POPULATION ECOLOGY OF THE EASTERN BOX TURTLE (*TERRAPENE CAROLINA CAROLINA*) IN A FRAGMENTED LANDSCAPE

by

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A thesis submitted to the Faculty of the University of Delaware in partial fulfillment of the requirements for the degree of Masters of Science in Entomology and Applied Ecology

Summer 2003

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ACKNOWLEDGMENTS

I express my sincere appreciation to my major professor, Dr. J. L. Bowman, and my other committee members, A. Doolittle, Dr. D. C. Forester, Dr. R. R. Roth, and Dr. D. W. Tallamy for their knowledge and guidance. I thank all those who helped with radio-telemetry and capture of turtles, in particular R. Baity, S. Bussells, J. Doughty, C. Howey, R. Kipp, R. Iglay, J. Johnston, J. Judy, I. Lajoie, and A. Porter. I also thank J. Longcore, Dr. E. P. Catts, Dr. R. R. Roth and their many graduate students and research assistants who kept detailed capture records of box turtles in the University of Delaware Woodlot since 1965. I would like to express my sincere gratitude to M. Frederick and the Frederick family for their interest in conservation and for allowing us to use the Turkey Run property. I thank the Delaware Division of Parks and Recreation and White Clay Creek State Park for allowing us access to the property and for waiving the park entrance fee. I thank J. White for taking photographs and for encouraging and spurring my interest in box turtles and herpetology many years ago. Additionally, I would like to thank Dr. J. W. Gibbons for review of my methods. I also gratefully acknowledge the MacIntire-Stennis Forestry Research Program, which provided funding for this project. Finally, I thank my parents, Debbie and Hank Nazdrowicz, whose love, support, encouragement, and understanding has contributed greatly to my success.

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ABSTRACT

In the mid-Atlantic region, urban sprawl and development have resulted in habitat loss and fragmentation; however, the effect on eastern box turtle (*Terrapene carolina carolina*) populations remains undetermined. I employed mark-recapture to study box turtle population ecology and investigate the status of box turtle populations in a fragmented landscape. From April 2001 through October 2002, I used 4 study sites with differing degrees of disturbance in northern New Castle County, Delaware, for my research. Two study sites (University of Delaware Woodlot and University of Delaware Webb Farm) were isolated forest fragments; 1 site (Turkey Run) was a young forest fragmented by small fields and was contiguous to adjacent forested and undeveloped habitat; and 1 site (White Clay Creek) was an interior forest. I used data collected by intensive searches, incidental finds, and radio-telemetry to estimate population abundances and densities, sex ratio, age structure, and survival rates at each study site.

We captured 268 turtles 892 times. I estimated adult population densities of 0.81-0.93, 2.12-3.69, 2.44-4.56, and 2.76-4.99 turtles/ha at the Woodlot, Webb Farm, Turkey Run, and White Clay Creek study sites, respectively. Sex ratios (male:female) were male biased at the Woodlot (3.00:1.00) and at White Clay Creek (2.07:1.00 females), whereas Webb Farm and Turkey Run had balanced sex ratios. I tested the validity of aging box turtles by counting annuli on the costal scutes of the carapace. I concluded this method was accurate for estimating age of turtles with 1-10 annuli, less accurate for turtles with 11 annuli, and inaccurate for turtles with ≥12 annuli. Proportion of juveniles in the total population were 0%, 6%, 25%, and 32% at the Woodlot, White Clay Creek, Webb Farm, and Turkey Run, respectively. I estimated an annual survival rate of 0.98 and a seasonal survival rate of 0.99 for Webb Farm, Turkey Run, and White Clay Creek combined because very few deaths were documented. At the Woodlot, I estimated an annual survival rate of 0.83 and seasonal survival rate of 0.94. Causes of most natural mortalities were undetermined, but 3 resulted from exposure to excessive heat or freezing conditions. Mowing and harvesting agricultural fields were the predominant causes of human induced mortalities.

The combination of human management practices, isolation, and lack of early successional areas appears to have the most influence on box turtle populations. We found no evidence of population change at Webb Farm, Turkey Run, or White Clay Creek. However, the Woodlot population was declining due to low survival and little recruitment. In order to preserve box turtle populations, I suggest mowing at a height of ≥15 cm or planting agricultural crops that do not require mowing on areas adjacent to forest habitats whenever possible.

Chapter 1

INTRODUCTION

Eastern box turtles (*Terrapene carolina*) predominantly inhabit moist woodlands across their range in eastern North America but also occur in pastures and marshy meadows (Ernst et al. 1994). In parts of their range, urban sprawl and development have resulted in habitat alterations, primarily habitat fragmentation and destruction. However, the effect of these habitat changes on populations of eastern box turtles has not been quantified. While many studies have addressed demographic characteristics (Stickel 1950, Williams 1961, Schwartz and Schwartz 1974, Schwartz et al. 1984, Langtimm et al. 1996, Pilgrim et al. 1997, Dodd 1997, Dodd 1998, Niederriter 2000), only a few have addressed population stochasticity on a long-term basis (24 years, Schwartz and Schwartz 1991; 27 years, Williams and Parker 1987; 30 years, Stickel 1978; 35 years, Schwartz 2000; and 50 years, Hall et al. 1999), and none have investigated multiple populations in close proximity simultaneously.

A paucity of research exists addressing the effects of fragmented landscapes on population ecology of eastern box turtles. Williams and Parker (1987) suggested loss of surrounding habitat contributed to a decline of an eastern box turtle (*T. c. carolina*) population at Allee Memorial Woods in Indiana. Stickel (1978) suggested development of a highway system may have increased mortality of adult nesting female eastern box turtles in a declining population at Patuxent Wildlife Research Center in Maryland. Additionally, Niederriter (2000) attributed a declining population and low population abundance of the eastern box turtle at the University of Delaware Woodlot in Newark, Delaware, to isolation and fragmentation. However, no studies have tested the effects of fragmentation by comparing eastern box turtle ecology among multiple study sites. The focus of this study was to compare population abundance, sex ratio, age distribution, and survival rate of the eastern box turtle among 4 study sites with differing degrees of disturbance in northern Delaware to investigate the effects of fragmented landscapes on eastern box turtle populations. The ultimate goal of this study was to obtain information applicable to conserving eastern box turtle populations in fragmented landscapes.

Population Abundance

Estimating overall population abundance of turtles is best employed with mark–recapture techniques. Mark–recapture studies of a population require multiple sampling occasions wherein every captured individual is marked with a unique code and released back into the population (Lancia et al. 1996). Populations are classified as either “open” or “closed,” depending on whether change occurs in the population during the course of the study. For an open population, individuals may enter (births, recruitment, and/or immigration) or leave (death and/or emigration) the population. For a closed population, no births, deaths, immigrations, or emigrations can occur.

When using mark recapture techniques, the number of individuals captured can be used to establish a crude population size since marking distinguishes individuals. More commonly though, mark-recapture is used for estimating population abundance with the use of statistical mark-recapture population models. However, these models of open or closed populations require specific assumptions, otherwise estimates of population abundance will be invalid.

For modeling closed populations, 3 assumptions must be met (Pollock et al. 1990):

1. The population must be closed: individuals cannot enter (birth or immigration) or leave (death or emigration) the population.
2. All animals have equal capture probability in each sample.
3. Marks cannot be lost and must be correctly recognized.

Assumption (1) is often violated in natural populations; but, if sampling periods are short, then birth/immigration and death/emigration can be considered non-influential (Langtimm et al. 1996). Additionally, open population models and some closed population models allow this assumption to be relaxed. Violation of assumption (2) also often occurs in natural populations because capture probabilities can vary by time, behavioral responses, and heterogeneity of individuals. Additionally, habitat quality may not be uniform, causing animals to congregate in certain areas rather than be randomly distributed. Seber (1982) described 8 closed population models that allow for variation in time, behavior, and heterogeneity within a population. In turtle populations, violation of assumption (3) is minimal, assuming the correct techniques are employed. A method for marking the carapace developed by Cagle (1939) leaves a permanent notch in the marginal scutes. Occasionally, however, the carapace is chewed by predators or other damages causes obliteration of one or several of the notches (N. Nazdrowicz, personal observation).

Open population models can be used to estimate population size as well as estimating capture and survival probabilities. The Jolly-Seber model is the basic model for open populations and must meet the following assumptions (Pollock et al 1990):

1. Every animal present in the population at the time of the *i*th sample has the same probability of capture.
2. Every marked animal in the population immediately after the *i*th sample has the same probably of surviving to time (i + 1).
3. Marks are not lost and must be correctly recognized.
4. All samples are instantaneous, and each release is made immediately after the sample.

Additionally, an implied assumption is that emigration from the study site is permanent, and therefore, any temporary emigration within a population could bias the estimates (Pollock et al. 1990).

Except in data sets with many recaptures, the general Jolly-Seber model is a poor estimator because a large number of parameters need to be estimated (Pollock et al. 1990). Through modifications of the Jolly-Seber model, the number of estimated parameters can be reduced, making the model more precise (Pollock et al. 1990). In estimating populations of box turtles, the latter 2 assumptions are not usually violated. However, time variation, behavioral responses, and heterogeneity can lead to violations in assumptions (1) and (2) (White et al. 1982). This can be overcome by using modifications of the Jolly-Seber model to fit specific assumptions of the study population.

The methods used in estimating population size in box turtle studies are varied. Most report the total number of turtles captured (Legler 1960, Blair 1976, Pligrim et al. 1997) or use simple hand-calculated open (Dolbeer 1969, Schwartz et al. 1984) or closed population models (Stickel 1950, Williams 1961, Schwartz and Schwartz 1974, Williams and Parker 1987). Recently, development of computer-based open population models has provided an assemblage of options to more appropriately fit the assumptions of the study population (Schwarz and Seber 1999). For example, in estimating population size of Florida box turtles (*T. c. bauri*), Langtimm et al. (1996) used goodness-of-fit tests in program RELEASE to test for violations of assumptions and then applied appropriate open population models using program JOLLY.

Population Density

Population abundance is often converted to density so comparisons among study populations can be made. When calculating density estimates, sources of bias such as border residents and proportion of transients must be considered. High density estimates can result from border residents being included in the population (Stickel 1950). Dice (1938) reported that animals collected on a given area will represent the population living on that area and on the area surrounding the study site with a width equal to one-half the average home range of the animal. Consequently, several studies included this border strip in their density estimates to alleviate an inflated estimate (Stickel 1950, Williams 1961, Reagan 1972, Williams and Parker 1987). However, when the study area is large enough that many more turtles occupy home ranges within the study site compared to turtles whose home ranges overlap the border, overestimates from border residents are insignificant (Stickel 1950). A large number of transient turtles within a population can also inflate density estimates (Stickel 1950). True transients are defined as turtles that wander through the environment without ever establishing a home range (Schwartz et al. 1984, Dodd 2001), whereas other turtles may become temporary transients moving through a study area to exploit a temporary food source, to access nesting habitat, or as a result of a natural displacement or human induced perturbation (Dodd 2001). Stickel (1950) considered all turtles captured only once as transients and excluded them from her estimates to avoid such biases.

Reported densities of eastern box turtles are varied (Table 1). Estimates derived from closed population models range from 2.7-5.7 turtles/ha in Indiana (Williams and Parker 1987) to 9.9-12.4 turtles/ha in Maryland (Stickel 1950). These densities also incorporate modifications from Dice (1938). Estimates derived from open population models are higher and do not use modifications from Dice (1938): 14.9 turtles/ha in Florida (Langtimm et al. 1996) to 26.9 turtles/ha in Missouri (Schwartz et al. 1984). These estimates represent populations in a variety of habitats and habitat quality (Dodd 2001).

In addition to density, Iverson (1982) and Dodd (1998) indexed box turtle population densities using biomass per hectare (kg/ha), which can be used in understanding community organization, energy flow, and ecosystem productivity (Congdon and Gibbons 1989). However, since biomass demonstrates relationships

Table 1. Summary of reported population densities of eastern box turtles (*Terrapene carolina*).

Subspecies	Study	Turtles / ha	Estimation Method
T. c. bauri	Langtimm et al. (1996)	14.9 (11.4-18.5)[1,2]	Jolly-Seber Model A / area
T. c. bauri	Pilgrim et al. (1997)	16.3[2]	asymptotic estimation / area
T. c. carolina	Dolbeer (1969)	18.8 (16.8-36.3)[1,2]	Jolly-Seber model / area
T. c. carolina	Stickle (1950)	9.9-12.4[2]	various[4] / area + border strip[5]
T. c. carolina	Williams (1961)	9.0[2]	Lincoln Index / area + border strip[5]
T. c. carolina	Williams & Parker (1987)	2.7-5.7[3,6]	Schnabel method / area + border strip[5]
T. c. triunguis	Reagan (1972)	5.9[2]	number found / area + border strip[5]
T. c. triunguis	Schwartz et al. (1984)	18.4-26.9 (17.4-28.1)[1,3,6]	Jolly-Seber model / area

[1]95% Confidence Interval
[2]Estimate of adult turtles only
[3]Range of densities over years
[4]Estimated range based on number of turtles found 2 or more times, Schnabel method, and Underhill method
[5]Modification of Dice (1938), which states that animals collected on a given area represent the population of that area plus a border area equal to 0.5 the average home range of the animal, used to alleviate an inflated estimate due to the effect of border residents.
[6]Estimate of all turtles (juveniles and adults)

among species on a community and ecosystem level, rather than within species among populations, it was not considered in this study.

Sex Ratios

Fisher (1930) considered a sex ratio of 1:1 evolutionarily stable. However, deviations from a 1:1 sex ratio, both male and female biased, have been reported for several turtle species (Hailey 1990, Edmonds and Brooks 1996, Souza and Abe 1997, Chen and Lue 1999, Hailey and Willemsen 2000). Possible causes of uneven sex ratios in turtle populations are sampling bias, skewed primary sex ratios, sex-specific mortality rate differences, sex-specific differences in age at maturity, and sex-specific differences in movement (Gibbons 1970, 1990; Lovich and Gibbons 1990; Edmonds and Brooks 1996; Hailey and Willemsen 2000).

Sampling biases caused by collecting technique, microhabitat sampled, sex-specific behavior, and age or size at maturity may explain some reported uneven sex ratios in turtles (Gibbons 1970, 1990; Lovich and Gibbons 1990). Reagan (1974) tested the effect of sampling bias on sex ratios of the three-toed box turtle (*T. c. triunguis*). The sex ratio of the three-toed box turtle collected randomly along roadsides was female biased, whereas the sex ratio within the study site (8.4 ha) was not different from 1:1 (Reagan 1972). Other studies reporting unbalanced sex ratios may not have considered sampling biases (Gibbons 1970). Individual ability to locate turtles and turtle behavior can influence sampling bias. For example, habitat type and accessibility can vary among and within study sites, making locating turtles difficult in certain areas. Sexual segregation into different microhabitats and seasonal behaviors may make one sex appear more abundant (Lovich and Gibbons 1990). Gibbons (1990) reported that concentrating collection efforts during the nesting season produced female-biased samples in most species of turtles, whereas high capture rates of males at other times may reflect increased mating activity (Lovich and Gibbons 1990). Improper determination of sex or sexual maturity may also skew sex ratios (Gibbons 1970). This factor is especially important for box turtle species because juvenile box turtles physically resemble adult females (St. Clair 1998), potentially skewing the sex ratio toward female bias. Therefore, sampling biases must be minimized before demographic differences between sexes are considered as the cause of uneven sex ratios in natural populations (Lovich and Gibbons 1990).

Sex determination is temperature dependent in box turtles (Ewert and Nelson 1991) and many other reptile taxa (Bull 1980). For reptiles in general, low temperatures typically produce males, whereas high temperatures produce females with a threshold temperature around 27°-31°C (Bull 1980). The same holds true for box turtles; however, the exact threshold temperature remains unknown (Dodd 2001). Since location of a nest determines incubation temperatures, nest site selection may produce biased primary sex ratios (Lovich and Gibbons 1990, Hailey and Willemsen 2000). Dodd (1997) reported a male-biased sex ratio (1.6:1.0) in the Florida box turtle at Edgemont Key Island, Florida. He found no variation in sex ratio among years, months, or sampling periods. Dodd (1997) believed the male-biased sex ratio resulted from nesting conditions. Favorable soil for nesting occurred in the forest interior of the island, whereas, in the warmer, less vegetated and open areas, compact crushed shells made digging difficult (Dodd 1997).

As a result, eggs laid in the cooler forest interior were probably male biased (Dodd 1997). Within a population, variation occurs in nest site selection and temperature during each year and throughout a female's reproductive life (Lovich and Gibbons 1990). Therefore, the overall sex ratio of the population may be balanced by differences in sex ratios among individual nests and year-to-year biases (Mrosovsky et al. 1984, Lovich and Gibbons 1990). Zweifel (1989) reported sex ratios of maturing painted turtles (*Chrysemys picta*) fluctuated from male- to female-bias over a 5 year period. However, collectively the sex ratio remained 1:1 (Zweifel 1989).

Following hatching, differential mortality rates of the sexes could cause adult sex ratios to be skewed (Gibbons 1970, 1990; Lovich and Gibbons 1990; Hailey and Willemsen 2000). No evidence exists supporting sex-specific mortality in juvenile turtles (Gibbons 1990, Lovich and Gibbons 1990), but, at maturity, differences in size and behavior may influence mortality (Lovich and Gibbons 1990). In sexually dimorphic species, the earlier maturing sex or smaller sex may have an increased mortality risk. Although behavioral changes occur at maturity, differential mortality between juveniles of one sex and adults of the other sex within the same age cohort of any turtle species has not been observed (Gibbons 1990). However, Gibbons (1990) reported that female-biased sex ratios in the slider turtle (*Trachemys scripta*) resulted from greater predation on the smaller males. In box turtles, sex-biased growth varies among subspecies (Pilgrim et al. 1997). In the eastern box turtle, males mature earlier and at a smaller size, but females are smaller as adults even though they have a greater carapace height (Stickel and Bunck 1989). Probability of mortality may also be influenced by sex-specific behavioral differences among adults (Gibbons 1990). Seigel (1980) found higher mortality rates in nesting female diamondback terrapins (*Malaclemys terrapin*), whereas Schwartz and Schwartz (1974) reported a higher mortality of male three-toed box turtles occurred during hibernation.

Early maturation of one sex, can produce a skewed sex ratio toward that sex (Gibbons 1990). Lovich et al. (1990) documented female-biased sex ratios in wood turtles (*Clemmys insculpta*), a species in which females mature earlier and at a smaller size than males, whereas Lovich and Gibbons (1990) reported that male-biased sex ratios in the diamondback terrapin were the result of earlier maturation of males. Consequently, in turtles with differential maturity, a single age or size cohort may contain mature individuals of one sex and juveniles of the other. Gibbons (1990) documented that when juvenile slider turtles within this cohort were included, the sex ratio more closely approached 1:1. Therefore, in sexually dimorphic species, sex ratios will be biased toward the earlier maturing sex when no other sex ratio factors are involved (Gibbons 1990, Lovich and Gibbons 1990). However, in long-lived species such as box turtles, the proportion of the earlier maturing sex to the overall adult population is small, having little effect on the sex ratio.

Movement among populations also affects sex ratios. Male turtles often move greater distances and more often among populations than females (Gibbons 1990, Lovich and Gibbons 1990). Lovich and Gibbons (1990) hypothesized that these movement differences were the result of different reproductive strategies. Male turtles may be active earlier in the season and move greater distances to increase their chances of mating with multiple females (Lovich and Gibbons 1990), and during the nesting season, female movements may increase as they search for nest sites (Stickel 1950, Lovich and Gibbons 1990). Both male and female box turtles have been documented to occasionally leave their home range for unexplained reasons (Stickel 1950, Langtimm et al. 1996). Although differential movement of the sexes may cause fluctuation in sex ratio, Lovich and Gibbons (1990) noted that sex ratio of an area may be balanced by movement in and out of a population. Conversely, greater interpopulation movements of one sex may result in an overestimate of the proportion of that sex in the population (Gibbons 1990).

For box turtles, most studies reported an even sex ratio (Table 2). However, Dodd (1997) reported a male biased sex ratio of 1.6:1 over a 5-year period for Florida box turtles. After considering causes of possible bias, he concluded the sex ratio was natural and attributed it to nesting conditions (Dodd 1997). Williams and Parker (1987) also reported sex ratios that favored males although significance only occurred during 2 of the 8 years tested.

Age Structure and Distribution

Determining age of individuals can be used to ascertain important parameters such as recruitment rate, longevity, and overall stochasticity of a population. A common technique used for determining ages of turtles, including box turtles, is counting growth annuli formed by deposition of scute layers on the carapace or plastron (Zug 1991, Germano and Bury 1998), despite a lack of data validating this technique (Wilson et al. 2003). Ewing (1939) reported that in box turtles 1 growth annulus is usually formed each year per scute, but warned that false annuli occasionally form between true annuli.

Table 2. Summary of adult sex ratios reported in population studies of eastern box turtles (*Terrapene carolina*).

Subspecies	Study	Sex Ratio (M:F)	$P \geq 0.05$
T. c. bauri	Dodd (1997)	1.6:1.0	yes
T. c. bauri	Pilgrim et al. (1997)	0.9:1.0	no
T. c. carolina	Bayless (1984)	1.1:1.0	no
T. c. carolina	Dolbeer (1969)	1.0:0.6	not reported
T. c. carolina	Stickel (1950)	0.91:1.0	no
T. c. carolina	Williams & Parker (1987)	male bias[1]	yes
T. c. triunguis	Leuck & Carpenter (1981)	1.15:1.0	no
T. c. triunguis	Reagan (1972)	0.67:1.0	no
T. c. triunguis	Schwartz & Schwartz (1974)	1.2:1.0	not reported

[1]Study conducted from 1957-1984, significance reported in years 1959 and 1983.

Evidence, however, suggests that this method may only be accurate for aging young box turtles (Ewing 1939, Schwartz et al. 1984, Germano and Bury 1998, Schwartz 2000). Nichols (1939) examined 16 eastern box turtles and found the annuli added equaled the number of years elapsed in only 5 turtles, and Stickel (1978) found this occurred 32% of the time. Stickel and Bunck (1989) determined that in 21 of 52 turtles, the number of annuli corresponded to years elapsed in eastern box turtles that were 13 years or younger when first captured. Schwartz (2000) reported accuracy for three-toed box turtles 10 years or younger. Consequently, age-class structure of box turtles may be difficult to assess because age estimates of adults are difficult to determine. Therefore, most researchers reporting age distribution for box turtles group individuals into two cohorts: juveniles and adults, with adult turtles typically having 10 or more growth annuli (Schwartz et al. 1984, Pilgrim et al. 1997) or a carapace length ≥100-120 mm (Stickel 1950, Schwartz and Schwartz 1974, Langtimm et al. 1996, Dodd 1997). Shell wear may also aid in age determination (Zug 1991). As box turtles age, the scutes become worn, making annuli difficult to count (Stickel 1978, Schwartz et al. 1984). Schwartz et al. (1984) used shell wear to distinguish young adults (10-32 years) from old adults (33-51 years). Additionally, for long-term studies, ages of adults can be estimated based on number of years known alive.

Estimations of the juvenile cohort may be biased because juvenile box turtles are difficult to find due to their small size and habitat use (Ernst et al. 1994, Dodd 2001). Juveniles often seek shelter under vegetation and debris (Ernst et al. 1994, Dodd 1997). Dodd et al. (1994) documented that juvenile Florida box turtles preferred areas with abundant organic soil and ground cover, which may provide protection from predators and environmental conditions in addition to greater prey abundance. Therefore, the proportion of juveniles reported is variable (Table 3), and juvenile abundance may be underrepresented in some studies (Ernst et al.1994). Schwartz et al. (1984) reported juvenile three-toed box turtles comprised on average 46% of the population by year between 1965-1980. However, Pilgrim et al. (1997) reported a much lower proportion of only 3.1% juveniles for a Florida box turtle population. Most studies report proportions of juveniles between 10-25% (Table 3).

An unstable age distribution may be the result of low or non-existent recruitment in some years due to nest predators and low female reproduction. Additionally, changes in age distribution may call attention to perturbations affecting recruitment and survival (Dodd 1997). For example, Hall et al. (1999) reported a changing age structure of an eastern box turtle population over a 40-year period with percentage of juveniles being 4.2%, 6.2%, 4.8%, and 15.7% in 1945, 1955, 1965, and 1995, respectively. The higher percentage of juveniles in 1995 may have resulted from fewer adult turtles in the population due to a flooding event in 1972, which greatly reduced the adult turtle population (Hall et al. 1999, Dodd 2001).

Mortality and Survival Rates

Box turtle mortality is caused by numerous factors including predation, parasites and disease, food availability, environmental conditions, natural disasters, and human-induced mortality (Ernst et al. 1994, Dodd 2001). Documented natural predators of juvenile box turtles and nests include badgers (*Taxidea taxus*), skunks (*Mephitis mephitis,*

Table 3. Percentage of juveniles reported in population studies of eastern box turtles (*Terrapene carolina*).

Subspecies	Study	% of Juveniles	Definition of Juvenile
T. c. bauri	Pilgrim et al. (1997)	3.1%	<10 rings
T. c. carolina	Stickel (1950)	10.9%	<108 mm
T. c. triunguis	Dodd (1997)	18%	<120 mm
T. c. triunguis	Reagan (1972)	4.2%	not reported
T. c. triunguis	Schwartz & Schwartz (1974)	18-25%	<110 mm
T. c. triunguis	Schwartz et al. (1984)	46%	<10 rings

Spilogale putorius), minks (*Mustela vison*) and weasels (*Mustela* spp.) foxes (*Urocyon cinereoargenteus*, *Vulpes vulpes*), raccoons (*Procyon lotor*), coatis (*Nasua narica*), rats (*Rattus* spp.), nine-banded armadillos (*Dasypus novemcinctus*) crows (*Corvus brachyrhynchos, C. cryptoleucus*), vultures (*Cathartes aura*, *Coragyps* spp.), Mississippi kites (*Ictinia mississippiensis*), barn owls (*Tyto alba*) and snakes (*Agkistrodon piscivorus, A. contortrix*, *Cemophora*, *Coluber* spp., *Heterodon* spp., *Lampropeltis* spp.) (Ernst et al. 1994, Dodd 2001). Predators of adult box turtles are few but include raccoons, skunks, coyotes (*Canis latrans*), dogs (*Canis familiaris*), and foxes (Ernst et al. 1994, Dodd 2001). Ectoparasites, such as mites, ticks, and files, and endoparasites are probably present in small numbers in box turtle populations (Dodd 2001). However, their effect on natural populations has not been quantified (Dodd 2001). Additionally, the extent of disease in box turtle populations is also poorly understood (Dodd 2001). Other causes for mortality include exposure to environmental extremes and human activity. Schwartz and Schwartz (1974) documented that 68% of all mortalities in three-toed box turtles occurred during hibernation in central Missouri. Mortality of ornate box turtles (*T. ornata*) in south-central Wisconsin resulted from human activity (i.e., automobiles, farm machinery, and lawnmowers; Doroff and Keith 1990), and Stickel (1978) hypothesized increased mortality of the eastern box turtle due to increased road construction.

Mortality rates of box turtles can be sex-, age-, or size-specific. Sex-specific differences in box turtles may be due to differences in behavior and movements. Schwartz and Schwartz (1974) reported a sex-specific adult mortality; three-toed box turtle males comprised 64% of mortality during hibernation and 34% during the active period. The researchers hypothesized that this difference was due to longer activity in fall and earlier activity in spring by males searching for mates, and therefore being subjected to early or late winter freezes (Schwartz and Schwartz 1974). However, review of male and female activity in fall and spring did not support this hypothesis (Schwartz and Schwartz 1974). Predation on box turtles is age- and size-specific: nests and juveniles are most vulnerable, whereas adult box turtles have few predators (Ernst et al. 1994).

Since box turtles are long-lived species, annual survival rates should be high once they reach adulthood (Gibbons 1987). Yahner (1974) estimated a 0.80 annual survival rate for the eastern box turtle between 1968-1972, a value similar to the mean annual survival rate of 0.81 reported by Doroff and Keith (1990) in ornate box turtles. Although these numbers are high, Wilbur and Morin (1988) noted that even with an annual rate as high as 0.90 only 1 in 100 turtles would be alive after 44 years. Doroff and Keith (1990) estimated an annual survival rate of 0.95 would be necessary for a stable population of ornate box turtles.

Summary

Information on population ecology of the eastern box turtle is highly variable among studies addressing population parameters. This variability may be attributed to biases, latitudinal gradient, habitat quality, and/or biological differences of the subspecies, but may also be a result of differences in past land-use history and present degree of disturbance of sites and surrounding areas. These latter issues and their relationship to box turtle population ecology have not adequately been quantified. Past box turtle population studies have been conducted primarily on protected sites in contiguous habitats where human influence was minimal. Some long-term studies documented population declines associated with the recent development of surrounding areas (Stickel 1978, Williams and Parker 1987), but the influences of these changes on the population were not directly observed. Additionally, Schwartz (2000) reported recent development of adjacent areas to a study site in Missouri but has yet to report the effects on the box turtle population.

I chose 4 study sites that differed in the degree of disturbance to investigate eastern box turtle population ecology in a fragmented landscape. On each study site, I estimated population abundance and density, sex ratio, age structure, and survival rate. I compared these estimates among study sites to better understand the effect of fragmentation on population ecology.

Chapter 2

STUDY SITES

To study the effects of forest fragmentation on the eastern box turtle, we chose 4 study sites with differing degrees of disturbance on the northern Delmarva Peninsula in New Castle County, Delaware. The University of Delaware Woodlot and University of Delaware Webb Farm were isolated forest fragments located within the city limits of Newark, Delaware. Turkey Run consisted of patchy forest habitat that was contiguous to adjacent forest habitat, and White Clay Creek was an interior forest. These latter two study sites were located in Delaware about 8 km north of the Woodlot and Webb Farm (Figure 1).

The Woodlot

The University of Delaware Woodlot study site (18.5 ha) was an isolated forest fragment (Figure 2). The western and northern portions of this forest were over 130 years old, while the southern and eastern portions were approximately 70 years old (Gorman and Roth 1989). A standard 2-m high chain-link fence surrounding the Woodlot created a sharp barrier between mature forest and a human manipulated landscape; however, early successional habitat existed along the length of the southeastern and eastern boarder (1-4 m wide along most of the stretch with a small section spanning 35 m in width). At the junction of the southeastern and eastern edge, a

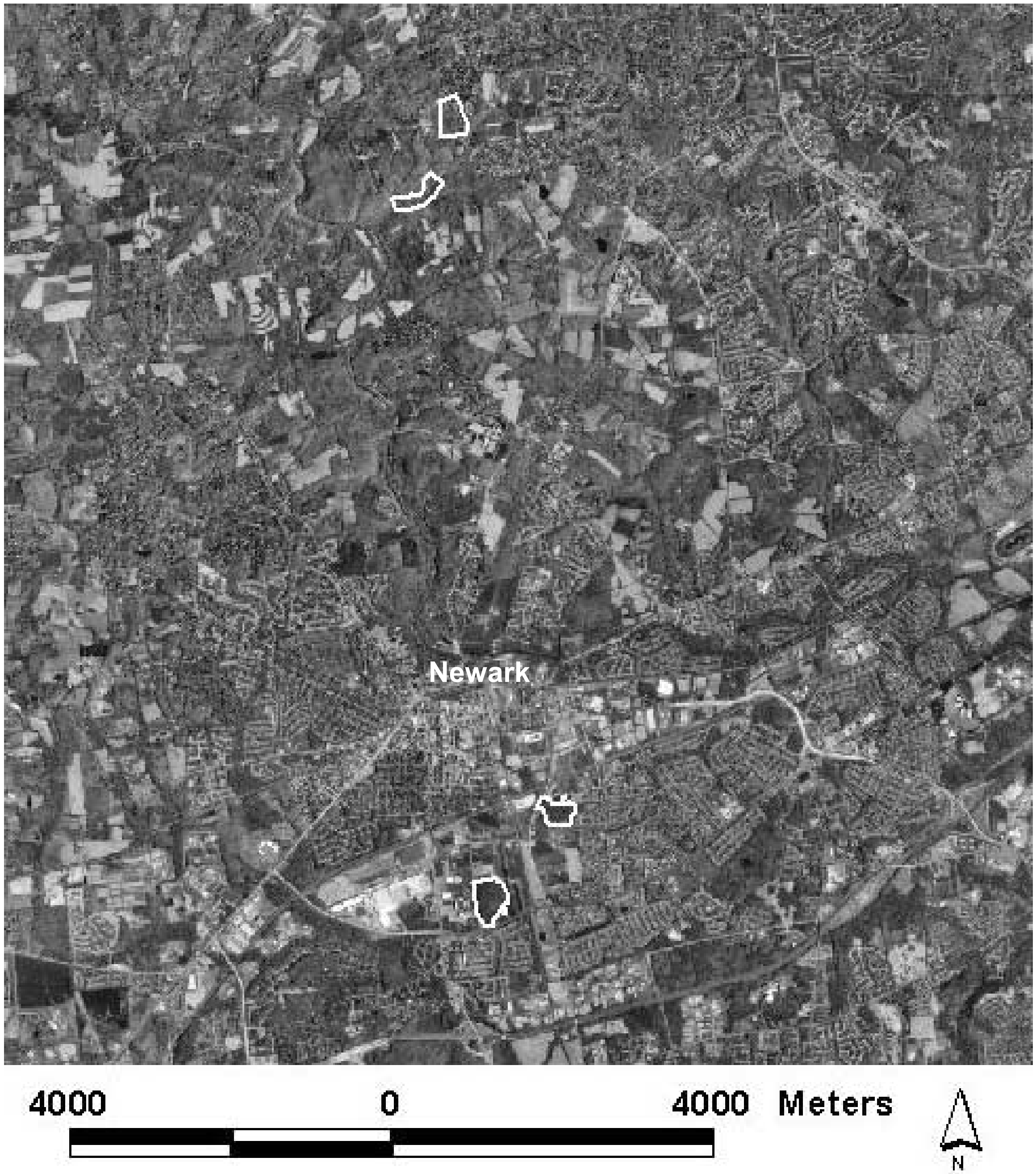

Figure 1. Aerial photograph (1997) of Newark, Delaware area showing the University of Delaware Woodlot (bottom left), University of Delaware Webb Farm (bottom right), Turkey Run (top right), and White Clay Creek (top left) study sites.

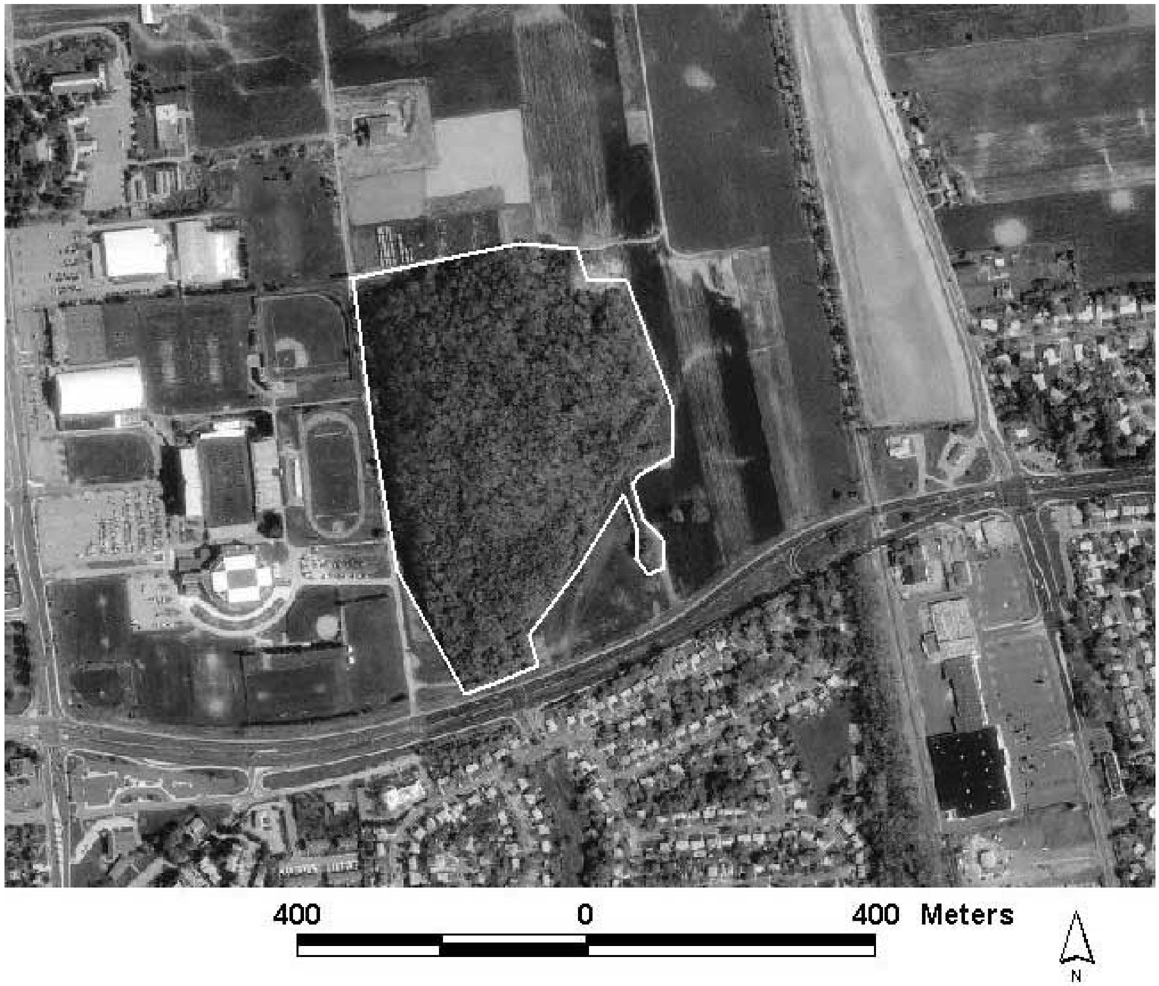

Figure 2. Aerial photograph (1997) of the University of Delaware Woodlot study site (18.5 ha) in Newark, Delaware. Major features bordering the Woodlot include Route 4 to the south, University Athletic Complex to the west, and agricultural fields to the north and east.

southward running fencerow allowed for additional early successional habitat (about 2 m wide) connecting a small patch of trees. These areas of early successional habitats were included in the Woodlot study site.

To the north, a gravel road separated the Woodlot from a small experimental orchard and agricultural fields planted in corn. A University-access paved road ran the length of the western border, with the University Athletic Complex, which contained sports fields, a stadium, and parking lots, farther to the west. A divided 4-lane highway (Route 4) with a 20-cm vertical curb bordered the southern edge. A narrow hedgerow of mostly exotic shrubs grew along a ditch adjacent to Route 4. Another gravel road crossed the southern portion of the Woodlot 20 m from Route 4 connecting the University-access road to an athletic field along the southeastern edge of the Woodlot. An agricultural field planted in alfalfa bordered the eastern edge, and a small meadow occurred along the northeastern corner of the Woodlot.

Aerial photographs show the Woodlot has been isolated from other forest habitats by agricultural fields and development since as early as 1937. However, forest tracts comparable in size persisted to the south until the mid-1960s when Robscott Manor subdivision was built. Additionally, in the mid-1960s, approximately 5 ha of forest along the western border of the Woodlot were cleared for construction of the University Athletic Complex.

Topography of the Woodlot sloped gradually to the south with elevations ranging from 23 m to 31 m above sea level (Bray et al. 1966). A small stream, which flowed southward through the Woodlot from the western edge, and several low areas, especially towards the southern end, periodically flooded after heavy rains. Hickories (*Carya* spp.), oaks (*Quercus* spp.), red maple (*Acer rubrum*), sweet gum (*Liquidambar styraciflua*), and tulip poplar (*Liriodendron tulipifera*) dominated the overstory canopy, while pepperbush (*Clethra alnifolia*), poison ivy (*Toxicodendron radicans*), spicebush (*Lindera benzoin*), and *Viburnum* spp. dominated the understory. The native greenbriar (*Smilax* spp.) and exotic multiflora rose (*Rosa multiflora*) formed thickets in certain areas.

The areas adjacent to the Woodlot experienced intensive management. Grass along the northern, western, southern, and southeastern edges of the Woodlot was maintained as a lawn-type landscape by mowing at a height of 5 cm. Within the orchard, grass grew taller but was still mowed at a height of 5 cm a few times a month. The alfalfa field was harvested 3-4 times a year with a mower height of 5 cm, and the meadow was mowed 3-4 times a year to a height of about 15 cm. Additionally, portions of the early successional habitat along the eastern boundary of the Woodlot were mowed once a year to about 15 cm.

Other researchers and students used the University of Delaware Woodlot throughout the year. However, entry was prohibited without permission. Box turtles had been captured and marked on this area since 1965. In the first year, J. Longcore captured and marked 63 turtles (Bray et al. 1966). During 1999-2000, Niederriter (2000) used radio-telemetry to study this box turtle population.

Webb Farm

Northeast of the Woodlot (920 m) was the University of Delaware Webb Farm study site. Agricultural fields (alfalfa and corn), a single row of railroad tracks, and a heavily traveled 2-lane highway (Route 72) with a 20-cm vertical curb separated these areas. Due to these barriers and lack of hedgerow corridors, turtle movement between the Woodlot and Webb Farm seemed unlikely.

Webb Farm (10.9 ha) was comprised of a forest fragment and an early successional meadow along the southern boundary (Figure 3). The eastern half of this forest fragment was approximately 50 years old, while the western portion was about 70 years old. Adjacent forest habitat was present along the eastern border, but was not included in the study site due to the proximity of a single-family home subdivision (Brookside) built up to the tree line to the south and east and a subdivision of town houses (White Chapel) built up to the tree line to the north of these woods. To the north of Webb Farm, a hedgerow that connected Webb Farm to a small early successional area bisected 2 agricultural fields planted in corn. North of these fields, 4 rows of railroad tracks ran east-west. Two small wet meadows were located along the western and eastern edges of the southern cornfield, and we included these areas within the Webb Farm boundary. A standard 2-m high chain link fence separated Webb Farm from Route 72 on the northwestern edge, and a cow pasture bordered the southwestern edge. A small stream flowing southward entered Webb Farm from Route 72 at the northwestern corner. This stream flowed through the forest until it reached the southwestern corner, where it joined with another stream and flowed eastward forming the southern boundary of Webb Farm, separating the early successional meadow from several horse pastures. A second small stream flowed southward from a storm-water retention pond north of Webb Farm. This stream bisected the eastern portion of the forest before flowing into the first stream

Figure 3. Aerial photograph (1997) of the University of Delaware Webb Farm study site (10.9 ha) in Newark, Delaware. Major features bordering Webb Farm include cattle and horse pastures to the south, Route 72 to the west, cornfields and railroad tracks to the north, and White Chapel and Brookside housing communities to the east.

forming the southeastern corner of Webb Farm.

Aerial photographs from 1940 and 1954 showed that Webb Farm and adjacent areas were used for agricultural purposes, but as Webb Farm succeeded to secondary forest, connectivity to other forest habitats existed periodically via narrow early successional corridors along the streams. With the development of Brookside to the southeast circa 1954, Route 72 to the west circa 1977, and White Chapel to the northeast in the late 1980s, Webb Farm became increasingly isolated. This development destroyed habitat and corridors and created barriers to turtle movement. In the summer of 2002, I documented box turtles in a small early successional area directly across Route 72. However, the 20-cm vertical curb along Route 72 was probably a physical barrier to turtles. I hypothesized turtles could move between these two areas by passing under Route 72 via an underpass 200 m north of Webb Farm along the railroad tracks. Additionally, during the summer of 2002, Route 72 and its 20-cm vertical curb was completely removed for a construction project. When the road was rebuilt, the 20-cm curb was replaced with a lower, more rounded 10-cm curb, which may no longer be a physical barrier to turtle movement. However, movement between areas on opposite sides of Route 72 have not been documented or adequately investigated. I also documented box turtles in early successional areas north of Webb Farm across the cornfield, which prior to the 1990s extended eastward 280 m along the railroad tracks to Marrows Road. Hedgerows along these railroad tracks may be suitable corridors for turtle movements.

Topography of Webb Farm was flat with elevations ranging from approximately

21 m to 24 m above sea level. The early successional meadow and several low-lying areas within the forest were inundated with water following heavy rains. Black cherry (*Prunus serotina*), black gum (*Nyssa sylvatica*), oaks, red maple, and sweet gum dominated the overstory, while greenbriar, multiflora rose, and *Viburnum* spp. were common in the understory. Vegetation in the meadow was dominated by grasses, sedges, goldenrod (*Solidago* spp.), and ragweed (*Ambrosia trifolia*). Greenbriar and *Rubus* spp. formed thickets in dry areas, while buttonbush (*Cephalanthus occidentalis*) was common in wetter areas of the meadow.

Management around Webb Farm was less disruptive than at the Woodlot, although areas are more developed. Mowing occurred on properties of the subdivisions and along the highway right-of-way. The wet meadows along the northern boundary of Webb Farm were mowed once a year to about 15 cm. The cornfields were plowed twice a year in early spring and fall. Other University researchers or students did not use Webb Farm during the duration of this study. However, residents from nearby subdivisions often entered Webb Farm, and on few occasions, we observed residents capturing box turtles. Additionally, some residents placed fruits at the edge of their property to feed turtles.

Turkey Run

Turkey Run study site (14.4 ha) was a privately owned, 30-year-old forest interspersed with small fields and surrounded by a primarily rural landscape (Figure 4). A secondary paved road (Corner Ketch Road) ran along the northern boundary.

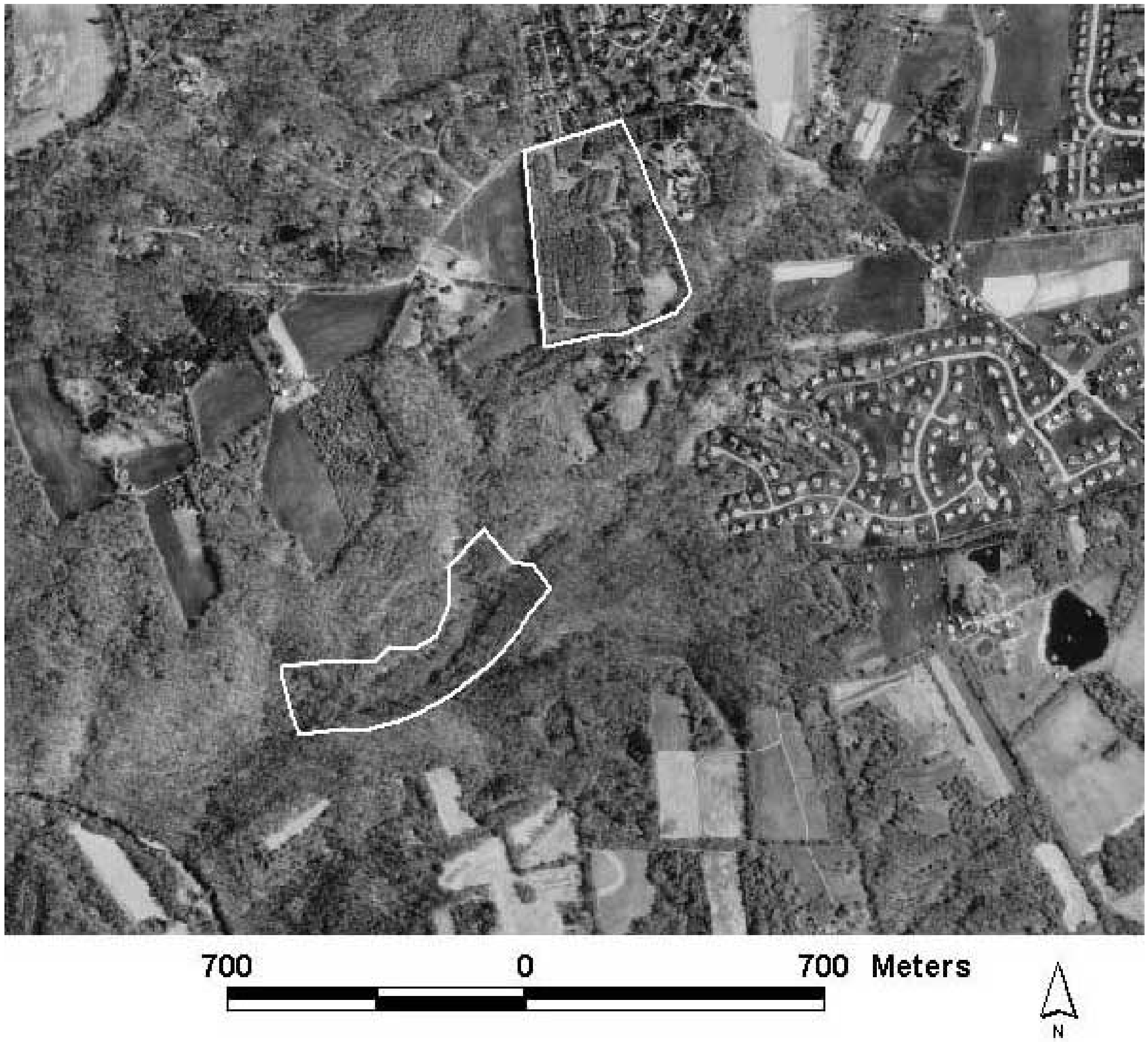

Figure 4. Aerial photograph (1997) of Turkey Run (14.4 ha, top) and White Clay Creek (11.3 ha, bottom) study sites in Newark, Delaware. Associated areas where radio-tagged turtles frequented included fields west and south of Turkey Run and north and southeast of White Clay Creek.

Subdivisions of single-family homes (~ 0.4 ha lots) were built north of Corner Ketch Road in the 1980s. Agricultural fields planted in hay bordered the western side of Turkey Run. These fields were part of White Clay Creek State Park, which included 1,284 ha of contiguous agricultural fields and forest in Delaware and 507 ha in Pennsylvania. To the south was a farmhouse and nineteenth century barn surrounded by fields and forest. A small stream originating from a springhead in the northeastern corner of Turkey Run flowed southward along the eastern border through forest estimated at 60 years of age. Across from this patch of forest to the northeast was a house built circa 1950.

Aerial photographs from 1940 show Turkey Run was used for agriculture. Mature stands of forest existed several hundred meters to the south and east in 1940, while forests adjacent to Turkey Run on the south and east were not present until 1954. Between 1952 and 1976, the western two-thirds of the study site was used by Millcreek Nursery to grow trees and other ornamental shrubs. In the fall of 1976, Millcreek Nursery closed, and the property was abandoned. Many trees and shrubs were dug up and auctioned off leaving large holes and depressions scattered across the property. Mowing occurred periodically in certain areas but was otherwise allowed to succeed to forest, thus creating a matrix of open field and forest patches.

Topography of Turkey Run was of high elevation ranging from approximately 88 m to 110 m above sea level with steep slopes occurring only along the southeastern corner. The overstory canopy was primarily tulip poplar and oaks with flowering dogwood (*Cornus floridanus*) in the understory. The exotic autumn olive (*Elaeagnus umbellata*) and multiflora rose formed dense thickets especially along the forest edge and in light gaps.

Mowing at Turkey Run occurred 3 times a year in late May, late August, and late October/early November to a height of about 15 cm. Hay was harvested from the agricultural fields to the west of Turkey Run twice a year in late June and late October at a height of 5-8 cm. South of Turkey Run, hay was harvested in mid-June and mowed in late August at a height of 5-8 cm in 2001. In 2002, these fields were mowed in mid-November at a height of 5-8 cm. I marked box turtles at Turkey Run and adjacent areas between 1994-2000. I released 6 adult turtles, which I captured from various other localities, at Turkey Run during this period. Additionally, during September of 1995 and 1996, I removed 20 hatchlings from their nests and raised them indoors. I released 14 of these turtles at Turkey Run on 1 June 1997, while the remaining 6 turtles were released at another location.

White Clay Creek

White Clay Creek study site (11.3 ha) was an interior forest approximately 60 years old within White Clay Creek State Park (Figure 4). The closest non-forested areas were agricultural fields 140 m to the south and 230 m to the north. Two remnant open canopy areas existed near the northern corner of the study site about 30 m away. These areas were about 0.01 ha each and were characterized by early successional grasses. A closed-canopy park road (Thompson's Station Road) delineated the southern boundary of the study site, and a park trail bisected the eastern end. Five small tributaries on the study site fed a second-order stream that ran southwest though the center. White Clay Creek study site was 460 m south southwest of Turkey Run and was connected by continuous forest, making movements between sites possible.

Aerial photographs from 1940 show White Clay Creek study site was an open field but was probably no longer in agricultural use. The western and eastern ends were adjacent to mature stands of forest with a matrix of agricultural fields and early successional forests to the north and south. By 1954, White Clay Creek was an early successional forest, and all nearby agricultural fields were succeeding to forest.

Topography ranged from flat along both sides of the central stream to sloped north of the stream with elevation ranging from approximately 40 m to 80 m above sea level. American sycamore (*Platanus occidentalis*), black walnut (*Juglans nigra*), red maple, and tulip poplar were common in the overstory canopy. Flowering dogwood and spicebush subsisted in the understory. However, exotic species dominated the understory canopy; multiflora rose and Chinese privet (*Ligustrum sinense*) were most common along the stream where they formed dense thickets, while autumn olive dominated the upland slopes.

Recreational use of White Clay Creek study site by the public was limited to hiking, mountain biking, and deer hunting between dawn and dusk. While hikers and mountain bikers commonly used Thompson's Station Road, which was open to vehicular traffic during daylight hours Monday though Friday, use of the park trail that bisected the eastern end of White Clay Creek study site was traveled less frequently. Deer hunting (archery and shotgun), which required hunters to use designated deer stands, only occurred during several weeks in November, December, and January.

Chapter 3

METHODS

This thesis work was part of a more comprehensive study focusing on the ecology of eastern box turtles in a fragmented landscape. By using radio-telemetry and mark-recapture, our collective goal was to investigate aspects of box turtle ecology including home range, movement rates, nesting ecology, macro- and micro-habitat use, hibernaculum selection, population ecology (the focus of this thesis), and the effects of fragmentation on these parameters. As a result of a collaborative effort by several researchers working on this study, I use "we" to denote when several researchers helped in the data collection. All capture and handling procedures were approved by the University of Delaware Institutional Animal Care and Use Committee (#1083).

Turtle Handling

From 15 April 2001 through 31 October 2002, we captured box turtles by incidental finds and visual searches on and within close proximity of our 4 study sites. Upon first capture, we measured, weighed, sexed, aged, marked, and released each turtle at the capture location. We recorded data in the field except for research technicians who brought turtles indoors. In such cases, we used cloth sacks to hold and transport individual turtles, and we housed turtles individually in 10-L buckets. We kept turtles indoors <24 hours. To prevent disease transmission, we quarantined turtles from different study sites.

For all new and previously captured turtles, we recorded date, time, activity, and turtle location with a GPS unit (GeoExplorer 3, Trimble Navigation Ltd., Sunnyvale, Calif.). We designated turtle activity as active or not active and further described their activity as head out, head and feet out, resting, resting form, buried under leaves, hibernaculum, basking, feeding, mating, nesting, walking, or other. We differentially corrected location data from 2 base stations. We used Reedy Point, Delaware, base station as our primary source of data, which was approximately 23 km south-southeast of the study sites, and Dover, Delaware, base station located 63 km to the south as a back-up.

We added extensions to the measuring tines of digital calipers to accurately measure straight carapace length (along the midline from the nuchal to the articulation of the 12th marginal scutes), straight carapace width (across the articulation of 2nd and 3rd vertebral scutes), straight carapace height (at the articulation of 2nd and 3rd vertebral scutes), straight plastron length (anterior and posterior plastron length along the midline measured separately), and plastron width (at hinge) to the nearest 1.0 mm. To measure turtle mass, we used Pesola spring scales (600±5 g, 300±2 g, 30±0.25 g). We recorded length measurements once per year and weight measurements at each capture.

We marked each adult turtle by filing a unique combination of permanent notches (~2-3 mm deep) in the marginal scutes (Cagle 1939) with a file or hacksaw blade. Starting at the head and continuing around to the tail, we numbered marginal scutes on the left and right side as 1 through 12. The fifth, sixth, and seventh marginal scutes were usually not marked due to their proximity to the bridge, and we made no more than 2 notches per scute. This method does not injure the turtle or affect survival (Cagle 1939). We marked hatchling turtles by cutting a triangular shaped notch into the marginal scutes with fine-point dissecting scissors. This notch was approximately 2 mm deep and removed about one-third to half of the area of the scute. We chose the largest marginal scutes for marking hatchings to allow the largest possible notches. We did not mark the fifth, sixth, or seventh marginal scutes due to their proximity to the bridge. Additionally, for most hatchlings, we did not mark the first, eleventh, or twelfth marginal scutes due to their small size. Turtle marking codes did not overlap among study sites, except between the Woodlot and Turkey Run where box turtles had previously been marked; however, these areas were approximately 8 km apart with no possibility of movement between sites without human assistance.

We aged turtles at first capture and in subsequent years by counting annuli on the first, second, and third pair of costal scutes of the carapace. In temperate-zone turtles, 1 annulus is usually formed each year and, therefore, may be a reliable estimate of age for turtles (Zug 1991). However, the accuracy of this method has not been adequately quantified in box turtles (Wilson et al. 2003). Stickel and Bunck (1989) reported determining age by growth annuli was less reliable at >13 annuli and new annuli become indiscernible past 18-21annuli (Stickel 1978). Additionally, scutes of very old turtles are often worn smooth (Stickel 1978), making age estimates less accurate. I tested the accuracy of this method by making age estimates of recaptured turtles in the subsequent year without prior knowledge of age and then compared additional annuli growth to the 1 year elapsed. Turtles with ≥10 annuli, I classified as adults (Schwartz et al. 1984, Pilgrim et al. 1997).

For determining gender, we considered 4 physical characteristics: iris color, tail length, hind claw characteristics, and concavity of the plastron. Male box turtles typically have orange or red irises; a long, thick tail with the anus beyond the margin of the carapace; long, robust, curved hind claws; and a concave plastron (Ernst et al. 1994). In contrast, female box turtles have yellow or brown irises; a shorter, more tapered tail with the anus inside the margin of the carapace; slender and straighter hind claws; and a flat, slightly concave, or slightly convex plastron (Ernst et al. 1994).

Transmitter Attachment and Radio Tracking

Beginning 26 April 2001, we attached a 26.5 g transmitter (Series R2100; 164 MHz; Advanced Telemetry Systems, Inc., Isanti, Minn.) to the first 10 male and 10 female box turtles captured at each study site. In instances of turtle mortality, we moved the transmitter to the first turtle captured of the same sex on the study site. We attached all 20 transmitters to turtles by 29 May 2001 at Turkey Run, 8 June 2001 at White Clay Creek, and 12 June 2001 at Webb Farm. At the Woodlot, transmitters were already attached to 8 turtles (5 males, 3 females) from a previous study (Niederriter 2000). Due to low population abundance at this study site (<20 turtles captured) we attached transmitters to every turtle found throughout the study, with the last transmitter being attached on 19 September 2002.

To attach the transmitter, we brought turtles indoors and housed them individually in 10-L buckets. We used PC-7 heavy-duty epoxy (Protective Coating Co., Allentown, Penn.) to attach the transmitter to either the left or right second costal scute of the carapace (except on 1 female where we attached a transmitter to the first costal scute) so not to interfere with daily activities and mating (Boarman et al. 1998). We did not attach transmitters to damaged or flaking scutes. Additionally, to prevent obstructing shell growth we did not cover the growth margin around the scute with epoxy (Boarman et al. 1998). To allow the epoxy to thoroughly dry, we kept turtles indoors overnight. Prior to releasing a turtle at its capture location, we removed excess epoxy from around the transmitter with a razor blade.

We located turtles by homing with an IC-R10 receiver (Icom Inc., Bellevue, Wash.) or a Telonics TR-2 receiver (Telonics Inc., Mesa, Ariz.) and hand-held H-antenna ≥5 times a week from 1 May to 31 October. During the transition period when turtles were entering and emerging from hibernation (~3 to 4 weeks in fall and spring), we located turtles 3 times a week. After all turtles had entered hibernation, we located turtles once a week. Transmitters were on a duty cycle (11 hours on; 13 hours off) and had a battery life of approximately 1,100 days. To adjust transmitter on-air times, we brought turtles indoors and housed them individually, quarantined by study site, in divided plastic bins. For females, this occurred approximately 15 May in 2001and 2002 to accommodate checking for nesting females in late evening; then, approximately 15 July in 2001and 2002, females' transmitters were reset to earlier times. Males were rarely brought in for transmitter on-air time readjustments. We varied tracking time among sites so that we located turtles throughout the day, which for most turtles occurred between 0800 and 1700 hours eastern standard time.

Intensive Searches

I conducted intensive 1-day visual searches for both radio-tagged and non-radio-tagged turtles once a week from the last week in May through August 2001-2002 at each study site. During the first and third weeks in September, I conducted 2 additional searches at each study site. With the goal of finding as many turtles as possible, I conducted searches during optimum times (early morning to mid-afternoon) and searched the entire study site while focusing on areas of optimal habitat. Each search lasted between 2-6 hours and was not conducted in the rain. Stickel (1950) used similar search methods. To avoid bias toward finding radio-tagged turtles, I did not conduct radio-telemetry $\leq$2 days prior to each search.

Mortalities

To document mortalities, we used radio telemetry, incidental finds, and active searches. When we found dead turtles, we recorded date, location, and possible cause of mortality. If the date of mortality was uncertain, I approximated length of time dead by examining the extent of body decomposition. For turtles in which the body was fully decomposed and only the shell remained, I used the midpoint date between when the turtle was last seen alive and date found dead. Following mowing of agricultural fields within or adjacent to each study site or fields frequented by radio-tagged turtles, we actively searched for dead turtles along the edges (1-2 m) and recorded grass height.

Analyses

We captured box turtles during intensive searches and by incidental finds while visiting the study sites or conducting radio-telemetry. However, due to bias involved with the radio-telemetry equipment, I only recorded captures of radio-tagged turtles on intensive searches. Therefore, I used 2 approaches to estimating population abundances, densities, and sex ratios at each study site in this thesis: analyzing data from all captures (turtles captured on intensive searches and on incidental finds), and analyzing data from intensive searches only. Additionally, I used time spent searching during intensive searches to calculate catch per unit effort (CPUE). I used all turtles captured to estimate age structure, and radio telemetry to calculate survival rates for each study site. Due to the very low population abundance at the Woodlot, this study site was excluded from some analyses. Additionally, long-term capture data existed for the Woodlot and Turkey Run, and I presented analyses of these data separately.

Catch Per Unit Effort

As a method for comparing population abundance among sites, I calculated CPUE for intensive searches by dividing the number of turtles captured by time (hours) spent searching. Assuming that turtles had a similar probability of capture among sites, study sites with similar CPUE should have similar abundances. Additionally, seasonal differences in CPUE may determine the best time of year to capture turtles. I compared CPUE of all turtles captured and adult turtles captured among seasons and study sites blocking on year using an Analysis of Variance (ANOVA; Peterson 1985). I used a

Fisher's Protected Least Significant Difference (LSD) mean separation test to investigate differences among seasons and study sites (Peterson 1985).

Mortalities and Survival

I documented mortalities at each study site and in associated areas and grouped these mortalities as natural, human induced, or other unnatural. I used radio-telemetry to determine cause-specific mortality and to estimate annual survival rates by year using the Kaplan-Meier procedure (Allison 1995). Since I documented very few mortalities for Webb Farm, Turkey Run, and White Clay Creek, I pooled data from these areas to estimate annual survival rate. I estimated annual survival rate for the Woodlot separately. Because of the low number of mortalities and their even distribution among the seasons, I used the annual survival rate estimates to estimate a seasonal survival rate that was constant across seasons (spring, 16 April to 15 July; summer, 16 July to 31 August; fall, 1 September to 14 November; winter, 15 November to 15 April) for each study site.

Sex Ratio

I compared adult sex ratio among years within study sites using a log likelihood ratio Chi-squared analysis (Stokes et al. 1995) for all turtles captures and intensive searches. When sex ratio did not differ by years within study sites, I pooled data and compared sex ratios among study sites. Additionally, I tested sex ratios within study sites for parity using a log likelihood ratio Chi-squared analysis (Stokes et al. 1995).

Aging Technique

To determine approximate ages of turtles, I calculated the mean number of annuli counted on the first, second, and third pair of costal scutes of the carapace. To determine a maximum age at which age could reliably be estimated for most turtles, I compared precision in the number of annuli counted across the first, second, and third pair of costal scutes of the carapace. If counts were imprecise, I concluded the turtle could not reliably be aged. I also compared accuracy in the number of annuli added in subsequent years to years elapsed per scute. If the number of new annuli was imprecise across all scutes or was not accurate with the number of years elapsed, I concluded the turtle could not reliably be aged. Finally, I compared amount of shell wear, which would denote very old turtles, to the number of countable annuli present. To minimize observer bias, I only used annuli counts that I recorded.

Age Structure

After I determined the maximum age at which age could reliably be estimated for most turtles, I standardized 2001and 2002 ages to 2001 ages and grouped turtles by age cohorts and compared trends in abundance across cohorts and among study sites. I also grouped juveniles and adults to determine juvenile percentage per study site.

Population Abundance and Density

I used mark-recapture to estimate adult population abundance at each study site using both open and closed population models, and I made comparisons among model types. Due to differences in survival and capture probabilities, I excluded juveniles (<10 years of age) from the population estimates.

I used the immigration/emigration joint hypergeometric maximum likelihood estimator (JHE) in program NOREMARK to estimate abundance from mark-recapture data collected on intensive searches by year at each study site (Neal et al. 1993). This model assumed demographic but not geographic closure and incorporated sightings of radio-tagged animals to estimate population abundance (Neal et al. 1993). I estimated and compared densities between years and among study sites using confidence intervals. If confidence intervals overlapped, I assumed densities did not differ.

For the open population models, I investigated the validity of the assumption for my data. I tested for violation of the assumptions of equal capture and survival probabilities by using the program RELEASE within program MARK for all turtles captured and turtles captured during intensive searches (White and Burnham 1999). Using RELEASE, I used TEST 2 to test for equal capture probability and TEST 3 to test for violations of equal survival probability. Additionally, I used the Jolly-Seber model in program MARK to estimate abundance with data from all turtles captured and from intensive searches at each study site (White and Burnham 1999). For both data sets, I pooled captures within seasons (n = 6), excluding the winter season (15 November to 15April) since no turtles were captured during this time, and grouped individuals by sex. Abundance estimates represented population size for the beginning of the study (2001), because models only provided estimates of initial abundance.

The general Jolly-Seber model provided estimates of 4 variables: survival rate (Phi), capture rate (p), population growth rate (Lambda), and population size (N). Based on observations from ratio telemetry and goodness-of-fit tests of survival and capture probabilities, I chose 4 reduced candidate models that were subsets of the general Jolly-Seber model for analyzing the mark-recapture data (Table 4). Based on the few mortalities and turtles recruited into the population observed, I assumed survival rate was constant and recruitment was negligible over the course of the study. I calculated average seasonal survival rates for each study site from the estimated annual survival rate, and I fixed survival rate to this estimate for the reduced models. Because I considered recruitment to be zero, I fixed population growth rate for the reduced models to equal survival rate since population growth rate is a function of the recruitment rate plus the survival rate of the population. However, since I could not confirm turtles had equal capture probability, I allowed capture rate to vary by sex and over time (Model 1), over time (Model 2), by sex (Model 3) or remain constant (Model 4), and I allowed population size to vary by sex. I used the model with the lowest corrected Akaike's Information Criterion (AICc) value as the most parsimonious model (White and Burnham 1999). I estimated and compared density estimates from MARK using the most parsimonious model among study sites and between MARK and NOREMARK for 2001 using confidence intervals. If confidence intervals overlapped, I assumed densities did not differ.

<u>Long-term Data</u>

For the University of Delaware Woodlot (1965-2002) and Turkey Run (1994-2002) long-term data, I pooled captures by year. Because I was interested in annual variation in population abundance, which the models in program MARK did not provide,

Table 4. Definitions for the Jolly-Seber general and reduced models used to estimate population abundance of eastern box turtles from all captures and intensive searches at the University of Delaware Woodlot, University of Delaware Webb Farm, Turkey Run, and White Clay Creek study sites. Survival rate, capture rate, population growth rate, and population size either varied by sex and time, time, sex, remained constant, or were fixed to an estimated value.

Model	Survival Rate (Phi)	Capture Rate (p)	Population Growth Rate (λ)	Population Size (N)
General Model	sex and time	sex and time	sex and time	sex and time
Reduced Models				
Model 1	fixed[1]	sex and time	fixed[1]	sex
Model 2	fixed[1]	time	fixed[1]	sex
Model 3	fixed[1]	sex	fixed[1]	sex
Model 4	fixed[1]	constant	fixed[1]	sex

[1]Fixed to 0.9943 for University of Delaware Webb Farm, Turkey Run, and White Clay Creek study site estimates, and to 0.9421 for University of Delaware Woodlot study site estimates.

I used the Jolly-Seber full model, the modified Jolly-Seber full model, and the Jolly-Dickson full model in program POPAN to estimate annual population abundance (Arnason 1999). The Jolly-Seber full model allowed for capture probability to vary over every sample time and for births and deaths to occur, but did not allow for temporary immigration or emigration (Arnason 1999). Additionally, this model was limited in that it could not estimate parameters near the beginning or end of the sample chain (Arnason 1999). The modified Jolly-Seber full model added heterogeneity among survival rate of individuals to the Jolly-Seber full model (Arnason 1999). The Jolly-Dickson full model allowed survival rate and capture rate to vary over time and could estimate parameters near the beginning and end of the sample period (Arnason 1999).

For the Woodlot long-term data set, researchers using the Woodlot from 1965-2002 captured turtles by incidental finds. Additionally, from 1999-2002, Niederriter (2000) and this study captured turtles with intensive searches. Due to these differences in capture effort, I used 2 data sets to estimate population abundance: all captures recorded from 1965-2002 and captures from 1965-2002 excluding intensive searches by recent box turtle researchers during 1999-2002 but included incidental find by other researchers using the Woodlot. For Turkey Run, search effort in 1994-1996 was similar to effort during this study (2001-2002), although I conducted searches mainly during the months of June, July, and August in 1994-1996. Between 1997-2000, I made very few captures, and therefore, excluded these years from the analyses.

For the Woodlot, I calculated sex ratio of individual turtles from all captures pooled over 5 year periods (i.e., if a turtle was caught every year it was only included once per period) to avoid year-to-year biases. I tested for differences among periods using a Mantel-Haenszel Chi-square and for parity using a log likelihood ratio Chi-squared analysis (Stokes et al. 1995). For Turkey Run, I calculated sex ratio of individual turtles for the period of 1994-1996. I tested for differences among years and between 1994-1996 sex ratio and 2001-2002 sex ratio using a Mantel-Haenszel Chi-square and for parity using a log likelihood ratio Chi-squared analysis (Stokes et al. 1995). I also compared age structure among years at the Woodlot for all captures from 1965-2002 and Turkey Run between 1994-1996 period and 2001-2002 period.

Chapter 4

RESULTS

From 16 April 2001 through 14 November 2002, we captured 268 turtles 892 times on the 4 study sites. We captured 16 turtles 77 times at the University of Delaware Woodlot (Table 5). Intensive searches accounted for 94% of these turtles (n = 15) and 84% of capture events (n = 65; Table 6). In addition to these captures, other turtles were known to occur at the Woodlot. Two turtles that had transmitters attached prior to 16 April 2001 were known to have home ranges within the Woodlot but were never captured. Additionally, we collected 2 hatchlings in September 2002 from a nest along Route 4 laid by a resident turtle. We marked and released these hatchlings along the southern edge of the Woodlot. We captured and marked 64 turtles 260 times at Webb Farm (Table 5). Intensive searches accounted for 80% of these turtles (n = 51) and 58% of the capture events (n = 152; Table 6). At Turkey Run, we captured 97 turtles 253 times with 76% of these turtles (n = 74) and 58% of capture events (n = 147) occurring on intensive searches (Table 5, 6). At White Clay Creek, we captured 91 turtles 302 times with 69% (n = 63) and 57% (n = 171) occurring on intensive searches, respectively (Table 5, 6).

Capture frequency for individual adult turtles at the Woodlot and Webb Farm was greater than that at Turkey Run and White Clay Creek. Over the course of the study,

Table 5. Number of individual eastern box turtles captured and capture events from incidental finds and intensive searches during 2001, 2002, and over the course of the study (2001-02) for University of Delaware Woodlot, University of Delaware Webb Farm, Turkey Run, and White Clay Creek study sites.

	2001		2002		2001-02	
	n	events	*n*	events	*n*	events
Woodlot						
All Turtles	15[1]	42	11[1]	35	16[1]	77
Adults	15[1]	42	11[1]	35	16[1]	77
Juveniles	0	0	0	0	0	0
Males	12[1]	35	9[1]	30	12[1]	65
Females	3[1]	7	2[1]	5	4[1]	12
Webb Farm						
All Turtles	53	148	52[1]	112	64	260
Adults	44	129	41[1]	92	48	221
Juveniles	9	19	11	20	16	39
Males	24	60	24[1]	57	26	117
Females	20	69	17[1]	35	22	104
Turkey Run						
All Turtles	75[1]	151	62[1]	102	97	253
Adults	56[1]	116	44[1]	78	68[2]	194
Juveniles	20[2]	35	18	24	31	60
Males	29	65	24[1]	47	36	112
Females	27[1]	51	20[1,2]	31	32[2]	82
White Clay Creek						
All Turtles	70	185	55[1]	117	91	302
Adults	68	183	52[1]	112	86	295
Juveniles	2	2	3	5	5	7
Males	46	131	35[1]	83	58	214
Females	22	52	17[1]	29	28	81

[1]Not included are several radio-tagged turtles that were known to be on the study sites during for at least part of the study but were never captured: 1 male and 1 female at the University of Delaware Woodlot in 2001; 2 males and 3 females at the University of Delaware Woodlot in 2002; 1 male and 1 female at the University of Delaware Woodlot in 2001-02; 1 male and 2 females at the University of Delaware Webb Farm in 2002; 1 female at Turkey Run in 2001; 4 males and 3 females at Turkey Run in 2002; 5 males and 1 female at White Clay Creek in 2002.
[2]One turtle captured in 2001 as a juvenile was recruited into the adult population as a female in 2002. This turtle was counted as a female in the total count (2001-02).

Table 6. Number of individual eastern box turtles captured and capture events from intensive searches during 2001, 2002, and over the course of the study (2001-02) for the University of Delaware Woodlot, University of Delaware Webb Farm, Turkey Run, and White Clay Creek study sites.

	2001		2002		2001-02	
	n	events	*n*	events	*n*	events
Woodlot						
All Turtles	13	34	11	31	15	65
Adults	13	34	11	31	15	65
Juveniles	0	0	0	0	0	0
Males	10	28	9	27	11	55
Females	3	6	2	4	4	10
Webb Farm						
All Turtles	43	87	30	65	51	152
Adults	36	77	25	65	41	133
Juveniles	7	10	5	9	10	19
Males	19	33	15	35	23	68
Females	17	44	10	21	18	65
Turkey Run						
All Turtles	56	89	38	58	74	147
Adults	44	71	31	48	58	119
Juveniles	12	18	7	10	16	28
Males	24	41	17	26	33	67
Females	20	30	14	22	25	52
White Clay Creek						
All Turtles	44	101	42	70	63	171
Adults	43	100	40	67	60	167
Juveniles	1	1	2	3	3	4
Males	27	66	24	43	37	109
Females	16	34	16	24	23	58

Turkey Run had 18 adult turtles (26%) captured only once and White Clay Creek had 32 adult turtles (37%) captured only once, whereas we captured 2 (13%) and 3 (6%) adult turtles only once at the Woodlot and Webb Farm, respectively (Table 7, 8). We captured most adult turtles ≥4 times at the Woodlot (63%) and Webb Farm (58%), whereas at Turkey Run and White Clay Creek, we captured most adult turtles <4 times with only 32% and 31% being captured ≥4 times, respectively (Table 8). Radio-tagged turtles had a greater frequency of capture than marked turtles especially at Turkey Run and White Clay Creek (Table 8). When I excluded radio-tagged turtles from the capture histories, including their initial captures, the percentage of turtles captured ≥4 for Webb Farm, Turkey Run, and White Clay Creek was 43%, 18%, and 22%, respectively.

Turkey Run and White Clay Creek had a greater turnover of adult turtles per year than did the Woodlot or Webb Farm (Table 7). At Turkey Run, 43% of adult turtles captured in 2001 were not recaptured in 2002, and 18% of adult turtles captured in 2002 were new captures (Table 9). At White Clay Creek, 50% of adult turtles captured in 2001 were not recaptured in 2002, and 35% of turtles captured in 2002 were new captures (Table 9). At Webb Farm, 16% of adult turtles captured in 2001 were not recaptured in 2002, and 10% of adult turtles captured in 2002 were new captures (Table 9). At the Woodlot, 33% of adult turtles captured in 2001 were not recaptured in 2002, and 9% of adult turtles captured in 2002 were new captures (Table 9).

Table 7. Frequency of capture for male, female, and juvenile eastern box turtles for 2001, 2002, and over the course of the study (2001-02) captured during incidental finds and intensive searches for University of Delaware Woodlot, University of Delaware Webb Farm, Turkey Run, and White Clay Creek study sites.

	2001			2002			2001-02		
	Males	Females	Juveniles	Males	Females	Juveniles	Males	Females	Juveniles
Woodlot									
Captured 1 time	5	1	0	1	0	0	2	0	0
Captured 2 times	2	1	0	2	1	0	1	2	0
Captured 3 times	2	0	0	3	1	0	1	0	0
Captured 4 times	0	1	0	1	0	0	1	2	0
Captured 5 times	1	0	0	0	0	0	1	0	0
Captured >5 times	2	0	0	2	0	0	6	0	0
Webb Farm									
Captured 1 time	7	3	4	9	9	7	1	2	7
Captured 2 times	6	7	4	7	2	1	3	5	4
Captured 3 times	6	2	0	3	3	1	7	2	3
Captured 4 times	4	2	0	2	2	2	3	3	1
Captured 5 times	0	2	0	1	1	0	7	4	0
Captured >5 times	1	4	1	2	0	0	5	6	1

Table 7. Cont.

	2001			2002			2001-02		
	Males	Females	Juveniles	Males	Females	Juveniles	Males	Females	Juveniles
Turkey Run									
Captured 1 time	11	13	11	11	10[1]	12	6	12[1]	19
Captured 2 times	6	5[1]	6	7	9	6	10	6	4[1]
Captured 3 times	8	4	1	6	1	0	7	5	2
Captured 4 times	2	4	1	1	0	0	6	3	3
Captured 5 times	2	0	1	0	0	0	2	5	3
Captured >5 times	0	0	0	0	0	0	5	1	0
White Clay Creek									
Captured 1 time	17	11	2	16	9	2	20	12	4
Captured 2 times	11	4	0	9	5	0	13	4	0
Captured 3 times	6	1	0	4	2	1	6	4	1
Captured 4 times	4	2	0	1	1	0	3	2	0
Captured 5 times	3	2	0	3	0	0	5	1	0
Captured >5 times	5	2	0	2	0	0	11	5	0

[1]One turtle was captured in 2001 as a juvenile and was recruited into the adult population as a female in 2002. This turtle appears in both the female and juvenile columns for the total count (2001-02).

Table 8. Capture frequency of all adult eastern box turtles, radio-tagged box turtles, and adult box turtles without transmitters captured over the course of the study (2001-02) during intensive searches and incidental finds for University of Delaware Woodlot, University of Delaware Webb Farm, Turkey Run, and White Clay Creek study sites. Juveniles were excluded due to differences in capture probability.

	Adult Turtles		Radio-tagged Turtles[1]		Non-radio-tagged Turtles	
	n	%	*n*	%	*n*	%
Woodlot[2]						
Captured 1 time	2	0.13				
Captured 2 times	3	0.19				
Captured 3 times	1	0.06				
Captured 4 times	3	0.19				
Captured 5 times	1	0.06				
Captured >5 times	6	0.38				
Webb Farm						
Captured 1 time	3	0.06	0	0.00	4	0.14
Captured 2 times	8	0.17	8	0.32	5	0.18
Captured 3 times	9	0.19	4	0.16	7	0.25
Captured 4 times	6	0.13	2	0.08	5	0.18
Captured 5 times	11	0.23	3	0.12	5	0.18
Captured >5 times	11	0.23	8	0.32	2	0.07
Turkey Run						
Captured 1 time	18	0.26	4	0.17	17	0.35
Captured 2 times	16	0.24	4	0.17	12	0.25
Captured 3 times	12	0.18	6	0.25	11	0.22
Captured 4 times	9	0.13	3	0.13	6	0.12
Captured 5 times	7	0.10	4	0.17	3	0.06
Captured >5 times	6	0.09	3	0.13	0	0.00
White Clay Creek						
Captured 1 time	32	0.37	5	0.24	27	0.41
Captured 2 times	17	0.20	2	0.10	16	0.24
Captured 3 times	10	0.12	4	0.19	7	0.11
Captured 4 times	5	0.06	2	0.10	3	0.05
Captured 5 times	6	0.07	1	0.05	4	0.06
Captured >5 times	16	0.19	7	0.33	9	0.14

[1]Includes initial capture of radio-tagged turtles.
[2]Radio-tagged turtles and non-radio-tagged turtle columns were excluded since all turtles captured at the Woodlot received transmitters.

Table 9. Number of individual eastern box turtles captured on the study sites only in 2001, captured on the study sites for the first time in 2002, and captured on the study sites in both 2002 and 2001 by incidental finds and intensive searches for University of Delaware Woodlot, University of Delaware Webb Farm, Turkey Run, and White Clay Creek study sites.

	Woodlot			Webb Farm			Turkey Run			White Clay Creek		
	2001	2002	Both	2001	2002	Both	2001	2002	Both	2001	2002	Both
All Turtles	5	1	10	12	11	41	36[1]	22	39	36[1]	21[1]	34
Adults	5	1	10	7	4	37	24[1]	8	32	34[1]	18[1]	34
Juveniles	0	0	0	5	7	5	12	10	8	2	3	0
Males	3	0	9	2	2	22	12[1]	7	17	23[1]	12[1]	23
Females	2	1	1	5	2	15	11[1]	5	16	11[1]	6[1]	11

[1]Of the turtles captured on the study sites, a few were captured off the study sites in either the preceding year or the following year: 1 male and 1 female at Turkey Run were captured on the study site in 2001 and captured off the study site in 2002; 3 males and 1 female at White Clay Creek were captured on the study site in 2001 and captured off the study site in 2002; 2 males and 2 females at White Clay Creek were captured off the study site in 2001 and then captured on the study site in 2002.

Catch Per Unit Effort

Season and study site did not interact to affect CPUE for all captures ($F_{6,11}$ = 0.84, P = 0.565) or for adults ($F_{6,11}$ = 0.87, P = 0.548). Additionally, CPUE did not differ among seasons for all turtles captured ($F_{2,11}$ = 1.75, P = 0.218) or for adults ($F_{2,11}$ = 1.38, P = 0.291) but did differ among study sites for all turtles captured ($F_{3,11}$ = 5.71, P = 0.013) and for adults ($F_{3,11}$ = 6.34, P = 0.009; Table 10). For adults, CPUE of the Woodlot and Turkey Run was less than White Clay Creek; however, Webb Farm was intermediate and did not differ from either Turkey Run or White Clay Creek (Table 10). For all turtles, CPUE of the Woodlot was less than Webb Farm, Turkey Run, and White Clay Creek study sites (Table 10).

Survival

We recorded 15 human induced mortalities, 14 natural mortalities and 1 unnatural mortality of 8 radio-tagged, 6 marked, and 16 unmarked turtles on the study sites or in associated areas frequented by radio-tagged turtles (Table 11). Of the marked and unmarked turtle mortalities, 13 were human induced, 8 were natural, and 1 was unnatural, whereas of the radio-tagged turtles, 6 were natural and 2 were human induced mortalities. From all the study sties, 16 male (Woodlot = 5, Webb Farm = 1, Turkey Run = 4, White Clay Creek = 3, Turkey Run/White Clay Creek associated fields = 3) and 6 female (Woodlot = 0, Webb Farm = 1, Turkey Run = 3, White Clay Creek = 1, Turkey Run/ White Clay Creek associated fields = 1) mortalities were documented.

Radio telemetry allowed us to determine cause-specific mortality in 6 instances. We documented 3 deaths from exposure to excessive heat or freezing conditions. In the

Table 10. Catch-per-unit-effort (CPUE) for adult and all eastern box turtles captured over 6 seasons in 2001 and 2002 at the University of Delaware Woodlot, University of Delaware Webb Farm, Turkey Run, and White Clay Creek study sites.

		Adults			All Turtles		
	n	CPUE	SE	LSD[1]	CPUE	SE	LSD[1]
Woodlot	6	0.6415	0.1084	C	0.6415	0.1084	B
Webb Farm	6	1.2256	0.1542	AB	1.3862	0.1829	A
Turkey Run	6	0.8809	0.1283	CB	1.1144	0.1778	A
White Clay Creek	6	1.3335	0.1355	A	1.3476	0.1338	A

[1]Least significant difference: values with the same letter are not significantly different.

Table 11. Summary of eastern box turtle mortalities recorded at University of Delaware Woodlot (WL), University of Delaware Webb Farm (WF), Turkey Run (TR), and White Clay Creek (WC) study sites and associated areas in 2001 and 2002.

Year	Area	Cause	Sex[1]	Turtle History on Study Site
2001	WL	Natural[2]	m	radio-tagged
2001	WF	Natural[3]	u	not marked
2001	TR	Natural[3]	m	not marked
2001	TR	Mowing	j	not marked
2001	TR	Mowing	j	marked
2001	WL – associated field	Mowing	m	radio-tagged
2001	TR/WC – associated fields	Mowing	m	not marked
2001	TR/WC – associated fields	Mowing	m	not marked
2001	TR/WC – associated fields	Natural[3]	f	not marked
2001	TR/WC – associated fields	Mowing	m	not marked
2001	WC – park road	Automobile	m	not marked
2001	WC – park road	Automobile	m	not marked
2002	WL	Natural[3]	m	radio-tagged
2002	WL	Natural[3]	m	radio-tagged
2002	WF	Natural[3]	f	marked
2002	WF	Natural[4]	m	radio-tagged
2002	TR	Mowing	f	not marked
2002	TR	Natural[3]	m	marked
2002	TR	Natural[3]	f	marked
2002	TR	Natural[3]	m	radio-tagged
2002	TR	Natural[4]	m	radio-tagged
2002	WC	Natural[3]	m	marked
2002	WL – associated field	Mowing	m	radio-tagged
2002	WF – associated field	Unnatural[5]	j	not marked
2002	TR – associated woodland	Brush removal	f	not marked
2002	TR – associated woodland	Brush removal	j	not marked
2002	TR/WC – associated fields	Mowing	u	not marked
2002	TR/WC – associated fields	Mowing	u	not marked
2002	TR/WC – associated fields	Mowing	j	marked
2002	WC – associated woodland	Natural[3]	f	not marked

[1]Sex: m = male, f = female, j = juvenile, u = unknown.
[2]Turtle was found outside its hibernacula, presumably removed by a predator and died from exposure.
[3]Natural cause of unknown origin. In most cases only an empty carapace was found.
[4]Turtle was found dead upside-down and presumably died from heat exposure.
[5]The carapace of this turtle was found crushed in a cattle pasture. Exact cause of death could not be determined but was assumed that a cow stepped on it.

winter of 2002, 1 radio-tagged turtle at the Woodlot was found dead completely closed up in its shell about 1 m from its hibernaculum on 7 January 2002. When I checked on this turtle 2 days later, it was found turned upside-down. I suspected a predator flipped it over and possibly removed it from its hibernaculum exposing it to freezing conditions. During the active season in 2002 at both Webb Farm and Turkey Run, we found 1 radio-tagged turtle upside-down. Posture of these dead turtles made it appear as though they were trying to right themselves before they died. Both deaths occurred in late July to mid-August 2002, and I believe these turtles died from exposure to excessive heat. On 28 May 2002, a radio-tagged turtle from the Woodlot fell down a hole approximately 30 cm in diameter and 1 m deep. This hole was a straight vertical drop that appeared to be connected to an animal burrow that ran parallel to the ground. The apron of a woodchuck (*Marmota monax*) burrow was in close vicinity; however, the hole the turtle fell down had no apron, and it was unknown whether the tunnel at the bottom of the hole was connected to the nearby woodchuck burrow. This turtle remained in the hole for 40 days, and on 7 July 2002, I decided to dig him out since I suspected he was dead. However, he was still alive, although he was emaciated, and his eyes were swollen shut. I released him near the entrance; but he moved no more than 70 m after being removed from the hole and died on 11 September 2002, presumably unable to recover from his weakened state. Additionally, 1 radio-tagged turtle in 2001 and 1 radio-tagged turtle in 2002 were killed by mowing equipment in an alfalfa field, which was adjacent to the eastern edge of the Woodlot. This field was mowed to a height of 5 cm.

Of our radio-tagged turtles, we only documented mortalities in males. Additionally, we documented few mortalities of radio-tagged turtles on Webb Farm (n = 1), Turkey Run (n =2), and White Clay Creek (n = 0); however, 28% of the radio-tagged turtles (n = 5) at the Woodlot died during this study. I used these data to estimate survival rate at each study site. I estimated a combined annual survival rate of 0.98 (SE = 0.017) and a combined seasonal survival rate of 0.99 for Webb Farm, Turkey Run, and White Clay Creek. I calculated survival rate of the Woodlot separately since a large proportion of turtles known on the study site died over the course of the study. I estimated an annual survival rate of 0.83 (SE = 0.091) and seasonal survival rate at 0.94 for this study site.

I was unable to determine causes of the 8 natural mortalities documented in marked and unmarked turtles; however, I was able to determine an unnatural cause of mortality and 9 human induced mortalities in marked and unmarked turtles. Near Webb Farm, a juvenile's carapace was found crushed in the cow pasture bordering the western edge of the study site in 2002. Since no mowing occurred in this pasture, I assumed a cow stepped on it. After examining the shell, I concluded this turtle was stepped on while it was alive, as dried flesh connected broken pieces of shell.

Mortalities of marked and unmarked turtles from mowing resulted from either being hit by mower blades or run over by the tractor's tire. While mowing mortalities occurred primarily off the study sites in associated areas frequented by radio-tagged turtles, Turkey Run was the only study site in which mowing occurred within the boundaries. Two juvenile mortalities in 2001 and 1 adult mortality in 2002 occurred due to mowing at Turkey Run (Table 11). In associated areas frequented by radio-tagged turtles to the north and northeast of White Clay Creek and to the south and west of Turkey Run, we documented 1 juvenile and 5 adult mortalities due to mowing of fields (Table 11). These areas were mowed at a height of 5-8 cm, whereas mowing at Turkey Run was at a height of 15 cm, which was high enough to mow over turtles without harm. On several occasions, I observed radio-tagged turtles along the edge of the field immediately before mowing at Turkey Run. After mowing, I checked on these turtles again, and they were unharmed and had moved out of the fields into the edge of the woods. I also documented that turtles were present in the grass during mowing at this height but were unharmed by evidence of damaged transmitters. Mower blades cut transmitter wires in half and in 2 instances knocked transmitters off the turtles' carapace without injury to the turtles. Additionally, clearing of brush with large mowing machinery south of Turkey Run resulted in 1 juvenile and 1 adult death in 2002.

Cars were the other cause of human induced mortality documented off the study site for non-radio-tagged turtles. I documented 2 male turtles killed by cars on Thompson's Station Road, which borders White Clay Creek study site. However, it should be noted that these turtles were unmarked and approximately 275 m from the western edge of the study site. I documented radio-tagged and marked turtles crossing both Thompson's Station Road along White Clay Creek study site and Corner Ketch Road along Turkey Run. These turtles were mostly females that probably crossed the roads to find nesting habitat.

Immigration/Emigration

Using radio-telemetry, I was able to observe temporary and permanent immigration and emigration at the study sites. The Woodlot and Webb Farm experienced little temporary emigration and no permanent emigration, whereas Turkey Run and White Clay Creek experienced the most temporary immigration and emigration and some permanent emigration. At the Woodlot, 14 of 18 (78%) radio-tagged turtles remained within the study site boundaries, as did 20 of 25 (80%) turtles at Webb Farm. I did not document any permanent immigration for either the Woodlot or Webb Farm. At Turkey Run only 13 of 24 (54%) radio-tagged turtles remained on the study site, and at White Clay Creek only 2 of 22 (9%) turtles remained on the study site. I also observed permanent to semi-permanent emigration from these study sites. At White Clay Creek, 5 radio-tagged turtles initially captured on the study site, emigrated off the site and never returned, while 1 radio-tagged turtle from Turkey Run and 1 from White Clay Creek, only returned to the study site to hibernate. Additionally, I observed temporary immigration in 1 radio-tagged female whose home range was over 1 km away and moved to Turkey Run each year to nest. Female turtles from White Clay Creek emigrated to nearby fields during the nesting season, and 1 radio-tagged and 2 marked turtles immigrated to Turkey Run.

The occurrence of transient box turtles at our study sites was rarely observed. I observed transient behavior in only 1 radio-tagged turtle. This turtle was originally captured on the study site on 5 May 2001 and remained in a small area; then around 6 August 2001 he began traveling northwest off the study site. On 18 August 2001, he turned back toward the study site. Between 20 August and 19 September 2001, he traveled across the study site and continued moving until he hibernated 440 m southeast of the study site. Following hibernation, the turtle continued to travel away from the study site. This turtle then hibernated again at a straight line distance of 900 m from his original capture location. Additionally, several radio-tagged turtles were originally captured on the study site only to leave and apparently establish a home range some distance from the study site, while another female stayed near her nesting site for most of the active season only to return near her original site of capture on the study site to hibernate in September. Without the aid of radio telemetry, such turtles found once and never seen again could be mistaken for transient turtles rather than temporary emigration or spatial and temporal shifting of home ranges. One radio-tagged turtle originally captured in the middle of White Clay Creek occupied a home range on the outside edge of the study site but never reentered.

Sex Ratio

Sex ratios did not differ among years within study areas (Table 12), and did not differ among study sites for all captures ($\chi^2_3 = 5.66$, $P = 0.129$) or intensive searches ($\chi^2_3 = 1.73$, $P = 0.631$). Sex ratios were not balanced at some sites. Webb Farm and Turkey Run had even sex ratios, whereas the Woodlot and White Clay Creek had male-biased sex ratios (Table 13).

Table 12. Sex ratio of eastern box turtles in 2001 and 2002 for all captures and intensive searches at the University of Delaware Woodlot, University of Delaware Webb Farm, Turkey Run, and White Clay Creek study sites.

	2001		2002			
	M	F	M	F	χ^2_1	*P*
All Captures						
Woodlot	12	3	9	2	0.01	0.907
Webb Farm	24	20	24	17	0.14	0.711
Turkey Run	29	27	24	20	0.08	0.784
White Clay Creek	46	22	35	17	<0.01	0.969
Intensive Searches						
Woodlot	10	3	9	2	0.09	0.768
Webb Farm	19	17	15	10	0.31	0.576
Turkey Run	24	20	17	14	<0.01	0.980
White Clay Creek	27	16	24	16	0.07	0.794

Table 13. Sex ratio of eastern box turtles from all captures and intensive searches over the course of the study (2001-02) for University of Delaware Woodlot, University of Delaware Webb Farm, Turkey Run, and White Clay Creek study sites.

	Males	Females	Sex Ratio[1]	χ^2_1	*P*
All Captures					
Woodlot	12	4	3.00	4.00	0.046
Webb Farm	26	22	1.18	0.33	0.564
Turkey Run	36	32	1.13	0.24	0.628
White Clay Creek	58	28	2.07	10.47	0.001
Intensive Searches					
Woodlot	11	4	2.75	3.27	0.071
Webb Farm	23	18	1.28	0.61	0.435
Turkey Run	33	25	1.32	1.10	0.294
White Clay Creek	37	23	1.61	3.27	0.071

[1]Number of males per female.

Aging Technique

Counts were precise across scutes for every turtle with 1-8 annuli (Figure 5). For turtles with 9-10 annuli, counts were precise across scutes in 85% of the turtles, and for turtles with 11 annuli, 60% of the turtles had a precise count of annuli across scutes (Figure 5). For turtles with a mean count of 12-13 annuli, counts of annuli across scutes were precise for 46% of the turtles, and for turtles with 14-20 annuli, annuli counts across scutes were imprecise about 80% of the time (Figure 5). Subsequent year counts for turtles with 1-10 mean annuli increased by 1 year for each scute for most turtles (Table 14). For turtles with 11-12 annuli, subsequent year counts showed less accuracy, whereas turtles with 13-20 annuli did not demonstrate accuracy with years elapsed for each scute (Table 14). For 29 turtles, annuli counted in 2002 were less than the number of annuli counted in 2001, which likely was due to imprecision in counting technique rather than a physical loss of annuli (Table 14). Additionally, turtles with a carapace that showed signs of wear and were presumably very old usually had only 12-13 countable annuli. Therefore, I concluded turtles with 1-10 annuli could be aged accurately by counting annuli on the costal scutes of the carapace, while age determination of turtles with 11 annuli was less accurate, and I could not determine ages of turtles with ≥12 annuli.

Age Structure

We captured no juveniles at the Woodlot, though 1 turtle captured in 2001 was estimated at 10 years of age. Juveniles accounted for 6%, 25%, and 32% of the all turtles captured at White Clay Creek, Webb Farm, and Turkey Run, respectively (Table 5). Intensive searches produced slightly fewer juveniles than all captures combined (Table

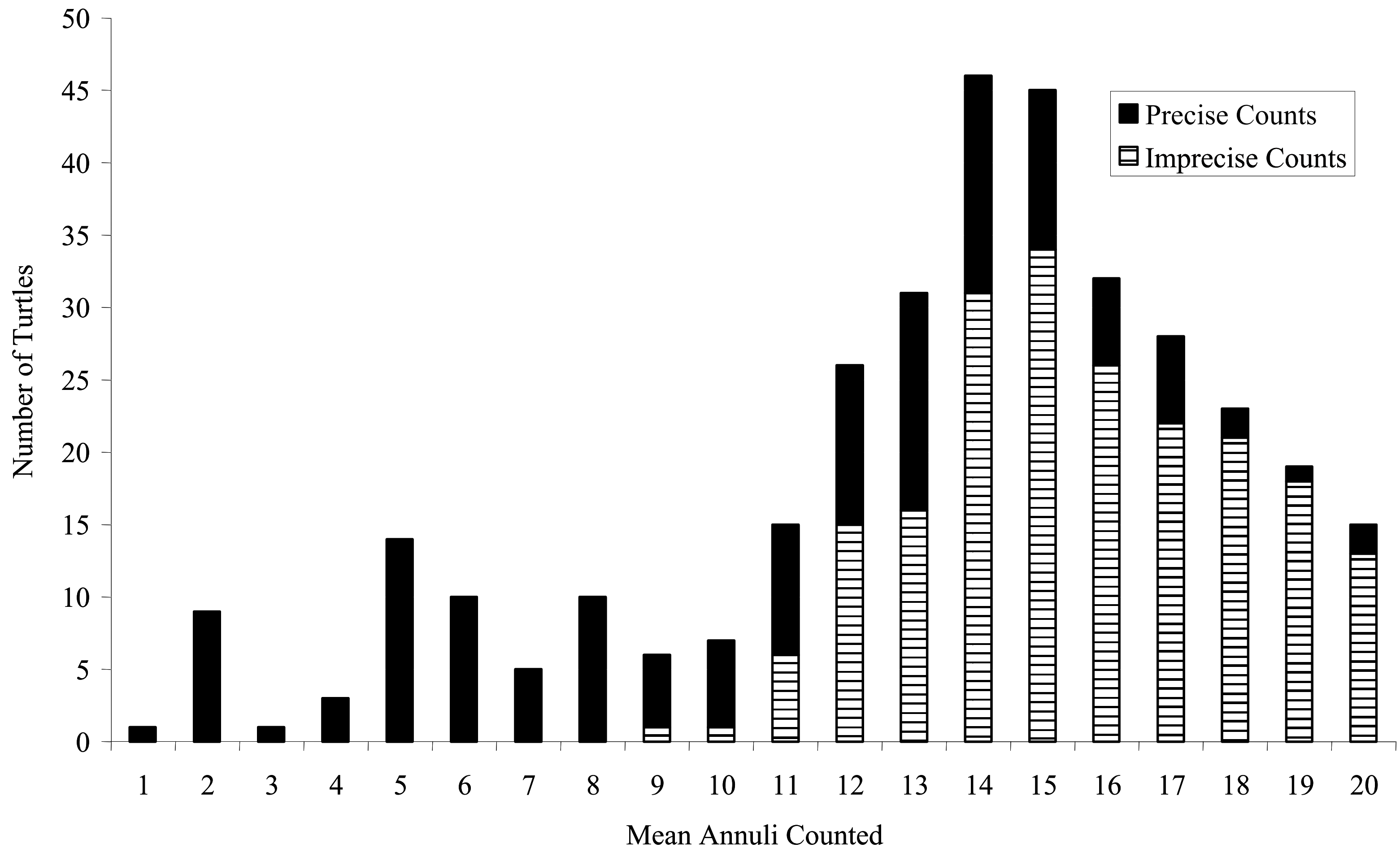

Figure 5. Number of eastern box turtles per mean annuli counted on the first, second, and third pair of costal scutes of the carapace for precise and imprecise annuli counts across scutes.

Table 14. Mean annuli added after 1 year for eastern box turtles at the University of Delaware Woodlot, University of Delaware Webb Farm, Turkey Run and White Clay Creek study sites. Shaded area represents the number of turtles whose annuli increased by 1 annulus after 1 year elapsed.

Mean Annuli	Mean Annuli Added in 2002						
In 2001	-3	-2	-1	0	+1	+2	+3
1							
2							
3							
4					1		
5				2	1		
6					2		
7					1		
8				1	1	1	1
9				1			
10					1		
11		1		2			
12			1	2	2		
13		1		6	2	1	
14		2	2	6	6		
15	1	1	5	4	3	1	
16			4	5	2		1
17	1		3	3	1		
18		1	2	2			
19	1		2	1	4	1	
20			1	2			

6). Additionally, we captured juveniles less frequently than adults (Table 7). At Webb Farm, Turkey Run, and White Clay Creek, we captured most juvenile turtles <4 times (Table 7). Recapture rate per year was lower for juveniles than for adults (Table 9). At Webb Farm, 50% of juveniles captured in 2001 were not recaptured in 2002 and 58% of juveniles captured in 2002 were new captures (Table 9). At Turkey Run, 60% of juveniles captured in 2001 were not recaptured in 2002 and 56% of juveniles captured in 2002 were new captures (Table 9). At White Clay Creek, we did not recapture any juveniles in 2002 (Table 9). We captured juveniles from all ages with greatest abundances occurring at age 1 and 5 (Figure 6). At Turkey Run, all ages between 1-9 were represented with age 5 containing the most individuals (Figure 6). Age 2, 4, and 9 were not represented at Webb Farm (Figure 6). White Clay Creek was only represented by age 4, 5, 7, and 9. Recruitment was greater in 2001 than in 2002, with 9 turtles recruited in 2001 and 3 turtles recruited in 2002 for all study areas (Figure 6).

Population Abundance Estimates

Data from all captures and intensive searches met the assumptions of equal capture and survival probability except at White Clay Creek study site where survival probabilities were not equal for all captures ($\chi^2_{10} = 27.10$; $P = 0.003$; Table 15). For mark-recapture data collected from all captures, the most parsimonious model for the Woodlot and Webb Farm was Model 1 (Table 4), the least restrictive candidate model, which allowed capture rate to vary by sex and over time (Table 16). For Turkey Run and White Clay Creek, the most parsimonious model was Model 2 (Table 4) in which capture rate varied over time (Table 16). The most parsimonious models for mark-

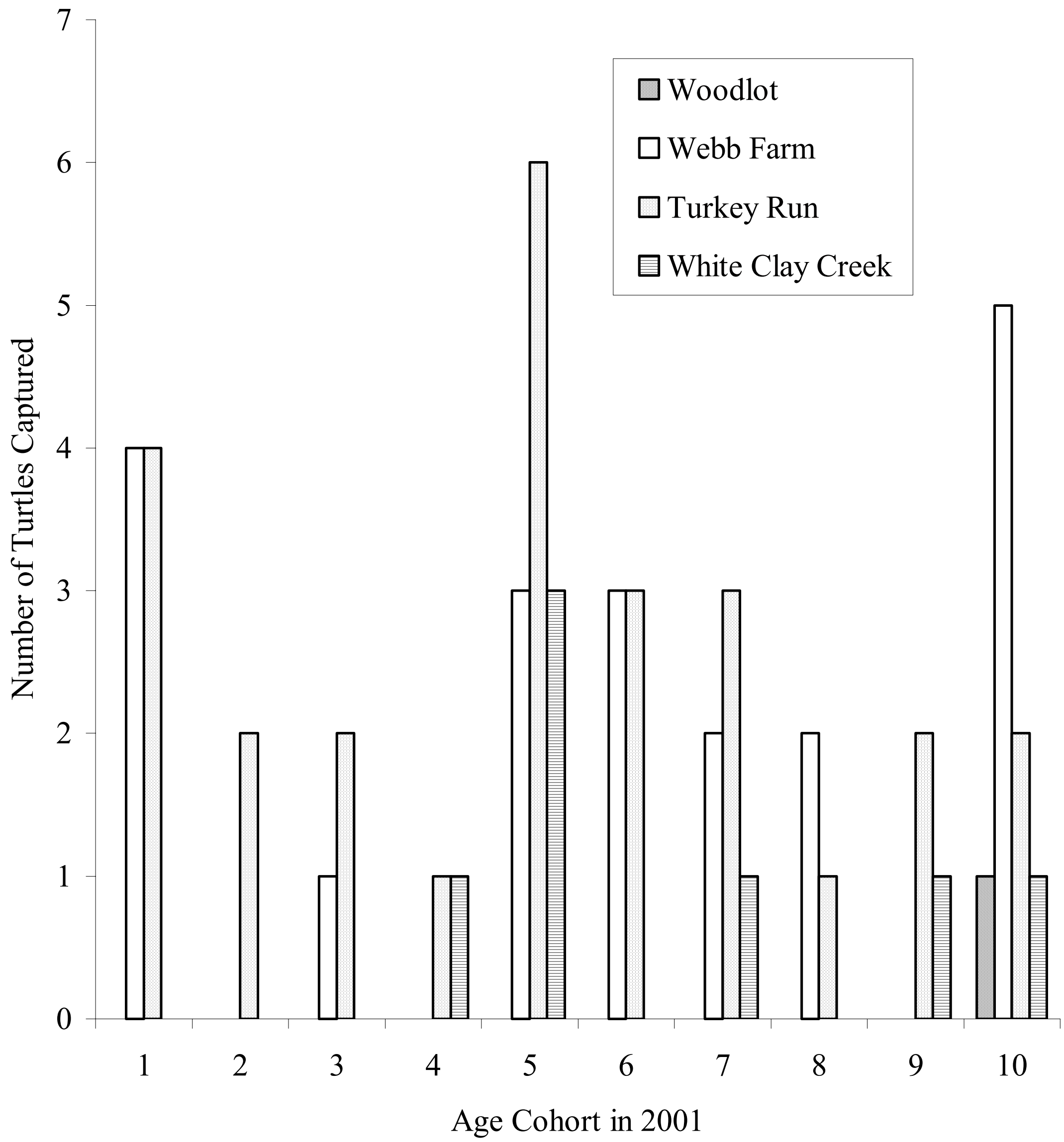

Figure 6. Number of juvenile eastern box turtles captured in each age cohort during 2001 and 2002 with all ages standardized to 2001 ages for the University of Delaware Woodlot, University of Delaware Webb Farm, Turkey Run, and White Clay Creek study sites. Since turtles captured represents true abundance and not density, direct comparison among study sites is not valid. Age cohort 9 represent turtles recruited into the adult population in 2002 and age cohort 10 were recruited into the population in 2001.

Table 15. Results from testing the assumptions of equal capture probability (TEST 2) and equal survival probability (TEST 3) in program RELEASE of for all captures and intensive searches for University of Delaware Woodlot, University of Delaware Webb Farm, Turkey Run, and White Clay Creek study sites.

	Capture Probability			Survival Probability		
	χ^2	*df*	*P*	χ^2	*df*	*P*
All Captures						
Woodlot	0.00	3	1.000	0.71	3	0.871
Webb Farm	2.19	6	0.902	1.30	8	0.996
Turkey Run	0.26	6	1.000	3.23	10	0.976
White Clay Creek	2.58	6	0.859	27.10	10	0.003
Intensive Searches						
Woodlot	1.79	3	0.617	1.42	2	0.493
Webb Farm	2.58	4	0.631	3.62	7	0.822
Turkey Run	7.17	6	0.305	2.18	7	0.949
White Clay Creek	4.90	6	0.556	10.27	10	0.417

Table 16. Corrected Akaike's Information Criterion (AICc), AICc weight, and model deviance values for candidate models of the Jolly-Seber model in program MARK for all captures and intensive searches for the University of Delaware Woodlot, University of Delaware Webb Farm, Turkey Run, and White Clay Creek study sites. The lowest AICc value (denoted with an asterisk) was used to determine the most parsimonious model, which was used to estimate population densities.

	Woodlot			Webb Farm		
	AICc	AICc Weight	Deviance	AICc	AICc Weight	Deviance
All Captures						
Model 1[1]	94.43*	0.95	47.91	304.51*	0.85	104.70
Model 2[2]	100.51	0.05	53.99	307.99	0.15	108.18
Model 3[3]	119.80	0.00	66.25	329.66	0.00	129.85
Model 4[4]	122.08	0.00	75.56	330.02	0.00	130.21
Intensive Searches						
Model 1[1]	122.68	0.00	83.41	202.54*	1.00	67.11
Model 2[2]	93.31*	0.99	56.30	224.19	0.00	73.07
Model 3[3]	109.11	0.00	64.85	271.84	0.00	129.99
Model 4[4]	103.78	0.01	66.77	271.11	0.00	131.45

Table 16. Cont.

	Turkey Run			White Clay Creek		
	AICc	AICc Weight	Deviance	AICc	AICc Weight	Deviance
All Captures						
Model 1[1]	370.25	0.14	104.92	457.14	0.01	167.752
Model 2[2]	366.68*	0.86	115.52	446.97*	0.99	171.244
Model 3[3]	410.00	0.00	169.72	477.68	0.00	212.638
Model 4[4]	410.53	0.00	168.15	479.13	0.00	211.999
Intensive Searches						
Model 1[1]	256.13	0.00	90.37	311.86	0.00	131.363
Model 2[2]	242.56*	0.99	92.38	297.86*	0.99	132.183
Model 3[3]	285.29	0.00	144.34	328.88	0.00	172.149
Model 4[4]	283.63	0.00	144.86	326.79	0.00	172.201

[1]Model 1: Capture rate varying by sex and over time
[2]Model 2: Capture rate varying by time
[3]Model 3: Capture rate varying by sex
[4]Model 4: Capture rate constant

recapture data collected on intensive searches were the same as for all captures except at the Woodlot where Model 2 was the best model (Table 16).

Population Density Estimates

Density estimates from the immigration/emigration JHE model ranged from 0.59-2.21, 0.22-1.53, and 0.81-3.62 turtles/ha for males, females, and all adults, respectively. Density estimates did not differ between years for each study site for males, females, or adults except at the Woodlot where density estimates for males in 2002 were lower than in 2001 (Table 17). Among study sites, densities did not differ except for the Woodlot where densities for males, females, and all adults in 2001 and 2002 were lower than the other study sites (Table 17). Additionally, male and female density estimates revealed a trend similar to calculated sex ratios. Male and female densities did not differ for Webb Farm and Turkey Run in 2001 and 2002; however, male densities were greater than female densities for the Woodlot and White Clay Creek except for the Woodlot in 2002 where male and female density estimates did not differ (Table 17).

Density estimates from the Jolly-Seber model ranged from 0.61-5.53, 0.22-2.65, and 0.83-8.81turtles/ha for males, females, and all adults, respectively (Table 18). Density estimates for all captures did not differ from density estimates for intensive searches for males, females, or all adults at each study site except for females at Webb Farm and for males and all adults at White Clay Creek where densities were lower for intensive searches (Table 18). For all captures and intensive searches, the Woodlot had the lowest density estimates of 0.52-0.79, 0.22-0.22, and 0.72-0.98 turtles/ha for males, females, and all adults, respectively (Table 18). Webb Farm and Turkey Run had similar

Table 17. Density estimates per ha derived from program NOREMARK using the immigration/emigration joint hypergeometric maximum likelihood estimator (JHE) model for adult, male, and female eastern box turtles captured during intensive searches in 2001 and 2002 for the University of Delaware Woodlot, University of Delaware Webb Farm, Turkey Run, and White Clay Creek study sites. Point estimates and 95% confidence intervals represent estimated population density for each study site over the sampling period (late May to mid-September, 2001 and 2002).

	2001		2002	
	Point Estimate	95% CI	Point Estimate	95% CI
Adults				
Woodlot	0.86	0.86-0.93	0.81	0.81-0.86
Webb Farm	3.04	2.57-3.69	2.30	2.12-2.64
Turkey Run	3.27	2.59-4.37	3.20	2.44-4.56
White Clay Creek	3.53	2.93-4.44	3.62	2.76-4.99
Males				
Woodlot	0.65	0.65-0.71	0.59	0.59-0.64
Webb Farm	1.75	1.23-2.88	1.11	1.01-1.35
Turkey Run	1.74	1.27-2.62	1.46	1.02-2.47
White Clay Creek	2.21	1.71-3.03	2.12	1.46-3.37
Females				
Woodlot	0.22	0.22-0.33	0.27	0.27-0.78
Webb Farm	1.47	1.29-1.78	1.20	1.20-1.35
Turkey Run	1.53	1.09-2.35	1.39	1.02-2.21
White Clay Creek	1.15	1.15-1.59	1.23	0.88-1.94

Table 18. Density estimates per ha calculated using the Jolly-Seber model in program MARK for male, female, and all adult eastern box turtles captured on all captures (incidental finds plus intensive searches) and during intensive searches only for the University of Delaware Woodlot, University of Delaware Webb Farm, Turkey Run, and White Clay Creek study sites for 2001-02. Point estimates and 95% confidence intervals represents estimated population density for each study site at the beginning of the study in 2001.

	Males			Females			Adults		
	Point Estimate	SE	95% CI	Point Estimate	SE	95% CI	Point Estimate	SE	95% CI
All Captures									
Woodlot[1]	0.66	0.052	0.58-0.79	0.22	0.000	0.22-0.22	0.87	0.052	0.78-0.98
Webb Farm[1]	2.39	0.000	2.40-2.40	2.02	0.081	1.89-2.21	4.41	0.081	4.25-4.57
Turkey Run[2]	2.65	0.131	2.43-2.95	2.35	0.124	2.15-2.63	5.10	0.179	4.67-5.37
White Clay Creek[2]	5.53	0.234	5.10-6.02	2.65	0.154	2.38-2.99	8.18	0.280	7.65-8.75
Intensive Searches									
Woodlot[2]	0.61	0.058	0.52-0.75	0.22	0.000	0.22-0.22	0.83	0.058	0.72-0.95
Webb Farm[1]	2.26	0.173	1.98-2.67	1.65	0.000	1.66-1.66	3.91	0.173	3.59-4.27
Turkey Run[2]	2.82	0.279	2.37-3.49	2.13	0.232	1.76-2.69	4.96	0.363	4.29-5.72
White Clay Creek[2]	3.59	0.217	3.21-4.06	2.22	0.164	1.93-2.58	5.81	0.272	5.30-6.37

[1]Model 1: Capture rate varying by sex and over time
[2]Model 2: Capture rate varying by time

densities ranging from 1.98-3.49, 1.66-2.69, and 3.59-5.72 for males, females, and all adults, respectively (Table 18). White Clay Creek had the greatest density estimates for all captures for males and all adults; however, densities did not differ from Turkey Run for females for all captures or for males, females, and all adults for intensive searches (Table 18). Males had a greater density than females for the Woodlot, Webb Farm, and Turkey Run for all captures and intensive searches (Table 18).

Density estimates for 2001 from the JHE model for males, females, and all adults did not differ from Jolly-Seber estimates from intensive searches except for White Clay Creek where the Jolly-Seber estimate for all adults was greater than the JHE estimate. For all captures, the Jolly Seber model produced greater estimates for males at White Clay Creek, for females at Webb Farm and White Clay Creek, and for all adults at Webb Farm, Turkey Run, and White Clay Creek.

Long-term Data

The Woodlot (1965-2002)

From 1965-2002, 213 turtles were captured and marked in the Woodlot. By the end of this study in 2002, only 13 adult turtles were known to be alive in the Woodlot. Within the last 4 years (1999-2002), 24 adult turtles were captured in the Woodlot, of which 7 died and 9 were new captures (Table 19). Four turtles captured in 1999 were not recaptured during this study (Table 19). Seven of the 13 remaining turtles in 2002 were first captured within the last 4 years (1999-2002), whereas 1 turtle was first captured in

Table 19. Capture history for eastern box turtles captured between 1999-2002 at the University of Delaware Woodlot.

Turtle No.	Year First Captured	Year Last Seen	Status at End of Study[1]
0001	1966	2002	Alive
0002	1995	2001	Dead
0003	1999	2002	Alive
0004	1997	2002	Alive
0005	1966	2002	Alive
0006	1999	2002	Alive
0007	1977	2001	Dead
0008	1990	2000	Dead
0009	1965	2000	Dead
0010	1965	2002	Alive
0011	1999	1999	Unknown
0012	1965	2002	Dead
0013	1984	2000	Unknown
0014	1999	2002	Alive
0015	1977	1999	Unknown
0016	1965	2002	Alive
0017	1965	2002	Alive
0018	1994	1999	Unknown
0500	2000	2002	Alive
0501	2001	2002	Alive
0502	1995	2002	Dead
0504	2001	2002	Alive
0505	2001	2002	Dead
0508	2002	2002	Alive

[1]Alive denotes turtles monitored via radio telemetry until the end of the study, dead denotes turtles mortalities documented in the year last seen, unknown denotes turtles captured in year last seen but not fixed with a radio transmitter.

1997, 2 turtles were first captured in 1966, and 3 turtles were first captured in 1965 (Table 19).

Population estimates for 1965-2002 demonstrate that the box turtle population at the Woodlot has declined from approximately 100 turtles (5.4 turtles/ha) in 1968 to approximately 10-17 turtles (0.54-0.92 turtles/ha) in 2001 (Figure 7). Point estimates for 2001 from the Jolly-Seber full model (n = 17.2), the modified Jolly-Seber full model (n = 17.2), and the Jolly-Dickson full model (n = 17.4) from all captures at the Woodlot are similar to the total number of adult turtles captured (n = 18) over the course of this study (Table 20). Only the Jolly-Dickson full model provided an estimate for 2002, which was 14.0 turtles and was similar to the number of adult turtles known (n = 13) alive at the end of this study (Table 20). Estimates from a second data set, which did not include captures recorded by turtle researchers from this study or Niederriter (2000), had point estimates of 9.6, 8.4, and 15.4 turtles in 2001 for the Jolly-Seber full model, the modified Jolly-Seber full model, and the Jolly-Dickson full model, respectively (Table 21). For 2002, the Jolly-Dickson full model provided a point estimate of 4.0 turtles (Table 21).

Sex ratio pooled over 5 years differed among periods ($\chi^2_7 = 4.25$, $P = 0.039$). Although the first period (1965-1969) was marginally male biased, a male-biased sex ratio was evident beginning in the period 1970-1974 (Table 22). This male-biased sex ratio steadily increased to a peak of 3.00 males to females during 1990-1999 (Table 22), which was equal to the sex ratio determined for 2001-2002 (Table 13); however, over the period 2000-2002, the sex ratio was 2.50 males to females (Table 22).

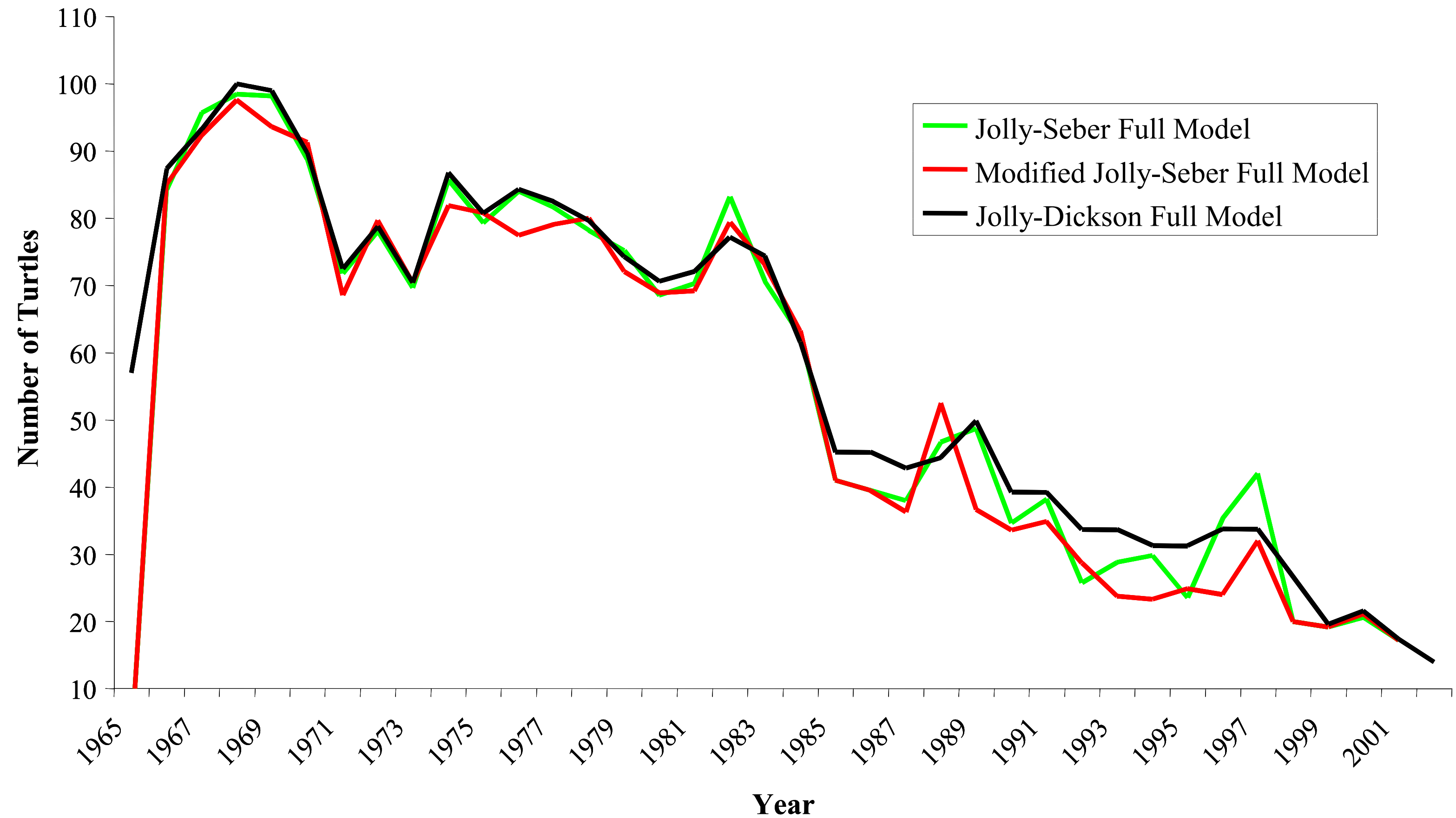

Figure 7. Population abundance for all captures of eastern box turtles recorded from 1965 to 2002 for the University of Delaware Woodlot study site using the Jolly-Seber full model, the modified Jolly-Seber full model, and the Jolly-Dickson model.

Table 20. Population abundance estimates for all captures of eastern box turtles recorded from 1965-2002 for University of Delaware Woodlot study site using the Jolly-Seber full model, the modified Jolly-Seber full model, and the Jolly-Dickson full model from program POPAN.

	Jolly-Seber Full Model			Modified Jolly-Seber Model			Jolly-Dickson Full Model		
Year	Point Estimate	SE	95% CI	Point Estimate	SE	95% CI	Point Estimate	SE	95% CI
1965	0.0[1]	0.00[1]	0.00[1]	0.0[1]	0.00[1]	0.00[1]	57.0	6.40	45.8-71.0
1966	84.3	7.94	70.2-101.4	85.1	8.27	70.4-102.9	87.4	11.12	68.2-112.0
1967	95.7	5.95	84.8-108.2	92.4	4.97	83.1-102.7	93.3	8.49	78.1-111.5
1968	98.5	11.53	78.4-123.8	97.6	11.71	77.2-123.4	100.0	10.37	81.7-122.5
1969	98.2	10.09	80.3-120.1	93.6	8.82	77.8-112.5	99.0	13.37	76.1-128.2
1970	88.8	9.43	72.2-109.3	91.3	10.70	72.6-114.8	89.8	11.93	69.3-116.4
1971	71.8	5.39	62.0-83.2	68.6	4.11	61.0-77.1	72.5	8.48	57.7-91.1
1972	78.1	8.62	63.0-96.9	79.7	9.54	63.1-100.7	78.8	9.89	61.7-100.7
1973	69.7	6.22	58.5-83.0	70.4	6.67	58.5-84.7	70.4	8.94	54.9-90.2
1974	85.7	8.52	70.6-104.1	81.9	7.42	68.6-97.8	86.8	10.51	68.5-110.0
1975	79.3	7.92	65.2-96.4	80.8	8.78	65.3-99.9	80.7	10.29	62.9-103.5
1976	84.0	9.14	67.9-103.9	77.5	6.82	65.2-92.1	84.3	10.09	66.7-106.5
1977	81.6	8.05	67.3-99.0	79.1	7.40	65.9-95.0	82.5	10.78	63.9-106.5
1978	78.2	11.81	58.3-105.0	80.0	13.34	57.8-110.7	79.7	11.42	60.3-105.4
1979	75.2	6.66	63.2-89.4	72.1	5.59	56.7-91.7	74.3	8.75	59.0-93.5
1980	68.5	6.59	56.8-82.7	68.9	6.92	56.6-83.8	70.6	9.49	54.3-91.8
1981	70.3	4.88	61.4-80.5	69.2	4.57	60.8-78.8	72.1	8.48	57.3-90.7
1982	83.2	13.31	60.9-113.6	79.4	12.19	58.9-107.1	77.2	8.81	61.8-96.5
1983	70.6	14.58	47.3-105.4	73.1	16.61	47.1-113.5	74.4	16.63	48.3-114.7
1984	62.6	9.87	46.0-85.1	63.3	10.86	45.3-88.4	61.6	11.41	43.0-88.3

Table 20. Cont.

Year	Jolly-Seber Full Model			Modified Jolly-Seber Model			Jolly-Dickson Full Model		
	Point Estimate	SE	95% CI	Point Estimate	SE	95% CI	Point Estimate	SE	95% CI
1985	41.0[2]	7.99[2]	28.1-59.9	41.0[2]	7.99[2]	28.1-59.9	45.2	10.97	28.3-72.2
1986	39.5[2]	27.21[2]	11.6-134.0	39.5[2]	27.21[2]	11.6-134.0	45.2	10.96	28.3-72.2
1987	38.0	7.50	25.9-55.7	36.3	6.79	25.2-52.2	42.8	10.27	26.9-68.1
1988	46.7	19.45	21.3-102.3	52.5	28.32	19.5-141.4	44.4	11.57	26.9-73.4
1989	48.7	21.18	21.5-110.1	36.7	11.91	19.7-68.2	49.9	10.27	33.5-74.4
1990	34.7	8.99	21.1-57.2	33.6	8.81	20.3-55.7	39.3	10.49	23.5-65.7
1991	38.2	16.33	17.2-85.3	34.9	13.91	16.4-74.0	39.3	10.49	23.5-65.7
1992	25.8	13.28	10.0-66.7	28.7	21.44	7.8-105.9	33.7	14.05	15.4-73.9
1993	28.8	15.27	10.9-76.4	23.8	10.46	10.4-54.2	33.7	14.05	15.4-73.9
1994	29.8	9.56	16.1-55.0	23.3	5.17	15.2-35.8	31.3	8.69	18.3-53.4
1995	23.6	6.71	13.7-40.8	24.9	8.51	13.0-47.8	31.3	8.69	18.3-53.4
1996	35.3	31.65	7.8-159.1	24.0	13.27	8.7-66.0	33.8	7.20	22.4-51.1
1997	42.0	33.44	10.6-165.8	32.0	21.54	9.7-106.0	33.8	7.20	22.4-51.1
1998	20.0[2]	4.87[2]	12.5-32.0	20.0[2]	4.87[2]	12.5-32.0	26.7	8.49	14.5-49.1
1999	19.2	0.83	17.6-20.9	19.2	0.79	17.7-20.8	19.6	4.46	12.6-30.4
2000	20.6	4.36	13.7-31.0	21.1	5.33	13.0-34.4	21.6	6.53	12.1-38.6
2001	17.2	0.73	15.8-18.7	17.2	0.81	15.7-18.9	17.4	4.27	10.8-28.0
2002	0.0[1]	0.00[1]	0.00[1]	0.0[1]	0.00[1]	0.00[1]	14.0	3.93	8.2-24.0

[1]No estimate provided, the Jolly-Seber model cannot estimate values near the beginning or end of the sample period.
[2]No unmarked animals were captured so estimate may be invalid.

Table 21. Population abundance estimates for data collected on incidental finds of eastern box turtles from 1965-2002 excluding captures made on intensive searches by recent box turtle researchers (1999-2002) for University of Delaware Woodlot study site using the Jolly-Seber full model, the modified Jolly-Seber full model, and the Jolly-Dickson full model from program POPAN.

	Jolly-Seber Full Model			Modified Jolly-Seber Model			Jolly-Dickson Full Model		
Year	Point Estimate	SE	95% CI	Point Estimate	SE	95% CI	Point Estimate	SE	95% CI
1965	0.0[1]	0.00[1]	0.00[1]	0.0[1]	0.00[1]	0.00[1]	56.0	6.40	44.8-70.0
1966	84.1	8.27	69.4-101.9	84.8	8.62	69.5-103.4	87.3	11.38	67.7-112.6
1967	95.1	6.08	83.9-107.8	91.7	5.08	82.3-102.2	92.5	8.51	77.3-110.7
1968	102.1	12.86	79.8-130.6	101.9	13.46	78.7-131.9	100.6	9.75	83.2-121.6
1969	98.2	10.09	80.3-120.0	93.6	8.82	77.8-112.5	99.6	9.75	82.2-120.6
1970	88.8	9.43	72.2-109.3	91.3	10.70	72.6-114.8	90.3	11.57	70.3-116.0
1971	71.8	5.39	62.0-83.2	68.6	4.11	61.0-77.1	72.5	8.45	57.7-91.0
1972	78.1	8.62	62.9-96.9	79.7	9.54	63.1-100.7	78.8	9.86	61.7-100.6
1973	69.7	6.22	58.5-83.0	70.4	6.67	58.5-84.7	70.4	8.92	55.0-90.2
1974	85.7	8.52	70.6-104.1	81.9	7.42	68.6-97.8	86.8	10.48	68.6-109.9
1975	79.3	7.92	65.2-96.4	80.8	8.78	65.3-99.9	80.7	10.26	63.0-103.4
1976	84.0	9.14	67.9-103.9	77.5	6.82	65.2-92.1	84.2	10.07	66.7-106.4
1977	81.6	8.05	67.3-99.0	79.1	7.40	65.9-95.0	82.5	10.75	64.0-106.4
1978	78.2	11.81	58.3-105.0	80.0	13.34	57.8-110.7	79.7	11.40	60.3-105.3
1979	75.2	6.66	63.2-89.4	72.1	5.59	56.7-91.7	74.3	8.72	59.1-93.4
1980	68.5	6.59	56.8-82.7	68.9	6.92	56.6-83.8	70.6	9.47	54.3-91.7
1981	70.3	4.88	61.4-80.5	69.2	4.57	60.8-78.8	72.1	8.46	57.3-90.7
1982	83.2	13.31	60.9-113.6	79.4	12.19	58.9-107.1	77.2	8.78	61.8-96.4
1983	70.6	14.58	47.3-105.4	73.1	16.61	47.1-113.5	74.4	16.62	48.3-114.7
1984	62.6	9.87	46.0-85.0	63.3	10.86	45.3-88.4	61.6	11.40	43.0-88.3

Table 21. Cont.

Year	Jolly-Seber Full Model			Modified Jolly-Seber Model			Jolly-Dickson Full Model		
	Point Estimate	SE	95% CI	Point Estimate	SE	95% CI	Point Estimate	SE	95% CI
1985	41.0[2]	7.99[2]	28.1-59.9	41.0[2]	7.99[2]	28.1-59.9	45.2	10.96	28.3-72.2
1986	39.5[2]	27.21[2]	11.6-134.0	39.5[2]	27.21[2]	11.6-134.0	45.2	10.96	28.3-72.2
1987	38.0	7.50	25.9-55.7	36.3	6.79	25.2-52.2	42.8	10.25	26.9-68.0
1988	46.7	19.45	21.3-102.3	52.5	28.32	19.5-141.4	44.4	11.57	26.9-73.4
1989	48.7	21.18	21.5-110.1	36.7	11.91	19.7-68.2	49.9	10.26	33.5-74.4
1990	34.7	8.99	21.1-57.2	33.6	8.81	20.3-55.7	39.3	10.48	23.5-65.7
1991	38.2	16.33	17.1-85.3	34.9	13.91	16.4-74.1	39.3	10.48	23.5-65.7
1992	25.8	13.28	10.0-66.7	28.7	21.44	7.8-105.9	33.7	14.04	15.4-73.8
1993	28.8	15.27	10.9-76.4	23.8	10.46	10.4-54.2	33.7	14.04	15.4-73.8
1994	33.3	12.30	16.5-67.1	23.3	5.17	15.2-35.8	36.5	11.12	20.4-65.4
1995	30.1	13.56	13.0-69.9	40.6	33.97	9.7-169.3	36.5	11.12	20.4-65.4
1996	28.5	25.48	6.3-128.0	19.5	10.67	7.2-53.2	38.1	9.71	23.3-62.3
1997	50.0	53.54	9.0-277.3	26.0	17.29	7.9-85.1	38.1	9.71	23.3-62.3
1998	18.3[2]	7.60[2]	8.4-40.0	18.3[2]	7.60[2]	8.4-40.0	38.1	9.71	23.3-62.3
1999	18.3	9.36	7.1-47.1	15.4	6.41	7.0-33.7	22.0	11.22	8.6-56.5
2000	13.6	5.16	6.6-27.9	12.1	3.45	7.0-20.9	15.5	6.50	7.0-34.1
2001	9.6	5.25	3.5-26.2	8.4	3.37	3.9-17.9	15.4	6.71	6.8-34.9
2002	0.0[1]	0.00[1]	0.00[1]	0.0[1]	0.00[1]	0.00[1]	4.0	2.10	1.5-10.5

[1]No estimate provided, the Jolly-Seber model cannot estimate values near the beginning or end of the sample period.
[2]No unmarked animals were captured so estimate may be invalid.

Table 22. Sex ratio of eastern box turtles captured over 5 year periods for University of Delaware Woodlot study site for 1965-2002.

Year	Males	Females	Sex Ratio[1]	χ^2_1	*P*
1965-69	58	40	1.45	3.31	0.069
1970-74	50	28	1.79	6.21	0.013
1975-79	44	21	2.10	8.14	0.004
1980-84	42	19	2.21	8.67	0.003
1985-89	19	7	2.71	5.54	0.019
1990-94	18	6	3.00	6.00	0.014
1995-99	18	6	3.00	6.00	0.014
2000-02	15	6	2.50	3.86	0.050

[1]Number of males per female.

No more than 2 juveniles were captured per year at the Woodlot except between 1965-69 and in 1971 and 1979. Additionally, no juveniles have been captured in the Woodlot since 1992. However, we documented 1 successful nest with 2 hatchlings outside of the Woodlot in 2002 (Kipp unpublished data). We released these hatchlings along the southern boundary. This lack of juveniles captured coincides with a 50% reduction of female turtles captured that occurred in the Woodlot between the 1965-1969 period when 40 females were captured and the 1975-1979 period when 21 females were captured (Table 22).

Turkey Run (1994-2002)

Between 1994-1999, I captured and marked 79 turtles at Turkey Run. Additionally, I captured and released 1 female in 1995, 1 male in 1996, 1 female and 1 male in 1997, and 2 females in 1999 onto Turkey Run from various locations off the study site, and in 1997, I released 14 juveniles at Turkey Run, which I originally removed from their nest in 1995 and 1996. During 2001-2002, we captured 61 new turtles and recaptured 36 marked turtles from previous years. Additionally, we recaptured 5 of the 14 released juveniles during 2001-2002; however, we did not recapture any of the adult turtles released at Turkey Run.

During 1994-1996, I captured 32 male and 38 female turtles. Sex ratio for this period did not differ from all captures ($\chi^2_1 = 0.72$, $P = 0.396$) or intensive searches ($\chi^2_1 = 1.59$, $P = 0.207$) in 2001-2002. Additionally, 17% of captures during this period were juveniles ($n = 12$). This percentage was lower then the percentage of juvenile captured for 2001-2002.

Population abundance estimates from the Jolly-Seber full model, the modified Jolly-Seber full model, and the Jolly-Dickson full model did not differ among years except in 2001 for the Jolly-Seber full model where population abundance was lower (Table 23). Density estimates ranged from 2.27-6.00, 4.33-5.77, and 2.15-6.04 for the Jolly-Seber full model, the modified Jolly-Seber full model, and the Jolly-Dickson full model, respectively. These estimates did not differ from the estimates from the most parsimonious Jolly-Seber model in program MARK or the JHE model estimates.

Table 23. Population abundance estimates for all captures of eastern box turtles from 1994-2002 for Turkey Run study site using the Jolly-Seber full model, the modified Jolly-Seber full model, and the Jolly-Dickson full model from program POPAN. No captures occurred during 1997-2000; 1996 estimates were adjusted for 5 year time lapse.

Year	Jolly-Seber Full Model			Modified Jolly-Seber Model			Jolly-Dickson Full Model		
	Point Estimate	SE	95% CI	Point Estimate	SE	95% CI	Point Estimate	SE	95% CI
1994	0.0[1]	0.00[1]	0.00[1]	0.0[1]	0.00[1]	0.00[1]	31.0	4.86	22.8-42.1
1995	86.4	17.99	57.7-129.4	83.1	18.50	54.0-127.9	87.0	14.66	62.7-120.8
1996	65.1	10.10	48.1-88.0	62.3	9.45	46.4-83.7	67.1	12.04	47.3-95.1
2001	32.7	6.43	22.3-47.9	68.1	5.32	58.4-79.3	71.9	8.89	56.5-91.5
2002	0.0[1]	0.00[1]	0.00[1]	0.0[1]	0.00[1]	0.00[1]	48.0	5.46	38.4-59.9

[1]No estimate provided, the Jolly-Seber model cannot estimate values near the beginning or end of the sample period.

Chapter 5

DISCUSSION

Immigration/Emigration

Turtle movement reflected the study sites' degree of isolation from other habitats. At the Woodlot, the most isolated site, I observed some temporary emigration, but I did not document any temporary immigration and found no evidence of permanent immigration or emigration. At Webb Farm, temporary emigration also occurred, and an effect of border residents occurred on the east side of the study site which was adjacent to forest habitat. Additional box turtle habitat existed to the west separated by Route 72 and to the north separated by a cornfield, but I observed no evidence of movement between these areas, and I believe the bias from movement between these sites was minimal. Due to the minimal movement observed between adjacent areas at these study sites, I considered these box turtle populations geographically closed.

At Turkey Run and White Clay Creek, habitat was contiguous between and around study sites, and I observed temporary and permanent movement between study sites and among surrounding areas. Border residents at theses study sites probably accounted for a large source of bias. At Turkey Run and White Clay Creek, temporary immigration/emigration was common, and permanent emigration was documented. With such extensive movements occurring, Turkey Run and White Clay Creek possibly comprised part of a single, larger population. However, I treated these 2 areas as separate study populations since surrounding habitat was not adequately sampled.

At White Clay Creek, tests of the assumptions of open population models detected a violation of equal survival probability, which probably resulted from individuals being captured only once, since we recorded no deaths in radio-tagged turtles and only 1 marked turtle death. Therefore, this violation represented bias from transient turtles or border residents. Several studies have suspected transient turtles as part of the population (Stickel 1950, Schwartz and Schwartz 1974, Kiester et al. 1982, Schwartz et al. 1984, Williams and Parker 1987, Langtimm et al. 1996). Most studies viewed transients as turtles captured only once or within 1 year, but only Kiester et al. (1982) tested this hypothesis by using radio telemetry. Of 7 turtles radio-tagged, 3 appeared to be true transients, while 4 were border residents (Kiester et al. 1982). Stickel (1950) also noted that border residents could also have been captured only once, but believed in most cases these turtles were transients. Langtimm et al. (1996) used goodness-of-fit tests to detect transients in their data by testing for violations of equal survival probability. Based on radio telemetry from our study, I believe transients were an insignificant part of the adult population, considering I only detected 1 transient in 89 radio-tagged turtles, and contrary to Stickel (1950), I believe most turtles captured only once in our population were border residents.

Mortalities and Survival

Despite nearly equal numbers in natural and human induced mortality, active searches for human induced mortalities off the study sites biased our results, and data from radio telemetry suggested natural causes were the primary source of mortality. Human induced mortality resulted from mowers and automobiles, but we documented few human induced mortalities on the study sites, since mowing only occurred within the study site boundary at Turkey Run. Natural mortalities included exposure to heat and freezing conditions and occurred on the study sites, but causes were primarily unknown. Schwartz and Schwartz (1974) documented winter mortality in a population of three-toed box turtles accounted for 68% of known mortality, whereas Doroff and Keith (1990) reported that human induced mortality was the only known cause of death in a population of ornate box turtles.

Only Yahner (1974), Schwartz et al. (1984), and Doroff and Keith (1990) estimated annual survival rates for box turtles; however these rates were much lower than our estimates of annual survival rate for Webb Farm, Turkey Run, and White Clay Creek. Yahner (1974) estimated a 0.80 annual survival rate for the eastern box turtle, and Schwartz et al. (1984) estimated a 0.82 annual survival rate that ranged from 0.72-0.92 by year for three-toed box turtles. A similar mean annual rate of 0.81 was estimated for ornate box turtles (Doroff and Keith 1990). These rates were similar to annual estimates for the Woodlot; however, both Yahner (1974) and Schwartz et al. (1984) included juveniles in their survival estimates, whereas the Woodlot estimates did not. Additionally, Schwartz et al. (1984) and Doroff and Keith (1990) estimated rates using the Jolly-Seber model. This model included loss from death, as well as loss from emigration in the survival estimates. If a high amount of emigration occurred in these populations, estimates will be negatively biased.

Aging Technique

I determined counting annuli of the first, second, and third pair of costal scutes of the carapace was a poor method to estimate age for individuals with ≥12 annuli. For individuals with ≥12 annuli, counts were imprecise across scutes and new annuli added were inaccurate with years elapsed. Other box turtle researcher who tested the accuracy of this technique also found that annuli often did not corresponded to years elapsed. Nichols (1939), Stickel (1978), and Stickel and Bunck (1989) observed accuracy in 31%, 32%, and 40% of all turtles examined, respectively. Reasons for this imprecision may be the result of not being able to distinguish false growth rings on certain scutes or among years (Ewing 1939). For turtles with <12 annuli, the technique was more accurate but not free of error. Although this technique is a common method used for aging turtles, few studies have tested its validity among ages (Wilson et al. 2003). I believe this technique can be used for age determination for juveniles with accuracy, but researchers should also test its validity to avoid inaccuracy from observer bias. Although the technique was not used in this study, the use of a digital camera may aid in testing the validity of this technique. Comparing photographs of same scutes for different years will more easily show additions of new annuli rather than researchers depending on their counting ability in the field for comparisons. This technique may strengthen the accuracy of aging of juveniles and extend the minimum age of young adults.

Age Structure

Juvenile abundance was related to macrohabitat characteristics. The percentage of juveniles in the population was similar between Webb Farm and Turkey Run and these areas had similar habitat characteristics with both sites having large areas of early successional habitat. Conversely, the Woodlot and White Clay Creek had very little early successional habitat and had similar percentages of juveniles. The Woodlot, however, also had a very low female abundance, and therefore, comparisons of juvenile abundance from this study site may not be valid.

Although juvenile abundance was low at the Woodlot and White Clay Creek, I believe these numbers were valid because search technique was similar among study sites. The wide range of juvenile composition we observed among study sites was consistent with the wide range reported in the literature (Table 3). Pilgrim et al. (1997) reported juveniles comprised about 3% of a population of Florida box turtles. This proportion was similar to White Clay Creek possibly because this study site (forest surrounded by freshwater marsh on 3 sides and levee and shallow impoundment on the other; Pilgrim et al. 1997) and White Clay Creek lacked suitable nesting sites. Hall et al. (1999) reported that juveniles 5-10 years of age represented 4.2%, 6.2%, 4.8%, and 15.7% of the population in 1945, 1955, 1965, and 1995, respectively, whereas Dodd (1997) reported 18% for an island population of Florida box turtles. However, definitions of juveniles in the literature lacks consistency with some researchers using size and others using annuli to determine age (Table 3). For example, Dodd (1997) considered turtles <120 mm juveniles; however, in our populations we captured turtles with shells worn smooth from old age at sizes <110 mm.

Sex Ratio

Understanding sex ratio dynamics is important in determining the health of a population because it affects the availability of sexual encounters and the potential number of eggs produced (Lovich and Gibbons 1990). Most researchers reported a balanced sex ratio in box turtles (Table 2), which I also documented at Webb Farm and Turkey Run. However, the Woodlot and White Clay Creek had male-biased sex ratios, and the Woodlot has had a male-biased sex ratio since 1965. Williams and Parker (1987) reported a male-biased sex ratio occurred in 2 out of 8 years; however, this bias likely resulted from variation among years. Dodd (1997) reported a male-biased sex ratio for a population of Florida box turtles that resulted from good nesting locations being located in the cooler forest interior and these cooler nests produced more male offspring. At White Clay Creek, nesting conditions became cooler as surrounding areas succeeded to forest. Females continuing to nest in these areas probably produced more male-biased nests. However, the lack of juveniles found at White Clay Creek suggests that successful nesting within or adjacent to the study site was not common. Additionally, radio telemetry demonstrated gravid females from our study sites (with the exception of 1 turtle at White Clay Creek, Kipp unpublished data) nested in open fields where nests would likely produce balanced or female-biased sex ratios.

Other possible causes of uneven sex ratios in turtle populations may be due to sampling bias, sex-specific mortality rate differences, sex-specific differences in age at maturity, and sex-specific differences in movement (Gibbons 1970, 1990; Lovich and Gibbons 1990). I believe that sampling biases and differences in age at maturity were not factors. Also, despite documenting a male-biased sex ratio at 2 study sites, I did not document a differential mortality rate favoring females. Conversely, at the Woodlot, I documented a mortality rate favoring males. However, more male mortalities at the Woodlot may have simply been because more males were present in this population.

With radio telemetry, I observed differential movement of the sexes. In geographically closed populations such as the Woodlot and Webb Farm, differential immigration/emigration were not considered a significant source of bias. However, differential immigration or emigration could be a significant bias at Turkey Run and White Clay Creek since these study sites were located adjacent to undeveloped habitats that allowed turtles to move freely. At White Clay Creek, female box turtles left the study site and migrated to nearby fields to nest, making them unavailable for capture during that part of the year. If nesting females from interior forests did not return to the study site some years after nesting, as observed at White Clay Creek, sex ratios would appear male biased in those years. Consequently, female turtles moved to Turkey Run to nest making them available for capture. If a large number of female turtles moved to Turkey Run during the nesting season, this could skew the sex ratio toward female bias or make a male-biased sex ratio appear balanced. At Turkey Run, I observed a balanced sex ratio, but several marked females and 2 radio-tagged females were known to have moved to Turkey Run during the nesting season. Additionally, 13 females at Turkey Run were captured only during the nesting season on the study site, which accounts for almost half (41%) of all female turtles captured at Turkey Run. At Webb Farm, I also observed a balanced sex ratio; however, I did not observe an influx of females during the nesting season as I did at Turkey Run. Additionally, most females nesting at Webb Farm nested in the early successional meadow and cornfields, which were free from mowing, whereas females at the Woodlot and White Clay Creek nested in fields where I documented mortalities due to mowing. Turkey Run was intermediate in that mowing was not a factor on the study site, but it bordered a field to the west where I documented mowing mortalities.

Population Abundance

Langtimm et al. (1996) documented that capture probabilities differed between juvenile and adult Florida box turtles, and therefore, concluded that including juveniles in the population estimate was not valid. I did not have a sufficient sample size to test for differences between juveniles and adults; however, since we captured juveniles less frequently than adults (Table 7), I assumed capture probabilities differed between juveniles and adults and computed population density estimates for adult turtles only.

The survival parameter in the Jolly-Seber model did not distinguish between mortality and emigration, which implied that emigration from the study site was permanent, and therefore, any temporary emigration could be a significant source of bias (Pollock et al. 1990). I accounted for this bias by not including emigration in the survival parameter, which resulted in positively biased abundance estimates at study sites where emigration occurred. Our density estimates from the Jolly-Seber model at White Clay Creek were higher than the JHE model estimates, which accounted for immigration/ emigration. The high amount of temporary and permanent emigration, as well as border residents, observed at this study site probably caused the Jolly-Seber model to overestimate abundance.

Since I documented little recruitment and a very high survival rate at Webb Farm, Turkey Run, and White Clay Creek, these populations could be consider demographically closed. Therefore, densities from the immigration/ emigration JHE model may be the more valid estimates, since this model assumed demographic but not geographic closure. Density estimates for the Woodlot may also be more valid from this model because all turtles in the population were radio-tagged, and therefore, the JHE model accounted for the mortality losses. Additionally, these estimates did not differ among years or study sites except at the Woodlot, which was the only study site where I observed a population decline.

Density estimates of our 4 study sites were lower than reported by other studies. Most studies of eastern box turtles estimated densities between 9-18 turtles/ha (Table 1). Densities estimated by Williams and Parker (1987) for eastern box turtles in Indiana, which declined from 4.4-5.7 turtles/ha between 1960-1967 to 2.7 turtles/ha in 1983, were most comparable to our study; however, these estimates included juveniles which comprised 11-25% of the population. Schwartz et al. (1984) also estimated densities based on all turtles captured, which ranged from 18.4-26.9 turtles/ha between 1966-1979. Since juveniles comprised 46% of the population and only had an annual survival rate of 0.66 (Schwartz et al. 1984), these estimates were probably double the adult population. Despite our low population densities in comparison with other studies, I believe these numbers accurately represent the true densities at our study sites, due to the low proportion of new adult turtles found in 2002 and the small confidence intervals of our estimates (Table 17).

Study Site Effects

The amount of bias among study sites due to border residents and turtle movements (immigration/emigration) ranged from least at the Woodlot, our most isolated site, to most at White Clay Creek, our undisturbed area. This probably occurred because less isolated sites were less restrictive on turtle movements, allowing turtles to emigrate from other areas, and allowed more habitat for border residents.

At Webb Farm, Turkey Run, and White Clay Creek, the few number of turtles recruited I observed was similar to the calculated mortality rate, which indicated these populations were stable. However, the Woodlot had a high mortality rate and only 1 turtle recruited, which indicated that this population was declining. Additionally, juvenile abundance at White Clay Creek and the Woodlot was very low. At the Woodlot, this was mostly likely due to low female abundance; however, at White Clay Creek, this indicated that nesting was not common within the study site and that very few turtles dispersed at an age <10 years.

I found no evidence that mortality influenced the male-biased sex ratios at the Woodlot or White Clay Creek, even though females nested in fields disturbed by human management practices (e.g., mowing). However, this evidence does not preclude that sex ratios were altered by differential mortality rates in the past. At Webb Farm and Turkey Run, I observed a balanced sex ratio. However, unlike Webb Farm, Turkey Run was also influenced by mowing along the western border and within the study site, although to a lesser extent than the Woodlot and White Clay Creek since mowing on the study site was not considered a significant source of mortality. Additionally, a large influx of females observed during the nesting season may have biased this sex ratio, whereas at Webb Farm mowing did not occur at female nesting locations, and I did not observed an influx of females during the nesting season.

Based on only 2 active seasons of data, I could not conclusively determine whether these box turtle populations were stable or declining, since year-to-year variation may have been significant (Dodd 2001). However, I found no evidence to conclude box turtle populations were unhealthy except at the University of Delaware Woodlot where I documented extremely low density estimates, a low survival and recruitment rate, and a male-biased sex ratio. This conclusion was confirmed by long-term data from 1965-2002, which showed this population was in decline, whereas long-term data from Turkey Run suggested a stable population. Other long-term studies have documented decreases in population abundance over time (Stickel 1978, Williams and Parker 1987, Hall et al. 1999). Hall et al. (1999) documented that a decrease in population abundance coincided with a male-biased sex ratio starting in 1975. Additionally, Williams and Parker (1987) attributed population declines to an unknown effect of human activity in surrounding areas, and Stickel (1978) suggested development of a nearby highway system led to increased mortality.

The combination of human management practices, isolation, and lack of early successional areas appears to have the most influence on box turtle populations. At the Woodlot, where these factors were most extreme, I documented a declining population and male-biased sex ratio. Webb Farm was primarily free from human management and had large early successional areas. Although Webb Farm was relatively isolated, the box turtle population appeared to have a healthy age and sex distribution. Turkey Run also appeared to have a healthy age and sex distribution, although mowing occurred on and adjacent to the study site and the balanced sex ratio may be biased from immigration of nesting female turtles. The unbalanced sex ratio at White Clay Creek was most likely the result of differential immigration/emigration and human induced mortalities, although differential mortalities may no longer be impacting the sex ratio. While this population experienced a high survival rate and showed no evidence of decline during this study, this population is most subject to decline should mortality rate increase from mowing of fields, diseases, or natural disasters due to its low juvenile abundance.

Management Recommendations

Harvesting agricultural fields for hay and alfalfa and mowing tall grass was the greatest human induced threat to box turtles, which usually occurred within 1-2 m from the forest edge. To minimize such mortalities, agricultural fields adjacent to box turtle populations should be planted with crops that do not require mowing (e.g., corn). I suggest if fields are mowed periodically to maintain open areas, that fields be mowed at a height of ≥15 cm during the hottest part of the day and in seasons when turtles are least likely to occupy fields (mid-July to August; late fall, e.g., November; or early spring, e.g., early April). If fields are used for agricultural purposes that require mowing, then a 2-4 m buffer mowed to a height of ≥15 cm should be maintained between the agricultural field and forest edge. The Woodlot had a 1-2 m buffer between the forest edge and alfalfa field, which was used by turtles but was not wide enough to prevent the death of some turtles. Searching for turtles before mowing by walking the edge of the field may also prevent deaths. For areas that are overgrown with exotic vegetation, management should include hand cutting and herbicides, rather than using large machinery.

I documented few box turtles deaths from automobiles, even though other researchers have observed significant road mortalities (Dodd et al. 1989). Though little can be done to prevent turtles from crossing roads or restricting traffic on state roads, unnecessary deaths due to automobiles can be avoided on park roads by enforcing speed limits or restricting large trucks from traveling these narrow roads.

Past studies have used various search methods for studying box turtle demographics. I suggest mark-recapture techniques should include structured weekly intensive searches spanning across the active season in addition to turtles captured on incidental finds. For my study, sex ratios calculated from intensive searches were similar to all captures at each study site, and intensive searches allowed for use of the JHE model, which provided the best density estimates. Additionally, intensive searches accounted for most captures in my study. Because intensive searches were an effective means of determining sex ratio and population density, this method may be the most time effective way to determine demographics of box turtle populations.

My research demonstrated the importance of studying box turtles in multiple locations to determine the status and demographics of box turtle populations in fragmented landscapes. Since methods vary considerably among researchers, comparisons among populations from different studies are problematic. Comparison among our 4 study sites revealed that box turtle population may be stable in fragmented landscapes that are not affected by human management practices in habitat patches of approximately 10-20 ha. However, to determine the true status of these populations, they will need to be studied on a long-term basis. Since box turtles are a long-lived species, changes in population structure may be subtle and not detected in studies carried out over a short period of time (Dodd 2001). Over the long term, other factors such as lack of genetic variability, influx of disease, or catastrophic events may negatively impact these isolated population.

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