Loben Sels, 1976; Shine, 1977; Joanen and McNease, 1980; McPherson and Marion, 1981a; White, et al., 1982). Seminiferous tubule diameter was used as a parametric measure of the spermatogenic cycle. Variances of testis weight samples were heterogeneous when examined in relation to each of the independent

Table 2. Descriptive statistics of seminiferous tubule diameter and height of the epithelium by spermatogenic stage for Chrysemys picta. N is sample size and means are followed by one standard deviation.

Stage	N	Seminiferous Tubule Diameter (μm)	Epithelial Height (μm)
1	11	61.50 ± 2.50	11.30 ± 0.33
2	45	56.24 ± 1.09	13.52 ± 0.30
3	17	58.34 ± 1.59	17.94 ± 0.75
4	15	80.67 ± 3.79	24.10 ± 1.57
5	29	101.88 ± 2.96	28.64 ± 1.01
6	35	123.79 ± 2.88	32.80 ± 1.10
7	13	85.92 ± 4.29	12.18 ± 0.94
8	3	72.27 ± 7.99	14.17 ± 2.28

variables (B=1.60-18.0, P<0.01). Testis weights were then transformed to their logarithms, which increased the linearity of the relationships, as well as corrected the heterogeneity (B=0.73-3.05, P>0.05). As shown in Table 3, 67.6% of the variation is due to the effect of the spermatogenic cycle, presumably due to the changes in tubule diameter July through September. Plastron length and month were the second and third variables entered in the equation, accounting for 10.5% and 1.58% of testis weight variation, respectively. The variable year accounted for only 0.006% of the observed variation. The remaining variance (19.8%) was due to errors in measurement and variation among stages within months.

Reproduction in Male Sternotherus odoratus

Body size and age at maturity. Average carapace length for 113 S. odoratus adult males was 82.6±15.2 mm (51.0-118.5) and average plastron length was 56.5±9.8 mm (35.4-79.9). Four two-year old males collected September through November (51.0, 51.3, 52.3, 52.4 mm carapace length) were in advanced stages of spermatogenesis and contained varying amounts of spermatozoa in the testicular lumen. Each had a mature penial organ in the enlarged tail base. All larger males in the sample were mature. Stinkpots mature in their second year and store spermatozoa in the epididymes for use in matings during their third year.

Testicular weight cycle. The hypothesis that testis weight variation was not significantly affected by carapace length, a measure of body size, was tested with an ANCOVA design identical to that used

Table 3. Forward, stepwise multiple regression of log-testis weight versus seminiferous tubule diameter, plastron length, month and year for Chrysemys picta. Sample size is 170.

Step	Variable	Partial r	R^2	F
1	Tubule diameter	0.822	0.676	350.37***
2	Plastron length	0.370	0.780	296.74***
3	Month	0.593	0.796	216.13***
4	Year	0.061	0.802	167.29***

*** indicates significance below 0.001 level.

for C. picta. Plots of testis weight versus carapace length indicated the relationship to be linear. Results showed that testis weight variation was significantly affected by carapace length ($F=83.71$, 1, 112 d. f., $P<0.001$) and, therefore, testis weights were adjusted as for C. picta. Adjusted testis weights exhibited minimal values March through May, an increase June through July, peaks in August and regression September through November (Figure 4). Adjusted weights reached maximum regression in May of the following year. These seasonal changes in testis size are concordant with seasonal changes in the spermatogenic cycle (see below).

To determine if adjusted testis weights differed significantly between months (1980 and 1981 samples combined) and years, a multiple ANCOVA was designed and performed as was done for C. picta. Carapace length was included as the covariate. Results revealed a significant effect on testis weight due to month ($F=19.69$, 8, 112 d. f., $P<0.001$), but an insignificant effect due to year ($F=0.398$, 1, 112 d. f., $P=0.529$). Combined monthly sample variances were heterogeneous ($B=6.31$, $P<0.001$). Only the arctangent transformation (Nie, et al., 1975) of adjusted testis weights provided homogeneous variances ($B=1.337$, $P=0.149$). One-way ANOVA on these combined samples revealed a significant month effect ($F=13.53$, 8, 112 d. f., $P<0.001$). Tukey's HSD test showed that July through September and November samples were significantly different from all other monthly samples but not among themselves.

Spermatogenesis. Table 4 illustrates the seasonal distribution of spermatogenic stages for 1980 and 1981. Onset of spermatogenesis (stage 2) was in May, with mitotic divisions producing two to three

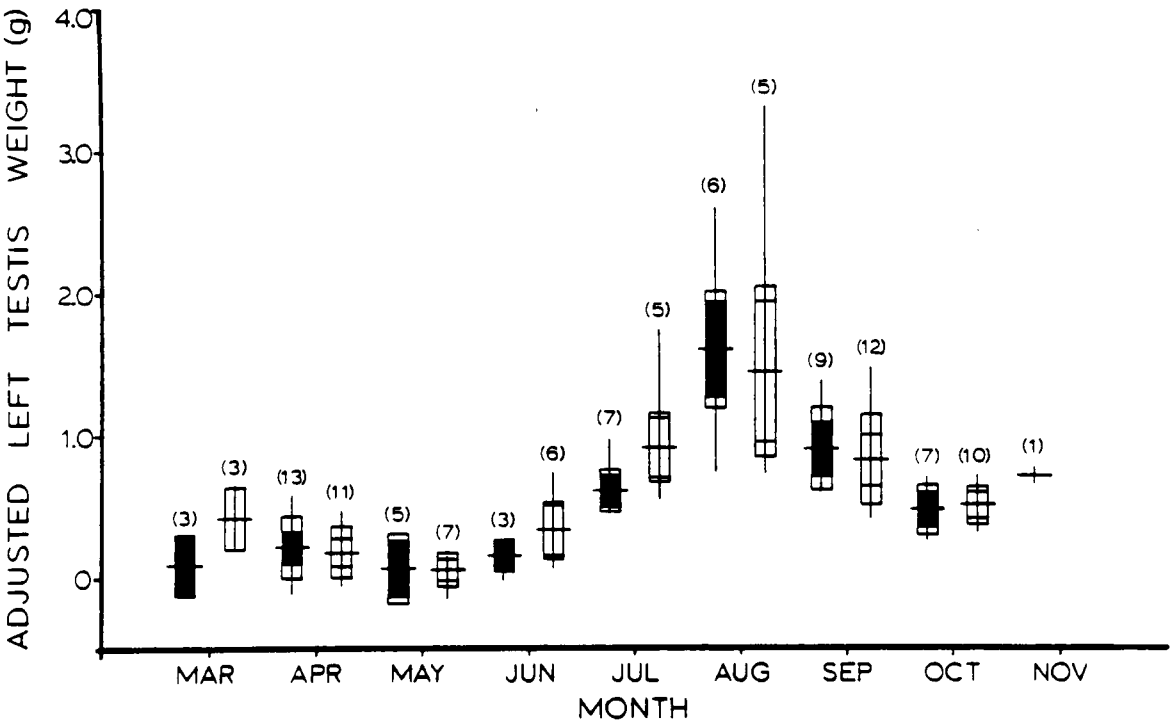

Figure 4. Seasonal variation in adjusted left testis weight for Sternotherus odoratus. Closed rectangles represent 1980 and open rectangles 1981. Symbols as in Figure 2.

Table 4. Seasonal changes in the spermatogenic cycle of Sternotherus odoratus. Numbers refer to number of turtles.

	Spermatogenic Stages							
	1	2	3	4	5	6	7	8
1980								
Mar	2							
Apr	13							
May		5						
Jun			1	2				
Jul					7			
Aug						6		
Sep						6	3	
Oct						1	5	1
Nov								1
1981								
Mar	1							
Apr	9							
May		7						
Jun		1	3	1	1			
Jul				1	4			
Aug					2	3		
Sep						12		
Oct						3	7	

layers of primary spermatocytes. Spermatozoa were abundant in the epididymes during this time and some turtles had some cellular debris in the tubular lumen, Tubule diameters were at minimal size and epithelial height began to increase (Figure 5). Secondary spermatocytes were very abundant by June and spermatids were visible one to two weeks later in some individuals. Meiosis II and differentiation of spermatids (stages 3 and 4) continued through July so that, by the end of the month, all turtles had abundant spermatids and germinal spermatozoa (stage 5). Cellular debris was almost nonexistent and there were a few spermatozoa in the reduced epididymes. Tubule diameter and epithelial height increased and reached maximum sizes in August (Figure 5). Peak spermiogenesis and spermiation (stage 6) were registered for most males that month. Spermiation continued into September and tubule diameters remained large. Spermatozoa were abundant in the lumen and epididymes and, by the end of September, some males exhibited a reduction in spermatocytes and spermatids (stage 7). Most October males had abundant spermatozoa, but few germinal spermatozoa and no spermatids could be found by the end of the month (stage 8). Most March and April males exhibited maximum involution with a few spermatogonia and scattered spermatozoa (stage 1). Minimal tubule diameters were reached by April and onset of spermatogenesis was concordant with minimum testis weights. Statistics in Table 5 describe the variation in seminiferous tubule diameter and epithelial hsight by stage and Figure 5 illustrates the seasonal changes by month and year. Photomicrographs illustrating the seasonal variation and stages are in Risley (1938) and McPherson and Marion (1981a).

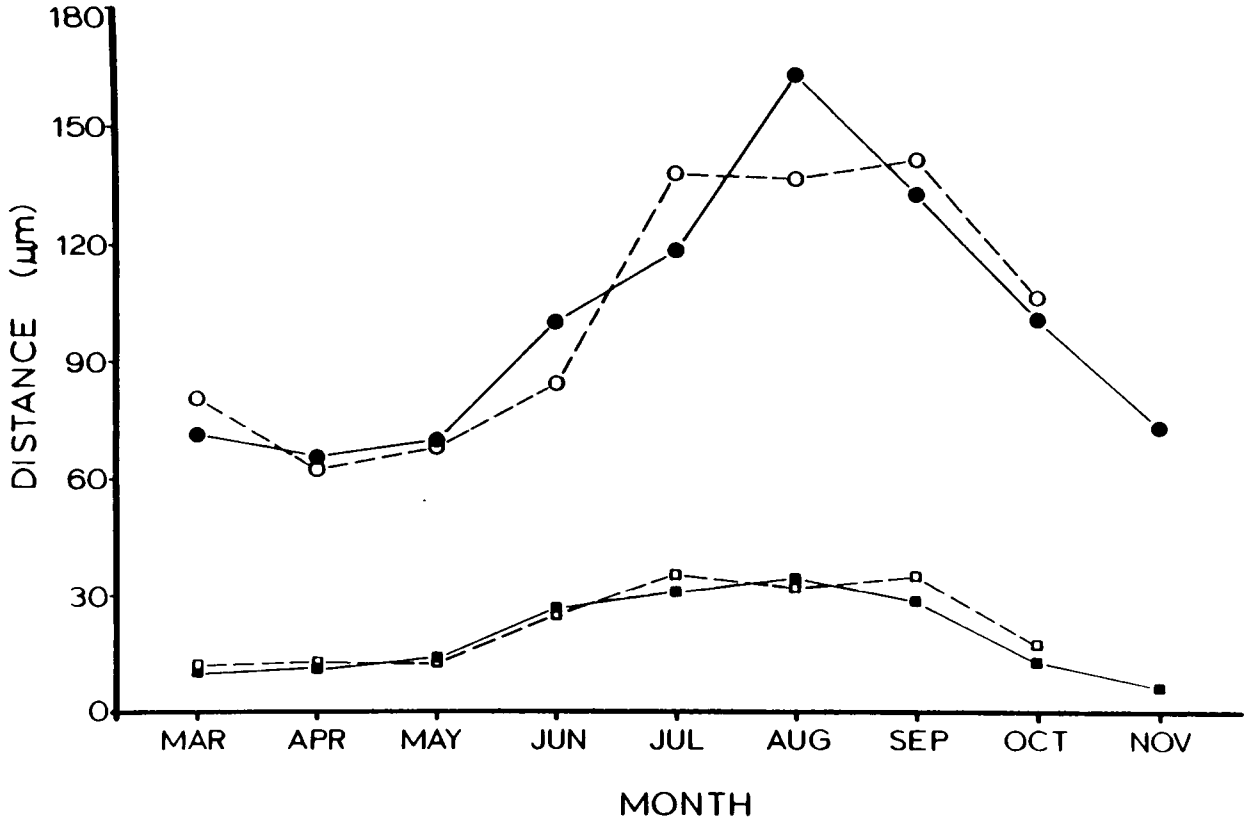

Figure 5. Seasonal changes in mean diameter of seminiferous tubules and height of the tubular epithelium (lower lines) for Sternotherus odoratus. Closed circles and boxes represent 1980 and open circles and boxes 1981. Sample sizes as in Figure 4.

Table 5. Descriptive statistics of seminiferous tubule diameter and height of the epithelium by spermatogenic stage for Sternotherus odoratus. N and statistics as in Table 2.

Stage	N	Seminiferous Tubule Diameter (μm)	Epithelial Height (μm)
1	25	64.62 ± 1.48	12.16 ± 0.39
2	13	68.48 ± 2.04	13.63 ± 0.64
3	4	83.30 ± 6.79	22.30 ± 2.86
4	4	101.45 ± 7.63	29.18 ± 3.55
5	14	128.60 ± 4.81	33.04 ± 1.04
6	31	146.99 ± 3.50	34.99 ± 0.70
7	17	93.68 ± 2.31	10.62 ± 0.57
8	5	74.48 ± 3.22	8.96 ± 1.12

Components of variation in the male cycle. Forward, stepwise, multiple linear regression of testis weight versus four independent variables (month, year, carapace length and seminiferous tubule diameter) was used to gain insight into the factors that contributed to the variation in the male reproductive cycle of S. odoratus. Testis weight variation was heterogeneous when examined in relation to each independent variable ($B=2.7-16.5$, $P<0.001$), except for year ($B=0.168$, $P=0.731$). A log-transformation corrected the variance heterogeneity ($B=0.55-1.04$, $P>0.39$) and increased the linear relationships between variables. The results (Table 6) showed that tubule diameter accounted for the majority of the variation (64%). This is apparently due to the increase in diameter July through September. The second and third variables, carapace length and month, contributed 24.9% and 0.4% to the observed variation, respectively. The fourth variable, year, accounted for only 0.1%. Error variance assumed the remaining 10.6%.

Reproduction in Female Chrysemys picta

Body size and age at maturity. Sixty-five adult female C. picta averaged 132.7±7.8 mm (112.5-148.2) carapace length and 124.1±8.1 mm (105.6-144.6) plastron length. Females without Class III follicles, oviductal eggs or corpora lutea were considered mature. Plastron lengths of 93.7, 95.4, 96.5, 97.5 99.6 and 104.4 mm were recorded for the largest subadult females. The oldest known female of this group, based on annuli counts, was six years of age (104.4 mm PL). Another six year old female (105.6 mm PL) was mature and contained one oviductal egg. All females larger than 105 mm plastron length were

Table 6. Forward, stepwise multiple regression of log-testis weight versus seminiferous tubule diameter, carapace length, month and year for Sternotherus odoratus. Sample size is 113.

Step	Variable	Partial r	R^2	F
1	Tubule diameter	0.800	0.640	197.13***
2	Carapace length	0.657	0.889	439.49***
3	Month	0.391	0.893	302.56***
4	Year	0.044	0.894	227.38***

*** indicates significance below 0.001 level.

mature and the youngest of this group was eight years of age (107 mm PL). Average size at maturity is thus, about 105 mm plastron length and is reached in the sixth or seventh year of growth.

Ovarian cycle. Vitellogenesis (=follicular development, Moll, 1973) began in August for most females after a quiescent period of about three weeks (Table 7). Ovary weights were minimal in August (mean=3.3 g, N=12), but increased 91% in September (mean=6.3 g, N=6). Most August and all September females contained Class II follicles. Vitellogenesis continued through April, but was probably interrupted during the coldest months of winter brumation. By April all females bore sets of Class II and Class III follicles. Ovary weights were maximal at this time (mean=15.4 g, N=5) and represents a 140% increase over September weights. The earliest collection date for a female with oviductal eggs was 14 May 1980 (no May 1981 ovigerous females were caught), indicating a mid-May ovulation of the first clutch. The latest dates for oviductal eggs were 22 June 1980 and 19 June 1981. Maximum follicle diameter was 17 mm and females collected between 14 May and 10 June 1980 and 8 May and 18 June 1981 contained follicles of this size. Ovary weights decreased 37% from May (mean=14.2 g, N=11) to June (mean=9.0 g, N=14) and an additional 35% in July (mean=4.0 g, N=16). Two July females (one each in 1980 and 1981) contained complete sets of Class III follicles, while five of six 1980 females had only one to two Class III follicles (Table 7). Apparently, some females lay a July clutch and others do not ovulate the entire complement of ova. Corpora lutea were found in 22 females caught between 14 May and

Table 7. Monthly percentages of mature Chrysemys picta females with Class II and Class III follicles (see text), oviductal eggs and corpora lutea.

	N	Follicles				Oviductal Eggs		Corpora Lutea	
		Class II		Class III					
		N	%	N	%	N	%	N	%
1980									
Apr	3	3	100	3	100	0	0	0	0
May	8	7	88	8	100	6	75	6	75
Jun	9	7	78	8	89	4	44	8	89[a]
Jul	6	2	33	1	50	0	0	0	0
Aug	10	7	70	0	0	0	0	0	0
Sep	6	6	100	0	0	0	0	0	0
1981									
Mar	1	1	100	1	100	0	0	1	100
Apr	2	2	100	2	100	0	0	0	0
May	3	3	100	3	100	0	0	1	33
Jun	7	7	100	6	86	3	43	6	86[a]
Jul	10	7	70	6	60	0	0	1	10
Aug	2	2	100	0	0	0	0	0	0

[a] indicates 3 females with 2 sets of corpora lutea.

22 June 1980 and 25 May and 19 June 1981. One female contained corpora lutea when caught on 27 March 1981. They were 4.5 mm in diameter and clearly identifiable. Commonly, however, corpora lutea regress to corpora albacantia (Ernst, 1971a) and cannot be seen in specimens taken in late-July or August.

Nine females, six in 1980 and three in 1981, with oviductal eggs and fresh corpora lutea exhibited transuterine migration of ova (Legler, 1958; Tinkle, 1959). Net migration was from the largest ovary to the smallest and, in one, an ovum moved from a balanced 2-2 to an unbalanced three on the right side and one on the left. The number of ova ovulated on the right reproductive tract (2.22 ± 1.4, N=9) was almost identical to the number ovulated on the left (2.11 ± 1.5).

There were no substantial differences between the 1980 and 1981 reproductive cycles (Table 7).

Clutch size and reproductive potential. Clutch sizes were not apparently different if determined from number of enlarged follicles, oviductal eggs or corpora lutea (Table 8). Modal clutch size was four. The use of enlarged follicles may overestimate clutch size, since not all females ovulate their entire clutches (see above). For this reason and to increase sample size, analyses of clutch data are based on counts of corpora lutea. Sample clutch variances for 1980 and 1981 were homogeneous (F_{max} test, F=1.096, P>0.05), and clutch means (Table 8) were not significantly different between years (t-test, t=-0.57, 20 d. f., P=0.575).

Clutch size was significantly correlated with plastron length (Figure 6) whether determined for 1980 samples (r=0.712, P=0.0021,

Table 8. Clutch statistics for Chrysemys picta. The mean is followed by 1 standard deviation, and sample size and range are in parentheses.

	1980	1981	Combined Sample
Enlarged follicles	4.25 ± 1.04 (8, 3-6)	4.00 ± 1.12 (8, 2-6)	4.13 ± 1.09 (16, 2-6)
Oviducal eggs	4.00 ± 1.41 (10, 1-6)	5.00 ± 1.73 (3, 4-7)	4.23 ± 1.48 (13, 1-7)
Corpora lutea	4.07 ± 1.21 (14, 1-6)	4.38 ± 1.19 (8, 3-7)	4.18 ± 1.18 (22, 1-7)
Total	4.14 ± 1.23 (22, 1-6)	4.19 ± 1.17 (16, 2-7)	4.16 ± 1.13 (38, 1-7)

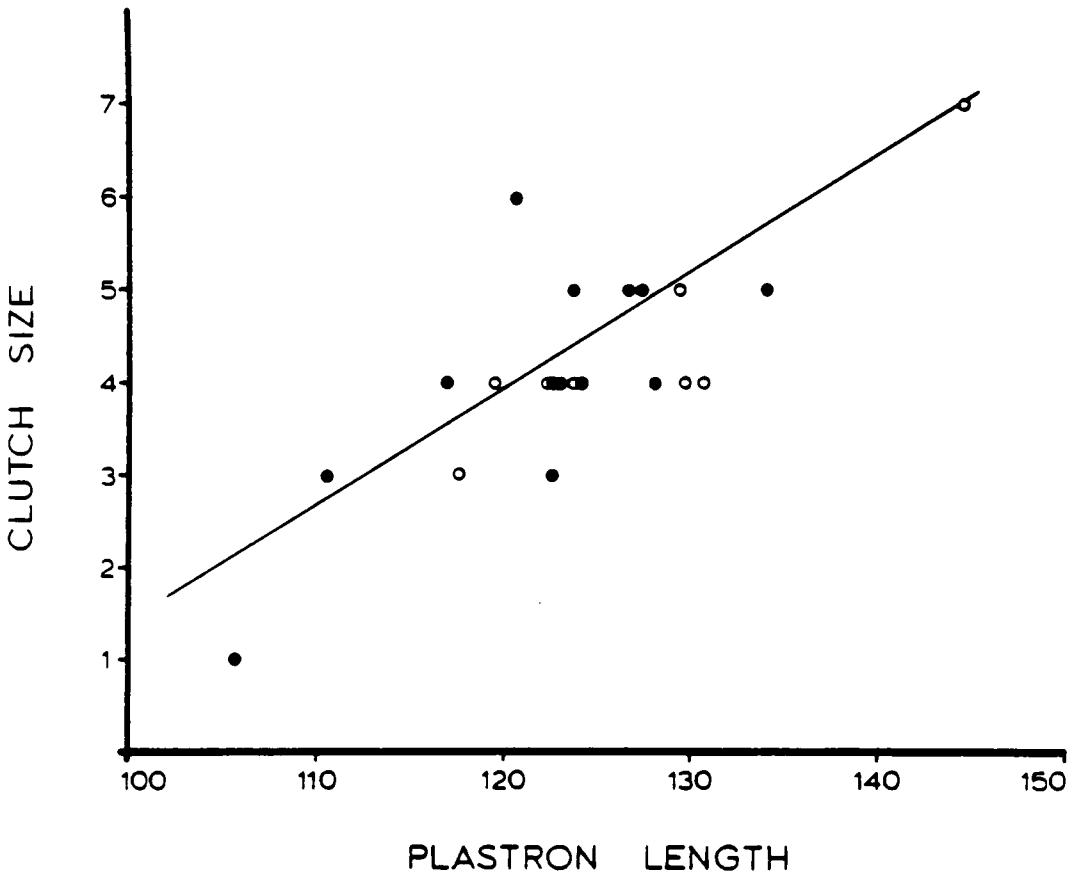

Figure 6. Relationship of clutch size with plastron length for Chrysemys picta. Closed circles respresent 1980 and open circles 1981. The regression equation is N = -9.822 + 0.133X (N=22).

N=14), for 1981 (r=0.871, P=0.0024, N=8) or for the total sample (r=0.766, P<0.001, N=22). Clutch size increases by one for every eight millimeters plastron length. Forward, stepwise multiple linear regression was used to determine which factors accounted for significant amounts of the variation in clutch size. A priori tests revealed that relationships of the dependent variable to each of the independent variables were linear and that variances were homogeneous (B=0.12-1.60, P>0.19). Results (Table 9) showed that 62.1% of clutch size variation is due to the effect of plastron length. Egg weight and month, the second and third variables entered in the equation, contributed 16.7% and 10.4% of the variation, respectively. These variables, along with egg length (1.1%), egg width (0.8%) and year (0.04%) explain 91.2% of clutch variance. Clutch size was positively correlated with plastron length, egg width and year and negatively correlated with the remaining three variables.

Virginia Chrysemys picta lay as many as two clutches of eggs per year. Three females each year (all collected in June) bore oviductal eggs and two distinct sets of corpora lutea. For the combined data, N=6, the first clutch averaged 4.33±1.4 (3-6) and the second 4.83±1.2 (4-7) eggs. The difference is insignificant (Paired sample t-test, t=-1.46, 5 d. f., P=0.203). Four females laid one egg more in the second clutch than in the first and one female one egg less. Based on collection dates of ovigerous females, the first clutch is laid mid- to late-May and the second about three weeks to a month later. At Grassy Swamp Lake an average size female C. picta lays about eight eggs per year.

Table 9. Forward, stepwise multiple regression of clutch size versus plastron length, egg weight, egg length and width, month and year for Chrysemys picta. Sample size is 12.

Step	Variable	Partial r	R^2	F
1	Plastron length	0.788	0.621	16.40**
2	Egg weight	-0.168	0.789	16.82**
3	Month	-0.019	0.893	22.33***
4	Egg length	-0.479	0.904	16.56**
5	Egg width	0.115	0.912	12.49**
6	Year	0.329	0.913	8.71*

*P<0.05, **P<0.001, ***P<0.001

Eggs, incubations and hatchlings. A summary of egg statistics is presented in Table 10. Between year differences in egg length, egg width and weight were insignificant (t-tests, t=0.42-1.03, 11 d. f., P=0.324-0.683); all variances were homogeneous (F_{max} test, F=3.48-16.61, P>0.05). Of the various comparisons of egg measurements with either plastron length or clutch size, only egg width versus plastron length showed a significant relationship (Table 11, Figure 7).

No females from Grassy Swamp Lake were observed nesting, but dates of nesting females elsewhere in Virginia are between late-May and mid-July (Richmond and Goin, 1938; personal observations). Incubation time was 71-76 days and hatching dates of two clutches were 7-9 August and 11-15 August. Mean carapace length of four neonates was 22.1±0.3 mm (21.8-22.4), mean plastron length was 20.7±0.7 mm (20.3-21.8) and mean weight was 3.7±0.2 g (3.5-3.9). Juveniles in their first year of growth caught and released at Grassy Swamp Lake were 47.7-60.2 mm plastron length (mean=53.3, N=14) and weighed 23-46 g (mean=33.8, N=14).

Reproduction in Female Sternotherus odoratus

Body size and age at maturity. Mean carapace length of 134 adult female S. odoratus was 85.9±8.8 mm (66.0-112.7) and mean plastron length was 64.3±6.9 mm (50.0-84.3). Carapace lengths of the two largest immature females were 62.0 and 72.2 mm and both were four years of age. One four-year old (68.8 mm CL) contained two Class III follicles 20 May 1980. Three other four-year olds (66.0, 69.5, 71.5 mm CL) contained vitellogenic follicles when collected in August and September. Except for the 72.2 mm individual, all females larger than 66 mm carapace

Table 10. Egg statistics for Chrysemys picta. Sample size (N) for length and width measurements is the number of eggs and N for weights is the number of clutches (clutch weight divided by clutch size provided an average egg weight per clutch).

	Length			Width			Weight		
Year	N	$\bar{X} \pm$ SD	Min - Max	N	$\bar{X} \pm$ SD	Min - Max	N	$\bar{X} \pm$ SD	Min - Max
1980	34	29.83 ± 2.37	25.7 - 33.7	34	16.08 ± 1.07	14.6 - 18.5	10	4.56 ± 2.13	3.44 - 5.78
1981	14	30.00 ± 0.98	28.1 - 31.6	14	17.14 ± 0.39	16.4 - 17.8	3	5.11 ± 0.54	4.50 - 5.50
Total	48	29.98 ± 2.05	25.7 - 33.7	48	16.39 ± 1.04	14.6 - 18.5	13	4.69 ± 0.84	3.44 - 5.78

Table 11. Regression statistics of egg sizes and egg weight versus plastron length (PL) and clutch size (CS) for Chrysemys picta. 1980 and 1981 samples are combined.

Sample	N	Regression Equation	r	Significance
Egg length - PL	12	N = 34.502 - 0.034X	-0.164	0.306
Egg width - PL	12	N = 9.175 + 0.059X	0.538	0.036
Egg weight - PL	13	N = 2.547 + 0.017X	0.195	0.262
Egg length - CS	12	N = 32.951 - 0.644X	-0.479	0.058
Egg width - CS	12	N = 16.042 + 0.799X	0.115	0.361
Egg weight - CS	13	N = 5.213 - 0.124X	-0.219	0.237

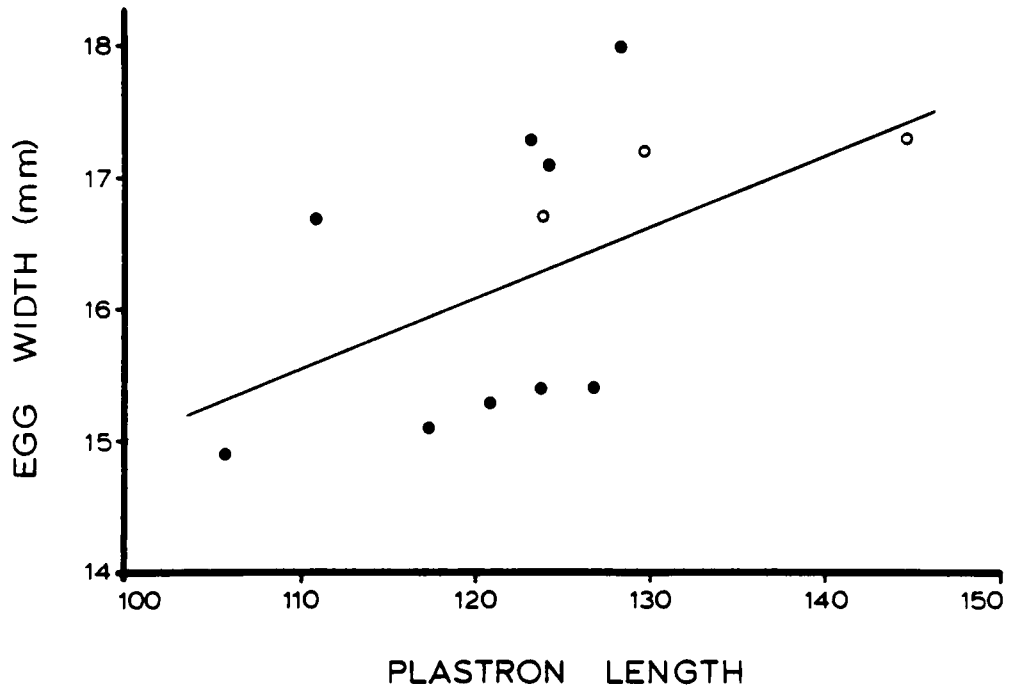

Figure 7. Relationship of egg width with plastron length for Chrysemys picta. Closed circles represent 1980 and open circles 1981. Refer to Table 11 for the regression equation.

length were mature. Age at maturity for females from Grassy Swamp Lake is four to five years.

Ovarian cycle. Vitellogenesis began in late-August after a quiescent period of about two to four weeks (Table 12). Some females possessed small Class III follicles by mid-September and all females had Class II follicles this month. Ovarian weights were lowest in August (mean=2.0 g, N=19), increased 30% in September (mean=2.6 g, N=20) and an additional 30% in October (mean=4.2 g, N=4). Rate of follicular enlargement decreased through the winter months, but all March females had Class II and Class III follicles (Table 12). Ovarian weights were only slightly larger in March (mean=4.5 g, N=3) and April (mean=4.5 g, N=7) than in October. Oviductal eggs were present in females collected 14 April to 14 July 1980 and 24 April to 16 July 1981. Thus, ovulation of the first clutch is about mid-April and most clutches are laid by the second week of July. Ovary weights were maximal in May (mean=5.3 g, N=23), decreased 40% by June (mean=3.2 g, N=27) and 22% further by July (mean=2.0 g, N=31). Class III follicles were found in fourteen females caught in July; four with one and one with two in 1980 and three with one and five with two in 1981. One female in 1981 (20 July) contained four follicles of preovulatory size and may have been in the process of laying a late clutch that year. As with C. picta, some females apparently do not ovulate their entire complement of Class III follicles. Corpora lutea were found from 16 April to 16 July 1980 and 24 April to 16 July 1981 (Table 12).

Nine 1980 females and twenty 1981 females exhibited transuterine migration of ova. In each case movement was from the side with the

Table 12. Monthly percentages of mature Sternotherus odoratus females based on Class II and Class III follicles (see Text), oviductal eggs and corpora lutea.

		Follicles				Oviductal Eggs		Corpora Lutea	
		Class II		Class III					
	N	N	%	N	%	N	%	N	%
1980									
Mar	1	1	100	1	100	0	0	0	0
Apr	4	3	75	1	25	3	75	3	75
May	8	7	88	8	100	6	75	7	88
Jun	11	11	100	7	64	8	73	11	100[a]
Jul	15	11	73	5	33	1	7	1	7
Aug	12	12	100	0	0	0	0	0	0
Sep	14	14	100	4	29	0	0	0	0
Oct	2	2	100	2	100	0	0	0	0
1981									
Mar	2	2	100	2	100	0	0	0	0
Apr	3	3	67	2	67	1	33	1	33
May	15	14	93	13	87	8	53	15	100[b]
Jun	11	10	91	9	82	10	91	11	100
Jul	16	9	56	9	56	1	6	3	19
Aug	7	6	86	1	14	0	0	0	0
Sep	6	6	100	0	0	0	0	0	0
Oct	2	2	100	1	50	0	0	0	0

[a] includes 3 females with 2 sets of corpora lutea.
[b] includes 7 females with 2 sets of corpora lutea.

smallest ovary. Number of ova ovulated in the right reproductive tract (mean=1.8±1.3 in 1980, 1.7±1.2 in 1981) averaged slightly higher than the number ovulated in the left (1.4±1.3 in 1980, 1.5±1.0 in 1981).

Except for slight differences in timing, usually by about one to 1.5 weeks, the ovarian cycles do not differ substantially between years (Table 12).

Clutch size and reproductive potential. When based on counts of enlarged follicles, mean clutch size was slightly below estimates based on oviductal eggs or corpora lutea (Table 13). Modal egg number was three. Statistical analyses of clutch data are based on counts of corpora lutea. Variances of clutch sizes between years were homogeneous (F_{max} test, F=1.67, 21, 31 d. f., P>0.05) and the means were not significantly different (Table 13) (t=1.17, 52 d. f., P=0.246).

Clutch size was significantly correlated to carapace length in 1980 (r=0.527, P=0.006, N=22), in 1981 (r=0.726, P<0.001, N=32) and in the total sample (r=0.642, P<0.001, N=54) (Figure 8). The number of eggs increases by one for every eleven millimeters carapace length. Age was determined for 24 females with complete sets of growth annuli and was used to determine if a significant relationship existed with clutch size. The regression of the number of eggs with age was positive and significant in 1980 (r=0.743, P=0.045, N=6), in 1981 (r=0.664, P=0.001, N=18) and in both years combined (r=0.662, P=0.0002, N=24) (Figure 9). Forward, stepwise, multiple regression was used to identify the factors that accounted for significant amounts of variation in clutch size. Clutch variance was heterogeneous when tested with the independent variables egg length and egg width (B=2.54-4.58, P=0.033-

Table 13. Clutch statistics for Sternotherus odoratus. Numbers and statistics as in Table 8.

	1980	1981	Combined Sample
Enlarged follicles	2.71 ± 0.69 (17, 1-4)	2.96 ± 1.26 (27, 1-5)	2.86 ± 1.07 (44, 1-5)
Oviducal eggs	3.41 ± 1.33 (17, 2-7)	3.00 ± 0.91 (25, 2-5)	3.17 ± 1.10 (42, 2-7)
Corpora lutea	3.41 ± 1.26 (22, 2-7)	3.06 ± 0.91 (32, 2-5)	3.20 ± 1.07 (54, 2-7)
Total	3.10 ± 1.10 (39, 1-7)	3.02 ± 1.08 (59, 1-5)	3.05 ± 1.09 (98, 1-7)

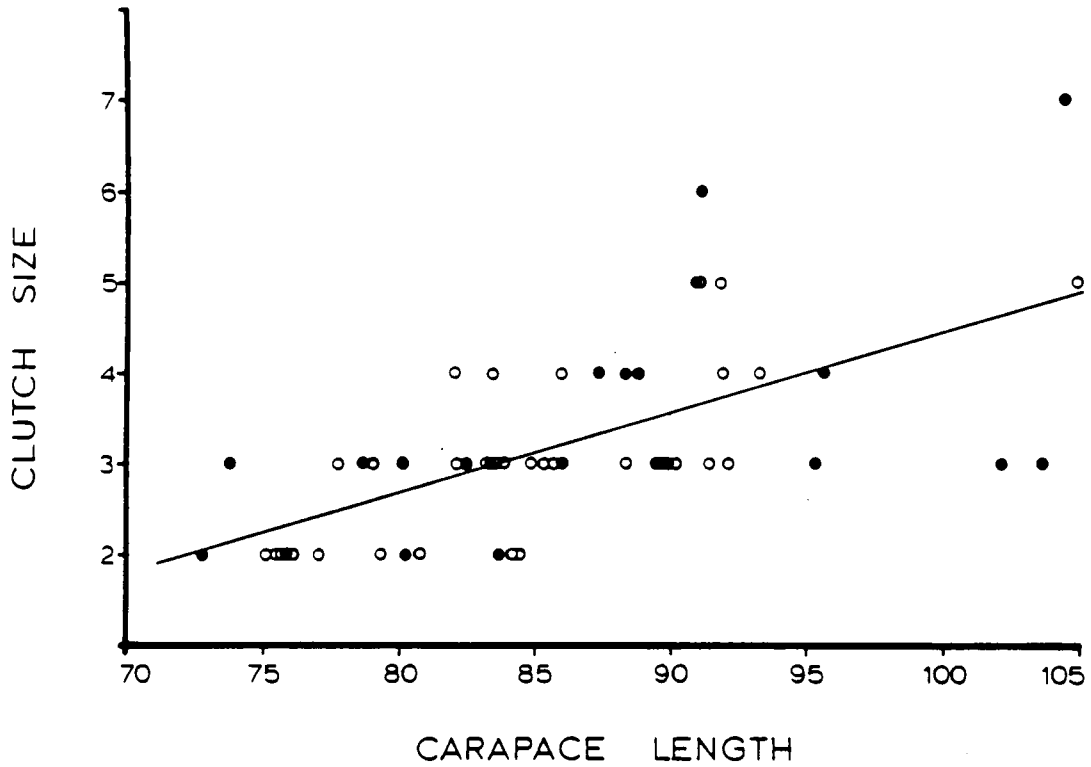

Figure 8. Relationship of clutch size with carapace length for Sternotherus odoratus. Closed circles represent 1980 and open circles 1981. The regression equation is N = -4.46 + 0.089X (N=54).

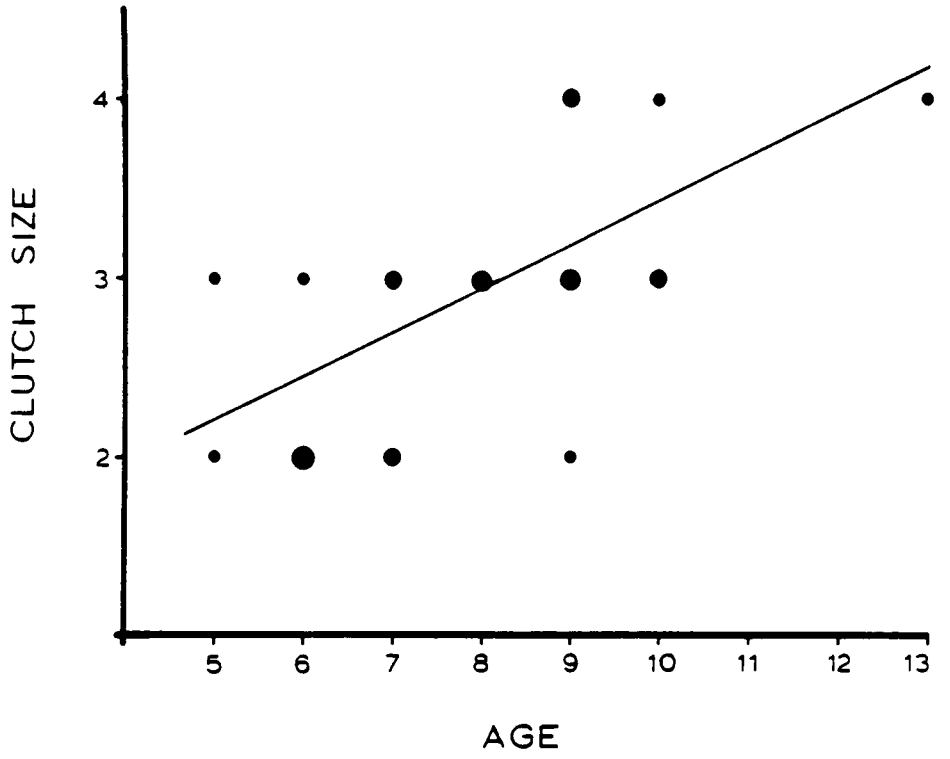

Figure 9. Relationship of clutch size with age for Sternotherus odoratus. Small circles represent one observation, intermediate circles two and large circles three observations. The regression equation is N = 0.926 + 0.242X (N=24). Age is in years.

0.038), but homogeneous when tested with the variables month, year and carapace length (B=0.124-2.68, P>0.1). A log-transformation of clutch size achieved homogeneity in all variables (B=0.341-1.06, P>0.3) and the regression model used these transformed clutch size data. Results of the model revealed that 43.4% of clutch size variation was explained by variation in carapace length (Table 14). Egg weight, width and length contributed 10.9%, 7.9% and 1.7% of the variation, respectively. Variations between years accounted for only 0.01%, whereas variation in months was insignificant. All five variables accounted for 63.9% of total clutch variance. Clutch size is positively correlated with carapace length and egg width and negatively correlated with egg length, egg weight and year.

Sternotherus odoratus in Virginia lay at least two clutches per year. Three females in 1980 and seven in 1981 bore two distinct sets of corpora lutea. These data were combined for comparison due to the small 1980 sample. The first clutch averaged 3.7±1.6 (3-6) eggs and the second 3.0±0.5 (2-4). Five females laid one egg less in the second clutch, one an egg more and one female laid six in the first clutch and three in the second. The results of a Paired sample t-test indicated no significant difference between clutch means (t=2.09, 9 d. f., P= 0.067). Based on collection dates of ovigerous females, the first clutch is deposited in early-May and the second approximately three weeks later in early-June. There was no direct evidence for production of three clutches by a single female. However, the length of time remaining in the activity season and the collection of ovigerous females in late-July suggest some females lay three clutches. If two clutches

Table 14. Forward, stepwise multiple regression of log-clutch size versus carapace length, egg weight, egg length and width, month[a] and year for Sternotherus odoratus. Sample size is 41.

Step	Variable	Partial r	R^2	F
1	Carapace length	0.658	0.433	30.60***
2	Egg width	0.538	0.513	20.52***
3	Egg weight	-0.074	0.622	20.84***
4	Egg length	-0.097	0.639	16.38***
5	Year	0.177	0.639	12.76***

[a] not included, remaining partial for month = -0.0098, P>0.05. ***P<0.001

are normally ovulated, an average size female lays six eggs per year.

Eggs, incubation and hatchlings. Table 15 presents a summary of egg statistics based on measurements of all oviductal eggs. Variances in egg measurements were homogeneous ($F=1.20-1.36$, $P>0.05$). Between year differences in egg length and weight were insignificant (t-tests, $t=0.78-1.15$, $P=0.257-0.440$), but differences in mean egg width were significant ($t=2.29$, $P=0.027$). Completely shelled, hard, eggs averaged 24.6 ± 1.7 mm ($N=56$) in length (1980: 24.9 ± 1.6, $N=27$; 1981: 24.3 ± 1.9, $N=29$) and 14.1 ± 0.6 mm in width (1980: 14.2 ± 0.4, $N=27$; 1981: 14.0 ± 0.7, $N=29$).

There was no correlation of egg length with carapace length, nor was there a significant relationship with clutch size. Egg weight and width were, however, significantly correlated with carapace length and exhibited positive relationships with clutch size (Table 16). Figure 10 illustrates the relationship of egg weight with carapace length and Figure 11 illustrates the relationship of egg width with clutch size. The relationships in 1981 were sufficiently strong to cause combined year samples to show highly significant relationships (Table 16).

Based on eggs dissected from ovigerous females from Grassy Swamp Lake, length of incubation varied from 70 to 80 days. Laboratory hatching dates of six clutches were 13-16 August and 21-27 August. Eleven neonates averaged 20.3 ± 0.8 mm (18.5-22.0) carapace length, 15.2 ± 0.7 mm (13.9-16.5) plastron length and 2.1 ± 0.2 g (1.8-2.5) body weight. The smallest stinkpot captured and released at Grassy Swamp Lake was a 37.9 mm carapace length and 9 gram juvenile.

Table 15. Egg statistics for Sternotherus odoratus. Sizes, weights and numbers as in Table 10.

	Length			Width			Weight		
Year	N	$\bar{X} \pm$ SD	Min - Max	N	$\bar{X} \pm$ SD	Min - Max	N	$\bar{X} \pm$ SD	Min - Max
1980	56	24.07 ± 2.21	18.5 - 29.0	56	14.25 ± 1.23	13.2 - 15.3	16	2.85 ± 0.39	2.10 - 3.50
1981	69	23.64 ± 1.75	17.9 - 27.9	69	13.58 ± 1.59	12.1 - 15.2	25	2.54 ± 0.36	1.85 - 3.66
Total	125	23.82 ± 1.97	17.9 - 29.0	125	13.72 ± 1.56	12.1 - 15.3	41	2.66 ± 0.40	1.85 - 3.66

Table 16. Regression statistics for egg sizes and egg weight versus carapace length (CL) and clutch size (CS) for Sternotherus odoratus. 1980 and 1981 samples are described separately followed by the total sample.

Sample		N	Regression Equation	r	Significance
Egg length - CL	1980	17	N = 24.542 - 0.003X	-0.015	0.477
	1981	25	N = 20.131 + 0.042X	0.213	0.153
	Total	42	N = 22.140 + 0.021X	0.011	0.259
Egg width - CL	1980	17	N = 13.249 + 0.009X	0.209	0.211
	1981	25	N = 9.067 + 0.054X	0.589	0.001
	Total	42	N = 11.178 + 0.031X	0.432	0.002
Egg weight CL	1980	16	N = 2.541 + 0.004X	0.094	0.364
	1981	25	N = -0.614 + 0.031X	0.595	<0.001
	Total	41	N = 1.206 + 0.017X	0.363	0.010
Egg length - CS	1980	17	N = 25.095 - 0.242X	-0.153	0.278
	1981	25	N = 23.540 + 0.040X	0.027	0.449
	Total	42	N = 24.126 - 0.069X	-0.045	0.389
Egg width - CS	1980	17	N = 13.600 + 0.133X	0.389	0.061
	1981	25	N = 12.447 + 0.395X	0.567	0.002
	Total	42	N = 12.945 + 0.269X	0.497	<0.001
Egg weight - CS	1980	16	N = 2.854 - 0.002X	-0.006	0.492
	1981	25	N = 1.991 + 0.183X	0.465	0.010
	Total	41	N = 2.335 + 0.105X	0.269	0.044

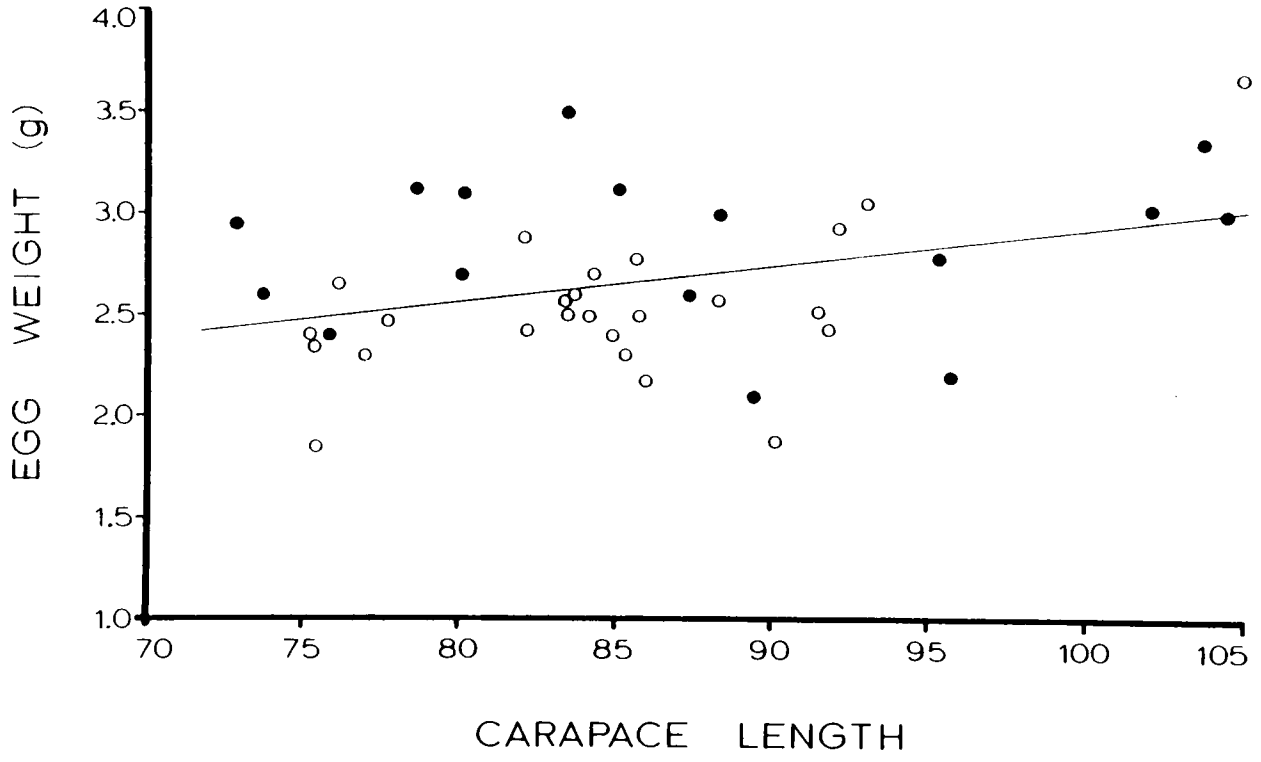

Figure 10. Relationship of egg weight with carapace length for Sternotherus odoratus. Closed circles represent 1980 and open circles 1981. Refer to Table 16 for the regression equation.

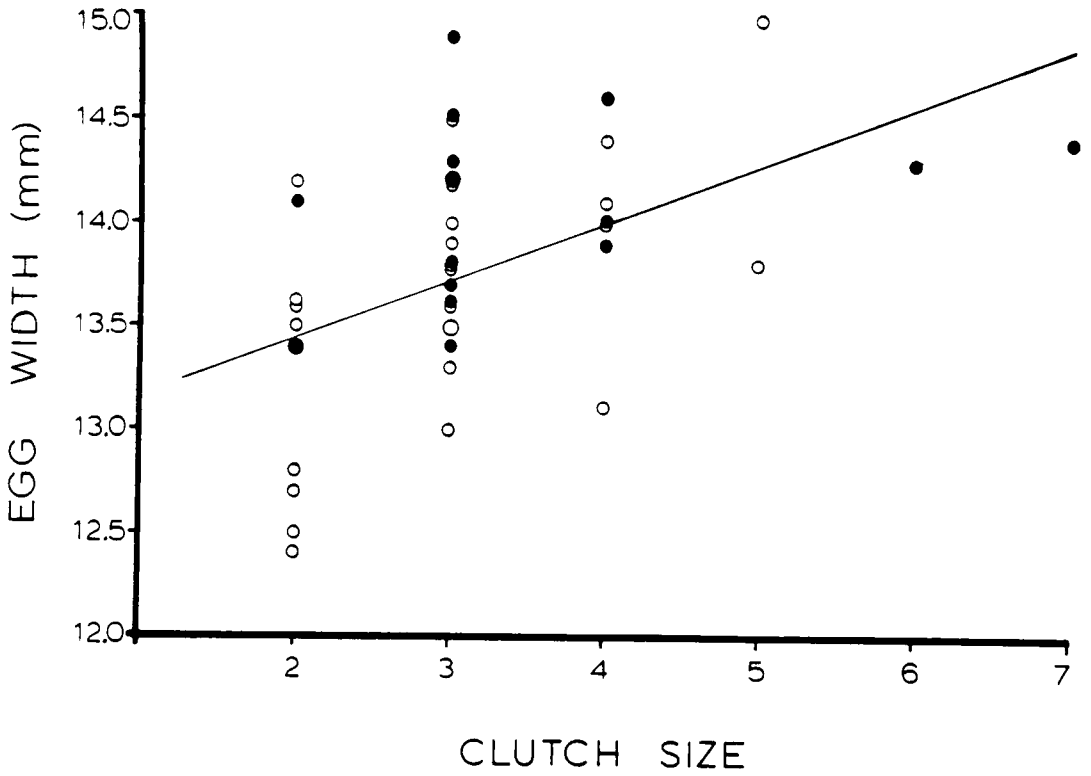

Figure 11. Relationship of egg width with clutch size for Sternotherus odoratus. Closed circles represent 1980 and open circles 1981. Refer to Table 16 for the regression equation.

Discussion

Reproduction in Male Chrysemys picta

That age at maturity for male Chrysemys picta varies geographically was demonstrated by Moll (1973). He showed that this life history feature varied more between subspecies than within subspecies. There are no published data on age at maturity for other populations of C. picta picta, the subspecies predominant in Virginia (Ernst and Barbour, 1972), for comparison with the results of this study. However, Ernst (1971a), who studied a C. picta picta X marginata population in southeastern Pennsylvania, determined that males matured at age four and mated for the first time at age five, one year older than the three and four years, respectively, reported here. Gibbons (1968c) found that marsh habitat males matured two years earlier than lake habitat males in the same area. This suggests age at maturity may be resource dependent.

Testis weights have been used to describe the testicular cycle in this species by Gibbons (1968c) and Ernst (1971a). Although they did not correct testis weights for variation in body size (Acthley, et al., 1976), the cycles were concordant with the one reported above for Virginia painted turtles. Correction for body size may explain the apparent egnima of the enlarged March testes recorded by Ernst (1971a). Moll (1973) and Moll and Christiansen (1973) used testis length and width measurements and found similar cycles for midwestern C. picta.

The spermatogenic cycle for C. picta males in Virginia does not

differ substantially from cycles examined in other locations (Ernst, 1971a; Moll, 1973; Moll and Christiansen, 1973). There are, however, slight differences in timing that may reflect climatic differences. Initiation of spermatogenesis (here defined as appearance of primary spermatocytes, stage 2 of McPherson and Marion, 1981a) is in April for Virginia, Louisiana and Pennsylvania populations, mid-May in Illinois and Tennessee and mid-June in Wisconsin (Ernst, 1971a; Moll, 1973). Primary spermatocytes were appearing when turtles were first caught on 16 April 1980 and 5 April 1981, however, not all males had initiated spermatogenesis when collected this month. Thus, yearly variation in initiation of spermatogenesis differed by about one week to ten days, about half the time indicated for populations in widely scattered locations. Spermatozoa first appeared in males caught 10 June 1980 and 21 June 1981 and spermiation (movement of sperm to epididymes) occurred from mid-September to late-March. These dates are in accordance with the timing of these events in other populations studied, except for Wisconsin and high elevation New Mexico populations (Ernst, 1971a; Moll; 1973; Moll and Christiansen, 1973).

The results of the forward, stepwise multiple regression model clearly showed that testis weight variation is primarily dependent on changes in the spermatogenic cycle. They also show that between year variation is insignificant when samples are compared at the month level. Significant annual differences could appear if samples of sufficient size were obtained at weekly or biweekly intervals. Sampling at this level has been done for some lizards (Ballinger, et al., 1972; Ballinger and Shrank, 1972), but not for turtles.

Reproduction in Male Sternotherus odoratus

Tinkle (1961) demonstrated clinal variation in body size for male stinkpots; southern males were smaller than northern males. Body sizes of stinkpots from Virginia support this trend by exhibiting intermediate lengths. Age at maturity for males from Virginia, two, is a year younger than the average reported for this species (Risley, 1933; Tinkle, 1961). All mature males Tinkle examined, except for a single one-year old southern male, were three or older. Carapace lengths of 51.0 and 51.3 mm reported herein are the smallest sizes yet reported for mature males (but see Chapter IV). Minimum carapace lengths of reproductive males reported range from 54 mm to 65 mm for this species (Tinkle, 1961; Mahmoud, 1969; McPherson and Marion, 1981a).

Seasonal changes in testis weight for males from Virginia are similar to the changes reported by Mahmoud and Klicka (1972) for populations from Arkansas and Oklahoma. Maximum testis weight was reached in August and declined sharply after September for all samples (mid-September in Mahmoud and Klicka). Minimum weights were reached after mid-September in their samples but not until the following May in Virginia samples. The testis weight cycle reported for a population from Alabama (McPherson and Marion, 1981a) differs from the two above in that autumnal weight decline did not occur until November and minimal weights occurred in February. It should be noted that peak weights occurred in August in all these populations.

Risley (1938) pioneered the description of reptilian spermatogenic cycles with his studies of S. odoratus from Michigan. His study and the recent one by McPherson and Marion (1981a) are the only available

to date that describe the entire cycle. There are marked differences among the three studies. In Michigan, primary spermatocytes did not appear until June, but by late-July spermiogenesis had begun. Primary spermatocytes were first observed in May in Virginia and March in Alabama. As in Michigan, spermatozoa appeared by late-July in turtles from these two areas. Spermatocytes decreased rapidly by late-September in Michigan and in October for most Virginia turtles. In contrast, spermiogenesis continued through October in Alabama and spermatocyte decline was not rapid until November (McPherson and Marion, 1981a). Peak spermatogenesis was in August for all these populations. These comparisons support Moll's (1979) hypothesis that peak sperm production is reached in August in the majority of temperate zone turtles. Moll's (1973) hypothesis that turtles in northern latitudes have shorter spermatogenic cycles that start later and end earlier than cycles of turtles in southern latitudes is also supported by these comparisons. Temperature related activity periods probably accounts for the latitudinal differences.

This study demonstrates that seasonal changes in the testis weight cycle is primarily a function of changes in the spermatogenic cycle. This is certainly true for all temperate zone turtles and probably true for turtles in tropical areas as well. Significant annual variation in the testicular cycle is minimal. Differences that exist between years (usually in spring) are probably due to variation in onset of warm weather.

Interspecific Comparisons and Conclusions on Male Reproduction

It is well known that age at maturity for Chrysemys picta and Sternotherus odoratus males differ by one to two years (Risley, 1938; Tinkle, 1961). This study demonstrates the differences may be as little as one year for syntopic populations. The close geographic uniformity for age at maturity for S. odoratus (Tinkle, 1961) and within subspecies of C. picta (Moll, 1973) suggests phylogenetic constraints and warrants further investigation. Gibbons, et al., (1981), however, showed that Pseudemys scripta males may mature early if growth rates allow a minimal size to be reached. This point is discussed further in Chapter IV.

Interspecific comparisons of testis weight and spermatogenic cycles indicate concordance in some aspects but discordance in others. Most C. picta males collected in April had initiated spermatogenesis that month, whereas initiation in S. odoratus did not begin until May. Stinkpots continued spermiogenesis into October in 1981, but painted turtles had completed this phase in September in both years. Comparisons of Figures 3 and 5 show that rates of seminiferous tubule diameter increase are similar between species when years are considered separately. Tubule diameters increased from May lows more sharply in 1980 than in 1981. The rate of diameter increase between June and July was faster in 1981 than in 1980 and mean 1980 maximum diameters in August exceeded mean diameters that month in 1981. These yearly similarities suggest rates of change in the spermatogenic cycle of these two species are under similar environmental influences. Spaet (1973) and McPherson and Marion (1981a) suggested water temperature and photoperiod are involved in

stimulating spermatogenic activity. They hypothesize that warm water temperatures in August and September (about 29 C), in association with decreased photoperiod, may cue maturation of spermatids. Prolonged spermatogenesis in southern populations may be a consequence of a gradual decline in fall water temperatures. These hypotheses could be tested by examination of spermatogenic cycles of turtles inhabiting spring upwellings (Berry, 1975; Cox and Marion, 1978) where water temperatures are constant. Laboratory experiments under controlled conditions might also elucidate these processes.

Male reproductive cycles of C. picta and S. odoratus probably represent adaptations to the female cycle. Sperm are produced after energy uptake through feeding in the spring and early summer and are stored in epididymes for spring matings. Fall matings are known to occur in stinkpots (McPherson and Marion, 1981a) and are thought to occur in painted turtles (Gibbons, 1968c). These matings take place at a time when female follicles are enlarging through vitellogenesis. Females of some turtles can store sperm in oviducts for fertilization in the spring (Moll, 1979) after vitellogenesis is complete. It seems likely that fall matings are early events of the mating phase of a normal cycle and that these events are merely interrupted by cold weather. It follows that fall matings will be encountered more often in southern latitudes.

Reproduction in Female Chrysemys picta

Age at maturity for female Chrysemys picta (6 years) is in agreement with ages reported for this species (6-10) by Gibbons (1968c),

Ernst (1971a) and Wilbur (1975b). Moll (1973), however, reported ages of four to six for Arkansas, Illinois and Tennessee and seven to eight for Wisconsin turtles. Age at maturity is considered by Ernst (1971a) to be a function of a minimum body size. Chapter IV contains a detailed discussion of this point.

The various phases of the ovarian cycle in painted turtles (vitellogenesis, ovulation, latent period and oviposition) are all generally concordant with cycles reported for other populations (Powell, 1967; Gibbons, 1968c; Ernst, 1971a; Moll, 1973; Moll and Christiansen, 1973). The primary differences are in the timing of events and represent adaptations to local environments. Vitellogenesis follows a variable quiescent period with little to no ovarian activity and continues into the following spring when ovulation occurs. Onset of oviposition ranges from mid- to late-May and terminates in early- to mid-July for all populations studied (cited above). Variations of timing among populations appear to be only slightly more variable than between years (Gibbons, 1968c; this study). Of all reproductive attributes, clutch size has received the most attention. Clutch size ranges from one to twenth (Ernst and Barbour, 1972; Moll, 1979). Moll (1973) stated that clutch size in C. picta falls within characteristic limits within subspecies but may vary due to environmental conditions. Powell (1967) reported a mean clutch size of 8.5 (5-11) for C. picta picta from Nova Scotia, twice the size for painted turtles from Virginia. He provided no size data, however, so it is difficult to determine if clutch size was a function of larger female size or an adaptation to maximize reproductive output by laying a large annual clutch. Multiple

clutches (usually two) have been confirmed for several populations of painted turtles in addition to the one studied here (Moll, 1973; Snow; 1980; Tinkle, et al., 1981).

Most investigators have found no significant correlations of clutch size with body size (Cagle, 1954; Gibbons and Tinkle, 1969; Ernst, 1971a). Thus, the highly significant correlation reported here was unexpected. Tinkle, et al. (1981) recently determined that clutch size increased significantly with body size for a population of painted turtles from Michigan. Their result was based on a sample of 82, but the regression line explained only 9% of the variance, compared to 62.1% in this study. Results herein demonstrate that some of the clutch variance is due to egg weight and variations in egg number by month. The number of eggs in successive clutches in a single season and in different years were insignificantly different in this study and in Tinkle, et al. (1981). In contrast, Gibbons, et al., (1979) found significant differences in successive clutches in a single season for Deirochelys reticularia.

Results illustrated in Figure 6 demonstrate that larger females lay eggs which are greater in width than small females. Thus, it is likely that the physical constraint of pelvis size plays a role in determining the size egg a female can lay (Tucker, et al., 1978). There was an insignificant decrease, however, in egg length and weight with increasing body size. Changes in egg weight due to corresponding width changes were probably not detected because of the method of weight determination. Egg size is frequently related to neonate size (Ewert, 1979) and small neonates may have lower survivorship than large neonates.

Reproduction in Female Sternotherus odoratus

Minimum age and size at maturity for Sternotherus odoratus females from Virginia are well within the variations in these attributes reported elsewhere. Tinkle (1961) found that most southern females mature at age three and northern females at ages four to seven. Virginia females are intermediate as would be predicted from his results. Risley (1933) reported nine years as age at maturity for stinkpots from Michigan, but Tinkle (1961) considered this to be an overestimate. Size at maturity ranges from 61 mm to 75 mm carapace length for southern females, including those in Virginia (66 mm), (Tinkle, 1961; Mahmoud, 1969; Gibbons, 1970c; McPherson and Marion, 1981b).

Sternotherus odoratus ovarian cycles have been quantified by Mahmoud and Klicka (1972) and McPherson and Marion (1981b) and are similar to the one reported for females in this study. Ovarian weights and follicle sizes are maximal in spring and decrease through the nesting season to minimal weights and sizes in August. Vitellogenesis begins in late-August or September and continues, with winter interruption, until spring ovulations. Oviductal eggs were found mid-May to mid-June by Mahmoud and Klicka (1972) and February to mid-July by Iverson (1977). Tinkle (1961) found oviductal eggs in southern females March through July and in northern females only in May and June. Risley (1933) stated that the egg-laying season in June through early-July for stinkpots from Michigan. The corresponding period for turtles from Virginia is most similar to that reported for S. odoratus from Alabama by McPherson and Marion (1981b), late-April to late-July.

There are no published studies comparing ovarian cycles between years for stinkpots, but the results of this study indicate onset of ovulation and the subsequent nesting period may vary by one to two weeks. This amount of variation in timing is within the range observed when comparing some of the dates for widely scattered populations (see above).

Clutch sizes have been shown to decrease north (range 2-9) to south (range 1-4) by Risley (1933), Tinkle (1961) and Gibbons (1970c), but average clutch sizes of 3.2 have been reported from Florida (Iverson, 1977), 3.0 from Arkansas, Oklahoma and Texas (Mahmoud and Klicka, 1972) and 2.6 from Alabama (McPherson and Marion, 1981b). Average clutch size for stinkpots from Virginia (3.2) is intermediate between northern and southern values and agrees with sizes reported for other middle latitude populations. McPherson and Marion (1981b) suggested that Iverson's (1977) clutch mean is probably an overestimate because of the predominately large females in his sample. The positive relationship of the number of eggs to body size has been demonstrated for other S. odoratus populations (Tinkle, 1961; Gibbons, 1970c; Iverson, 1977; McPherson and Marion, 1981b), and, as has been shown for stinkpots from Virginia, fecundity may also be a function of age. Over 43% of clutch variance is accounted for by variation in body size. Egg measurements account for another 17.7%. The remainder of the variance is due to error in measurements and probable differences in resource acquisition. The high error variance also suggests that individual clutch size variation between years should be as great as among individuals in the population in the same year. Comparisons of first and second clutch means were

insignificant, however. Similar results were reported by Iverson (1977) and McPherson and Marion (1981b) for successive clutches in their samples. This result, along with the lack of significant differences between years suggests that resource utilization may be the key to understanding clutch size variation in S. odoratus.

Clutch frequency for stinkpots in Virginia is two and possibly three for some females and is similar to that reported for Alabama turtles (McPherson and Marion, 1981b). Frequencies of three to four clutches have been reported for Florida stinkpots (Iverson, 1977) and a single annual clutch is known for northern populations (Risley, 1933; Tinkle, 1961).

Positive correlations of egg width and weight with body and clutch size for 1981 but not 1980 suggests annual differences in energy utilization. Larger females can produce larger eggs because they are less constrained by pelvis size and may be selected to utilize this tactic in unpredictable years to increase neonate size. As noted above, the drought of 1980 continued into 1981 and, along with a lowering of the water level by about 0.5 meter by the lake owner, could have been a cue to increase energy allocation in eggs the following year. Selection could favor females with the ability to produce larger neonates in years following a change in environmental conditions.

Interspecific Comparisons and Conclusions on Female Reproduction

Age at maturity differs by three years for the syntopic Chrysemys picta and Sternotherus odoratus at Grassy Swamp Lake, Virginia. In both species geographic variation in age at maturity suggests this

attribute is a complex function of growth rates, attainment of minimal adult size and constraints on egg size. Eggs above a minimum size should be selected to insure neonate survival and females must reach a minimal size to produce these eggs. These life history attributes are addressed in detail in Chapter IV.

Comparisons of the ovarian cycles of stinkpots and painted turtles in Virginia show the cycles are essentially similar except that S. odoratus has a longer nesting period and that some females may lay more than two clutches in a single season. Chrysemys picta females increase follicle size throughout the winter, whereas vitellogenesis in S. odoratus is almost nonexistent during that period. Differences in means of successive clutches and in clutch means between years were insignificant for both species and the same variables accounted for significant amounts of variation in clutch size.

CHAPTER III

GROWTH

Introduction

Growth in ectotherms is determined by two factors, natural selection of optimal growth rates operating within physical and physiological constraints (Case, 1978) and environmental variability, particularly in resource availability (Wilbur, et al., 1974). Experimental analyses of the former have not been done on any reptile to my knowledge, but it has been shown that reptilian growth rates are partly determined by levels of resource availability (Ballinger, 1977; Dunham, 1978, 1981).

It is well known that growth in freshwater turtles exhibits considerable variation. Growth rates have been shown to vary by sex and age in every species studied where age was determined (e.g., Legler, 1960; Moll and Legler, 1971; Ernst, et al., 1973; Ernst, 1975; Plummer, 1977; Christiansen and Burken, 1979; Iverson, 1979b; Vogt, 1980). Variation in growth between local populations has been attributed to food and high temperatures (Cagle, 1946), diet quality (Gibbons, 1967; Parmenter, 1980) and type of habitat substrate, indirectly related to diet quality (Quinn and Christiansen, 1972). The thermal environment has been shown to have a significant effect on growth rates (Gibbons, 1970b; Christy, et al., 1974; Gibbons, et al., 1981). Annual differences in length of growth seasons due to climatic variations (Sexton, 1959b, 1965) are thought to cause variations in

growth rate (i. e., amount of growth per season). Ernst (1971b) showed that growth in Chrysemys picta was reduced in a drought and cold spring year and Plummer (1977) demonstrated that there were annual differences in gorwth in Trionyx muticus. Wilbur (1975a), however, found no differences in annual growth in his study of C. picta. Growth in freshwater turtles exhibits geographic variation and depends on a variety of factors. Thus, to understand the life history of a population the causes of variation in individual growth rates must be elucidated.

This chapter presents the results of analyses of growth data collected from populations of Chrysemys picta and Sternotherus odoratus which inhabit an urban Virginia lake. Growth in C. picta has been studied in several other populations (Pearse, 1923; Cagle, 1954; Gibbons, 1971b; Ernst and Ernst, 1972; Wilbur, 1975a) and, therefore, considerable comparative data exists. Sternotherus odoratus growth, on the other hand, has been studied only superficially by Rigley (1933) and Mahmoud (1969). From these studies it was expected that age, sex and, perhaps year would emerge as significant factors affecting growth in these species. I chose to utilize Wilbur's (1975a) growth model to compare growth characteristics between his population of C. picta in southeastern Michigan and the one studied here. I also developed a similar model for S. odoratus for interspecific comparisons with the syntopic C. picta population. Age-specific growth rates for both species are examined in an effort to identify some of their life history tactics (sensu Stearns, 1976).

Materials and Methods

Analyses of growth were performed in data obtained on over 5400 captures of 820 Chrysemys picta and 634 Sternotherus odoratus inhabiting Laurel Lake between May 1979 and October 1981. Laurel Lake, about six kilometers northwest of Richmond, Virginia, in Henrico County, is a shallow, 2.75 hectare, eutrophic golf course lake and is located in a registered urbanized area (area classification based on the 1980 census, Federal Register, October 6, 1980, page 66185; personal communication, Cheryl Evans, Henrico County Planning Office). The study system consists of Laurel Lake and a section of Hungary Creek, along which are located two small beaver ponds. This system is described in detail in Chapter IV.

Most turtles were caught in baited funnel traps (Iverson, 1979c), but some were collected by hand and with a single basking trap. Processing was performed in the laboratory in 1979 but exclusively in the field 1980-1981. Turtles were returned to their original capture site within 24 hours (1979) or in less than three (1980-1981). Each turtle was assigned an individual number by filing notches in the shell margin. The coding system consisted of notching the first four carapacial marginals to either side of the cervical scute anteriorly and midline posteriorly. Numbers 1, 2, 4 and 7 were assigned in sequence as ones on the anterior left, tens on the anterior right, hundreds on the posterior left and thousands on the posterior right. Up to 9999 individuals of each species could be marked with this system. These numbers are also easily incorporated into computer files. Sex,

age (if possible), plastron and carapace length, medial length (0.1 mm) of all visible annuli on the right abdominal scute and weight (nearest gram) were noted for each capture. Male C. picta were considered mature if they had elongated foreclaws (usually over 8 mm) and an elongated tail base. Females were recorded as mature if they had no secondary male characteristics and were over 100 mm plastron length (determined by dissections, see Chapter II). Male S. odoratus do not have elongated foreclaws but are mature if the tail base is enlarged, enclosing a mature penis, and if scale patches (Rigley, 1930) are visible. Females lack the enlarged tail base and scale patches.

Medial annuli length does not vary significantly with body size for either species. Ratios of annuli length/plastron length (carapace length for S. odoratus) regressed on body size showed no significant relationships ($P>0.05$). The equation $PL_i = (A_i/A_j)(PL_j)$ was used to obtain body lengths at the beginning of previous growing seasons, where PL_i is the plastron length at the start of the ith growing season, A_i is the annulus length at the start of the ith growing season, A_j is the annulus length at the jth capture and PL_j is the plastron length at the jth capture (substitute carapace length for S. odoratus). These data provided lengths for ages 0 through n, where age 0 is the hatchling length.

Turtles which had two or fewer annuli missing (corresponding to ages 0 and 1) were assigned to an age class after counting the number of growth annuli. This method assumes the primary growth annuli, laid down during long periods of no growth (e.g., winter brumation), can be recognized from secondary annuli (Moll and Legler, 1971). For this

reason age samples are based primarily on 1980 and 1981 data and on data from turtles caught in 1979 which could then be aged with certainty. The use of counts of growth annuli for aging is dependent on recognizable annual growth. Reliability decreases with age, particularly because older turtles may not grow sufficiently some years (Moll and Lagler, 1971; Wilbur, 1975a). Many stinkpots bear complete sets of annuli, especially up to about ten years of age. Annuli in others were obscured by wear or by a black-brown deposit on the plastral scutes. If this was not very thick, it could be gently scraped away exposing the annuli below. All turtles which could be reliably aged constitute a known age sample and all age-specific analyses are based on these turtles.

The growth models are primarily based on growth increments determined by taking the difference between plastron (or carapace) lengths between growth seasons. The model assumes annuli and their measurements accurately reflect periods of growth and that the oldest are the first to be eroded (Wilbur, 1975a). These assumptions are considered to be valid for C. picta by Sexton (1959a) and Wilbur (1975a). Rigley (1933) and Mahmoud (1969) used annuli to age S. odoratus and made the same assumptions. My personal observations indicate stinkpots deposit growth rings in the latter half of the growth season and these are accurate indicators of age. In the model, body size (carapace or plastron length) is the mean of the distance between successive lengths. Throughout this chapter N represents the number of measurements.

Results

Growth in Chrysemys picta

Age-specific growth. Early spring emergence from the nest is documented for C. picta from Laurel Lake with the discovery of terrestrial hatchlings with umbilical scars 21 and 28 March, 1980 and 7 April, 1981. Turtles in their first year of growth were collected in the lake April through December. Recently hatched turtles (<10 grams) were caught March through May (8), June (9) and July (2) and most of these exhibited some growth. First year turtles averaged 41.6±7.1 mm plastron length (24.4-54.3, N=171) and weighed 18.88±7.43 grams (4.0-39.0, N=169). Growth increments averaged 23.0±4.4 mm (11-38, N=233).

Juvenile (=unsexed) C. picta more than double their body size in the first year and growth is logarithmic through age three (Figure 12). Female painted turtles follow this trend for the first two to three years, then assume a linear rate for ages three to ten (Figure 13). For males, growth is logarithmic until maturity is reached at age four (see Chapter IV) and linear thereafter. Females five to ten years of age grow faster than males in the same age group. There appears to be no abrupt change in growth rate after females reach maturity in their eighth year (see Chapter IV) (Figure 13). Old females (>125 mm PL) grow about one millimeter per year, if they grow at all in a given year. Mature females averaged 120.5±8.0 mm plastron length (97.2-142.0, N=735) and were considerably larger than males on the average (mean=96.4±10.9 mm, 71.0-121.0, N=1224). Immature females averaged 83.7±9.4 mm (59.8-100.0, N=173).

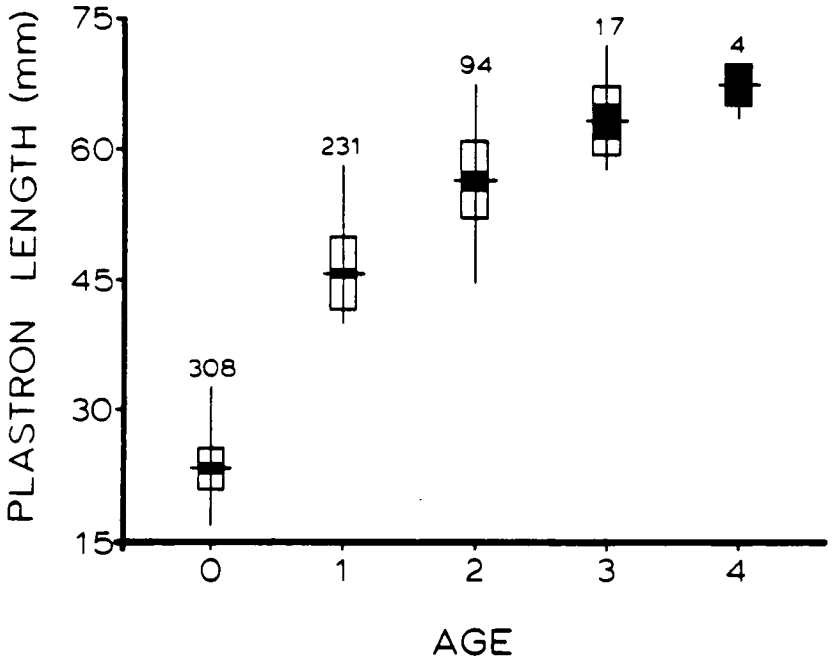

Figure 12. Relationship of plastron length with age for juvenile Chrysemys picta. Plastron length is the size at the start of the age interval. See Figure 2 for meaning of symbols.

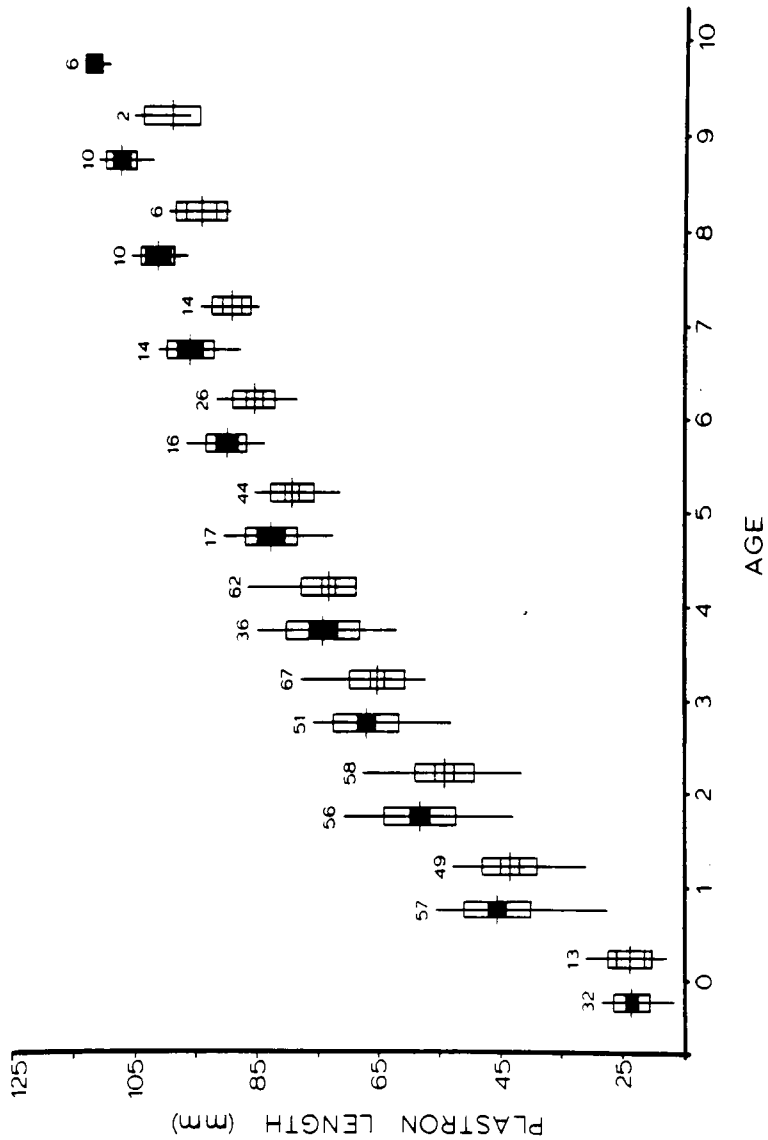

Figure 13. Age-specific growth for Chrysemys picta. Closed rectangles represent females and open rectangles males. See Figure 2 for meaning of symbols. Age is in years.

Since growth is likely to be more functionally linked to body weight than linear size (Wilbur, 1975a), relationships of body weight with plastron length were examined for all turtles in four sex and age groups. Weights were used for all juveniles, all mature males and immature females measured in 1980-1981 and adult females caught after the nesting season in 1980-1981. All relationships were log-log. The regression of the logarithm of body weight on the logarithm of plastron length adequately describes the relationships (Table 17). Over 93% of the variation in body weight is accounted for by body size in all but adult females (84.9%). Unexplained variation is likely due to water flux and measurement error. Variation in female weights also reflect differences in weights of vitellogenic follicles (see Chapter II).

Age-specific changes in body weight (Figure 14) reflect the slower growth rate of males after they have reached maturity and the continued higher rate of females through ages ten and eleven. Immature females average 109.0±30.4 g (46-173, N=169) body weight, mature females 283±52.2 g (150-458) and mature males 149±4.8 g (52-264, N=1143).

The growth model. The linear, additive model for Chrysemys picta from Laurel Lake (Table 18) was based on 718 measurements of growth increments. A classical multiple ANCOVA (Nie, et al., 1975) was used to determine if sex and year, independent variables, had significant effects on growth, the dependent variable. Age and plastron length were included as the covariates, since they significantly contribute to the variation in growth increments (Table 18). This model assumes that variances of the dependent variable relative to each independent

Table 17. Regression statistics of $\log_{10}$ (weight) = b + m $\log_{10}$ (plastron length), where b = $\log_{10}$I (= y-intercept), for Chrysemys picta. See text for descriptions of age-sex categories. N is sample size, m is slope of the regression line, S.E. is standard error and r^2 is the coefficient of determination

Category	N	$\log_{10}$I	S.E.	m	r^2
Juveniles	1040	-2.812	0.035	2.513	0.977
Adult males	866	-2.734	0.033	2.468	0.932
Immature Females	138	-2.696	0.035	2.458	0.934
Adult females	223	-2.964	0.032	2.599	0.849

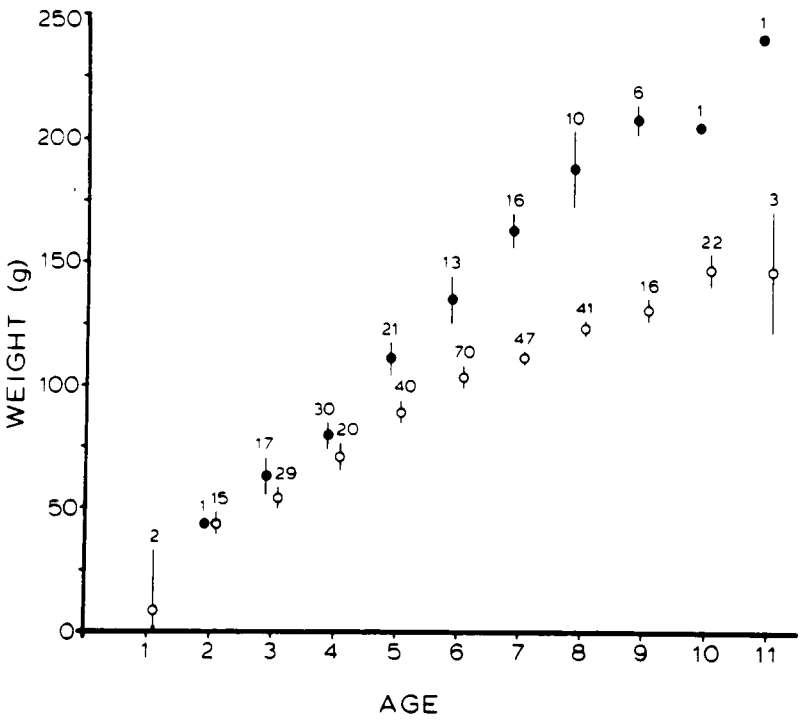

Figure 14. Relationship of weight with age for Chrysemys picta. Closed circles represent females and open circles males. The circle is the mean and the vertical line is the 95% confidence interval. Age is in years.

Table 18. Analysis of variance table for the growth model for Chrysemys picta.

Source	Sum of Squares	D.F.	Mean Square	F	Significance
Sex	478.93	2	239.46	10.596	<0.001
Year	322.879	3	107.626	4.762	0.003
Sex x year	319.07	6	53.18	2.353	0.029
Age[a]	116.59	1	116.59	5.159	0.023
Plastron length[a]	3742.17	1	3742.17	165.590	<0.001
Error	15909.71	704	22.60		
Total	44173.55	717	61.61		

[a]covariates

variable are homogeneous and normally distributed. Zar (1974) stated that the ANCOVA is sufficiently robust to allow testing without apriory examination of these assumptions. Relationships of growth increments to the independent variables appear linear as indicated by scatterplots of these data. In the classical design, growth increments are adjusted for each covariate before testing with each of the independent variables. The results (Table 18) demonstrate significant effects due to sex and year and their interactions. Removal of 1981 data (N=67) significantly alters the model and renders the effect of year ($F=2.698$, 2, 650 d. f., $P=0.068$), age ($F=3.256$, 1, 650 d. f., $P=0.072$) and the interactions between sex and year ($F=0.315$, 4, 650 d. f., $P=0.868$) insignificant. The insignificant F-value for age (Table 18) is due to the ANCOVA design wherein each covariate (age and plastron length) is tested while being adjusted for all other covariates (Nie, et al., 1975). The second covariate, plastron length, accounts for 61.1% of the growth variance (Forward, stepwise, multiple regression of growth with age, plastron length, sex and year: $F=1124.93$, 1, 716 d. f., $P<0.0001$), and age is directly related to it (Figures 12 and 13). The full model (including 1981 data) accounts for 87.4% of the variance in growth. Removal of 1981 data from the model only slightly decreases this estimate (86.3%). The error variance is probably due to measurement error, reproductive activities and short periods of growth cessation (Wilbur, 1975a). ANOVA comparisons of average growth for unsexed juveniles, males and females indicate significant differences among years (Table 19). Sample variances were homogeneous for juvenile C. picta and growth in 1981 was significantly less than in previous years (Tukey's HSD test, $P<0.05$).

Table 19. Comparisons of growth increment statistics for Chrysemys picta 1978 - 1981.

	Juveniles		Males		Females	
Year	N	$\bar{X} \pm$ SD	N	$\bar{X} \pm$ SD	N	$\bar{X} \pm$ SD
1978	76	19.91 ± 6.39	72	10.38 ± 5.23	70	12.88 ± 7.34
1979	161	17.45 ± 7.50	61	7.37 ± 3.59	65	9.55 ± 5.04
1980	87	18.42 ± 7.47	38	5.55 ± 3.89	21	10.23 ± 5.14
1981	48	12.46 ± 6.44	14	3.60 ± 3.44	5	6.80 ± 2.29
F		11.334		16.361		4.294
Significance		<0.001		<0.001		0.006

Male sample variances were heterogeneous (B=3.749, P=0.011) and Tukey's HSD test on sine-transformed growth increments (B=0.318, P=0.813) indicated that growth in 1981 was significantly less than in 1978-1980. Sample variances of female growth increments were also heterogeneous (B=4.808, P=0.002) and Tukey's HSD test on log-transformed increments (B=0.377, P=0.770) indicated that 1978 growth was significantly greater than growth in 1979, but not in 1980 or 1981.

Growth in Sternotherus odoratus

Age-specific growth. All Sternotherus odoratus known to be in their first year of growth were caught between 9 July and 30 December, indicating that few stinkpots, if any, overwinter in the nest. First year turtles averaged 38.3±6.0 mm carapace length (21.5-44.5, N=16) and weighed 10.8±3.2 grams (2.0-15.0, N=16).

Mean size at hatching (23.0±1.6 mm, 19.0-25.8, N=27) and after one year of growth (39.5±2.5 mm, 34.9-46.0, N=22) in unsexed juveniles compare favorably with calculated hatching size (age=0) for known males and females (Figure 15). Growth is logarithmic through age three for both sexes and is linear theafter through age eight. Growth in older individuals is considerably reduced and is variable. Individuals greater than about 90 mm grow about one millimeter annually. Mature females average 79.4±8.3 mm carapace length (60.0-104.6, N=1113) and mature males 79.0±12.3 mm (50.0-107.4, N=800).

The relationship of body weight with carapace length for S. odoratus was determined for all juveniles, males caught 1980-1981 and females weighed after the nesting season 1980-1981. All relationships

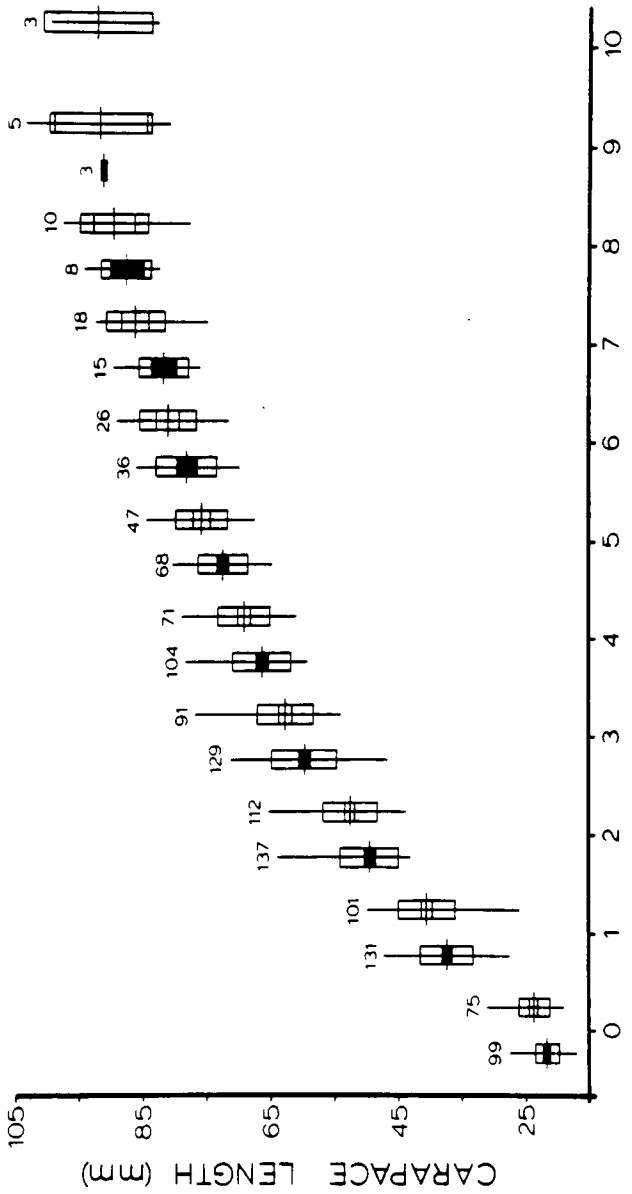

Figure 15. Age-specific growth for Sternotherus odoratus. Closed rectangles represent females and open rectangles males. See Figure 2 for meaning of symbols. Age is in years.

were log-log and regressions of the logarithm of weight against the logarithm of carapace length were highly significant (Table 20). Over 90% of the variance in body weight is determined by body size in all age and sex groups. As with C. picta, error variance is probably a function of measurement error, reproductive state and water flux.

Age-specific differences in body weight indicate separate life history tactics for males and females (Figure 16). Females exhibit a linear, rapid weight gain until age four when maturity is reached (see Chapter IV). This phase is followed by a three year slow weight gain period and then a second, variably linear phase. Weight gain in males is logarithmic until age four, then exponential through age eight. Growth in older males is roughly linear and highly variable. Mature females average 82.3±25.2 grams (34-170, N=1147) body weight and were slightly heavier than males (mean=76.7±33.5 g, 19=180, N=844).

The growth model. The growth model for stinkpots from Laurel Lake (Table 21) was based on 684 growth increment measurements and was designed as for C. picta. Scatterplots of growth data with sex and year indicate their relationships are linear. Results of the model show significant effects on growth due to sex, year and their interactions. If 1981 data are removed from the sample (N=64), sex ($F=1.587$, 2, 619 d. f., $P=0.205$), year ($F=1.684$, 2, 619 d. f., $P=0.187$) and their interactions ($F=1.112$, 3, 619 d. f., $P=0.343$) become insignificant. Age accounts for 60.5% of growth variance (Forward, stepwise regression of growth with age, carapace length, sex and year: $F=1041.95$, 1, 681 d. f., $P<0.0001$). The full model with 1981 data explains 91.3% of growth variance, whereas the model without 1981 data

Table 20. Regression statistics of $\log_{10}$ (weight) = b + m $\log_{10}$ (carpace length), where b = $\log_{10}$I (= y-intercept), for Sternotherus odoratus. See text for descriptions of age - sex categories and Table 17 for symbols.

Category	N	$\log_{10}$I	S.E.	m	r^2
Juveniles	159	-3.181	0.041	2.654	0.969
Adult males	684	-3.610	0.033	2.881	0.973
Adult females	656	-3.463	0.030	2.818	0.944

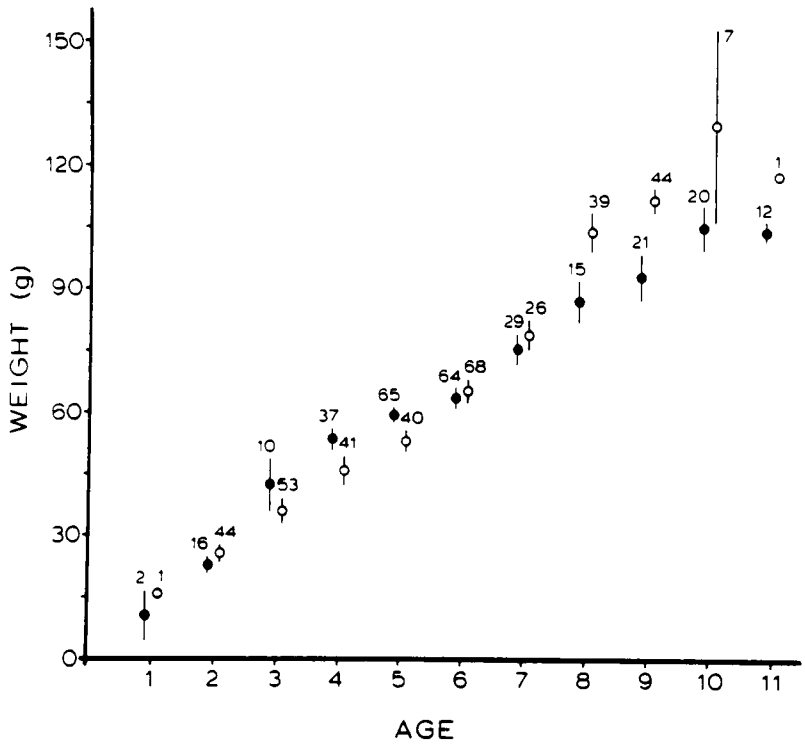

Figure 16. Relationship of weight with age for Sternotherus odoratus. Closed circles represent females and open circles males. The circle is the mean and the vertical line is the 95% confidence interval. Age is in years.

Table 21. Analysis of variance table for the growth model for Sternotherus odoratus.

Source	Sum of Squares	D.F.	Mean Square	F	Significance
Sex	129.01	2	64.51	7.359	0.001
Year	508.82	3	169.61	19.348	<0.001
Sex x year	153.45	5	27.09	3.090	0.009
Age[a]	481.23	1	481.23	54.898	<0.001
Carapace length[a]	263.12	1	263.12	30.017	<0.001
Error	5873.12	670	8.77		
Total	17281.79	682	25.34		

[a]covariates

explains 91.0%. Measurement error, reproductive state and summer brumation resulting in growth cessation probably account for the remaining variance in growth.

ANOVA comparisons of growth increments among years (Table 22) demonstrate significant differences for males and females, but insignificant differences for juveniles. Growth increment sample variances were homogeneous for both males ($B=0.084$, $P=0.969$) and females ($B=1.890$, $P=0.129$). Male and female stinkpot growth was significantly less in 1981 conpared to previous years and females in 1980 grew significantly less than in 1978 (Tukey's HSD test, $P<0.05$).

Discussion

Growth in Chrysemys picta

Delayed emergence, or overwintering in the nest, is a widespread phenomenon in turtles and has been confirmed for Chrysemys picta in five widely separated populations (Gibbons and Nelson, 1978). Based on observations of growth in most first-year turtles when caught initially in a season, the records of emergents in March and April and the lack of observations of emergents in late-summer, delayed emergence appears to be the tactic utilized by painted turtles from Laurel Lake. Delayed emergence increases the probability of survival since emergence at Laurel Lake occurs in the spring when rainfall is more predictable than in late-summer and fall, and dessication is less likely in the travel from the nest to water. All three terrestrial hatchlings were found on cloudy or rainy days. Emergence may be triggered by a period of winter

Table 22. Comparisons of growth increment statistics for Sternotherus odoratus 1978 - 1981.

	Juveniles		Males		Females	
Year	N	$\bar{X} \pm$ SD	N	$\bar{X} \pm$ SD	N	$\bar{X} \pm$ SD
1978	37	16.80 ± 3.79	91	10.73 ± 5.07	125	10.45 ± 4.42
1979	38	16.52 ± 3.65	115	10.41 ± 5.06	142	9.36 ± 4.08
1980	14	15.09 ± 3.11	68	8.81 ± 4.84	65	8.69 ± 4.45
1981	9	16.86 ± 1.98	24	4.55 ± 4.83	31	2.75 ± 3.12
F		0.865		11.262		28.384
Significance		0.462		<0.001		<0.001

temperatures, or release from them (Gibbons and Nelson. 1978). Emergents in summer face an unpredictable environment and potentially reduced resources due to the uncertainty of summer rainfall. Most rain occurring from June to September in central Virginia results from scattered thundershowers.

Ernst (1971b) stated that first-year growth in painted turtles depends on hatching (emergence) date and, although no data were presented, suggested that spring emergents grew to a larger size by year's end than summer emergents. First-year growth in painted turtles from Laurel Lake varied from eleven to 36 mm plastron length, suggesting some individuals in the sample emerged in the summer and grew comparatively less. It was not possible to accurately designate spring or summer emergents from annuli data. However, if the frequency distribution of growth increments is significantly bimodal, these two groups could be detected. The observed frequency distribution was not significantly different from a normal distribution with a mean of 22.99 (Komolgorov-Smirnov Goodness of Fit test, K-S Z=1.139, P=0.15). This result supports the observations that, at Laurel Lake, painted turtles delay emergence.

That age-specific growth rates are initially logarithmic and change to a linear rate after maturation has been demonstrated for other C. picta populations (Gibbons, 1968b; Ernst, 1971b; Wilbur, 1975a). This type of growth curve has been reported for other species of freshwater turtles as well (Moll and Legler, 1971; Plummer, 1977; Vogt, 1980). Mature females average considerably larger than mature males in all known populations and the difference is readily observed in body mass

and in the higher domed shells of females. Rapid female growth and delayed maturity are adaptations for increased body size and, therefore, increased clutch size (Wilbur, 1975a). It is probable that a female must reach a naturally selected minimum body size so that eggs she lays are large enough to produce viable neonates (see Chapter IV). Males have a slower age-specific growth rate, particularly after maturity. Early reproduction in males reflects the female-choice mating strategy (Berry and Shine, 1980), wherein small mobile males have an early advantage in seeking and courting females. Delaying maturity to achieve a larger body size increases risk of mortality and reduces chances to contribute to the next generation.

The growth model developed by Wilbur (1975a) for a Michigan population of C. picta demonstrated significant differences in growth between sexes but not ponds, years or the interactions of these three factors. Both covariates, age and plastron length, were highly significant in his study. Similarities between Wilbur's model and the one for painted turtles from Laurel Lake were found only in the effect of sex and in the significance of the covariates. Removal of 1981 data increases the number of similarities but also causes the covariate age to become insignificant (see Results). The primary difference between these models for year effects is probably due to the drought experienced in the southeastern United States during 1980 and 1981. Annual precipitation for 1978 through 1981 was 113 cm, 149.2 cm, 100.8 cm and 91.3 cm, respectively. Total rainfall for the normal turtle growth season, May to September, was 44.8 cm, 71.5 cm, 37.0 cm and 49.9 cm, respectively for 1978 through 1981 (U. S. weather data from Ashland,

Hanover County, Virginia; about 13 kilometers northeast of the study area, Anonymous, 1978-1979). The summer of 1980 was the driest in recorded history for this area (Anonymous, 1980: 24) and, although summer rainfall was higher in 1981, the average was still below normal (54.9 cm) for that period. Reduced growth between years is probably an indirect function of drought through reduction in resource levels and is, perhaps, a reflection of increased time in summer aestivation as well. Slow growth rates in 1981 may also be a result of reduced energy storage in 1980. Since there are no discernable differences in reproductive activities in 1980 and 1981, most energy available was, perhaps, used for this activity rather than partitioned into growth. The lack of significant year effects for the Michigan population (Wilbur, 1975a) is probably due to similar environmental conditions among the years of study.

Growth in Sternotherus odoratus

Although delayed emergence in S. odoratus has been confirmed (Gibbons and Nelson, 1978), most emergents at Laurel Lake enter the population in late-summer or early-fall. Eggs of this species have been found in shore debris, under logs, on stumps and in the open, as well as buried in soil at various distances from water (Cagle, 1937; Sanderson, 1970). Turtles in most of these sites would probably not survive winter temperatures. Selection would favor turtles emerging in the year the egg was laid. Overwintering in the aquatic environment where there is a less dramatic temperature flux would enhance survivorship. The fact that delayed emergence does exist in South

Carolina (Gibbons and Nelson, 1978) suggests there is geographic variation in this tactic. It is also possible that nest site selection could dictate which hatchlings emerge in the summer or fall and which delay emergence. Eggs buried in the soil could overwinter, whereas those above ground should hatch in the year of laying. The observed frequency distribution of growth increments (range, 9-27) was not significantly different from a normal distribution with a mean of 16.54 (K-S Z=1.006, P=0.263). Records of growth increments up to 27 mm suggests that not all stinkpots emerge the year of egg deposition, but no emergents were found in the spring during this study.

Age-specific growth curves illustrated by Risley (1933) and Mahmoud (1969) are similar in shape and slope to the one exhibited by turtles from Laurel Lake. The change in growth from logarithmic to linear occurs at about age five in Michigan and age three in Oklahoma and Virginia. This reflects the geographic variation in age at maturity exhibited by S. odoratus (Tinkle, 1961).

Age-specific changes in body weight are adaptations to the mating strategy employed by this species. Growth in females is rapid so that a naturally selected minimum body size is obtained. A female must be large enough for an egg of minimal size to pass through her pelvis and the inflexible egg must accomodate a neonate large enough to survive on his own. The decreased weight gain from ages four to six suggests that most energy available is being partitioned into reproduction. The second, accelerated phase of growth may be an adaptation to increase egg and clutch size (see Chapter II) during a period of reduced probability of survivorship. Males gain weight rapidly through age

five but surpass females by age six in an even greater accelerated phase of growth. Males mate by forced insemination where increased body mass is advantageous (Berry and Shine, 1980). Males of sizes equal to or greater than females should have a higher rate of success of insemination than smaller males, particularly if the female is large. This does not explain, however, the strategy employed by smaller males three to five years of age. Selection should favor rapid growth rates and an age at maturity that insures mating and offspring production. Yet, male S. odoratus from Virginia are able to mate for the first time in their third year but are smaller in mass than mature females until about age six. Mahmoud (1967) described the mating behavior of S. odoratus along with three other kinosternids and noted that small males mounted large females more toward the posterior portion of the carapace. The smallest male he examined was about 65 mm carapace length and was five years old. Three-year old males from Virginia are 49-50 mm. Is there a lower probability of mating for small males than large males? Do small males mate more often with small females? Are there separate mating behaviors employed by large and small males? Future research on stinkpot reproductive behavior should be directed toward these questions.

Interspecific Comparisons

The growth model for S. odoratus from Laurel Lake was identical to the one for the syntopic C. picta population when 1981 data were included. Removal of the 1981 data from the stinkpot model rendered the main factors, sex and year, as well as their interactions, insignificant. The overall concordance in age-specific growth between

sexes in stinkpots predicted this result. The model for C. picta showed a significant sex effect as would be expected from the results in Figure 13. Sex-specific growth appears to be the rule for painted turtles but not for stinkpots.

Annual differences in growth rates show similar patterns of reduction during drought years when compared interspecifically. This suggests the same environmental factors, probably associated with resource availability as noted above, are responsible for at least some of the variation in annual growth in both species. Growth tactics are reflections of the demographic characteristics of the populations and are further discussed in light of these in the summary.

CHAPTER IV

ECOLOGY AND DEMOGRAPHY

Introduction

Survival of a population in a particular environment depends on the suite of adaptations that characterize its life history tactic (Wilbur, et al., 1974, Stearns, 1976, 1977). These adaptations include age and size at maturity, fecundity, sex ratios and behavior. The trade-offs between alternative tactics depends on the demographic environment wherein these tactics evolve (Williams, 1966). An understanding of the structure of a population, its dynamics and its demographic characteristics should allow identification and assessment of its life history strategy.

Demographic properties of freshwater turtle populations have only recently been published. Wilbur (1975b) provided the first life table for turtles after a long term study of a Chrysemys picta population. Tinkle, et al. (1981), who have continued the investigation of that population, refined the life table estimates with additional information on clutch frequency and egg survivorship. Gibbons and his co-workers (e.g., Gibbons, 1969, 1970a,b; Gibbons and Coker, 1977; Gibbons and Greene, 1978; Gibbons, et al., 1981) are identifying demographic features of several species of freshwater turtles in southeastern North America, and are elucidating some of the causes of their variation, particularly in Pseudemys scripta. Demographic information on other species and other populations occupying different habitats is needed to test predictions that have evolved from these studies.

This chapter presents the results of an assessment of the ecological and demographic characteristics of syntopic populations of Chrysemys picta and Sternotherus odoratus inhabiting a lake located in a recognized urban area (see page 68). Results are based on over 5400 captures of these two species. The objectives were 1) to determine the structure and dynamics of the populations, 2) to identify their demographic characteristics, and 3) to compare these features interspecifically. It will be shown that urban lake populations of these two species do not differ appreciably from populations in areas less influenced by man's activities.

Materials and Methods

The study area is located 7 km northwest of Richmond, Virginia in Henrico County and consists of Laurel Lake, a section of Hungary Creek and two small beaver ponds (Figure 17). The creek is about six meters maximum width and less than one and half meter deep in the channel. Beavers constructed the dams in late 1978. Laurel Lake is a warm, polymictic reservoir at an elevation of 66 meters above mean sea level. The dam was built in 1927. The lower (southeastern) portion of the reservoir has received a considerable amount of silt from land clearing operations south of the westernmost beaver pond and water depth varies from less than 0.5 to one meter. The middle and upper portions have sandy substrates except for the corners where organic debris varies in depth from 0.1 to 0.5 meter. Water depth is less than 1.5 meters deep except for the channel which may be as deep as 2.5 meters. The water is turbid year round and the bottom cannot be seen except in areas of

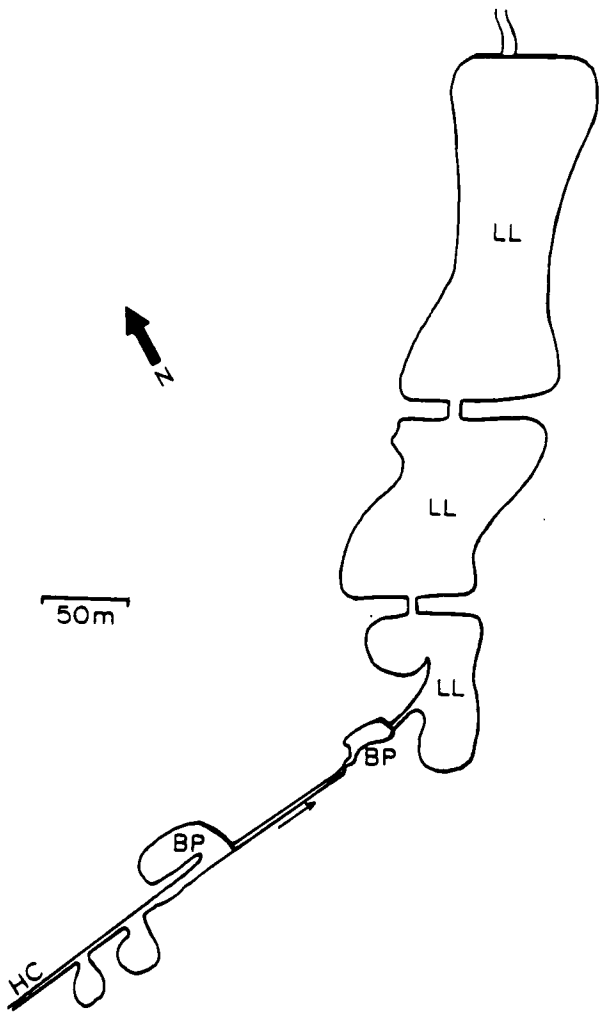

Figure 17. Map of Laurel Lake (LL) and associated Hungary Creek (HC). BP represents the beaver ponds and the arrow indicates the direction of stream flow.

less than 0.2 meters in water depth. Summer dissolved oxygen values averaged 6.3 mg/liter at the surface and 1.7 mg.liter at one meter depth and fall values averaged 12.2 mg/liter surface and 7.4 mg/liter at one meter.

Most of the study system is located in a now unused golf course. The lower part of the lake, the smaller beaver pond and parts of Hungary Creek are bordered by mixed stands of Acer rubrum L., Liquidambar styraciflua L., Pinus taeda L. and Populus alba L. Where it occurs, vegetation along the lake margin consists mainly of alder (Alnus serrulata (Aiton) Willdenow). Swamp rose (Rosea palustris Marshall) is present on the edge of the lake sections defined by road banks. A stand of oak (Quercus alba L.) borders most of the eastern side of the upper part of the lake. Aquatic vegetation consists of Nuphar luteum Sibthorp and Smith and Nymphea odorata Aiton in the silted areas and scattered patches of lizard's tail (Saururus cernuus L.), pickerel weed (Pontederia cordata L.) and some arrowleaf (Peltrandra virginica (L.) Kunth). Algal blooms are common. Yellow bullhead (Ictalurus natalis), creek chubsucker (Erimyzon oblongus), bluegill (Lepomus macrochirus), pumpkinseed (Lepomus gibbosus), crappie (Pomixis nigromaculatus), golden shiner (Notemigonus crysoleucus), largemouth bass (Micropterus salmoides) and eel (Anguilla rostrata) are occasionally caught in the traps. Eutrophication is probably due largely to fertilizer (phosphate) runoff from golf course lawns, as well as siltation.

The turtle community consists of two abundant species, Chrysemys picta and Sternotherus odoratus, the lesser abundant Chelydra

serpentina, Pseudemys rubriventris, Kinosternon subrubrum and the introduced Pseudemys scripta elegans. Clemmys guttata (2) have been captured above the upstream part of the study system. They were abundant in small ponds in a wooded area that is now the upper portion of the large field below the beaver pond (personal observations). That area was cleared in about 1975 for a shopping center, although it has yet to be built. The golf course was built in 1927 and was in use until late 1979. It was sold to a land developer that year. The lake has always been open to shoreline fishing and the surrounding area is used for various recreational activities. Litter from fishermen and recreationists frequently ends up in the lake.

Populations of C. picta and S. odoratus were censused from May 1979 (except June 1979) to 15 October 1981, in all months except January. Most turtles were caught in funnel traps (Iverson, 1979c) baited with sardines or chicken or fresh fish wrapped in hardware cloth. Traps were checked daily except for early spring and late fall months (every other day these months) and except for occasional two-three day trips. Some captures were made by hand or dipnet. During 1980 a small basking trap (MacCulloch and Gordon, 1978) was used but this proved to be less effective than funnel traps. All measurements of carapace length and plastron length, lengths of annuli on the right abdominal scute and weight were made by me to reduce errors. Sex, age, injuries, abnormalities, ectoparasites and carapacial coverage of algae were recorded. A number was assigned to each individual as described in Chapter III. Females were palped for oviductal eggs May through July; this was considerably more effective for stinkpots than painted turtles.

Reproductive data from turtles drowned in the traps (about 1% of each species) provided information on synchrony of reproductive cycles and estimates of clutch size.

Estimates of catchability were made with the conditional probability of capture procedure (Seber, 1973: 90) where, for each category in the sample, the number of 1980 captures of turtles captured in 1981 (C) was divided by the total number of turtles caught in 1981 that were originally caught in 1979 (R). The conditional probability of capture P(C/R), provides a measure of differences in catchability due to age or sex. These factors may be a source of bias in recapture estimates (Seber, 1973). Another source of bias results from turtles becoming trap shy or trap addicted. The use of Bailey's triple-catch method (Tanner, 1978) to estimate population parameters partially counteracts these problems.

Results

Ecology and Demography of Chrysemys picta

Population estimation. Estimates of catchability for Chrysemys picta were high for juveniles, adult males and immature females (Table 23). Turtles in these groups had greater than a 90% chance of being captured at least once during the active season. In contrast, adult females had only a 76.5% chance of capture each year. The difference is obvious in the field. Females were captured frequently until after the nesting season when rates declined. Capture rates of the other groups were high throughout the activity season.

Recapture rates were especially high for adult males but only

Table 23. Estimates of catchability for Chrysemys picta by age and sex. P(C/R) is the conditional probability of capture of at least once each year, where P = probability, C = the number captured in the second year and R = the number surviving three years.

Category	# Surviving 3 years	# Captured in 2nd year	P(C/R)
Juveniles	31	29	0.935
Adult males	83	75	0.904
Immature females	10	9	0.900
Adult females	81	62	0.765

moderately so for juveniles and adult females in comparison (Figure 18). Maximum number of recaptures varied by sex and age; 10 for immature females, 12 for juveniles, 17 for adult females and 24 for adult males. Frequencies were random for recaptures of immature and adult females, but significantly nonrandom for juveniles and adult males (Table 24). Since not all juveniles and adult males have an equal probability of capture, one of the basic assumptions of all mark-recapture estimates is violated. Wilbur and Landwehr (1974) suggest, under such circumstances, testing the recapture frequencies against a truncated or doubly truncated Poisson distribution. Table 24 includes statistics run under both these restrictions and demonstrates that double truncation, i.e., above zero and below 10 recaptures for juveniles and 1-14 for adult males, provides the only range of recapture frequencies that are significantly nonrandom.

Population size. The use of Bailey's triple-catch method to estimate population size avoids much of the inaccuracy associated with violation of equicatchability. This method identifies three capture periods (1979, 1980, 1981) and assumes that each turtle has an equal chance of being caught in each year, if it is alive. For computation, each individual was counted once in each year it was caught. This avoids making the assumption that each turtle has the same probability of being caught each day, week or month.

Triple-catch estimates of the size of the painted turtle population (Table 25) indicate there were 500 to 534 individuals alive in Laurel Lake and associated waters in 1980. The larger size of the adult male population compared to the number of females reflects their

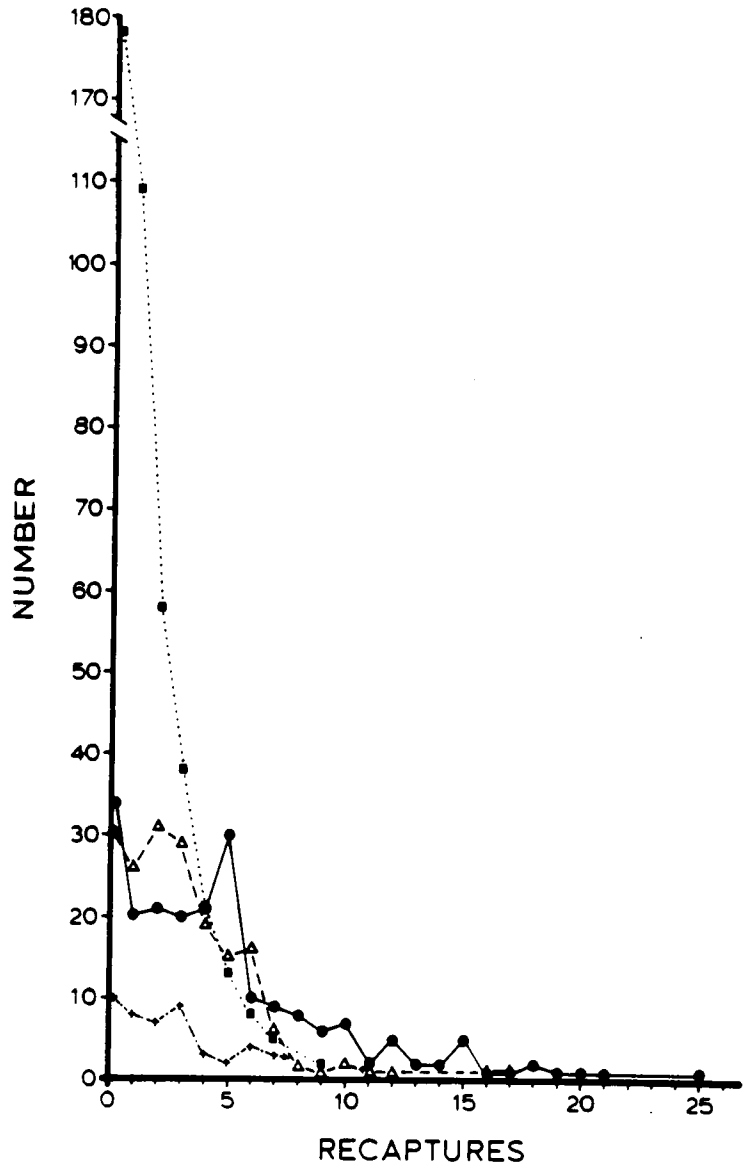

Figure 18. Capture frequencies for Chrysemys picta. Closed boxes represent juveniles, closed circles adult males, open triangles adult females and crosses immature females.

Table 24. Poisson distribution statistics of recapture data for Chrysemys picta. Cases is the total number of individuals, θ is the Poisson mean, K-S Z is the Kolomogorov - Smirnov statistic and P is the probability.

	Juveniles	Adult Males	Immature Females	Adult Females	Total
Cases	434	210	47	180	818
Recaptures	0-20	0-24	0-10	0-17	0-24
θ	2.436	5.910	3.681	4.133	3.933
K-S Z	2.278	2.865	0.650	1.158	5.456
P	<0.001	<0.001	0.792	0.137	<0.001
Truncated -					
Cases	256	176	37	150	607
Recaptures	1-20	1-24	1-10	1-17	1-24
θ	3.43	6.858	4.405	4.760	4.952
K-S Z	1.621	2.193	0.599	1.018	3.613
P	0.010	<0.001	0.865	0.251	<0.001
Doubly Truncated -					
Cases	254	163			563
Recaptures	1-10	1-14			1-9
θ	3.327	5.926			4.197
K-S Z	1.324	1.195			1.310
P	0.060	0.115			0.065

Table 25. Bailey triple-catch estimates of population size, survivorship, recruitment and losses for Chrysemys picta. $\hat{N}_2$ is the population size estimate, S_1 is the survivorship estimate and recruitment and losses are represented by b and d respectively.

Category	$\hat{N}_2$	$\hat{S}_1$	b	d	b-d
Juveniles	138 ± 5	0.457	21.2	1.0	20.2
Adult males	182 ± 3	0.956	10.7	0.9	9.8
Immature females	40 ± 4	0.944	4.4	0.9	3.5
Adult females	157 ± 5	0.963	4.7	0.8	3.9
Total	517 ± 17	0.834	41.0	3.6	37.4

higher rate of recapture in 1980 and may be a slight overestimate of their true abundance.

Population dynamics. Because it was not possible to enclose the study system and moniter all turtle activity, rates of emigration and immigration could not be accurately assessed. Mark-recapture data, however, suggest site fidelity. Two adult males and two adult females were trapped below the dam in the fall of 1979 (three had been previously marked in the lake) and were subsequently caught in the laker proper. Several turtles had fractures along the left or right posterior carapacial margin, an injury sustained only in a fall over the dam to the concrete slab below. Immigration probably occurs to some extent since another lake (Hoehns Lake) occurs only one kilometer upstream from Laurel Lake. Of the 48 new captures of adult turtles in 1981, 48.4% were caught in the upstream portion of the study system. Some immigration from upstream sources is, therefore, suggested.

Table 25 provides triple-catch estimates (Caughley, 1977) of recruitment (b) and losses (d). In these estimates recruitment combines natality and immigration and losses combine death and emigration. For each category recruitment was high and losses low. Comparisons of recruitment rates indicate that significant differences existed between juveniles and both immature females (G-test, $G=10.91$, $P<0.001$) and adult females ($G=10.32$, $P<0.005$). No significant differences were detected for the remaining comparisons ($G=0.073$-3.27, $P>0.05$). Combined with information on immigration (above), these results suggest that most recruitment results from natality. These rates provide estimates on the dynamics of the painted turtle

population between 1979 and 1980 and suggest considerable population growth.

Age at maturity. Laurel Lake Chrysemys picta males are reproductively mature at age four and are 71 mm in plastron length or larger. Some three-year olds were beginning to exhibit foreclaw growth but they did not have the enlarged tail base. All four-year old males had foreclaws 8 mm or longer and each had a mature penis. The smallest of this group was 71.3 mm plastron length.

Age at maturity for females was based on palpation of oviductal eggs, dissection of trap-drowned turtles, significant weight fluctuations in the nesting season and observation of individuals that had recently nested and had dirt around the rear legs and swollen cloacal vents. The smallest mature female at Laurel Lake was 97.3 mm plastron length and was eight years old. All other eight year olds examined (15) were greater than 100 mm and three of these were known to have laid eggs in that year of growth. Eleven seven-year olds were 95-103 mm plastron length and none of these were known to have reproduced. Thus, Laurel Lake females mature in their seventh year and lay their first clutch at age eight, most at a plastron length of 100 mm or larger.

Fecundity. The number of eggs per clutch was determined from dissection of seven females and counts of eggs in two nests. Clutch size averaged 4.1 (3-6). No single female was observed nesting twice in one year, but one female contained two distinct sets of corpora lutea when dissected on 1 July 1979 and another had preovulatory

follicles in addition to shelled eggs on 29 May 1981. Females contained oviductal eggs 20 May through 10 July and nesting females (3) were found between 30 May and 13 July. Several females were known to have laid eggs in successive years. Although there is no direct evidence of multiple clutches, data above indicate at least some Laurel Lake females lay two per year (also see Chapter II).

The correlation of clutch size with plastron length was positive ($r=0.378$) but insignificant ($N=-2.492 + 0.056X$, $P=0.158$), suggesting there is no age-specific increase in fecundity for Laurel Lake painted turtles (compare this result with Figure 6).

Age structure. Population structure refers to the proportions of the total population in each sex and age category (Tanner, 1978). An age was assigned to each turtle from analyses of growth annuli data and recent capture history (see Chapter III for details of methodology). Unsexed juveniles were assigned equally to sex and age classes. Since the structures are based on actual numbers of turtles and not estimates, it must be assumed that each sex and age class is representative of its relative proportion in the population (Wilbur, 1975). This does not appear to be an unwarranted assumption in this study since over 3000 captures of 820 individuals were obtained and it is likely most of the older age turtles were captured at least once.

In each of the years of the study the yearling age group was underrepresented in the samples, and may be a function of their habitat selection behavior. More adult males were distributed in age classes 4-10 than in ages 11 and older (Table 26). The majority of females, in contrast, were 11 years of age or older. Recruitment of new females into this reproductive group is apparently low.

Table 26. Age structure of Chrysemys picta in Laurel Lake. Unsexed juveniles of ages one to two equally assigned to sex groups.

	Age Class											
	1	2	3	4	5	6	7	8	9	10	11+	Total
Females												
1979	60	51.5	25	16	10	6	9	9	10	21	124	341.5
1980	48	55.5	49	21	14	10	5	9	9	10	133	363.5
1981	30.5	33	30.5	27	12	6	5	5	7	7	107	270
Males												
1979	58	46.5	34	27	26	25	33	15	20	11	39	334.5
1980	48	54.5	45	29	23	25	24	28	14	18	44	352.5
1981	30.5	32	31.5	24	16	15	16	18	16	11	47	257

Figure 19 illustrates the age structure of the 1980 population and allows a comparison of the proportions of individuals in each sex and age class. The distributions suggest that females live significantly longer than males, male survivorship is higher in ages 4-7 and a sharp increase in mortality occurs between ages three and four.

Sex ratios. The sex ratio of the total number of marked adult males (215) fours years old or older to marked females (184) seven years or older is not significantly different from a 1:1 ratio ($G=3.684$, $P>0.05$). The same result is obtained when using population size estimates (Table 25) ($G=0.921$, $P>0.25$). Comparisons of sex ratios by year (Table 27) show that there were significantly more adult males known to be alive than adult females in 1980 and 1981. Nine of fifteen adult turtles thought to be immigrants in 1981 (see above) were males, suggesting immigration during the drought year of 1980 may have contributed to the skewed sex ratio.

Survivorship. Survivorship from 1979 to 1980 was estimated with Bailey's triple-catch equations (Tanner, 1978). Individuals were recorded as surviving this period if they were caught anytime in 1980 or were known to be alive that year from their capture in 1981. Survivorship of immature females and adult males and females from 1979 to 1980 was estimated to be greater than 94% (Table 25). During this period juvenile survivorship was less than half this figure (45.7%).

Age-specific survivorship can be estimated from ratios of age classes between years, but assumes that all individuals in each age

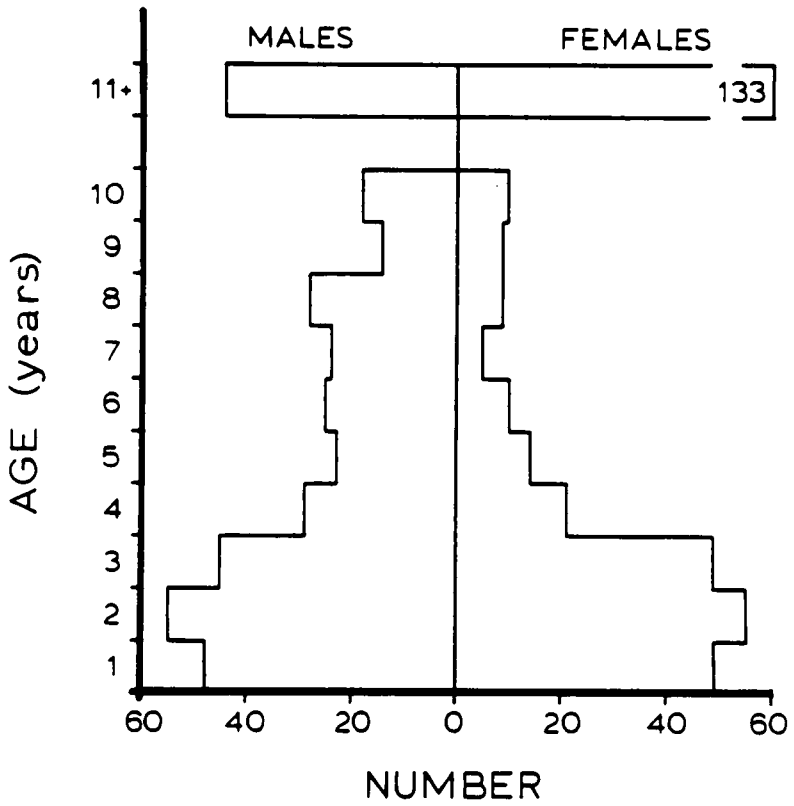

Figure 19. Age structure of the Chrysemys picta population in 1980.

Table 27. Adult sex ratios for Chrysemys picta 1979-1981.

Year	Males	Females	Ratio	G
1979	196	164	1.195	3.143
1980	205	161	1.273	5.470**
1981	163	126	1.294	4.375*

** $P<0.025$, * $P<0.05$

class were counted each year or were proportional to their actual abundance. The high rates of catchability for age classes above one, the use of only one capture record per year and the high recapture frequency suggest this assumption was not seriously violated. Survivorship for both sexes was higher for 1979-1980 than for 1980-1981 (Table 28). In 1980 adult females experienced 100% survivorship. Estimates for yearling survivorship are underestimated due to their underrepresentation in the sample, but all other estimates, especially for 1979-1980, are probably close to true survivorship for that period. The average of the two periods (79.5% females, 77.2% males) may approximate average annual survivorship over all age classes.

Survival rates of hatchling painted turtles (ages 0 to 1) could not be estimated with accuracy because nests were not monitered. An indirect estimation is based on the ratio of the number of yearlings in the following year's sample to the estimated number of eggs deposited by females in the previous year. This method assumes all hatchlings emerged from the nest in the spring and does not seem unwarranted in this study (see Chapter III). Total egg production in 1979 was calculated for 164 adult females, assuming each laid two clutches of 4.1 eggs. This is probably an overestimate because it is likely that not all females produced two clutches (Tinkle, et al., 1981). Yearling abundance in 1980 was calculated from mark-recapture data using the small-sample Lincoln Peterson estimate (Tanner, 1978). Hatchling survivorship based on this method was 16.2% for 1979-1980 (218.2 hatchlings, 1344.8 eggs). The estimate for 1980-1981 is only slightly higher (22.4%) based on 295 hatchlings and 1320.2 eggs.

Table 28. Estimates of age-specific annual survivorship for Chrysemys picta. These estimates are derived from data in Table 26.

	Age class									
	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	Average
Females										
1979-1980	0.925	0.951	0.840	0.903	1.000	0.833	1.000	1.000	1.000	0.939
1980-1981	0.688	0.550	0.551	0.571	0.429	0.500	1.000	0.778	0.778	0.650
Average	0.807	0.751	0.696	0.737	0.715	0.667	1.000	0.889	0.889	0.795
Males										
1979-1980	0.940	0.968	0.853	0.836	0.962	0.960	0.848	0.933	0.900	0.911
1980-1981	0.667	0.578	0.533	0.552	0.652	0.640	0.750	0.571	0.786	0.633
Average	0.804	0.773	0.693	0.679	0.807	0.800	0.799	0.752	0.843	0.772

Mortality. Mortality for turtles inhabiting urban lakes such as Laurel Lake is caused by a variety of factors other than natural ones. Unnatural causes of death were vehicular traffic (6), drowning in fish traps (4) and mutilation by grass mowers on the golf course (one adult female). This latter source of mortality was probably selective for nesting females since mowing was frequent in the nesting season. Local fishermen described decapitation of turtles they hooked and there were reports of shooting basking turtles. An unknown number of juveniles were removed each year by local boys. Of the known deaths, natural causes were raccoon (one adult female), heron (2 juveniles) and largemouth bass (one hatchling). Eight (3 females, 5 juveniles) died of unknown causes.

Ecology and Demography of Sternotherus odoratus

Population estimation. The estimate of catchability for adult female Sternotherus odoratus was higher than estimates for juveniles and adult males (Table 29). These differences reflect seasonal differences in activity. Adult males were captured less frequently than females late-May through August and males were captured at or greater than frequencies of female capture March to mid-May and September to November. Juvenile capture rates were low throughout the study period, but those that were marked had an 87.5% chance of recapture.

Recapture rates among age and sex categories are illustrated in Figure 20. More adult females were recaptured at higher frequencies than adult males, but several males were captured more than 16 times.

Table 29. Estimates of catchability for Sternotherus odoratus by age and sex. P(C/R) is the conditional probability of capture of at least once each year, where P = probability, C = the number captured in the second year and R = the number surviving three years.

Category	# Surviving 3 years	# Captured in 2nd year	P(C/R)
Juveniles	8	7	0.875
Adult males	37	30	0.811
Adult females	62	57	0.919

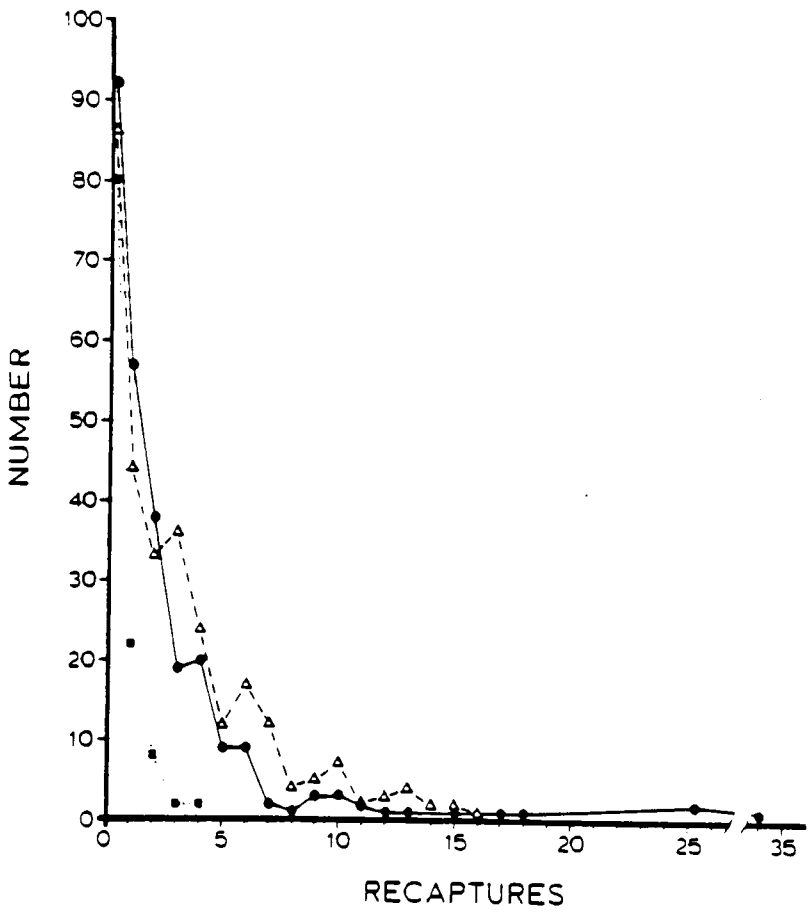

Figure 20. Capture frequencies for Sternotherus odoratus. Open triangles indicate adult females, closed circles males and closed boxes all juveniles.

Maximum number of recaptures was four for juveniles, 19 for adult females and 34 for adult males. Recapture frequencies were significantly nonrandom for all groups when analyses were based on all recapture data (Table 30). Truncating capture frequencies above zero for juveniles achieved randomness for this group. Double truncation was required for randomization for adult males and females and this occurred only after elimination of those individuals who were captured more than ten times for males and 13 times for females (Table 30).

Population size. Bailey's triple-catch method estimated a size of 534±45 for the Laurel Lake stinkpot population in 1980 (Table 31). Juveniles were underestimated because of the low capture frequency, and differences in number of males and females and the high variances are results of differences in catchability and recapture frequencies in 1980.

Population dynamics. Of five S. odoratus captured below the Laurel Lake dam, one, an adult male, was later recaptured in the lake. Although the data are scanty, site fidelity is suggested. Recapture data indicate that stinkpots remain in an area for considerable lengths of time before movement to another area is made. Several adult turtles had injuries along the left and right carapacial margin that indicated falls over the dam. Emigration downstream is suggested, but, since turtles with these injuries were found in the lake, the rate is not considered significant.

Triple-catch estimates of recruitment and losses and their

Table 30. Poisson distribution statistics of recapture data for Sternotherus odoratus. Definitions and symbols as in Table 24.

	Juveniles	Adult Males	Adult Females	Total
Cases	114	263	294	636
Recaptures	0-4	0-34	0-16	0-34
θ	1.456	3.392	4.031	3.527
K-S Z	1.379	3.652	3.575	5.395
P	0.045	<0.0001	<0.0001	<0.0001
Truncated -				
Cases	34	171	208	416
Recaptures	1-4	1-34	1-16	1-34
θ	2.529	4.678	5.284	4.863
K-S Z	0.764	3.170	2.179	3.948
P	0.603	<0.0001	0.0001	<0.0001
Doubly Truncated -				
Cases		158	196	373
Recaptures		1-9	1-12	1-9
θ		3.646	4.719	3.828
K-S Z		1.203	1.207	1.271
P		0.111	0.109	0.079

Table 31. Bailey triple-catch estimates of population size, survivorship, recruitment and losses for Sternotherus odoratus. Refer to Table 25 for meaning of symbols.

Category	$\hat{N}_2$	$\hat{S}_1$	b	d	b-d
Juveniles	82 ± 19	0.858	3.7	0.8	2.9
Adult males	217 ± 18	0.841	4.3	0.8	3.5
Adult females	235 ± 8	0.842	11.2	0.9	10.3
Total	534 ± 45	0.834	19.2	2.5	16.7

differences suggest a growing population (Table 31). The recruitment estimate for females was insignificantly higher than the estimate for juveniles (G=2.95, P>0.05) and males (G=2.30, P>0.05). These rates provided estimates of the dynamics of the S. odoratus population for the period 1979-1980.

Age at maturity. Sternotherus odoratus males from Laurel Lake mature in their second season and apparently mate for the first time in their third year. Onset of secondary sex characteristics, enlarged tail base and scale patches (Risley, 1930), were evident in all males by the end of their second year. Males were 50 mm carapace length or larger by that time. All three-year old males had these characteristics whether captured early or late in the season.

The youngest female stinkpot known to have contained at least one shelled egg was four years of age and 65.7 mm carapace length when palped on 6 June 1980. Five other females (mean=70.3 mm) were known to have laid eggs in their fourth year. No three year-olds were reproductive.

Fecundity. The number of eggs per clutch was determined by dissection of 13 females that had drowned in traps or were selected for this purpose. The average number of eggs, corpora lutea and preovulatory follicles was 2.7 (1-5). The smallest female contained one egg and was four years old. The correlation of clutch size to carapace length was positive (r=0.887) and significant (N=-5.78 + 0.109X, P=0.0017) demonstrating size-specific fecundity.

Oviductal eggs were detected in females by palpation between 5

May and 17 July. Of 71 records of oviductal eggs, 29.6% were in May, 64.8% in June and 5.6% in July. In 1980, 27 of 38 records occurred between 22 May and 9 June and eleven between 12 June and 7 July. Two of the 31 records for oviductal eggs in 1981 were between 5 and 13 May, while 19 were between 23 May and 7 June. Ten records were between 12 June and 3 July that year.

One female had oviductal eggs on 6 June and again on 25 June 1980. Another contained eggs 5 May and 31 May 1981. One female, dissected on 1 July 1981, had two distinct sets of corpora lutea. Seven females were known to have laid eggs in successive years. If 1980 records are used as an indicator, the late set of eleven records represents 28.9% of the total sample of females known to have reproduced that year. This value provides an estimation of the proportion of the female population that produced two clutches in 1980.

Age structure. Except for juveniles, the number of adult males and females in successive age classes probably represents the majority of that component of the population in Laurel Lake (Table 32). It is probable that with over 2240 captures and the high rate of adult catchability most were captured at least once during the study. Small stinkpots are vulnerable to predation by freshwater fish and probably snapping turtles, at least until they are about three years old. They probably select habitats that reduce their chances of mortality from these sources and thus, lower their representation in the sample. The number of adult females in age classes 4-6 were more numerous than in older age classes (Table 32) but few live beyond eleven years of age. Adult males show a similar age distribution. Figure 21 illustrates

Table 32. Age structure of Sternotherus odoratus in Laurel Lake. Unsexed juveniles of ages one to two are equally assigned to sex groups.

Sex	Age Class											Total
	1	2	3	4	5	6	7	8	9	10	11+	
Females												
1979	36	29	50	69	49	34	27	20	11	4	5	298
1980	18	35	28	49	65	49	31	26	17	11	7	336
1981	5	17	17	20	40	57	28	21	21	15	13	254
Males												
1979	39	49	49	43	34	12	12	9	6	5	17	275
1980	12	39	48	39	38	32	9	11	7	4	17	256
1981	4	9	25	25	27	27	21	8	10	4	17	177

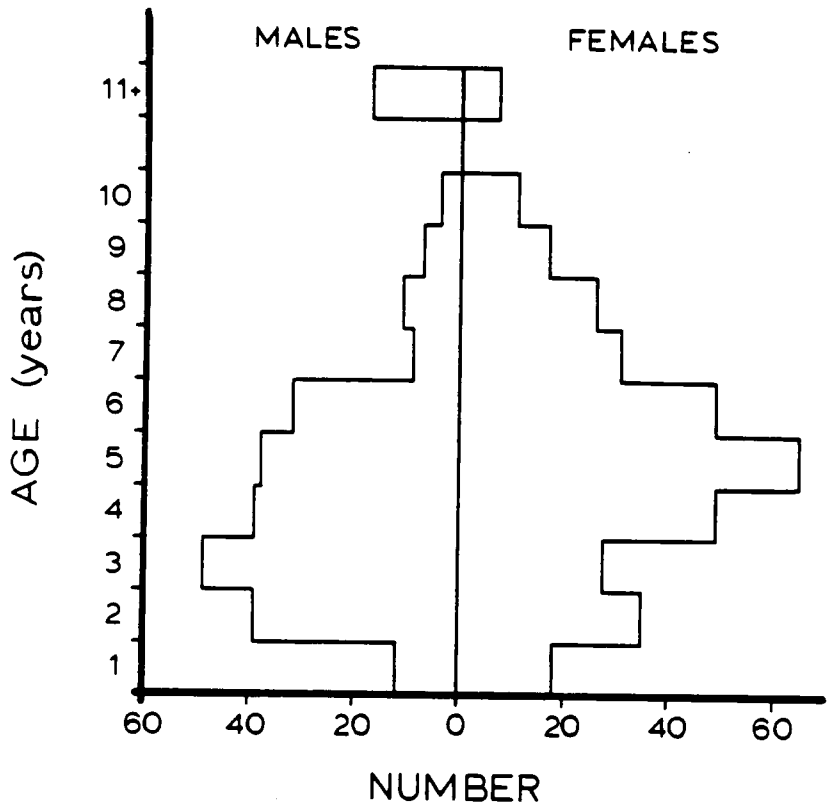

Figure 21. Age structure of the Sternotherus odoratus population in 1980.

the age distributions for 1980 and suggests that survivorship for older males (greater than eleven) is higher than for older females.

Sex ratios. The sex ratios of males two and older (266) to females four and older (290) in the total marked sample was not significantly different from unity ($G=1.082$, $P>0.25$), nor were they different based on estimated sizes of these two populations (Table 31) ($G=0.691$, $P>0.25$). Number of males to females differed significantly in 1981 (Table 33) but not in 1979 or 1980. This difference is probably a function of the lower catchability of males that year compared to females.

Survivorship. Triple-catch estimates of survivorship (Table 31) of all sex and age groups were above 84%. These numbers refer to the probability of survival between 1979 and 1980. Age-specific survivorship (Table 34) was based on age class ratios between years and one record per individual per year. Survivorship for females averaged 9.7% higher 1979-1980 than male survivorship that period. Rates for both sexes were less for 1980-1981 than for 1979-1980. Age-specific rates were variable between ages, sexes and years, and perhaps reflects the uncertainty of death for all these turtles in Laurel Lake. Overall averages for males (78.1%) and females (84.5%) can be considered indicators of annual average survivorship rates for these populations.

Rates of hatchling survival (ages 0-1) were estimated indirectly because no S. odoratus nests were found or monitered. Total egg production for 219 females, assuming two clutches per year and 2.7 eggs

Table 33. Adult sex ratios for Sternotherus odoratus 1979-1981.

Year	Males	Females	Ratio	G
1979	236	219	1.078	0.617
1980	244	255	0.957	0.243
1981	173	215	0.805	4.554*

* $P<0.05$

Table 34. Estimates of age-specific annual survivorship for Sternotherus odoratus. These estimates are derived from data in Table 32.

	Age class									
	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	Average
Females										
1979-1980	0.972	0.966	0.980	0.942	1.000	0.912	0.963	0.850	1.000	0.954
1980-1981	0.944	0.486	0.714	0.816	0.877	0.571	0.677	0.808	0.882	0.753
Average	0.958	0.726	0.847	0.879	0.939	0.742	0.820	0.829	0.941	0.854
Males										
1979-1980	1.000	0.980	0.796	0.884	0.941	0.750	0.917	0.778	0.667	0.857
1980-1981	0.750	0.641	0.521	0.692	0.711	0.656	0.889	0.909	0.571	0.704
Average	0.875	0.811	0.656	0.768	0.826	0.703	0.903	0.844	0.619	0.781

per clutch, was 1182.6. If, however, 28.9% of the female population deposits two clutches and the remainder only one, the total egg production was 932. Small sample Lincoln-Peterson estimates of yearling abundance that year was 91. The resulting survivorship estimate is 9.9%, almost certainly an underestimate.

Mortality. Few dead stinkpots or their shells were found in this study. The majority of deaths occur in water where shells disarticulate and decompose rapidly. Six died from drowning in a fish trap and two died from unknown causes. No predator deaths are known for Laurel Lake turtles and none were killed on roads by vehicles. Fishermen report that many are decapitated after being hooked on fishing lines. Their inconspicuousness affords than some protection from human related mortality.

Discussion

Chrysemys picta

Estimates of densities for painted turtle populations range from five to 239 per acre (Sexton, 1959b; Gibbons, 1968b; Ernst, 1971c; Bayless, 1975; Wilbur, 1975b; Bury, 1979). The density estimate for Laurel Lake, the associated area of Hungary Creek and the beaver ponds (2.75 hectares) is 188 per hectare (75 per acre). The wide range in densities is obviously due to differences in ecosystems and in variances in capture frequencies and estimates used. Age at maturity for C. picta from Laurel Lake is a year older than at Grassy Swamp Lake but size at maturity is approximately the same (see Chapter II).

Females from Laurel Lake mature one to two years later than females in Grassy Swamp Lake but all females are within three to five millimeters of 100 mm plastron length when maturity is reached. Age at maturity in other populations of this species ranges from four to ten and plastron lengths are 100 mm or longer (Bury, 1979). These comparisons support Ernst's (1971a) prediction that sexual maturity in this species is a function of size and not age. The age at which a turtle reaches a minimal size depends on growth rates. Grassy Swamp Lake turtles then, must grow at a faster rate in one or more age classes than turtles in Laurel Lake. Gibbons, et al. (1981) demonstrated that thermally enhanced accelerated growth rates in Pseudemys scripta resulted in a larger size but not greater age at maturity. Rates of growth between this population and a naturally occurring one were significantly different among juveniles, to which they attribute the primary cause of the differences. Fitness is maximized for turtles at Grassy Swamp Lake by their earlier age at maturity compared to Laurel Lake turtles. This result supports predictions developed by Cole (1954) and expanded by Williams (1966) and Stearns (1976) and others. Essentially, evolutionary fitness can be increased by achieving maturity earlier, thus offspring production is greater over a potentially longer lifetime. In light of these contrasting tactics, evolutionary strategies among emydid turtles may be more diverse than previously thought. Male size at maturity is probably a function of predator escape (Gibbons, et al., 1981) and physical constraints on mating size.

Reproductive cycles are synchronous in both sexes in Laurel Lake

and in Grassy Swamp Lake. Histological preparation of gonads from seven Laurel Lake males obtained at various times of the year were examined and found to be in similar spermatogenic stages as Grassy Swamp Lake males at those times. Female painted turtles in Laurel Lake contained oviductal eggs during the same weeks as females from Grassy Swamp Lake. Fecundity estimates for the two populations are almost identical and some females in both populations lay two clutches each year. Size-specific fecundity is demonstrated by the Grassy Swamp Lake data but not for Laurel Lake data. This discrepancy may be due to sampling error rather than a true difference, since there were no seven-year olds or old females (>127 mm PL) therein. It may also reflect increased fitness as noted above.

Comparable age structure data are available only for the Michigan population studied by Sexton (1959b) and Wilbur (1975b). There were large numbers of juveniles in Laurel Lake samples but not in the samples from Crane Pond. This is due to the different trapping and capture techniques rather than a true demographic difference. In each of the populations, adult females make up most of the population above ten years of age, while males were distributed between ages four and ten.

Sex ratios in this study do not differ significantly from unity except when considering separate years (1980 and 1981). These differences reflect variations in catchability between sexes and years and may involve immigration. Bull and Vogt (1979) and Bull, et al. (1982) determined that for C. picta low incubation temperatures (25 C) produce predominately males and high temperatures (28 C) females, and

that there were geographical differences in temperature effects. Selection of nesting sites by females could result in an altered sex ratio (Bull and Vogt, 1982) if mechanisms were not present in the population to counteract them. Since males outnumber females in Laurel Lake, nesting sites may have been located in predominately tree or shrub shaded areas.

Age-specific survivorship for Laurel Lake C. picta can be compared to estimates provided by Wilbur (1975b). He calculated an average annual survivorship of 76% for females older than three years of age. He assumed that over 90% of turtle mortality occurred through nest predation. Average annual survivorship for Laurel Lake females is 79.5% when based on age structure and 77.2% for males. Hatchling survivorship was estimated to be 16.2 to 22.4%, but the 67% estimate of survivorship of eggs to age one by Tinkle, et al. (1981) suggests these may be too low.

Sternotherus odoratus

Mahmoud (1969) found that the density of a S. odoratus population in an Oklahoma creek was 60.7 per acre. Density in Laurel Lake was 194 per hectare (77.4 per acre). Cahn (1937) and Thomas and Troutman (1937) commented on the high densities of stinkpots in a small swamp pond and ditch, respectively. Other authors, however, indicated low densities in other types of habitats (Tinkle, 1958a, b; Gibbons, 1970a; Ernst, 1971c).

Age and size at maturity for male and female stinkpots were identical for the Laurel Lake and Grassy Swamp Lake populations.

Growth rates must be similar in these populations, at least for the years up to maturity. Since age at maturity appears to vary more than size (Tinkle, 1961; Mahmoud, 1969; MacPherson and Marion, 1981a, b), it can be predicted that an increase in female S. odoratus fitness is achieved by reaching maturity at a minimal age.

Gonads from eight Laurel Lake males captured in different months were histologically prepared and staged as in Chapter II. Spermatogenic cycles appear synchronous for this population compared with the one in Grassy Swamp Lake. Sternotherus odoratus females in both populations contained oviductal eggs at similar times of the activity season. Fecundity estimates were higher for Grassy Swamp Lake stinkpots but this may be a function of the larger sample size and sizes of females. The clutch size difference may not be biologically significant. Some females in each population lay two clutches in some years. Fecundity is a positive function of body size and age in both populations. The discussion in Chapter II contains a more detailed examination of clutch size variation in this species.

Age structure in other populations of stinkpots is unknown. All immature ages are underestimated in the Laurel Lake sample, but this is not unique to this study. Agassiz (1857), Risley (1933) and Mahmoud (1969) commented on the difficulty of finding juveniles. Future studies of this species should incorporate methods to alleviate this problem. Perhaps juveniles are more terrestrial than heretofore known. Gibbons and Nelson (1978) mention a hatchling caught on land.

Adult age structure is probably a reflection of the mating strategy. High survivorship rates suggested by the ratios of adjacent

age classes of three through six (Figure 21) could be due to alternative mating tactic in these young males. Male body weight surpasses that of females at age six (Figure 16) and higher mortality may be a function of higher mobility and more frequent encounters with predators in older males. It follows that males in the younger group move less often than males in the older group. This argument is based on a stable age distribution and does not allow ruling out the possibility that the observed structure in 1980 is a function of higher fecundity rates or changes in survivorship in 1974 or 1975. Future research should determine if the distributions remain constant over the next few years or if the numbers shift with the age classes.

Most sex ratios of S. odoratus populations are reported as deviating from a 1:1 ratio (Gibbons, 1970d; Bury, 1979). These are usually based on samples of insufficient size collected at various times of the activity season (Risley, 1933; Cagle, 1942). As noted above, males and females differ in catchability by season, perhaps because males spend the summer months in deep water. Most types of turtle traps are set in shallow water and may not be placed in a male's summer home range. Tinkle (1961) found a sex ratio not different from unity based on museum specimens, although this result probably does not indicate true population sex ratios. Ratios presented in this study for Laurel Lake (except 1981) and Grassy Swamp Lake populations do not differ significantly from unity (Grassy Swamp Lake: $G=1.630$, $P>0.1$).

Survivorship rates are unavailable for other populations but estimates presented here from mark-recapture and age structure data

indicate they were high at Laurel Lake throughout the study period. The low capture rates of juveniles in this and other studies (e.g., Mahmoud, 1969) preclude realistic estimates for age classes one through two.

Interspecific comparisons

The assumption that each individual has an equal risk of capture throughout the study period was violated for most age and sex categories of both species when tested against the Poisson distribution. Bailey's triple-catch method, which registered only one capture per year for any individual, excluded most of the bias and provided accurate estimates of population size. Chrysemys picta is almost as equally abundant (517) in Laurel Lake as S. odoratus (534). This This result is counter to the results of Ernst (1971c) who found S. odoratus to be considerably less abundant than C. picta. Ream and Ream (1966) demonstrated that different capture methods resulted in biased estimates of sex ratio and size class distributions. With the exception of juvenile stinkpots, the variety of methods used in this study, as well as the length of study, probably eliminated serious bias. For these same reasons the estimates of population dynamics for 1979-1980 are considered accurate.

Assumptions of negligible emigration appear reasonable for both populations because of data indicating site fidelity. Immigration from upstream sources apparently accounts for some of the recruitment for C. picta. The only other source of immigrants is over six kilometers downstream. Immigration into the S. odoratus population

is probably low and insignificant because of the high home range fidelity exhibited by these turtles (Williams, 1952; Mahmoud; 1969). Although overland movement is known for this species (Ernst and Barbour, 1972), terrestrial immigration was not observed at Laurel Lake.

Some C. picta and S. odoratus females lay two clutches of eggs per year. Clutch size for these and other turtles is determined, in part, by physical constraints of the body cavity, the limitations on the size of the egg that can pass through the pelvis and the necessity to produce neonates large enough to survive on their own. Neonate strategy is to grow as fast as possible in the first few years to reduce the probability of being eaten. Small turtles are vulnerable to a wide variety of predators (Ernst and Barbour, 1972); the smaller the turtle the larger the number of predator taxa and sizes that can overpower and consume them. Baby painted turtles trade off exposure to predators with the need to bask, while stinkpots hide during this period.

Age structures of these syntopic populations differ markedly. Chrysemys picta are probably longer lived on the average than S. odoratus, although no actual longevity data are available for the turtles in these populations. Wilbur (1975b) found painted turtles known to be older than 25 years and predicted that many live to age 50. A captive record of 60 years is recorded for the stinkpot (Bowler, 1977), but natural longevity is unknown. Assuming the low stinkpot juvenile numbers are due to behavior and not high egg or juvenile mortality, both populations of turtles in Laurel Lake are

growing. Triple-catch estimates support this interpretation.

The results presented in this study contain no evidence that the urban Laurel Lake populations are structured or behave differently from populations in other types of aquatic systems (Cagle, 1942, 1944; Gibbons, 1968b; Ernst, 1971b; Mahmoud, 1969). Perhaps the only aspects unique to this and other similar urban systems are the unnatural sources of mortality, particularly mutilation of nesting females by grass mowers. The usual lack of high natural predator densities (e.g., raccoon) in these areas may be counterbalanced by the presence of man. Unless there are serious density-independent perturbations of the aquatic system, such as channelization, dredging, input of toxic chemicals or altering the land use to accommodate buildings, C. picta and S. odoratus populations in them are likely to be similar to those in other systems. If the system and populations are old enough, they should have a stable age distribution, but not necessarily the same ratios of age classes as those in Laurel Lake. Comparative population data are needed from river and swamp systems.

CHAPTER V

SUMMARY AND CONCLUSIONS

During this study over 6000 captures of Chrysemys picta (1062 individuals) and Sternotherus odoratus (881 individuals) were examined for details of reproduction, growth and population and demographic characteristics. Comparisons were made on populations inhabiting two lakes in central Virginia which contain similar turtle communities. Painted turtles and stinkpots were the most abundant species at both sites.

Male reproductive cycles were generally synchronous between species and between years within species. Onset of spermatogenesis for C. picta and S. odoratus in spring may respond to different environmental cues or perhaps different levels of these cues. Initiation of spermiogenesis appears to be synchronized, suggesting similar cues or cue levels for timing of this process. Ovarian cycles between species differ in length of egg laying period; stinkpot cycles are longer by about three weeks. There is considerable concordance with timing of vitellogenesis, oviposition and other events between species, years and localities (Moll, 1973; Moll, 1979).

Growth in C. picta is sex specific; females grow at faster rates than males. Growth in S. odoratus was not sex specific. It was demonstrated that growth differs significantly between years for both species. Rates were logarithmic initially but changed to a linear rate after maturity was reached. Growth of old individuals is highly variable.

The population of painted turtles in the urban Laurel Lake was estimated to be of similar size as the stinkpot population. Males outnumbered females in the former and females outnumbered males in the latter. Neither population differed significantly from a 1:1 sex ratio, however. The differences in numbers is partly a function of catchability differences between sexes. Juveniles were underrepresented in both population samples, particularly in the stinkpot sample. Until it is determined how to increase juvenile numbers in the samples, it will be difficult to construct realistic life tables.

Utilization of information such as that presented here is frequently discussed in light of life history theory. The formalization of r- and K- selection theory (MacArthur and Wilson, 1967) and its subsequent development (Pianka, 1970, 1972; Hairston, et al., 1970; Stearns, 1976) provided a framework around which reproductive and demographic data were discussed. Other theories (e.g., bet-hedging, Murphy, 1968; Stearns, 1976) demonstrated contrasting results and made interpretation of one's data difficult. The problems associated with definition and interpretation has led one recent author (Parry, 1981) to state that the r- and K- concept has outlived its usefulness. Stearns (1980) pointed out that life history tactics are more likely to be perceived above the species level and, indeed, has been done so by several authors (Pianka, 1970; Tinkle, et al., 1970). Examination of life histories from a standpoint of tradeoffs may, however, provide useful insights into patterns of life history (Parry, 1981). I will thus, summarize the life histories of C. picta and S. odoratus on an intraspecific level based on differences between

populations, as well as note primary interspecific differences.

Life history tactics of C. picta in Virginia are controlled largely by growth rates that allow females to reach a minimum selected size at maturity. Females in Laurel Lake reached maturity one to two years later than females in Grassy Swamp Lake, but at similar sizes. If a female achieves this size early, her lifetime reproductive potential is increased, as is her fitness. This minimum size, about 100 mm plastron length, presumably allows a female to produce a neonate large enough to survive on his own. Neonates are selected to grow at maximal rates during the first few years of life to achieve a size that reduces the number of predator taxa and sizes that can cause their death. Exposure to these predators is a tradeoff with the growth related need to bask. Male size at maturity was similar in the two populations studied, but age at maturity is one year earlier at Grassy Swamp Lake. Because of the lack of territoriality in this species, males have no advantage in delaying maturity to achieve a large size (Gibbons, et al., 1981). Size at maturity may be partly a function of minimal size needed for copulation. These arguments predict earlier ages at maturity in populations of C. picta picta that exhibit growth rates in excess of that described here.

Although no differences in age or size at maturity in S. odoratus were found between the populations studied allowing detection of tradeoffs, comparisons of the results in this study and the literature suggest minimizing age at maturity is the tactic utilized by females of this species. Mimimum sizes of most mature females are within 3-5 mm of 65 mm carapace length, suggesting there is a selected minimum

neonate size. Females must achieve a minimum body size before producing eggs. The small size of neonates in this species (Ernst and Barbour, 1972) is probably coupled with the evolutionary tactic of increasing fitness by laying several eggs on the average rather than one. The juvenile tactic is to hide during the most vulnerable period of life when risk of mortality is high. Fitness in males is maximized by rapid weight gain, although this does not explain how small males achieve maximal fitness since they are considerably smaller at maturity than the smallest mature female. The mating behavior of stinkpots should be examined from a standpoint of size.

Interspecific differences in age and sex-specific growth rates are probably a function of the behavior and microhabitats of these two species. Chrysemys picta is an aquatic-swimming (Berry and Shine, 1980) basking emydid. Basking presumably increases digestion rates and efficiencies (Boyer, 1965) and thus enhances growth. This may be particularly true for adults which eat more plant material than juveniles (Ernst and Barbour, 1972). Sternotherus odoratus, like other kinosternids, are highly aquatic bottom-walkers that bask infrequently. Growth rates in this species are thus dependent on water temperature. The type of food resource and length of time available in the season to obtain and digest it also influence growth rates (Parmenter, 1980). It is not known if syntopic painted turtles and stinkpots select different resources. Sexual size dimorphism in adults is more apparent in painted turtles because females grow at accelerated rates three or more years longer than males. Stinkpots do not exhibit sexual size dimorphism because males and females grow at similar rates. Because

of the size dimorphism in painted turtles, the smaller males must seek, court and stimulate females to achieve mating. They are thus highly mobile and are caught more frequently. Stinkpot males do not display elaborate courtship but forcibly restrain females to achieve mating (Mahmoud, 1967; Berry and Shine, 1980) and are thus less mobile and captured less frequently. Capture frequency is a function of mobility; an animal that moves infrequently has a lower probability of capture than one which moves more often. Population size estimates and related parameters (e.g., catchability) are, therefore, related to sexual differences in movement. Mahmoud (1969) found that male stinkpots had home ranges half the size of females, and that, for two other kinosternids, females had larger home ranges than males. Home range information is lacking for C. picta, but Gibbons (1968c) found that males moved more frequently in spring but females traveled further in summer, presumably in relation to nesting. It seems likely that other populations of these species will exhibit similar relationships of age and sex-specific growth rates, catchability and population estimates as those in this study, unless capture techniques override behavorial differences. Perhaps these same relationships will hold for other bottom-walkers (kinosternids) and aquatic-swimmers (emydids).

From the outset of this study it was thought that populations in urban lake systems should differ demographically from populations inhabiting lakes not disturbed directly by man's presence. Comparisons of population and demographic parameters in this study with those in the literature reveal no difference that could be attributed to this type of environment. Only in sources of mortality were there departures

from parameters on other populations. Except for density-independent perturbations, the size and structure of urban lake populations of freshwater turtles will depend on the physiognomic structure of the aquatic system and levels of resources therein. These same factors affect populations of turtles in natural systems.

Painted turtles and stinkpots possess attributes that enable them to adapt to a variety of aquatic systems, particularly urban lakes. They are omnivorous and can switch from one food resource to another depending on food availability (Lagler, 1943; Knight and Gibbons, 1968; Ernst and Barbour, 1972). They are able to lay eggs in a wide variety of soil conditions (Cagle, 1937; Richmond and Goin, 1938; Carr, 1952) or, as for some stinkpots, under debris or in the open (Risley, 1933; Cagle, 1937). Since eggs are usually laid at night, terrestrial females are seldom seen by people in urban areas, especially since most people do not frequent lakes and creeks at night. Finally, the highly aquatic stinkpots are seldom seen, even in daylight, and painted turtles are wary baskers and do not allow people to approach close enough to catch them; young boys not withstanding. The adaptability of these species may, in fact, enhance their growth and reproductive capabilities, particularly in highly eutrophic systems. Chelydra serpentina is certainly equally as adaptable since it has been collected in a host of man-altered habitats (Carr, 1952; Ernst and Barbour, 1972; Moll; 1980) and is known, like painted turtles and stinkpots, to consume carrion, along with vegetation, invertebrates and vertebrates (Lagler, 1943; Knight and Gibbon, 1968). Mud turtles, Kinosternon subrubrum, are bottom-walking omnivores (Mahmoud, 1969; Berry and Shine, 1980) and

are known from urban systems but, in light of the few numbers caught in this study (less than 15 at either lake), it appears urban lakes are only marginal habitats. Two species occurring in central Virginia, Pseudemys rubriventris and Clemmys guttata, are found in urban lakes only if resources required by them are available. Pseudemys rubriventris are primarily herbivores as adults (Ernst and Barbour, 1972) and require emergent macrophytes and other types of vegetation. Urban systems without these sources of food will be without these large basking turtles, except as relics of past populations. Spotted turtles, Clemmys guttata, are not found in urban lakes in Virginia except as populations inhabiting associated creek floodplains where the water is shallow and there is a canopy cover.

The land around Laurel Lake was bought for development and construction of houses and office buildings is expected in the near future (personal communication, Cheryl Evans, Henrico County, Virginia, Planning Office). Future alteration of the watershed will cause increased sedimentation and probably destruction of most lake-margin vegetation. Resource levels will decrease throughout the lake. Populations of all turtle species are expected to decrease through density-independent mortality, the severity of which depends on the time of year these perturbations occur. If construction around the lake is in winter, sedimentation could prevent emergence from brumation sites. If it occurs in summer, when at least some of the population is active, fewer animals will be directly affected. Long-term effects should involve density-dependent factors, particularly in competition for reduced resources. The Pseudemys rubriventris population will

probably not survive the changes, although some individuals may be able to survive for some years if they can switch to a carnivorous diet. If shallow-water emergents are able to recover, this species and Kinosternon subrubrum may survive, but at lower population levels than now exist. Populations of C. picta and S. odoratus will adjust to new resource levels and will remain in the lake, but at lower densities than at present. Silt deposits in the lake can be used, as they are now, for cover when vegetation cover is reduced. The constant turbidity of the water in Laurel Lake aids considerably in reducing the visibility of these turtles to man, and this would be expected to increase. These arguments predict that old urban lakes in Virginia with little aquatic vegetation and high siltation and turbidity levels will have a turtle community consisting primarily of Chelydra serpentina, Chrysemys picta and Sternotherus odoratus, and perhaps some introduced Pseudemys scripta elegans. If Pseudemys rubriventris are found, they will probably be old adults and very few in number. Kinosternon subrubrum and Clemmys guttata will not be found unless there is an associated creek with broad floodplain and overhead canopy. Urban lakes with aquatic vegetation will contain turtle communities similar to that presently in Laurel Lake.

A summary of the population and demographic characteristics of populations of Chrysemys picta and Sternotherus odoratus inhabiting urban lakes in Virginia is presented in Table 35.

Table 35. Comparisons of life history traits and population characteristics of Chrysemys picta with Sternotherus odoratus inhabiting urban lakes in Virginia. Where noted, variation in a trait is based on information from Grassy Swamp Lake (GSL) and Laurel Lake (LL). PL is plastron length and CL is carapace length.

Trait	Chrysemys picta	Sternotherus odoratus
Body size ♂	larger	smaller
♀	larger	smaller
♂-♀ within[a]	smaller	same
Reproduction	iteroparous	iteroparous
Age at maturity	3 (GSL), 4 (LL)	2[b]
	6 (GSL), 8 (LL)	4[b]
Size at maturity	71-72mm PL	50-51mm CL
	100mm PL	65-66mm CL
Number of clutches	2	2 (3?)
Clutch size	4.1 (GSL)	3.1 (GSL)
	4.2 (LL)	2.7 (LL)
Age specific fecundity	yes (GSL)	yes (GSL)
	no (LL)	yes (LL)
Egg size	larger	smaller
Population size[c]	517	538
Sex ratios	1:1	1:1
Survivorship adults	high, variable	high, variable
juveniles	low	?
Longevity ♂	longer	shorter
♀	longer	shorter
♂-♀ within[a]	shorter	longer
Net reproductive rate[d]	>1	>1
Generation time[d]	longer	shorter

[a] comparisons within species
[b] data from both lakes identical
[c] estimated from triple-catch equation
[d] estimated from age structure

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APPENDIX

Climatological Information

The study sites lie on the eastern edge of the Piedmont physiographic province in central Virginia and experience a temperate zone climate. The Applachian and Blue Ridge mountains to the west retard the progress of continental polar air masses and these are modified by the maritime conditions of the Chesapeake Bay and Atlantic Ocean to the east. Winter highs average 9.2°C and lows -1.7°C. Winter and early spring precipitation patterns are generally predictable and results from frontal activity. Weather in summer is dominated by thundershower activity and rainfall is local and generally unpredictable. Summer highs average 30.2°C and lows 18.5°C. Mean summer precipitation is 121.8 mm but highly variable. The normal frost-free season is May through mid-October. Monthly temperature and precipitation data are presented below for the study period (data recorded at Ashland, Virginia, 12 kilometers northeast of the study area, information from U.S. National Oceanic and Atmospheric Administration, monthly climatic summaries and Climatological Summary for Ashland).

	1979		1980		1981		Normal[c]	
Month	$\bar{X}$ Low - $\bar{X}$ High	Precip.	$\bar{X}$ Low - $\bar{X}$ High	Precip.	$\bar{X}$ Low - $\bar{X}$ High	Precip.	$\bar{X}$ Low - $\bar{X}$ High	Precip.
Jan	-3.9 - 6.7[a]	149[b]	-2.9 - 6.2	150	-7.3 - 5.0	22	-4.1 - 8.5	72
Feb	-8.3 - 2.8	176	-5.1 - 6.8	24	-2.1 - 12.2	92	-2.8 - 9.7	74
Mar	2.1 - 17.6	96	1.0 - 12.7	122	-0.6 - 13.4	40	0.5 - 14.5	86
Apr	6.8 - 20.4	100	6.9 - 21.0	105	8.1 - 22.7	74	6.3 - 20.7	73
May	12.5 - 24.6	107	12.1 - 25.2	178	10.5 - 23.4	143	11.4 - 25.3	85
Jun	14.2 - 27.7	90	15.6 - 27.9	9	18.4 - 30.0	25	15.6 - 29.1	90
Jul	18.4 - 29.1	68	19.3 - 31.7	84	19.2 - 30.0	193	18.0 - 30.8	105
Aug	18.6 - 29.6	182	19.4 - 32.4	56	17.2 - 28.1	71	17.4 - 30.2	115
Sep	16.1 - 25.3	268	16.8 - 29.4	43	13.1 - 25.4	67	13.4 - 27.0	84
Oct	7.3 - 19.9	114	6.9 - 19.3	153	5.9 - 18.6	70	7.0 - 21.4	83
Nov	4.3 - 17.5	104	0.7 - 13.2	68	2.6 - 14.4	18	1.3 - 15.6	80
Dec	-1.6 - 11.1	38	-3.1 - 8.8	16	-2.7 - 6.9	98	-3.3 - 9.3	81

[a] Temperatures in °C
[b] Precipitation in millimeters
[c] Averages for 1947-1969

VITA

Joseph Calvin Mitchell was born on 16 August 1948 in Lynchburg, Virginia. He attended secondary schools in Richmond, Virginia and received a diploma from Hermitage High School in 1966. He served in the United States Marine Corps from October 1966 to September 1970. He received his Bachelor of Science degree in Biology from Virginia Commonwealth University in 1974 and his Master's degree in Zoology from Arizona State University in 1976. A Doctor of Philosophy degree in Ecology was received from The University of Tennessee, Knoxville in 1982. During graduate school he held teaching assistantships and has been teaching at the University of Richmond since 1979. He has published over 30 technical and semitechnical papers and has received several research grants to study the systematics and ecology of reptiles and amphibians. His current research interests are in evolutionary, community and population ecology and biogeography. He is married to the former Wendy R. Hoilman and has a son, Joshua and a daughter, Tanya. He likes his kids, his Toyota Land Cruiser, Leo Kottke, John Hartford, Virginia and narrow-mouthed toad frog calls.