2014

Population structure, size, and the thermal ecology of Iowa wood turtles (Glyptemys insculpta): A comparison between suburban and rural populations

Samuel Wesley Berg

University of Northern Iowa

Recommended Citation

Berg, Samuel Wesley, "Population structure, size, and the thermal ecology of Iowa wood turtles (Glyptemys insculpta): A comparison between suburban and rural populations" (2014). *Dissertations and Theses @ UNI*. 65.
https://scholarworks.uni.edu/etd/65

POPULATION STRUCTURE, SIZE, AND THE THERMAL ECOLOGY OF IOWA WOOD TURTLES (*GLYPTEMYS INSCULPTA*):

A COMPARISON BETWEEN SUBURBAN AND RURAL POPULATIONS

An Abstract of a Thesis
Submitted
in Partial Fulfillment
of the Requirements for the Degree
Master of Science

Samuel Wesley Berg
University of Northern Iowa
August 2014

ABSTRACT

Population structure, population size, and the thermal ecology of wood turtles (*Glyptemys insculpta*) was studied in a suburban population in Black Hawk County (BHC) and compared to a rural population in Butler County (BC), Iowa. In a suburban population of 35 wood turtles, 32 (91.4%) were adults distributed in a 1:1 sex ratio [16 (45.7%) females and 16 (45.7%) males], and 3 (8.6%) were juveniles. In the rural population, 60 (98.4% of the total population) adult turtles were distributed in a 3:2 sex ratio [36 (59.0%) females and 24 (39.3%) males], and one (1.7%) juvenile was located. Population structure was similar at both study sites and indicates that these populations consist of older adults with low numbers of juveniles.

Thermal and ecological data were analyzed by population (study site), individual turtle, sex, and by activity period (Hibernation, Prenesting, Nesting, Postnesting, and Prehibernation). Between populations, mean annual body temperature was significantly greater among females when comparing BC 2004 data to BHC 2012 data. Males in BC had significantly higher annual mean body temperature when comparing both BC data from 2004 and 2005 to BHC 2012 data.

Annual mean turtle percent exposure (PE) was only significantly different analyzed between populations: annual mean PE of females in BC during 2004 and 2005 was significantly greater than that of females in BHC during 2012. Similarly, males in BC had significantly greater annual mean PE in 2004 and 2005 compared to males in BHC during 2012. During active periods, behavior differed between populations; BHC turtles were hiding in water (females: 47.8%; males: 64.2%) more often compared to BC

turtles (females: 19.7%; males: 16.0%). Female wood turtles in BC basked on land more frequently (27.2%) than BHC turtles (11.0%). In BHC, wood turtles (females: 14.5%; males: 12.6%) were observed hiding on land more frequently than BC turtles (females: 7.0%; males: 2.5%).

Wood turtles in BHC display altered patterns of habitat usage and behavior compared to wood turtles in BC. This is perhaps due to differences in site physiography and levels of human impact, and ultimately manifests in altered thermal environments at each site.

POPULATION STRUCTURE, SIZE, AND THE THERMAL ECOLOGY OF IOWA WOOD TURTLES (*GLYPTEMYS INSCULPTA*):

A COMPARISON BETWEEN SUBURBAN AND RURAL POPULATIONS

A Thesis

Submitted

in Partial Fulfillment

of the Requirements for the Degree

Master of Science

Samuel Wesley Berg

University of Northern Iowa

August 2014

This Study by: Samuel Wesley Berg

Entitled: Population Structure, Size, and the Thermal Ecology of Iowa Wood Turtles (*Glyptemys insculpta*): A Comparison Between Suburban and Rural Populations

Has been approved as meeting the thesis requirements for the

Degree of Master of Science

Date	Dr. Jeffrey W. Tamplin, Chair, Thesis Committee
Date	Dr. Mark Sherrard, Thesis Committee
Date	Dr. Theresa Spradling, Thesis Committee
Date	Dr. Michael J. Licari, Dean, Graduate College

ACKNOWLEDGMENTS

This project was partially funded by a Graduate Research Award for Student Projects (GRASP) from the College of Humanities, Arts, and Natural Sciences, by the Department of Biology, University of Northern Iowa, and an award to Dr. Jeffrey W. Tamplin, from the Black Hawk County Conservation Board. I am most grateful to my graduate thesis committee, Dr. Theresa Spradling and Dr. Mark Sherrard, who made the completion of my thesis possible. I could not have done it without their wise advice and keen insights.

Thank you to all of the undergraduate research assistants who helped over the course of two years: Amanda Holtz, Derek Miller, Katie Nelson, Mackenzie Smith, Jason Sholly, and Jeremy George. I also would like to thank my fellow researcher in this endeavor, Jessica Williams; my own research and thesis benefitted from her hard work on her thesis. Thank you to my family, and especially my Mom for putting up with hearing about turtles and research to no end over the last two years. Special thanks to my faithful friend Buzzy, for finding the turtles hidden to my human eyes, and keeping me company while ‘turtling’ all those days in the woods.

Most importantly though, thank you to Jeff, my graduate advisor. Your consistent patience and presence throughout the entirety of this project has been invaluable.

TABLE OF CONTENTS

PAGE

LIST OF TABLES

TABLE PAGE

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

Wood Turtle Natural History

Phylogeny of Emydid Turtles

The North American wood turtle is a member of the family Emydidae (semi-aquatic pond, marsh, and box turtles), which encompasses 12 genera and 50 species (Rhodin *et al.* 2010). Emydid turtles have historically occurred in Africa, the Americas, and Europe, but today the family is mostly a new world group, as only a single species (*Emys orbicularis*) occurs in Europe and parts of northern Africa. With a known fossil history of just 80 million years, it is the most recent of the 14 extant families of turtles, contains the largest number of species, and is most diverse (32 species) in North America (Bonin *et al.* 2006). The family is divided into two subfamilies: the Deirochelyinae (painted turtles, chicken turtles, map turtles, terrapins, cooters, and sliders; 39 species) and the Emydinae (western pond turtles, spotted turtles, Blanding's turtles, the European pond turtle, wood and bog turtles, and box turtles; 11 species).

The subfamily Emydinae consists of semi-aquatic and terrestrial turtles (Ernst and Lovich 2009, Rhodin *et al.* 2010). Based on molecular evidence using 339 parsimony-informing characters, Feldman and Parham (2002) recognized three monophyletic clades within the subfamily: 1) the genera *Actinemys*, *Emydoidea*, and *Emys*; 2) the genera *Glyptemys* and *Terrapene*; and, 3) a monotypic clade for *Clemmys guttata*. However, more recently, Weins *et al.* (2010) proposed three revised clades based on the analysis of several nuclear loci (NGFB, ETS, GAPD, ODC, R35, and Vim). This arrangement suggests that wood and bog turtles form a monophyletic clade, and places *Clemmys* within a larger clade containing western pond turtles, Blanding's and the European pond turtle, and box turtles (Figure 1).

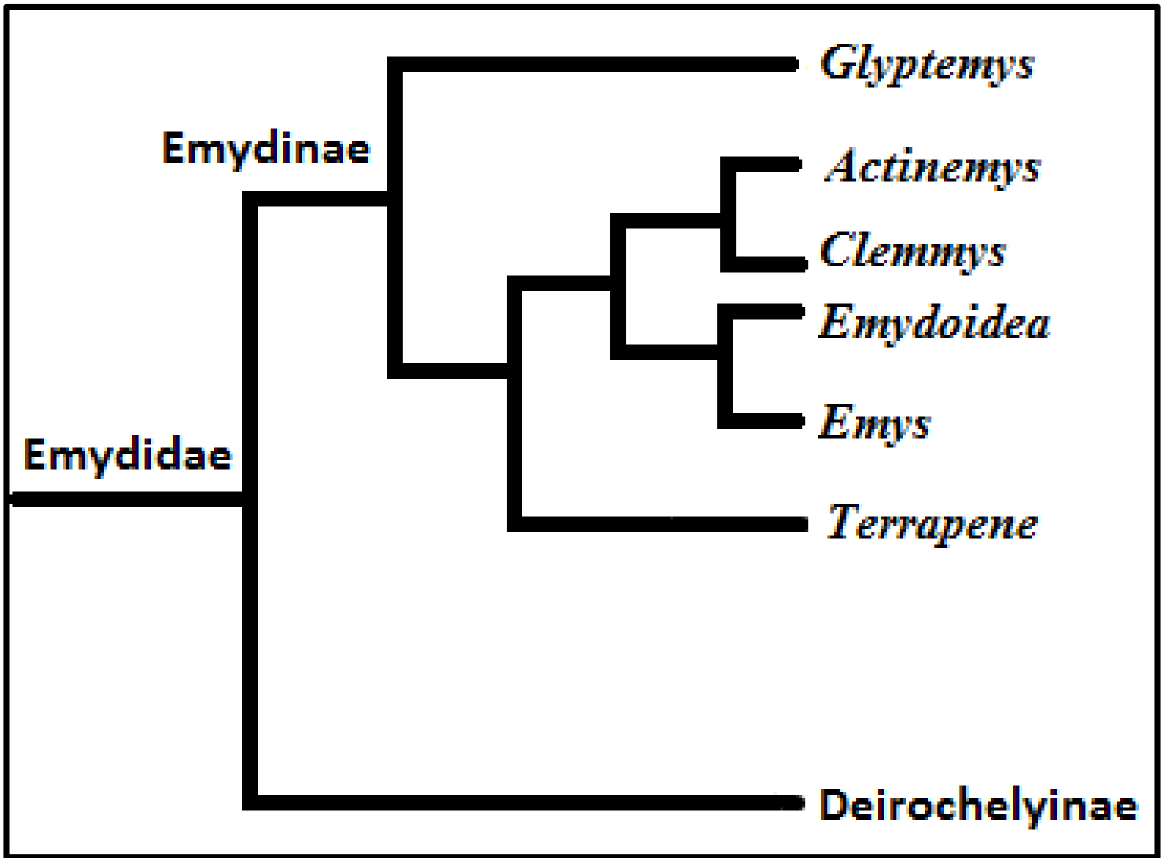

Figure 1. Phylogenetic tree of the family Emydidae, based on NGFB, ETS, GAPD, ODC, R35, and Vim nuclear loci (adapted from Wiens *et al.* 2010).

The North American wood turtle is a member of the genus *Glyptemys*, which it shares with its congener *G. muhlenbergii*, the bog turtle (Figure 2). Throughout the 20th century, wood and bog turtles were classified with several other Emydine species in the diverse genus *Clemmys*; upon analysis of fossil (Holman and Fritz 2001), morphological, and molecular sequence data of the mitochondrial cytochrome *b* gene (Feldman and Parham 2001, 2002), the genus *Clemmys* was determined to be paraphyletic. The genus *Glyptemys* was resurrected for wood and bog turtles, the western pond turtle was placed in the genus *Actinemys*, while leaving *Clemmys* as a monotypic genus containing only the spotted turtle (*Clemmys guttata*) (Parham and Feldman 2002).

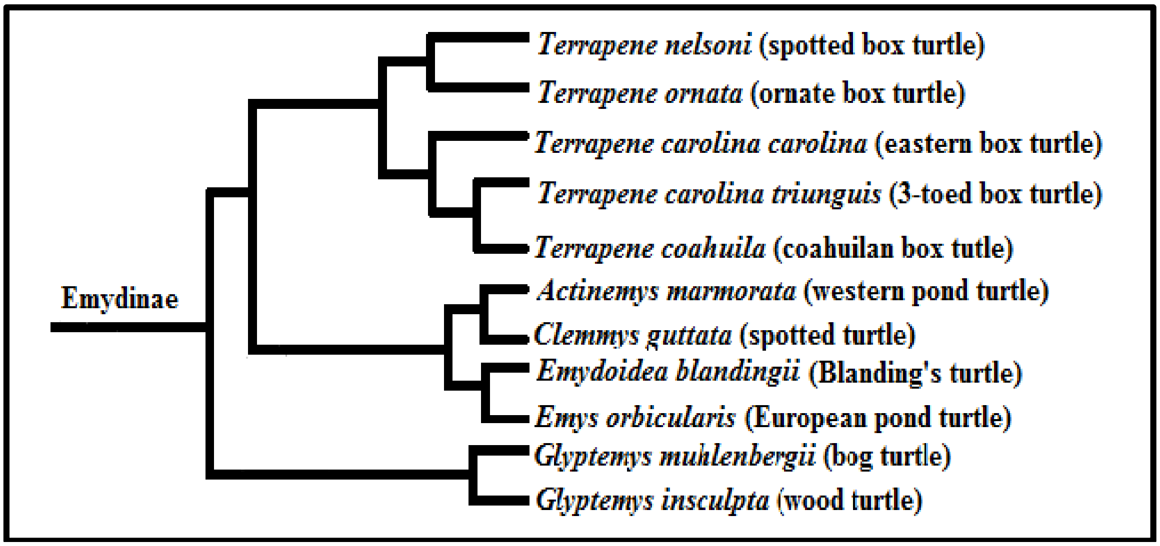

Figure 2. Phylogeny of the subfamily Emydinae, based on NGFB, ETS, GAPD, ODC, R35, and Vim nuclear loci (adapted from Wiens *et al.* 2010).

However, there is still disagreement regarding the arrangement of Emydine genera and the monophyly of *Clemmys*. Although monotypic genera are not preferable when generating a phylogeny, it is more parsimonious to leave *Clemmys* as a monotypic genus than to expand *Emys* to include all monotypic genera within the Emydinae (*Actinemys, Clemmys, Emydoidea,* and *Emys*) (Stephens and Wiens 2003). Furthermore, *Emys orbicularis* has a minimum of 4 geographically distinct haplotype clades that are morphologically detectable and may in the future be defined as distinct species, thus removing the issue of monophyly within *Emys* (Lenk *et al*. 1999).

Wood Turtle Distribution

International distribution. The wood turtle (*Glyptemys insculpta*) is a semi-aquatic turtle endemic to the Midwest and the Northeastern United States and Southeastern Canada (Figure 3). Wood turtles occur as far south as West Virginia and Virginia, as far West as Northeast Iowa, Eastern Minnesota, Wisconsin, and Michigan. In Canada, the range of this species is Southern Quebec, Ontario, Nova Scotia, and New Brunswick (Ernst and Lovich 2009). Wood turtle fossils are found as far south as Georgia, where this species existed until the end of the Wisconsin glaciation period (≈ 11,700 years ago). As the glaciers receded, this species retreated into its current northern distribution (Ernst and Lovich 2009).

Iowa distribution. Because of their rarity and cryptic habits, the historic and current distribution of wood turtles throughout Iowa is only loosely verified (Christiansen and Bailey 1997, Ernst and Lovich 2009, Spradling *et al.* 2010, LeClere 2013). However, all currently known populations exist in the Northeastern part of the state along the Cedar River drainage basin. The Lower Cedar, Middle Cedar, Upper Cedar, West Fork Cedar, Shell Rock, and Winnebago rivers are all sub-watersheds that comprise the

Cedar River Drainage Basin watershed (Iowa-Cedar Rivers UNESCO-HELP Basin 2013); the streams and riparian areas within this watershed may all contain wood turtle populations from the Iowa/Minnesota state border south through northwestern Black Hawk County (Figure 4).

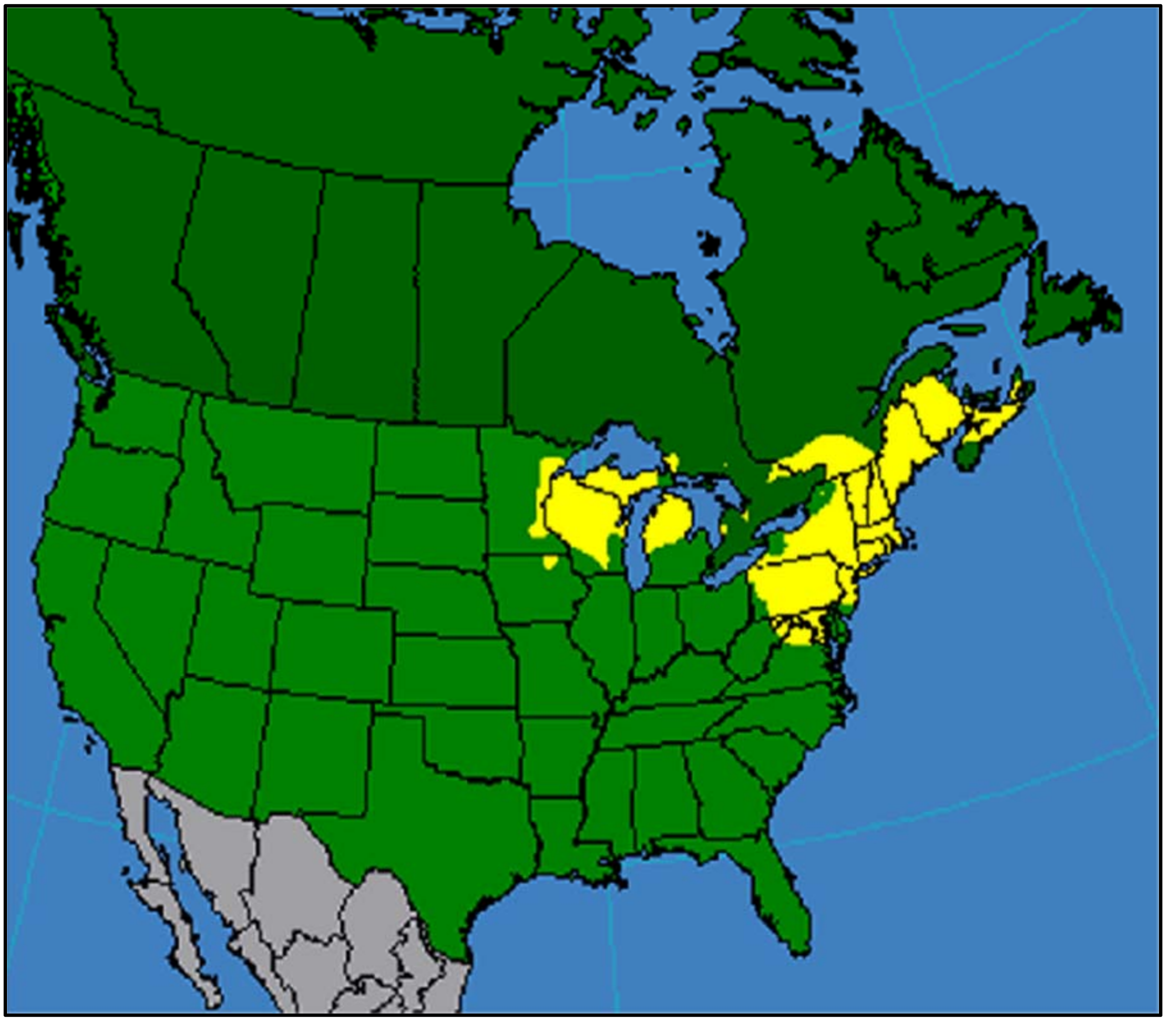

Figure 3. International distribution of the wood turtle (from Saumure 2010).

Several recently published Iowa wood turtle distribution maps (Ernst *et al.* 1994, Conant and Collins 1998, Ernst and Lovich 2009) indicate that the species' range terminates at the state's northern boundary and does not extend into southern Minnesota. However, because the Cedar River drainage basin headwaters originate in southern Minnesota (in Dodge, Freeborn, and Mower Counties) it is likely that the Iowa population of wood turtles extends into southern Minnesota.

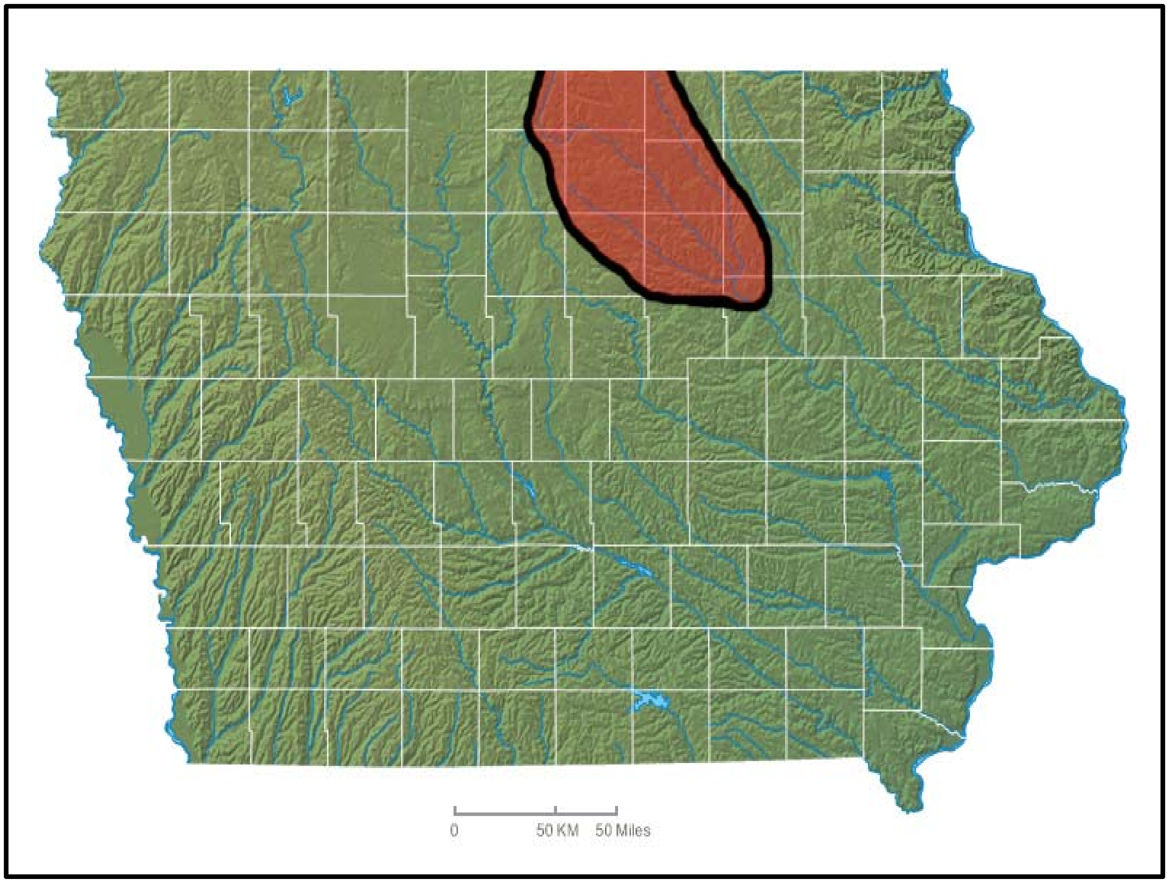

Figure 4. Current distribution of wood turtles in Iowa. Wood turtles are most likely to be found in or near creeks, streams, and rivers with the Cedar River drainage basin (Jeffrey W. Tamplin, personal observations 2003 – 2014).

Several wood turtles that were marked and radio tracked in Mower County, MN moved south across the border and hibernated in Iowa during the winter of 2011 – 2012 (Carol D. Hall, personal communication 2012). Thus, Harding's (1997) range map for *G. insculpta* is a more accurate depiction among those published in the general literature as it depicts wood turtles occurring in the head waters of the Cedar River in South-central Minnesota.

Iowa DNR occurrence records. According to the Iowa Department of Natural Resources (IA DNR), wood turtles occur in the following counties: Benton, Black Hawk, Bremer, Butler, Cerro Gordo, Delaware, Floyd, Franklin, Iowa, Mitchell, and Washington (IA DNR Natural Inventory 2013) (Figure 5). It is currently unknown if wood turtles occur in Hancock, Winnebago, and Worth counties, although the Shell Rock and the Winnebago Rivers pass through these counties and are known to harbor wood turtles in other portions of their drainage.

Records from Benton, Delaware, Iowa, and Washington counties are outliers to the majority of wood turtle accounts in Iowa, and represent localities that are not contiguous with the known species' state range. Because only solitary accounts exist in the same year (1989) for these four counties, it is most likely that these records represent misidentifications, pet releases, or perhaps result from stray wood turtles swept outside of their normal range by flooding.

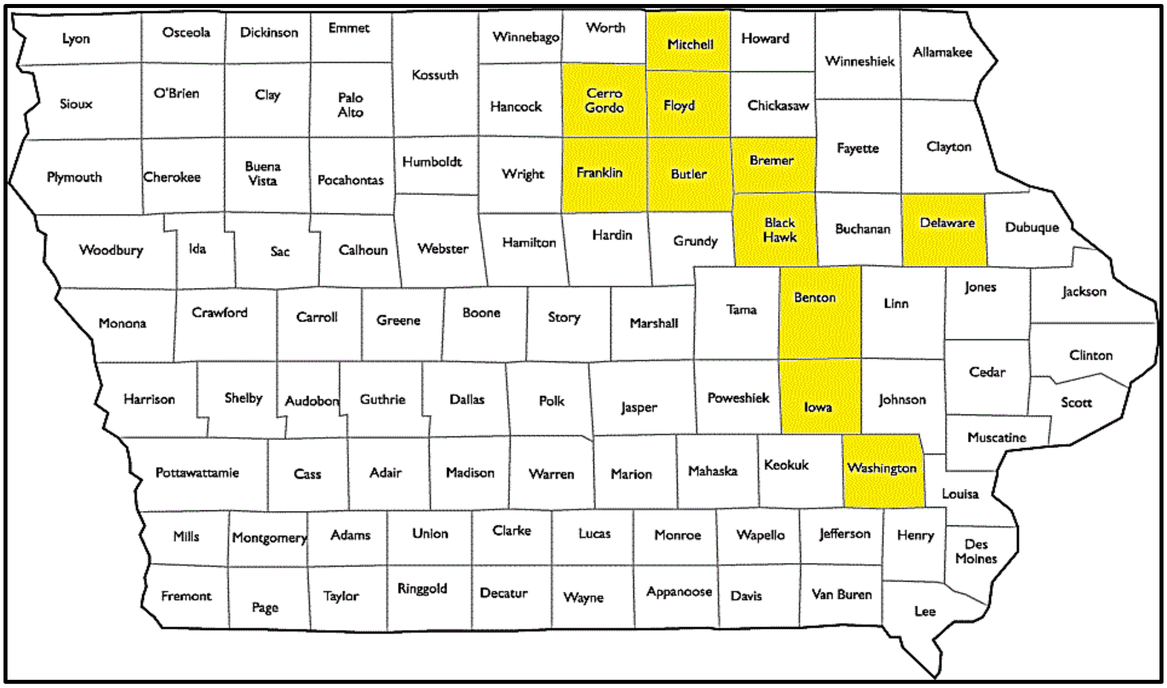

Figure 5. Distribution of the wood turtle in Iowa by county, according to records from the IA DNR (IA DNR Natural Inventory 2013).

Species Status

The wood turtle is not currently listed as federally endangered in the United States; however, due to the effects of anthropogenic habitat disturbance, collection for the pet trade, and agricultural and vehicular mortality (Levell 2000, Saumure *et al.* 2007, Ernst and Lovich 2009), most states in its range provide legal protection for the wood turtle. In the Midwest, Minnesota and Wisconsin list the species as Threatened and Michigan considers it a species of Special Concern. In Iowa, the wood turtle has been listed as endangered since 1997 due to its limited range, low population numbers, and heavy habitat disturbances (571-Chapter 77, Iowa Administrative Code; Christiansen and

Bailey 1997; IA Natural Resource Commission 2009). The IUCN Red List defines wood turtles as Endangered (Van Dijk and Harding 2012), and the Convention on International Trade of Endangered Species under Appendix II (CITES) (Buhlmann 1993) lists this species as illegal to trade.

Morphology

Species description. Adult wood turtles are medium-sized (≈ 14 – 20 cm) turtles with a maximum carapace length (CL) of 234 mm (Ernst and Lovich 2009). The carapace is keeled, ranges from brown to blackish in color, and often possesses radiating yellow lines on each scute. The plastron is yellow and black, with a specific pattern of splotches that develop during the first year of growth that are distinctive to each individual turtle. The plastron is unhinged and a V-shaped notch is present at the posterior end that facilitates tail extension (Harding 1997).

The common name of the species ("wood turtle") refers to not only the fact that the shell resembles sculptured wood, but also the characteristic that this species is commonly found in woodland habitats. The skin on the throat and the inner portions of the limbs of adults is a pale yellow to light orange color in Midwestern populations (Iowa, Michigan, Minnesota, and Wisconsin), but throughout its Eastern U.S. and Canadian distribution, the skin is bright orange to reddish in coloration (Ernst and Lovich 2009). In the Eastern U.S., the turtle is occasionally called "Ole red legs" or "Red leg" (Conant and Collins 1998)._ The intensity of these colors may vary seasonally and male coloration may be more vivid than female (Harding and Bloomer 1979). In Iowa, because lotic water sources are mostly turbid throughout much of the year, the brightly colored portions of the skin may be utilized in underwater mate recognition, for maintaining social hierarchy, and perhaps influences other intraspecific social behavior (Jeffrey W. Tamplin, personal observation).

Hatchling wood turtles (≤ 1 year of age) have concealing coloration; the carapace is unkeeled, pattern-less, and typically grayish-brown (Ernst and Lovich 2009); presumably the lack of color and distinct pattern is utilized to blend in with the substrate of their habitat. The plastron has a variable yellow background with black or brown mottled splotches that eventually become replaced by the characteristic adult pattern. Juveniles (≈ 1 – 8 years of age) and subadults (≈ 9 – 13 years of age) are typically strongly patterned; as they age, this pattern remains but may be increasingly obscured by weathering, algal growth, and the presence of dirt or mud.

The scientific name of the wood turtle, *Glyptemys insculpta*, refers to its highly sculptured shell. As wood turtles age, concentric growth rings (annuli) form on each carapace and plastron scute; the arrangement of annuli imparts the appearance of a flattened pyramid on each vertebral and costal scute and the carapace of younger individuals may give the impression of sculptured wood (Harding and Bloomer 1979, Ernst and Lovich 2009). Growth annuli can be used to estimate the age of wild individuals subjected to seasonal temperature cycles. Annuli are added yearly until maturity is reached between 14 – 18 years of age (Harding and Bloomer 1979, Farrell and Graham 1991). Growth continues throughout life, but after maturity is reached growth slows considerably and the CL of adult wood turtles may only increase by 1 mm per year or less (Lovich *et al.* 1990). After approximately 18 – 20 years of age, new annuli are no longer formed or are so small that they are practically indiscernible. From this point on, the shell begins to become environmentally abraded to such a degree that exact age can only be determined via mark and recapture studies (Walde *et al*. 2003, Ernst and Lovich 2009). However, age can be estimated in broad intervals (e.g., ≈ 21– 25, 26 – 30, 31 – 35) by assessing the amount of annuli erosion and shell weathering. Beyond 35 years of age, the shell may become so weathered, scarred, and pitted that the growth annuli no longer exist; these individuals are categorized as > 35 years old.

Sexual dimorphism and body size. Adult wood turtles display strong sexual dimorphism (Oldfield and Moriarty 1994, Ernst and Lovich 2009). Adult males have a concave plastron that is utilized to facilitate mating with females, an elongated tail with a cloacal opening that is distal to the shell margin, and a distinctly larger body size (CL range: 190 – 234 mm; mass range: ≈ 900 – 1200 g); females are typically smaller in size (CL range: 160 – 200 mm, mass range: ≈ 700 – 1000 g) and have a flat plastron (Lovich *et al*. 1990, Walde *et al*. 2003, Ernst and Lovich 2009) (Figure 6). Wood turtles with a CL ≤ 160 mm are classified as juveniles. Wood turtles ≥ 160 mm that are approaching adult size but do not display pronounced secondary sexual characteristics are categorized as subadults.

Figure 6. Sexual dimorphism in the wood turtle; adult females (left) have a flat plastron, smaller mean body size, and shorter tail with a more proximal cloaca compared to adult males (right), which possess a concave plastron, longer tails, and a larger head. Specimens from Butler County, Iowa: female CL = 168.4 mm, male CL = 186.1 mm. (Photo by Jeffrey W. Tamplin).

Seasonal Activity Periods

The wood turtle's annual activity cycle is divided into five activity periods; Hibernation, Prenesting, Nesting, Postnesting, and Prehibernation (Arvisais *et al*. 2002). During Hibernation, wood turtles are fully aquatic and dormant; metabolic activity is decreased as a response to low environmental temperatures (Arvisais *et al.* 2004). Upon emergence in the spring, mating occurs during the Prenesting period, and wood turtles often travel short distances and frequently bask terrestrially in riparian areas. The

Nesting period follows and is characterized by long distance terrestrial migrations by females and egg production and deposition. Increased terrestrial activity, reduced movements, and periods of aestivation characterize the Postnesting activity. Wood turtles again become mostly aquatic during the fall Prehibernation period and a second mating phase occurs.

Wood Turtle Habitat Usage

Wood turtles occur in streams, creeks, and rivers (lotic habitats) and in the riparian areas of associated woodlands, meadows, and farm fields. Across their range, habitat usage varies seasonally and geographically, and in some populations habitat selection may also differ between sexes (Ernst 1986, Quinn and Tate 1991, Kaufmann 1992a, Tuttle and Carroll 1997, Ernst and Lovich 2009). Except for box turtles (*Terrapene* spp.), wood turtles are the most terrestrial Emydid species in North America (Kaufmann 1992a). In terrestrial habitats, wood turtles are often located near the borders and margins of different habitat types; therefore, this species is characterized as an "edge species" (Kaufmann 1992a, Compton *et al*. 2002). The utilization of edge habitats allows wood turtles to maintain their dietary needs in areas that also facilitate optimal thermoregulation via "sun-shade shuttling" behavior during daily activity periods (Compton *et al*. 2002, Dubois *et al.* 2009).

Specific habitat use varies across its range; populations in the eastern United States populations are less aquatic than some Midwestern populations (Harding and Bloomer 1979, Ernst and Lovich 2009), an observation that may be related to climate differences between these two regions. In some populations, males may spend more time in aquatic settings than females, particularly during the warm summer periods when females typically aestivate terrestrially, and males use rivers and creeks as corridors to access various females (Kaufmann 1992a). New Hampshire females spent 80.0% and males spent 64.0% of the active season on land (Tuttle and Carroll 1997).

Seasonal habitat usage. During the Hibernation period, wood turtles are mostly dormant in lotic environments and exhibit little movement or activity (Ernst 1986). They hibernate (or more technically, brumate) on the bottom of rivers and creeks with a sandy or gravel substrate, typically in deep pools or under banks, flood debris, or submerged root masses (Walde 1998, Ernst and Lovich 2009). Wood turtles hibernate in streams with high levels of dissolved oxygen; these water sources tend not to freeze completely during winter and provide the turtles with continual access to oxygen (Greaves and Litzgus 2007). Wood turtles remain completing submerged during hibernation, and the combination of low temperatures and high oxygen tension allows wood turtles to remain aerobic when faced with long periods of cold temperatures (Seymour 1982, Graham and Forsberg 1991).

During the Prenesting period, *G. insculpta* spend most of their nights in aquatic habitats, and emerge on land to bask from mid-morning to late afternoon and then return to the water at night when air temperatures decrease (Arvisais *et al.* 2002, Ernst and Lovich 2009). Kaufmann (1992a) reported that 84.0% of wood turtles in Pennsylvania spent their nights in the creek when the air temperature was 10 ˚C or lower. Wood turtles utilize riparian habitats for terrestrial thermoregulation and do not typically bask aerially on logs like many “basking” emydids (e.g., painted and map turtles) (Ernst 1986).

During the Prenesting period, when daily temperature fluxes are high, it is crucial for wood turtles to maximize heat gain and to increase their body temperature above ambient levels (Walde 1998). This is especially important for females to enhance egg development and investment in thermoregulation activity during the spring may differ substantially across geographic regions (Ernst 1986, Dubois *et al.* 2009). In Maine, Compton *et al*. (2002) observed basking during 35.0 – 80.0% of morning locations from late April to mid-June, yet Ernst (1986) observed basking by only 13.7% of Pennsylvania wood turtles encountered during the morning hours. Aquatic basking may not be a common behavior in wood turtles, and is likely of greater thermoregulatory importance in several other emydine turtles [e.g., spotted (*Clemmys guttata*) and bog turtles (*G. muhlenbergii*)].

As ambient air temperatures rise, terrestrial activity increases; during the summer, turtles are located the farthest distance from water (Kaufmann 1992a). In Pennsylvania, turtles were often found between 100 – 400 m from the nearest water body during the Postnesting period (Ernst 1986). In Québec, Canada they spent much of July and August in dense vegetation, where they were hidden from detection by researchers (Walde 1998). During the Postnesting period in terrestrial habitats, *G. insculpta* use deciduous forests, Alder (*Alnus* sp.) thickets, emergent grasses, agricultural field edges, and areas dominated by Willow saplings (*Salix* sp.) (Compton *et al*. 2002, Ernst and Lovich, 2009).

Feeding

Wood turtles are opportunistic omnivores. They eat mostly vegetation and berries, but may supplement their diet with insects, worms, and even carrion (Ernst and

Lovich, 2009). In Pennsylvania, Strang (1983) reported that 31.4% of 51 different food items consumed by wood turtles were leaves. In West Virginia, Niederberger and Seidel (1999) recorded stomach contents of wood turtles; among the turtles sampled, 68% contained plant material, 46% contained earthworms, 38% contained insects and slugs, and 23% included carrion. Wood turtles in Butler County, Iowa consumed (in order of frequency of observations) grasses, slugs, violet leaves (*Viola* spp.), prairie ragwort leaves (*Senecio plattensis*), black raspberries (*Rubus* spp.), earthworms, snails, and dandelion leaves (*Taraxacum officinale*) (Tamplin 2006a). The observation that Iowa wood turtles feed on prairie ragwort is unusual because this plant is toxic to fish, lizards, birds, and several mammal species that do not transform the toxin. Wood turtle behavior was normal after ingesting this poisonous plant leading Tamplin (2006a) to surmise that the poison of prairie ragwort does not negatively impact wood turtles. Another distinctive feeding trait of this species is the behavior of thumping its plastron repeatedly on the ground, causing earthworms to surface (Ernst 1986, Buhlmann *et al*. 2008, Ernst and Lovich 2009).

Reproduction

Mating.

Wood turtles usually mate in aquatic environments twice a year (in Spring and Fall). Spring mating occurs between March and June and varies geographically and annually based on varying climate patterns (Harding and Bloomer 1979; Ernst and Lovich 2009). Fall mating typically occurs from September through November, but may occur during August or December, or any time that ambient temperatures elicit mating (Ernst and Lovich 2009). Farrell and Graham (1991) reported that mating occurred in early morning among wood turtles in a New Jersey population; in a Michigan population, Harding and Bloomer (1979) observed most mating events during late afternoons. In all populations mating usually occurs in the water, however, in Canada, Walde (1998) observed mating on land, as did Tamplin (personal observation) in Butler County, Iowa, and Ernst (1986) in Pennsylvania.

Nesting. This species nests on open sand bars along lotic water sources, or in sandy riparian woodland edges. Nesting usually occurs between May and June, but may extend into July in northern populations and/or during colder than normal climate periods. Females typically lay their eggs in sandy substrate during late afternoon, evening, or early morning (Harding and Bloomer 1979, Ernst and Lovich 2009). Nesting sites are most often located in areas with: 1) ample exposure to direct sunlight; 2) a sandy soil substrate that retains some moisture, yet is well-drained and not subject to flooding; and, 3) has a workable substrate that is free of rocks and thick vegetation (Harding and Bloomer 1979, Harding 1997). Nesting sites are often surrounded by ephemeral grasses, are located in sandy areas near bends in the river, and are maintained by the dynamics of water currents (Harding 1997). A female normally lays one clutch of eggs per year, but may not nest every year (Harding and Bloomer 1979, Ernst and Lovich 2009). Total clutch size ranges between 3 – 20 eggs, and varies geographically and by individual turtle. Harding and Bloomer (1979) reported clutch sizes between 5 – 18 eggs in Michigan; Brooks *et al*. (1992) reported clutch sizes between 3 – 13 eggs in Ontario, Canada; Tuttle and Carroll (1997) reported clutch sizes between 5 – 11 eggs in New Hampshire; Walde (1998) reported clutch sizes ranging from 5 – 20 eggs in Québec, Canada; and, Tamplin (in press) reported clutch sizes ranging between 6 – 13 eggs in Butler County, Iowa.

Egg incubation. The incubation period for *Glyptemys insculpta* eggs may last between 47 to 116 days, and is directly related to environmental temperatures (Harding and Bloomer 1979). In laboratory experiments, egg temperatures of 25 – 25.5 ˚C elicit hatching within 67 days and temperatures slightly above 30 ˚C usually produce hatchlings in < 50 days (Ewert and Nelson 1991, Ernst and Lovich 2009). The average incubation period for wild clutches is 67 days (range = 42 – 82 days; n = 9) (Farrell and Graham 1991). Unlike its congener the bog turtle (*Glyptemys muhlenbergii*) and many other emydids, wood turtle embryos do not display temperature dependent sex determination (TSD). Wood turtles have genetic sex determination (GSD) and the sexes are usually equally distributed in a clutch of eggs (Bull *et al*. 1985, Ewert and Nelson 1991). Depending on geographic location, hatchlings usually emerge from the nest between mid-August and early October and, with rare exceptions, do not overwinter in the nest (Parren and Rice 2004, Ernst and Lovich 2009).

Hybridization. Wood turtles may successfully hybridize with Blanding's turtles (*Emydoidea blandingii*); however, this is only known to have occurred in captivity when conspecific mates are limited or absent (Harding and Davis 1999).

Social Structure

Wood turtles are not territorial; however a social hierarchy occurs within populations. A linear rank hierarchy of dominance is maintained by repeated social interactions; a variety of aggressive, submissive, and neutral acts have been observed both between and within sexes, and typically the oldest, largest, and heaviest turtle is most dominant (Kaufmann 1992b). Using DNA fingerprinting, Galbraith (1991) determined that dominant male wood turtles fathered a significantly greater number of offspring than lower ranked males. Because higher ranked males demonstrate greater reproductive success, the establishment of a social hierarchy is likely driven by selection pressures (Kaufmann 1992b, Pearse and Avise 2001).

Significance of Temperature to Turtle Ecology

The environmental temperatures that turtles experience play a vital role in the behavioral patterns of many aquatic and semi-aquatic species; ambient temperature affects population structure (Gibbons 1968), habitat selection (Litzgus *et al*. 1999, Edwards and Blouin-Demers 2007, Dubois *et al*. 2009, Yagi and Litzgus 2013), feeding (Brown and Brooks 1991, Souza and Martins 2006), growth (Williamson *et al.* 1989, O'Steen 1998), and ultimately, survival. Aquatic and semi-aquatic turtles utilize both aerial and aquatic basking across a variety of habitats for thermoregulation. For some species, basking is critical to turtle fitness because it facilitates a rise in body temperature and may optimize locomotion, foraging, growth, and immune system function on a daily, monthly, and yearly basis (Hutchison and Maness 1979). However, not all species display similar behavior with respect to basking and thermoregulation. Many species bask after feeding in order to increase the rate of digestion and absorption efficiency, and yet several studies have indicated snapping turtles becoming inactive after feeding (Knight *et al.* 1990, Brown and Brooks 1991).

For some turtle species, in order to optimize physiologic function and to maximize energy gain, body temperatures are regulated and maintained within a preferred range (the "thermoregulatory set point" or T_{set}) during the active portions of their annual cycle (Dubois *et al.* 2008). For many reptile species, T_{set} is usually defined as the mean or the central range (25th or 75th quartiles) of selected body temperatures in an environment devoid of thermoregulatory costs (Pough and Gans 1982, Hertz *et al.* 1993). However, this definition is most appropriate for lizards and snakes and estimates of T_{set} that maximize the value of locomotion. In reptiles, physiological performance related to locomotion is usually stable within a small range of body temperatures, but food passage, digestion efficiency, and growth rates typically increase to a specific peak (the true "optimum temperature" or T_o) and then decrease sharply beyond T_o (Dubois *et al.* 2008). To maximize energy gain, ectotherms should select body temperatures that approximate, but do not exceed, T_o; this is particularly true for many turtle species in which optimizing locomotory speed is not a crucial component in capturing food or avoiding predators. At least for some turtle species, T_{set} is perhaps better defined as the upper 95th percentile of body temperatures selected in a thermal gradient, and thus more closely approximates T_o (Dubois *et al.* 2008). For turtles, the T_o for digestive efficiency is 29 – 30 ˚C and the T_o for developmental and growth rate is 30 – 31 ˚C (Parmenter 1980, Holt 2000); as such, the upper range of T_{set} for many turtles is likely near 30 ˚C and this value should equate to T_o for energy acquisition (Dubois *et al.* 2008).

Turtles that occupy temperate habitats and invest time and energy in thermoregulatory behavior should be favored by selective pressure to choose thermal niches that reduce thermoregulatory costs while maximizing energy gain. Thus, in the absence of other factors, turtles should select habitats that facilitate maintaining body temperatures that equate to the upper end of T_{set} (i.e., T_{upper}) rather than the lower end or the entire range (Dubois *et al.* 2008). This may be particularly evident in semi-aquatic species that utilize several different habitats throughout their daily and annual activity cycle and in northerly-distributed species that occupy thermally challenging habitats. In turtles, basking may be considered a thermoregulatory cost if it increases the risk of a predatory encounter, but this cost may be mitigated in many species by several factors: 1) the level of protection provided by the shell, 2) the ability of aquatic species to bask cryptically in shallow water habitats (by burying in the substrate or hiding in aquatic vegetation), or 3) the selection of terrestrial basking sites with dense vegetative cover by semi-aquatic and terrestrial species. Given the propensity of many turtles to actively thermoregulate via basking and/or the selection of specific warm microhabitats, the value of basking clearly outweighs the costs for most turtle species.

However, some aquatic turtle species do not thermoregulate at all; rather, these species are thermoconformers whose body temperature closely tracks ambient water temperatures (e.g., *Emydura* and *Hydromedusa*) (Chessman 1987, Manning and Grigg 1997, Souza and Martins 2006). Additionally, leatherback sea turtles (Dermochelyidae) do not appear to need to bask because they have adapted physiologic endothermy (Frair *et al.* 1972). If basking is not an essential behavior used to regulate body temperature in all species, but yet, coupled with the selection of specific microhabitats, is often utilized to raise body temperatures in certain species, then further studies are necessary to explain the observed variation in behavior that relates to how basking patterns, habitat selection, and thermal ecology differs across turtle species and populations.

Turtles represent one of the oldest extant orders of tetrapod animals and date back to the Permian Era. Throughout their history, turtle lineages have been exposed to many global thermal cycles, including periods of warming and dramatic cooling. There are still gaps in understanding the effects of environmental temperature on turtle biology and range from embryonic processes such as sex determination, hatchling body size, and incubation period, to post-hatching phenotypic patterns in adult body size, performance, immune system health, regulation of body temperature, thermal preference, and habitat selection (Telemeco *et al.* 2012, Mitchell *et al*. 2013, Rafferty and Reina 2014). Excluding a few well-studied taxa such as painted turtles (*Chrysemys picta*) and Eastern snapping turtles (*Chelydra serpentina*), the thermal ecology of most species of turtles is poorly understood. Furthermore, due to increasing anthropogenic factors, turtles are considered the most at risk group of vertebrates, even more so than amphibians (Rhodin *et al*. 2010). Therefore, turtles merit in-depth study to reveal patterns and causes of the observed variation in their thermoregulatory behavior, and to better develop effective conservation and management policies to help sustain the diversity of this ancient order of animals.

Thermal Ecology of Emydine Turtles

Thermoregulation and Active Temperatures

Emydine turtles occur across a large geographic range and are exposed to a wide variety of daily, seasonal, and annual temperature fluctuations. Both populations and species of emydine turtles have adapted to varying temperature and climate regimes by altering which environmental and body temperatures induce various activities, including the induction and cessation of hibernation and/or aestivation cycles, and specific events such as feeding, mating, and nesting behavior (Ernst and Lovich 2009). Thus, thermal responses and the ambient temperatures that elicit specific activities typically differ between emydine species and populations. Certain species (e.g., Blanding's and spotted turtles) are active at moderate to cold temperatures, while other species (e.g., box and bog turtles) are active at temperatures that are substantially higher than those observed in other emydids. Environmental temperatures that stimulate emydids to begin or to end hibernation, to bask either aerially or aquatically, and to feed or to mate, may all occur in either a broad or narrow range, and be higher or lower, even among closely related species.

Wood turtles. Unlike its congener the bog turtle, wood turtles (*Glyptemys insculpta*) are active throughout a wide temperature range and are often found to be active at relatively low environmental temperatures. In a Pennsylvania population studied by Ernst (1986), wood turtles were active during the months of April – October at body temperatures that ranged between 7.5 – 30 ˚C; in this population, mean internal temperature was 21.0 ˚C when active. In New Jersey, the body temperatures of active wood turtles ranged from 3.4 – 31.0 ˚C (mean = 16.2 ˚C) (Farrell and Graham 1991). Tuttle (1996) determined the body temperature of active wood turtles in New Hampshire ranged from 16.0 – 32.0 ˚C.

During the spring months, wood turtles emerge from their aquatic hibernation sites and begin to bask in riparian habitats. Perhaps because the sexes differ in size (and thus surface area to volume ratio is different), initial basking temperatures may differ between male and female wood turtles. In Pennsylvania, males generally emerge from hibernation a few days before females, and begin terrestrial basking at a lower environmental temperature (14 ˚C); female turtles begin basking at 17 ˚C (Ernst 1986). In the spring, when daytime temperatures may be warm but nighttime temperatures are cold, wood turtles remain near the riverbank and return to water at night because it represents a thermal refuge; they then reemerge to bask aerially during late morning hours. Profitt and Chance (2004) reported that wood turtles along the coastal plain of Maryland thermoregulate by basking until they raise their body temperature to a peak of 37 ˚C, then maintain body temperatures between 20 – 25 ˚C during the rest of the day; in this population, body temperatures decreased to 15 – 20 ˚C at night during the active phase of their annual cycle. In an Ontario, Canada population, Greaves and Litzgus (2007) reported the air temperature was 8.5 ˚C and the water temperature was 5.0 ˚C during the last wood turtle basking event of the fall (on October 30th).

Dubois *et al.* (2009) determined that free-ranging wood turtles in Quebec, Canada thermoregulated, but noted that the habitat at this northern location was thermally constraining and T_{set} (defined as T_{upper} and ≈ 30 ˚C) was only obtainable during a narrow

5-hour time period on sunny days. Regulation of T_b in this population was imprecise, but wood turtles maintained T_b values that were above ambient values in terrestrial habitats and exceeded river temperatures from 1000 to 1700 h on sunny days. On cloudy days, air temperatures in the terrestrial habitats used by wood turtles only marginally exceeded river temperature. Wood turtles at this site selected terrestrial locations with an open canopy (naturally warmer microhabitats) and used "sun-shade shuttling" to regulate T_b primarily between 0900 and 1600 h on sunny days.

Mating usually occurs at water temperatures ranging from 9.5 – 20 ˚C, but has been observed at temperatures as low as 1 ˚C (Ernst 1986, Niederberger and Seidel 1999, Ernst and Lovich 2009). Greaves and Litzgus (2007) observed mating at 5.0 ˚C in Ontario, Canada. In lotic water in Pennsylvania, mating occurs at a range of 10 – 20 ˚C, while in non-aquatic habitats mating has been observed within a temperature range of 11 – 23 ˚C (Ernst 1986).

The temperature at which feeding occurs apparently does not differ between adult male and female wood turtles. In Pennsylvania, wood turtles begin feeding in water when the temperature approaches 17 ˚C; on land, turtles begin feeding at 23 ˚C (Ernst 1986). In a laboratory study utilizing a terrestrial thermal gradient, Dubois *et al.* (2008) determined that fed juveniles selected significantly higher body temperatures (26.6 ˚C) than starved juveniles (23.1 ˚C), but this pattern was only evident when basking time was constrained to 5 hours per day. In the same study, food availability and basking time did not affect the temperature selection of adult male wood turtles, suggesting that maximizing energy gain is more important for juveniles than adults (Dubois *et al.* 2008).

Based on temperature selection patterns in a laboratory thermal gradient, Dubois *et al.* (2008) determined that T_{upper} for wood turtles from a Canadian population was approximately 30 ˚C. Several other laboratory-based thermal gradient studies have suggested that wood turtles are adept at detecting ambient temperature differences and prefer body temperatures that approach 30 ˚C. Nutting and Graham (1993) determined that the preferred body temperature of adults in a thermal gradient was 27.5 ˚C (range = 21.3 – 31.9 ˚C); Tamplin (2006b) reported that 6 hatchling wood turtles overwhelmingly selected the warmest temperature available in an aquatic thermal gradient within their normal active range (12 – 27 ˚C); similarly, juvenile wood turtles of 3 different age classes (3, 6, and 12 months of age) selected 30 ˚C in a thermal gradient of 15 – 30 ˚C; patterns of temperature selection differed between ages, but each age class selected the warmest temperature available and efficacy of temperature selection was related to ontogeny rather than body size (Tamplin 2009).

Other Emydine turtles. *Glyptemys muhlenbergii*, the federally endangered bog turtle, is another semi-aquatic species of the subfamily Emydinae. Bog Turtles are active within a temperature range of 16 – 31 ˚C; basking behavior begins in mid-morning after emergence from vegetative cover or *Sphagnum* bogs (Herman 1981). In North Carolina, Pittman and Dorcas (2009) observed bog turtles being active and basking from late April – August between 1000 – 1500 hours, with externally recorded maximum body temperatures of 35.2 – 40.6 ˚C. No significant difference in temperatures between males and females were observed between the months of June – July. Furthermore, Pittman and Dorcas (2009) observed that daily maximum temperatures averaged 31.5 ˚C from May –

July; therefore, turtles were presumed to maintain mean body temperatures well above the average environmental temperature(s). Because this is a bog dwelling species that frequently buries, it was concluded that the bog turtle shell temperatures are most closely correlated with shallow mud temperatures, and that the turtle shell temperatures during the warmest months (May – July) typically exceeded the environmental bog temperatures due to basking behavior (Pittman and Dorcas 2009).

The Blanding's turtle (*Emydoidea blandingii*), has a northern distribution (e.g., Nebraska, Iowa, the Great Lake states, the Northeastern U.S., and the Southeastern border of Canada) and is generally active throughout its range from late March – mid-November in lentic marshes and wetlands. Yet at the E.S. George Reserve in Michigan, Blanding's turtles were observed remaining active in a lentic habitat until early December; hibernation was terminated and turtles became active by March 1 when body temperatures were still below 3 ˚C (Congdon *et al*. 2008). In Southeastern Minnesota, during the month of March when ice was still present, Blanding's turtles emerged from hibernation with body temperatures of 2.3 – 5.2 ˚C, and began moving about searching for mates at internal temperatures ranging between 4.4 – 16.6 ˚C (Congdon *et al*. 2008). Blanding's turtles display peak mating behavior from March – April when water temperatures are 4 – 6 ˚C; mating is observed throughout the year in Minnesota except during December – February (Congdon and Keinath 2006). Female Blanding's turtles nest from late May – mid-June, and may initiate nesting earlier in May if yearly temperatures exceed typical norms (Congdon and Keinath 2006). In laboratory-based thermal gradient studies, male and female Blanding's turtles selected different water temperatures; males selected a mean of 22.5 ˚C and females selected a mean of 24.8 ˚C (Nutting and Graham 1993). Blanding's turtles are considered a cold-adapted species, as their distribution and ability to remain active at low temperatures clearly reflects.

Similarly, spotted turtles (*Clemmys guttata*), a semi-aquatic lentic (e.g., bog, marsh, pond) species, become active at environmental temperatures as low as 2 – 3 ˚C (Ernst 1982, Litzgus and Brooks 2000). Their range extends from Southeastern Canada, the Midwestern Great Lakes states, and along the east coast from Maine to Florida. Other emydid turtles (e.g., painted, bog, and some populations of wood turtles) only become active once temperatures reach at least 8 – 10 ˚C (Ernst 1972, 1977, 1986). Spotted turtles in Pennsylvania are active at internal temperatures ranging from 3 – 32 ˚C, and feeding only occurs when internal body temperatures approach 15 ˚C (Ernst 1982). Furthermore, due to their larger body size, male spotted turtles remain active at cooler temperatures for longer time periods than females, while females remain active for longer periods during warmer temperatures, presumably to enhance egg development (Ernst 1982). Environmental temperatures that elicit reproductive behavior may vary geographically; spotted turtles in Ontario, Canada court and mate when body temperatures average 15 ˚C (Litzgus and Brooks 2000), while spotted turtles in a more southern population in Pennsylvania mate when internal temperatures are 8 ˚C (Ernst 1982). Other emydid turtles that occupy lentic habitats are active at comparable environmental temperature ranges.

Relative to other emydine taxa, the ornate box turtle (*Terrapene ornata*) has a southern distribution and is found in the dry and moderately arid habitats of the US

Southwest and Plains states. It is active from early to mid-morning and mid- to late-afternoon, and basking behavior occurs at a mean internal body temperature of 26 ˚C in Kansas (Legler 1960) and Arizona (Plummer 2003), and 21 ˚C at its most northern distribution, in Wisconsin (Curtin 1995). In Kansas and Arizona populations, internal body temperatures during locomotion range between a mean of 28 – 30 ˚C (Legler 1960, Plummer 2003), and are between 24 – 25 ˚C in Wisconsin (Curtin 1995). At its southern-most distribution (Southwestern Arizona), this species is 95% subterranean, and is active only during the monsoon months of July – September; yet behaviors such as mating and foraging occur underground even during months of apparent inactivity (Plummer 2003). Most other emydid species are active at these temperatures, but may also be active at a much lower range of temperatures; this may be a consequence of their historic more northerly distribution when compared to the ornate box turtle.

Inactive Temperatures

The species-specific preference for maintaining body temperatures within a preferred range (T_{set}) is evident primarily during active periods, but different temperatures may elicit periods of inactivity across emydine species as well. Extremes of high and low temperatures determine when ectotherms aestivate or hibernate. Closely related species of emydine turtles become inactive at different temperature extremes, and at different times throughout the year.

To overcome the lack of available food associated with the winter season, and to compensate for the low environmental temperatures that prevent the digestion and absorption of food, turtles drastically lower their metabolic rate when faced with extended cold ambient temperatures. The depression of metabolic activity in reptiles and other ectotherms is termed “brumation.” Although many turtle species in southern populations exhibit only temporary periods of brumation and may become active on warm winter days, many northern populations enter a longer period of winter dormancy that can be referred to as “hibernation,” although in turtles this term does not entail the severity of physiologic effects observed in truly hibernating animals. Aquatic turtles enter hibernation during cold winter months either in flowing water, lakes or ponds, and submerged in mud. Terrestrial species bury down into the earth below the frost line (Ernst and Lovich 2009).

In contrast, during peak summer temperatures, turtles avoid reaching dangerously high (and potentially lethal) temperatures by aestivating (i.e., becoming inactive) and seeking out cool water sources, shaded areas, or burying into the substrate. The Critical Thermal Maximum (CTM) temperature is the temperature that initiates a cascade of metabolic events that, if not immediately mitigated, leads to mortality (Hutchison *et al.* 1966). In turtles, the CTM typically differs between species and the CTM may be substantially higher in terrestrial species when compared to aquatic species. In addition, intraspecific populations that occur in different geographic areas often display local adaptations that may produce “physiologic races.” These populations may be differentially adapted to slightly different temperatures, and thus exhibit different CTMs. Prolonged exposure to a temperature just slightly below the CTM may prove fatal to some species if it results in the loss of muscular and neurological control that is associated with the loss of a righting response (Hutchison *et al.* 1966). In turtles, the loss of righting response is typically fatal. Thus, the CTM of turtles varies between and within species, and most turtles have adaptive behavior that minimizes the potential for exposure to this temperature.

In summary, different species of Emydine turtles exhibit a range of environmental temperatures that promote them to become inactive. These temperatures may result in metabolic and behavioral adjustments that prevent exposure to sub-freezing temperatures and/or to high temperatures that would result in molecular-, cell-, and tissue-level destruction.

Wood turtles. Across their range, wood turtles become inactive during the months of mid-November through mid-March when air temperatures fall below 7.5 ˚C and water temperatures are between 4 and 5 ˚C (Greaves and Litzgus 2007, Ernst and Lovich 2009). During this time period, turtles hibernate in partially frozen lotic water sources and may not move more than a few meters (Harding and Bloomer 1979, Ernst 1986). Their body temperature equals that of the surrounding water and is typically at or slightly below freezing (Ernst 1986, Greaves and Litzgus 2007). Wood turtles use hibernacula such as underwater forms (e.g., submerged logs, flood debris, tree roots, and beaver or muskrat dens) or reside on the substrate of aquatic habitats to protect themselves from predation and select areas of low to moderate current to prevent being dislodged. Because wood turtles are anoxia intolerant, they utilize underwater areas with high dissolved oxygen content and moderate current to facilitate a limited degree of aquatic aerobic respiration during winter months (Graham and Forsberg 1991). Wood turtles stop feeding below 17 ˚C. As environmental temperatures consistently drop below this level in the fall, wood turtles become less active and begin utilizing fat stores for energy during the months associated with hibernation.

However, the months of hibernation are not the only time during the year that wood turtles become inactive; they may also become inactive during peak temperatures in the summer months as well. In Pennsylvania, wood turtles are largely inactive at temperatures exceeding 30 ˚C, and turtles commonly use shaded refuges during periods when ambient temperatures exceed this level (Ernst 1986). In a laboratory study, the CTM for wood turtles was 41.3 ˚C (range = 39.6 – 42.5 ˚C) and the mean loss of righting response was 39.8 ˚C (range = 39.0 – 40.5 ˚C) (Hutchison *et al.* 1966, Cloudsley-Thompson 1971); this value is well above the summer temperatures that are shown to elicit inactivity in this species. During peak summer temperatures, wood turtles seek shade and water sources and become relatively inactive when environmental temperatures approach their CTM. Wood turtles desiccate faster than some other terrestrial emydids (e.g., *Terrapene carolina*), therefore seeking shade not only prevents approaching the CTM but also prevents desiccation (Ernst 1968). In Pennsylvania, wood turtles may mitigate water loss when in terrestrial environments by eating predominately green leaves as a source of water (Strang 1983).

Other Emydine turtles. The winter ecology of the bog turtle (*Glyptemys muhlenbergii*) is poorly understood. Bog turtles inhabit lentic habitats during active periods and inhabit lotic habitats during inactive periods. The only known study on bog turtle thermal ecology demonstrates behavioral inactivity from October − early April in North Carolina (Pittman and Dorcas 2009). Bog turtles chose hibernacula such as crawfish burrows or bury in muddy substrate and under tree roots in small lotic water sources that do not freeze solid. Bog turtles usually maintain body temperatures above freezing (1.5 – 6.1 ˚C), however one turtle hibernated in a lentic bog experiencing temperatures as low as -1.5 ˚C (Pittman and Dorcas 2009). Throughout the hibernation period, bog turtles averaged external shell temperatures of 8 – 10.7 ˚C; because turtles did not move more than 5 meters (m) during the inactive months, it may be inferred that these were the average temperatures of their hibernacula. Similar to the bog turtle, wood turtles also become inactive during winter in aquatic hibernacula.

The Blanding's turtle (*Emydoidea blandingii*) is also a northern-distributed, lentic habitat species, similar to the bog turtle. This species has a mean CTM of 39.55 ˚C (Hutchison *et al*. 1966). Blanding's turtles become inactive when ambient temperatures approach their CTM; they seek out lentic and occasionally lotic water sources where they typically bury into the substrate. Hibernation in Illinois occurs from October – March (Rowe and Moll 1991), and in Wisconsin, when water temperatures approach 10 – 13 ˚C, communal hibernation occurs (Ross and Anderson 1990). In Nova Scotia, Canada, Blanding's turtles hibernate from mid-November – late March; even at temperatures below 1.5 ˚C, they make marginal movements of 7 meters or less (Newton and Herman 2009). This suggests that temperatures low enough to prompt complete inactivity in other species do not elicit the same response in all species of emydid turtles.

The spotted turtle (*Clemmys guttata*) ranges farther north into Ontario, Canada (45'N, 80'W) compared to box turtles (Litzgus *et al.* 1999). This species aestivates during warm periods, but aestivation occurs at much lower temperatures than in box turtles.

Spotted turtles burrow into the mud or other wet substrate when environmental temperatures exceed 20 – 21.5 ˚C in the most northern populations (Ontario, Canada) (Litzgus and Brooks 2000), yet their mean CTM observed in a laboratory study is 41.98 ˚C (Hutchison *et al*. 1966). This is unusual in turtles; it is much more typical for turtles to aestivate when ambient temperatures are close to their CTM (Cloudsley-Thompson 1971). In Pennsylvania, spotted turtles become inactive and aestivate when water temperatures reach 30 ˚C, and they shift their daily activity from afternoon in spring to mid-morning during the summer (Ernst 1982). Becoming inactive at ambient temperatures well below their CTM may infer that spotted turtles are a cool temperature-acclimated species that avoid even moderately high temperatures. Environmental temperatures falling below 2 ˚C also cause spotted turtles to become inactive and begin their yearly hibernation. During winter, they burrow into the muddy substrates of aquatic habitats, and select hibernacula that are not prone to freezing solid (Ernst 1982, Litzgus and Brooks 2000).

Terrapene ornata, the ornate box turtle, has a CTM approaching 41 ˚C. This species becomes inactive and either burrows into the earth, utilizes small mammal burrows, or hides under vegetation when environmental temperatures reach 33 – 36 ˚C (Legler 1960, Plummer *et al*. 2003). Similarly, throughout its geographic range the ornate box turtle is inactive during the winter months, and spends the months of November – February burrowed in the earth (Plummer *et al*. 2003). In Iowa, *T. ornata* enters hibernation as early as mid-October at air temperatures between 10 – 15 ˚C (Bernstein and Black 2005). In northern populations, *T. ornata* burrow gradually deeper down to avoid mortality as the frost layer reaches further into the soil (Legler 1960). However, in Iowa, several turtles were observed as surviving over a month of freezing soil temperatures with no obvious side effects (Bernstein and Black 2005).

The eastern box turtle (*Terrapene carolina*), a congener of the ornate box turtle, must also endure subzero temperatures across the northern portion of its range. Eastern box turtles do not burrow as deeply into the soil to mitigate freezing temperatures as ornate box turtles. Costanzo *et al*. (1993) demonstrated that *T. carolina* creates shallow burrows in the soil and is physiologically adapted to withstand freezing for several days at a time due to increased levels of glucose and withdrawal of water from their tissues, thus protecting their vital organs. The CTM of *T. carolina* (42.53 – 43.00 ˚C) is slightly higher than that of *T. ornata* (≈ 41 ˚C) (Hutchison *et al*. 1966); this similarity in CTM could reflect the evolutionary history of this genus and the relatively broad distribution of both species across North America.

Winter dormancy varies within the subfamily Emydinae. Inactivity is initiated at temperatures as low as 1.5 ˚C in one of the most northerly distributed species (Blanding's turtles) to a high of 15 ˚C in species with southern or only marginally-northern distributions (box turtles). Inactivity at warm temperatures depends on the species' CTM and geographic range; the most northerly distributed species (spotted turtles) aestivate at relatively low summer temperatures that are well below their CTM, while turtles with mid-latitudinal ranges (e.g., box turtle populations extending as far south as Mexico, Texas, and Florida) only become inactive at temperatures approaching their CTM.

Emydine Thermal Ecology Summary

The thermal ecology patterns of wood turtles are mostly known from populations in the Northeastern United States and Canada; these populations have been studied much more frequently than those in Iowa and the Midwest. Midwestern populations merit further observation to determine if their thermal ecology is similar to, or contrasts with, populations from Northeastern U.S. and Canada. Several species within the subfamily Emydinae have similar patterns of thermal tolerance; however, previous research suggests that the thermal ecology of wood turtles may be different from other Emydine turtles. Wood turtles begin to become active at temperatures approaching 7 – 8 ˚C (4 – 5 ˚C in northern populations); this is a higher temperature range than spotted and Blanding's turtles, species that become active at temperatures as low as 2 ˚C, and lower than bog turtles, a species that does not become active until environmental temperatures approach ≈15 ˚C. The relationship between inactivity and CTM is also different between wood turtles and other emydine species. In some populations, wood turtles become inactive at temperatures close to 30 ˚C, a value that is well below their CTM, while box turtles (CTM = ≈ 41 ˚C) and Blanding's turtles (CTM = ≈ 39 ˚C) don't become inactive until environmental temperatures approach their CTM.

Because turtles are ectothermic, environmental temperature is good predictor of behavioral activity state. In fact, in species that bask terrestrially, thermoregulatory behavior is not only dependent on ambient air temperatures and available solar radiation, but also habitat type. Some emydid turtle species (e.g., painted turtles and sliders) are more general in their habitat requirements, while other species (e.g., wood and bog turtles) may require specific canopy cover and plant species associations in order to optimally thermoregulate. Due to increased anthropogenic habitat destruction and fragmentation, this is a conservation issue that is particularly important to endangered species. Most turtle species cannot successfully mitigate habitat destruction due to their life history patterns of late maturity, low recruitment, and high levels of egg predation (Dodd 1990, Congdon *et al*. 1993). Large tracts of undisturbed land, once ideal for turtle species to function within, are now disturbed and suboptimal, sometimes drastically affecting the population structure of turtle communities.

Population Dynamics

Non-Suburban Populations

A non-suburban population is defined as one that exists away from excessive human interaction and is found on larger tracts of relatively unfragmented natural land. Larger, less disturbed tracts of land are associated with increased species diversity and individual species success (Fahrig 2003). Some animal species that are considered “habitat generalists” (e.g., white-tailed deer and fox squirrels) function well in fragmented landscapes at the edges of human suburban sprawl (DeStefano and DeGraff 2003). Yet there are numerous species that are “habitat specialists” requiring undisturbed heterogeneous landscapes. Furthermore, certain species like the Northern spotted owl need large tracts of unfragmented land, and require greater areas of interior habitat to prosper (Lamberson *et al*. 2002). Semi-aquatic turtle species (e.g., wood turtles) utilize multiple different habitat types throughout their yearly cycle, therefore these species are particularly sensitive to the anthropocentric changes of habitat fragmentation, and may not thrive in disturbed suburban habitats (Pittman and Dorcas 2009). Unfortunately, as human population growth and urbanization increases suburban sprawl, it also breaks up large tracts of undisturbed land, forcing what were once non-suburban animal populations to exist as suburban populations.

Suburban Populations

Suburban populations are those densities of animals existing within the outskirts of cities before the onset of open non-suburban land (DeStefano and DeGraff 2003) (Figure 7). These are animals that essentially live in people's backyards, in public recreation areas (e.g., parks, recreational access areas, and golf courses, etc.), and in the fragments of natural land amongst the ever-growing suburban sprawl. Suburban sprawl is noted as one of the most detrimental causes existing today to the loss of species diversity, and is especially harmful to those species requiring large tracts of undisturbed land (Marzluff 2001). However, studies have also demonstrated that at intermediate levels of development, urbanization (or rather 'suburbanization') may offer new areas for certain species to flourish (Blair 1996). Species such as white-tailed deer, wild turkeys, and spiny softshell turtles seem to do remarkably well on habitats that are disturbed and considered suburban (DeStefano and DeGraff 2003, Plummer *et al*. 2008).

Figure 7. Suburban sprawl: the dark green sections between houses are where suburban populations of animals may exist (National Audubon Society 2013).

Unfortunately, species that are sensitive to landscape changes, require specific habitats, and are slow to grow and reproduce, are significantly affected by even moderate suburban development and may become locally extirpated (Destefano and Degraff 2003). Some fast growing species, such as raccoons (*Procyon lotor*), may thrive in human disturbed landscapes (Hoffman and Gottschang 1977). However many slow growing turtle and amphibian species are only marginally successful on suburban landscapes (Gibbs 1998, Baldwin *et al*. 2004). It has been demonstrated that turtle species that move large distances for nesting, mating, and/or feeding often encounter disturbed areas of landscape, such as the presence of roads which produce an increased risk of mortality (Gibbs and Shriver 2002, Baldwin *et al*. 2004). Furthermore, in suburban landscapes the greater density of egg predators such as raccoons put turtle nest sites at increased risk of predation, and as a result turtle populations experience decreased annual recruitment (Marchand and Litvaitis 2004).

Areas that were once wild and natural, and absent regular human presence, are now converted to recreational access areas and public parks in the wake of suburban sprawl. Species that were once isolated, such as the wood turtle (*Glyptemys insculpta*), are now at risk. This is due to regular exposure to humans, human-subsidized predators (primarily raccoons and skunks), and the lack of ideal habitat in the wake of habitat conversion to suburban areas. Species that are particularly sensitive to human disturbance, such as the wood turtle, are in danger of extirpation when their habitat is no longer isolated from human contact (Garber and Burger 1995).

Iowa Wood Turtle Ecological Studies

To date, ecological research has been conducted on only two Iowa wood turtle populations: 1) a 2003 – 2006 study (Tamplin 2006a, Spradling *et al.* 2010, Tamplin in press) surveying the population that occurs along the West Fork of the Cedar River in Butler County (BC) [including the state-owned Big Marsh Wildlife Management Area (BMWMA) and the county-owned West Fork Access Area (WFAA) and adjacent private property], and 2) a 2009 – 2012 study (Williams 2013), analyzing the Black Hawk County (BHC) population located in the Beaver Creek drainage basin [encompassing the county-owned Beaver Creek Falls Access Area (BCFAA) and the surrounding private property].

The BC wood turtle population was intensely surveyed from 2003 – 2006 (and periodically through 2009) by a research group from the University of Northern Iowa. This survey focused on wood turtles inhabiting the southeast corner of BMWMA (East of Highway 14), and the WFAA and the adjacent private property near the junction of the West Fork and the Cedar River near County T55 and Temple Avenue. This population is genetically distinct from wood turtle populations in the Northeastern United States and Minnesota (Spradling *et al*. 2010), and therefore represents a peripheral isolate that is a possible reservoir for distinct alleles absent in populations outside of Iowa. This population is described as a rural population that has exposure to agriculture and limited exposure to human development.

The Black Hawk County population was initially surveyed from 2009 – 2012 (continuing to the present) in BCFAA (a forested floodplain containing 469 hectares and a public access area commonly used for hunting, canoeing, and hiking) (My County Parks 2013) and the adjacent private property that is heavily impacted by anthropogenic development. This wood turtle population is best described as a suburban population consistently in the presence of human disturbance and development. The present analysis utilizes data generated in conjunction with both of these two prior studies; a detailed description of each study site is provided in the materials and methods section, and data on population size and structure is presented in the results section.

Objectives of Study

Temperature selection is critical to all ectotherms and, in particular wood turtles, because they inhabit northern locations that may be thermally challenging, and because they frequently utilize both aquatic and terrestrial habitats. Thus, compared to many other emydid species, wood turtles have a wider range of daily and seasonal ambient temperatures from which to choose. To better develop management and conservation policies for this state endangered species, the thermal ecology, state distribution, population status, and habitat usage of this species must be better understood. Wood turtle activity patterns and their relation to temperature have been documented by only a few studies conducted in Canada and other states (Ernst 1982, Greaves and Litzgus 2007, Dubois *et al*. 2008, 2009). Currently, no published studies exist on the thermal ecology of wood turtles in suburban populations, nor in Iowa, which would potentially reveal how thermal patterns may differ from those of non-suburban populations. Studies have shown wood turtle populations decline in the presence of regular human activities by as much as 100% (Garber and Burger 1995, Willoughby *et al*. 2013). Therefore, assessing differences in behavior and population status as they relate to thermal ecology dynamics in suburban and non-suburban populations is vital to maintaining this species.

The goals of this study are to determine behavioral and habitat usage patterns as they relate to the thermal ecology of Iowa wood turtles, to compare data from a fragmented and smaller suburban population located in Black Hawk County with an adjacent larger rural population in Butler County, and to generate optimal conservation recommendations for each population as they relate to habitat restoration and maintenance. Hypotheses tested are as follows: 1) males will emerge from winter hibernation at lower ambient temperatures than females, this is predicted because males have a larger body size compared to females, and because males are documented as seeking out mates during the early Prenesting period.; 2) males remain active at cooler air and water temperatures when compared to females, this is hypothesized due to male wood turtles having a larger body size compared with female wood turtles; 3) females maintain higher internal body temperatures than males during the Prenesting and Nesting period (e.g., optimize egg development), and 4) turtles of both sexes will maximize optimal thermal gain by differentially utilizing available habitats based on corresponding ambient environmental temperatures, this is hypothesized because wood turtles are known to utilize a variety of habitats throughout their yearly activity cycle as ambient temperatures fluctuate.

CHAPTER 2

MATERIALS AND METHODS

Wood Turtle Sampling

This study was conducted under the Iowa Department of Natural Resources scientific collector's permit SC-647. Wood turtles were tracked intensively in Black Hawk County (BHC) from August 2011 to May 2013, and the present study includes data collected on 7 turtles that were periodically sampled from May 2009 until August 2011. To facilitate comparisons between study sites, the present analysis also incorporates data on wood turtles that were regularly tracked in Butler County (BC) from August 2003 to May 2006 and were to be occasionally sampled until May 2009.

Newly captured turtles were taken back to McCollum Science Hall, University of Northern Iowa for processing. Each turtle was given a unique numerical code and marked by drilling holes along the edges of the posterior marginal carapace scutes (modified from Cagle 1939). When each new turtle was captured, digital calipers (Fisher Scientific Calipers, model: 14-648-17, Grade 3) were used to measure carapace length (CL), plastron length (PL), carapace width (CW), shell height (SH), and head width (HW) to the nearest 0.1 mm. Total tail length (TTL) was calculated as plastron to vent (PV) plus vent to tail tip (VT) (mm) length to the nearest 0.1 mm. Turtles were weighed to determine the total mass (M) in grams (g) to the nearest 0.1 g (OHAUS ES series scale, model ES6R). After scrubbing the shells of each turtle to remove algae and detritus, they were photographed to document each turtle's unique appearance, including abnormalities and/or injuries.

Turtle age and sex (hatchling, juvenile, subadult or adult) were determined based on body size, number of growth annuli, and shell appearance. Age of adult turtles > 20 years of age was assessed in 5 year estimates (e.g., 21 – 25, 26 – 30 years of age, etc.), with turtles in the oldest category designated as being > 35 years of age. If captured near the nesting season (late-May to mid-June) female turtles were palpated for gravidity.

Radio Telemetry

For turtles that were designated for radio telemetry tracking, transmitters were attached with PC-7 (Protective Coatings, Inc.) epoxy to the right third and fourth costal scutes on the carapace (Eckler *et al*. 1990). The epoxy was allowed to dry for 24 – 48 hours, and then each turtle was released at its individual capture site (Figure 8). Each transmitter, including applied epoxy, weighed ≈ 46 g and represented 3.6 – 4.9% of each turtle's body mass. New adult wood turtles that were not designated for radio tracking were still processed and marked with marginal scute carapace holes in case of further encounters. In BHC, 25 adult turtles (13 females, 12 males) were equipped with a radio transmitter [Advanced Telemetry Systems (ATS) model R2220]. The battery life of each ATS transmitter is ≈ 9 years, so these transmitters were left attached to the turtle(s) for future research at this study site in BHC. In BC, 15 adult turtles (9 females, 6 males) were equipped with radio transmitters (HABIT Research VHF model 1010); because the battery life is shorter for this model, the BC radio transmitters were removed after ≈ 3 years of use.

Study Sites

Black Hawk County

Field data was collected in Beaver Creek Falls Access Area (BCFAA) and the surrounding private property in Black Hawk County, Iowa. This site is regularly disturbed by human presence (e.g., ATV use, bird blinds, hunting, canoeing, tubing, and hiking) and is divided into a West and East section by North Union Road (a paved county road). The West section of the study site (Figure 9) extends ≈ 0.93 kilometers (km) West of North Union Road and is significantly disturbed by suburban development; it contains private property including homes, city streets, Beaver Hills Country Club, a golf course, housing developments, and adjacent agricultural land found within 70 – 330 m from Beaver Creek.

The East section (Figure 10) of the field site is a protected, undeveloped forested floodplain (BCFAA) owned by BHC that runs parallel to the Cedar River and includes an elevated railroad line. North of the East section is leased agricultural land and South of the East section of the creek, to the western side of the railroad line is a small section of agricultural land that is used as cropland or a hayfield. The BCFAA is a heavily wooded area containing a variety of deciduous trees species such as American Elm (*Ulmus Americana*), Mulberry (*Morus rubra*), Silver Maple (*Acer saccharinum*), and Eastern Cottonwood (*Populus deltoides*) (Snyder 1994). Beaver Creek flows West to East, emptying into the Cedar River at latitude 42˚ 33' N and longitude 92˚ 29' W.

Figure 8. Adult male wood turtle (IA29) from Butler County with transmitter attached (Photo by Jeffrey W. Tamplin).

The Beaver Creek area is comprised of dense deciduous riparian woodlands impacted by the presence of the American beaver (*Castor canadensis*). Numerous areas along the West and East portions of the study site display evident beaver dams and stream structure and forms maintained by yearly flooding. In recent decades the Cedar River drainage basin, including Beaver Creek, has experienced a substantial increase in the frequency and the strength of flooding events, perhaps due to the effects of climate change as well as altered agricultural practices in the surrounding farmland (Spradling *et al.* 2010).

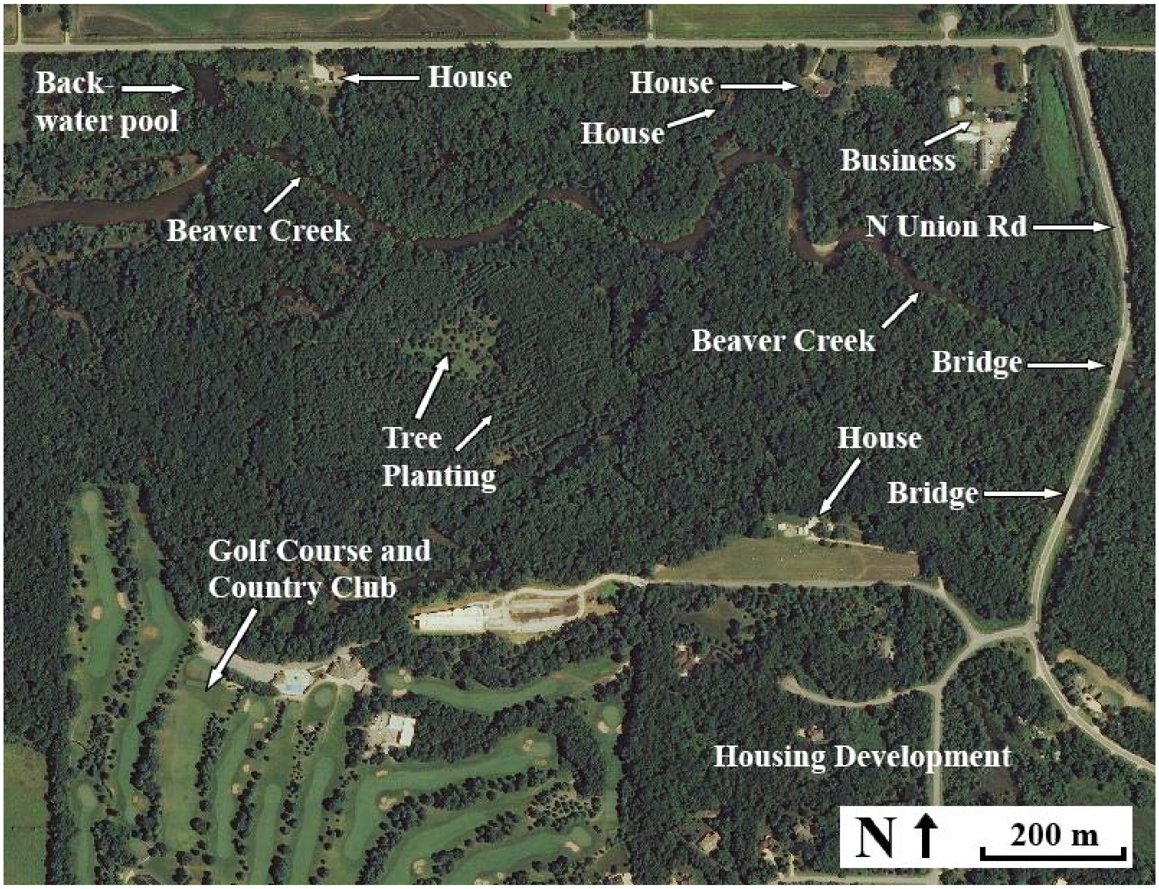

Figure 9. Aerial photo of the West section of the study site along Beaver Creek in Black Hawk County (BHC).

<u>Butler County</u>

Field data was also collected on a population of wood turtles in Butler County, Iowa, at two different sites along the West Fork Cedar River (WFCR): the state-owned Big Marsh Wildlife Management Area (BMWMA) (Figure 11) and the county-owned West Fork Access Area and the adjacent private property (WFAA/PP) (Figure 12).

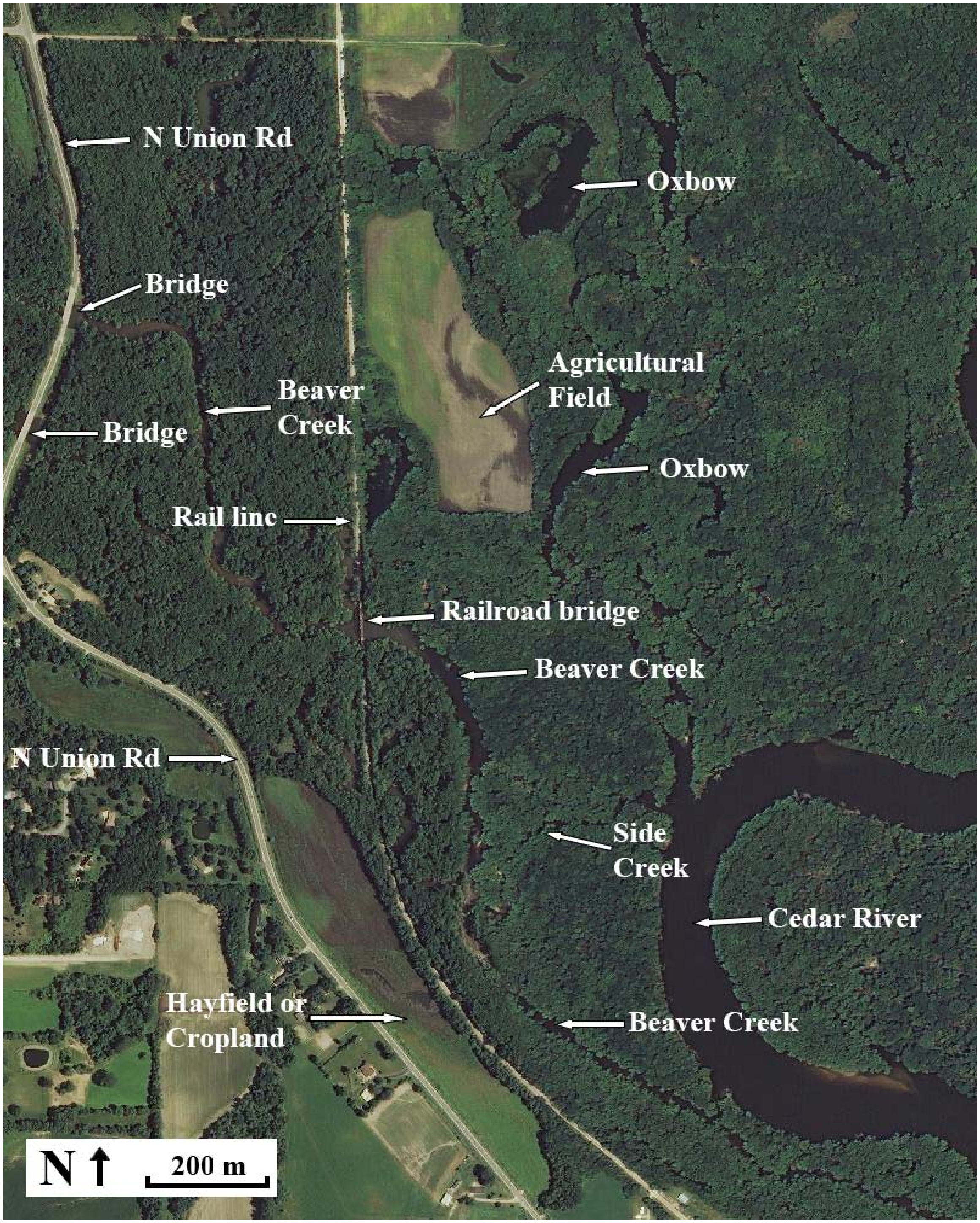

Figure 10. Aerial photo of the East section (BCFAA) of the study site along Beaver Creek in Black Hawk County (BHC).

These two areas are separated by ≈ 14 km along the WFCR but the surrounding riparian and forestland is similar and Spradling *et al.* (2010) considered this a single population. The BC population exists on larger tracts of land than the BHC population and is characterized by reduced levels of human disturbance.

Big Marsh Wildlife Management Area (latitude 42˚ 39’ N and longitude 92˚ 47’ W) is located six miles north of Parkersburg, contains 2,037.2 hectares, and is comprised of 50% grassland, 25% timber, and 25% wetland habitat (Big Marsh WMA 2013). The BMWMA is a partial refuge area for birds and other wildlife; hunting and non-motorized recreational activities are permitted in the area. In the present study, wood turtles were surveyed in the southeast corner of BMWMA, East of Highway 14. The location is comprised of mixed deciduous woodlands, with large pockets of open grassy clearings, bordered by private agricultural land, and is prone to yearly flooding events.

The WFAA/PP site (latitude 42˚ 38’ N and longitude 92˚ 38’ W) includes hayfields, a motocross track, a county hunting and recreation area and a portion of land was formerly used as cattle pasture several decades ago. Except for the motocross track, this land has been mostly maintained for conservation purposes for the past 30 – 40 years. The BC population of wood turtles is best described as a rural population that encounters limited human interaction; in the past 30 to 80 years, much of the anthropogenic disturbance on this population has been agricultural.

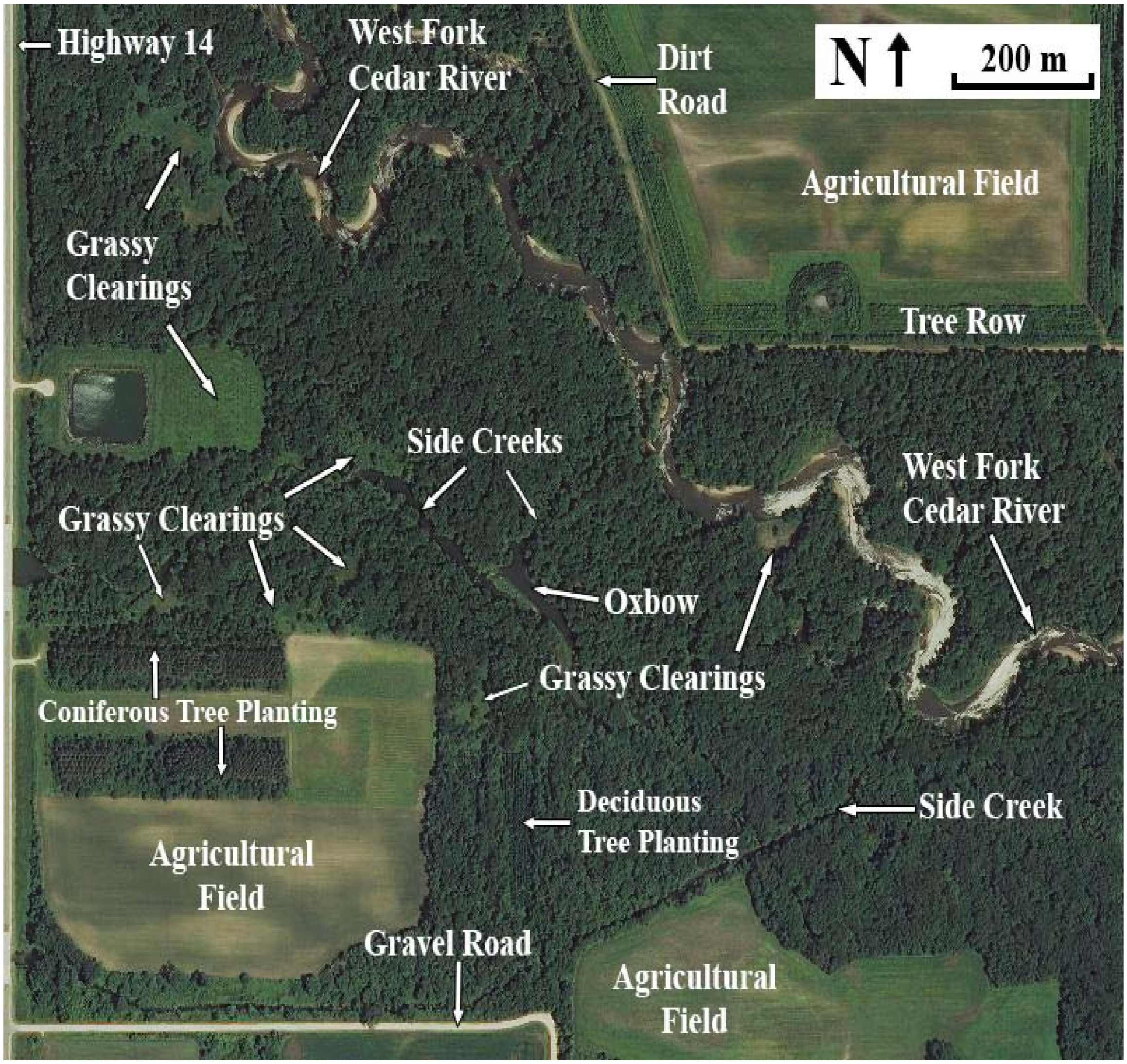

Figure 11. Aerial photo of the BMWMA study site along the West Fork Cedar River in Butler County (BC).

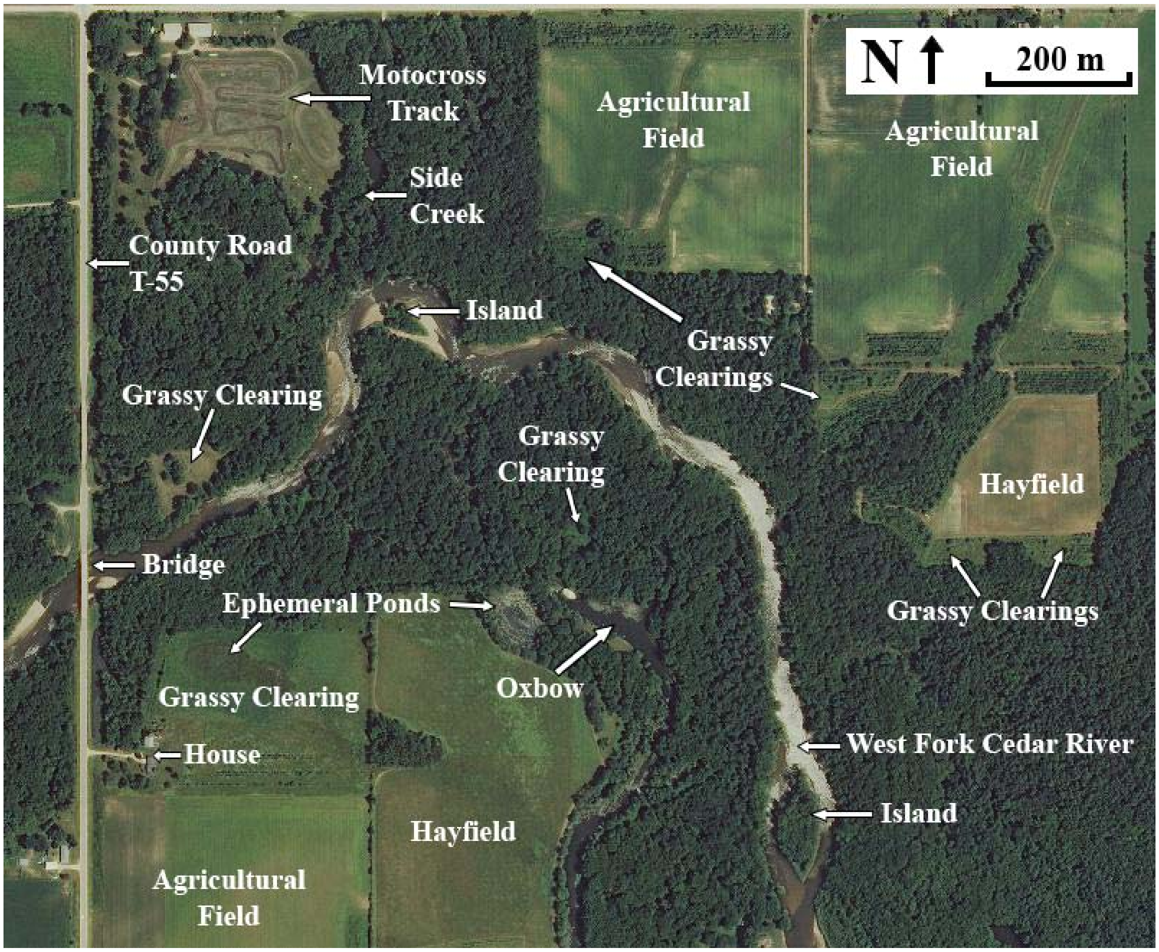

Figure 12. Aerial photo of the WFAA/PP study site along the West Fork Cedar River in Butler County (BC).

Data Sampling

During the winter months (mid-November to mid-March) turtles were tracked via radio telemetry once per week, as this species is well documented to be inactive and mostly non-mobile during its hibernation period (Ernst and Lovich 2009). During active months (March – November) turtles were tracked ≈ 3 times a week on non-consecutive days, and during nesting season (late-May – mid-June) turtles were tracked up to 5 days a week to identify as many nesting sites as possible. Data was analyzed by 5 predefined activity periods for wood turtles: Hibernation, Prenesting, Nesting, Postnesting, and Prehibernation (Arvisais *et al*., 2004). The exact dates encompassed by each activity period fluctuate annually based on seasonal climate patterns and yearly temperature variation.

At each study site, field data collection occurred between 1200 – 2000 hours in a manner designed to maximize the number of individual encounters without sampling the same turtle more than once per field day. In both BHC and BC, turtles were randomly selected for tracking on each field day and search patterns were not specific (i.e., the same sequence of locating individuals was not repeated on successive days). Due to field conditions, not every one of the radio-tracked turtles was located each time. Upon locating each turtle, the following data was recorded: GPS coordinates (latitude and longitude; elevation, in feet) (GARMIN GPS Map 60CSX), weather conditions (relative cloud cover, precipitation, humidity, and wind speed), turtle body temperature and corresponding environmental temperatures (see below for further description), habitat type (based on amount and type of canopy cover and dominant plant associations present), distance to water (if in a terrestrial location; in m), percent exposure of the turtle as observed from directly above (0 – 100% visibility in 5% intervals; value determined as an average from each field observer's response), sunlight intensity (if located in terrestrial habitats), water depth (if located in aquatic habitats), and any observed interactions between turtles (e.g., mating, aggressive or neutral social interactions).

When located, turtles were categorized as conducting 1 of 8 types of behaviors in either aquatic or terrestrial habitats. These include basking (≥ 20% exposed to direct sunlight), hiding (< 20% exposed to direct sunlight), walking, swimming, feeding, socializing, mating, and nesting. When turtles were located, the habitat was recorded as 1 of the 10 different types of basic habitats available at the study sites: lotic water (flowing), lentic water (stagnant), deciduous forest, emergent grasses and forbs, grasses and willow saplings, riverbank (with sparse cover), open riverbank (almost no cover), agricultural field, non-cultivated field, and other (e.g., private backyard, roadside ditch, railroad embankment, etc.).

Thermal data was recorded to the nearest 0.1 ˚C with a Fisher Scientific waterproof digital thermometer (model number 15-077-9D). When a turtle was located, internal body temperature (T_b) (cloacal) of each turtle and the corresponding environmental values [air (T_a) and soil (T_s) temperature at the turtle location, and water (T_w) temperature from the nearest permanent lotic or lentic water source] were recorded. In terrestrial habitats, sunlight exposure (value in Lux) of each turtle was recorded directly on the turtle's carapace with a Fisher Scientific Light Meter; in addition, corresponding environmental values of sunlight intensity were recorded within 10 m of the turtle location (minimum: values in the shadiest spot; maximum: value of the most sun exposed spot; and, an average value determined by the field observers to represent the dominant microhabitat type within 10 m of the turtle).

If the turtle was located in the water, I recorded water depth (in cm) of the turtle's location, maximum water depth, minimum water depth, and channel water depth within

10 m of the turtle's location was recorded. Environmental values on sunlight intensity and water depth from areas within 10 m of each turtle location were recorded to facilitate comparisons with the turtle's immediate habitat choice, including specific microhabitats. Other data collected included presence of ectoparasites (e.g., leeches, mosquitos), new injuries and abnormalities, and specific GPS coordinates of nest locations for an individual turtle.

In this study, thermal point data was utilized instead of continuous-sampling remote temperature data loggers so that exact location, habitat type, and turtle behavior could be correlated with temperature values. In addition, data loggers may not give accurate internal body temperature readings and are subject to disparities under extreme temperatures; data loggers are particularly inaccurate when equilibrating between air and water exposure (Ropert-Coudert and Wilson 2004, Edwards and Blouin-Demers 2007). This factor may be particularly exacerbated with semi-aquatic species such as wood turtles that select from a wide variety of aquatic and terrestrial habitats for thermoregulation. Although some studies have indicated that placement position of data loggers may mitigate the differences between internal body temperature and external shell temperature (Dubois *et al.* 2009), other studies utilizing external data loggers on turtles have produced temperatures that are above that species' CTM (Edwards and Blouin-Demers 2007). Dubois *et al.* (2009) were successful in demonstrating in wood turtles that surgically implanted data loggers (that yield a true internal body temperature) did not produce temperatures that were significantly different from those of data loggers glued to the skin of the inner hind leg cavity. However, given that wood turtles are an endangered species in Iowa, the risk of surgical implantation or any potential damage to the skin by affixing and later removing data loggers was not deemed appropriate.

Although studies utilizing data loggers may provide continuous thermal data and yield a larger quantity of data, a weakness of this type of data is the inability to correlate thermal values with habitat use and behavior. Data loggers are most useful when analyzing fully aquatic species or analyzing hibernation temperatures of semi-aquatic species that are inactive and constantly submerged during hibernation (Greaves and Litzgus 2007). In the present study, environmental and turtle body temperatures was sampled directly so these thermal data would directly correspond to turtle behavior and activity, to exact locations, and to eliminate inferred behavior (e.g., a temperature spike recorded by data logger being interpreted as a "basking event").

Data Analysis

All field data was partitioned and organized with StatView (ABACUS Concepts, Inc.). The Lincoln-Peterson Index was used to estimate population size based on the proportion of marked and unmarked wood turtles in the population, with a probability that the individuals will be recaptured from the same population. Significance level for all statistical analysis was set at alpha = 0.05, and unpaired two-tailed t-tests were used to determine if there were significant differences in body size (CL, PL, mass) between sexes and study sites. In StatView, the entire data sets for both the BC (2003 – 2009) and the BHC (2009 – 2013) wood turtles were utilized calculate mean values for temperatures, light intensities, distance to water, water depths, and percent exposure. This was done in order to deduce values that were true means across a broad range of study years, and to counteract seasonal extreme value fluctuations (e.g., temperatures and water depths during cold spells, flood events, heat wave and drought years, etc.).

For all other statistics, RStudio Version 0.98.501 – © 2009-2013 (RStudio, Inc.) was utilized to test for significance for all relevant data: turtle body temperature (˚C), turtle sunlight exposure (Lux), turtle water depth (cm), turtle distance to water (m), and turtle percent exposure. Data were analyzed to determine differences intersexually by activity periods within the same county (e.g., Black Hawk and Butler County), and intrasexually by activity periods between counties. A 2-way ANOVA was used to determine if significant variation occurred between the main effects of sex and activity period, and between the interactions of sex, activity period, and county. To address the issue of psuedoreplication and time in this data set, statistical tests using RStudio only compared Black Hawk County year 2012 to Butler County year(s) 2004 and 2005, and each "day" within each year was given an exact Julian calendar date (e.g., January 1 = 1). Additionally, the term "individual code" (e.g., IA10 or IA29) was included as a random factor to also counteract the psuedoreplication issue. Including the terms "day" and "individual code" eliminated any potential variation caused by differences between individuals.

Three fundamental equations were used within RStudio to test for significance and probability values:

1) Yearly Scale: (X ~ day + I(day^2) + sex + county, random =~ 1|code , data = X)

2) Yearly Scale without (day of year)^2: (X ~ day + sex + county, random =~ 1|code , data = X)

3) By Activity Periods: (X ~ day + sex + county, random =~ 1|code , data = X, subset = period=="X")

The day of year was computed as: (day of year)^2; the reasoning behind this is due to seasonal differences in ambient temperature [i.e., the beginning and end of the year are characterized by cold temperatures, and the middle portion of the annual cycle is comprised of warm/hot temperatures; therefore, the day of year would not be linearly related to the factors (e.g., turtle body temp, turtle water depth, etc.) among which significance was tested]. Rather, it may be a bell shaped curve, and therefore day of year^2 might also be a bell shaped curve. However, if a statistical test determined that a factor was of marginal significance across the entire year, then (day of year)^2 was removed. This was because including (day of year)^2 in the equation may have reduced some of the variation found within the data set. Furthermore, because the sample size may be considered reduced compared to other studies, data of marginal significance were not immediately discounted.

CHAPTER 3

RESULTS

Morphometrics, Population Size and Structure

Black Hawk County

In BHC from May 2009 – May 2013, a total of 35 turtles were captured and marked in the Beaver Creek watershed. Of the 35 captured turtles, 16 (45.7%) were females, 16 (45.7%) were males, and 3 (8.6%) were juveniles; one turtle (IA64) was initially captured as and 8-year-old juvenile in 2009 and matured into an adult female (based on carapace length) during the course of the study. The first 25 adult turtles (13 females and 12 males) captured were equipped with a radio transmitter and the remaining 10 turtles were marked for future identification so that if new turtles were located we would be able to distinguish new turtles from previously identified turtles. The adult sex ratio of the BHC population was 1:1 (50% female and 50% male); based on the Lincoln-Peterson Index mark-recapture method the total population size was estimated to be 39 turtles (95% confidence interval = 33 – 45) (Williams 2013).

Of the 35 turtles sampled, 6 (17.1%) were missing at least one limb and 13 (37.1%) were missing a substantial portion of their tail. During the first two years of the study period, only one death was documented: a > 25-year-old male that was potentially killed by a mesopredator. Adult survival frequency during the study period was 97.1%. Immediately after this study terminated, there was record flooding in the Beaver Creek watershed during the summer of 2013 and 4 additional deaths (two > 25-year-old males, and two > 25-year-old females) occurred, reducing adult survival frequency to 85.7% and increasing mortality to 14.3%.

For BHC wood turtles, the mean male CL was 198.2 mm (±8.5 SD; n=16), and the mean female CL was 186.1 mm (±5.7 SD; n=16) (Table 1). The mean CL for 3 juveniles was 138.8 mm (±27.2 SD; n=3). The mean PL for males (n=16) was 173.0 mm (± 28.9 SD) and the mean PL for females (n=16) was 179.6 mm (±8.8 SD); the mean PL for juveniles (n=3) was 124.8 mm (±25.1 SD).

Males had a significantly larger CL than females (unpaired T-test, df = 29, t-value = -4.7, P-value: < 0.001), however there was no significant difference in PL between males and females (unpaired T-test, df = 29, t-value = 2.0, P-value = 0.0531). Mean male mass was 998.3 g (±309.5 SD; n=16) and mean female mass was 989.1 g (±112.2 SD; n=16). The mean mass for the 3 juveniles was 345.3 g (±102.7 SD). There was no significant difference in mass between males and females (unpaired t-test, df = 29, t-value = -0.1, P-value = 0.8981). At the initial encounter, 88.6% of adult turtles in BHC were recorded as 21 years or older in age, with 30 (85.7% of the population) turtles of both sexes being of 26 years or older in age (Figure 13.).

Table 1. Morphometrics (mean CL, PL, M, SW, SH, HW, PV, VT, TTL) of turtles from BHC (females n=16, males n=16) and BC (females n=36, males n=24). In BC, three males and one female were first encountered dead and therefore soft tissue measurements (M, HW, PV, VT, and TTL) were not taken. Additionally, one BC male was encountered as a dismembered shell and age was the only measurement taken. All values are mm (±SD), except M = g (±SD).

	CL (±SD)	PL (±SD)	M (±SD) (g)	SW (±SD)	SH (±SD)	HW (±SD)	PV (±SD)	VT (±SD)	TTL (±SD)
	Range	Range	Range	Range	Range	Range	Range	Range	Range
BHC Female	186.1 (±5.7)	179.6 (±8.8)	989.1 (±112.2)	139.9 (±7.3)	72.3 (±3.8)	29.4 (±1.5)	19.6 (±3.9)	33.6 (±20.2)	53.2 (±21.7)
	178.0 – 196.7	160.9 – 191.2	702.0 – 1134.0	123.9 – 152.7	65.3 – 77.7	25.8 – 31.8	12.4 – 28.6	10.2 – 78.1	29.2 – 102.9
BC Female	181.7 (±6.9)	166.3 (±7.2)	943.8 (±105.2)	135.3 (±6.4)	71.5 (±3.0)	28.6 (±1.7)	19.6 (±5.4)	28.2 (±13.6)	47.8 (±15.5)
	168.4 – 195.8	151.2 – 189.7	738.0 – 1263.0	123.9 – 150.0	64.5 – 80.3	23.5 – 32.0	9.9 – 38.9	10.3 – 77.2	23.1 – 93.6
BHC Male	198.2 (±8.5)	173.0 (±9.5)	998.9 (±250.7)	142.3 (±5.3)	71.6 (±3.4)	37.0 (±7.7)	36.6 (±10.2)	45.9 (±20.0)	82.4 (±25.7)
	182.5 – 212.2	159.0 – 192.9	100.4 – 1180.4	133.0 – 150.9	66.6 – 76.5	28.7 – 64.5	14.1 – 47.7	18.8 – 79.4	44.5 – 127.1
BC Male	192.7 (±8.1)	163.0 (±6.1)	985.2 (±288.6)	135.9 (±5.2)	72.0 (±4.1)	35.0 (±2.1)	37.4 (±7.0)	46.2 (±15.1)	83.5 (±19.4)
	180.3 – 208.2	153.0 – 176.7	807.3 – 1140.0	127.1 – 145.7	62.2 – 77.6	29.6 – 37.6	18.6 – 46.1	21.6 – 70.2	40.3 – 113.4

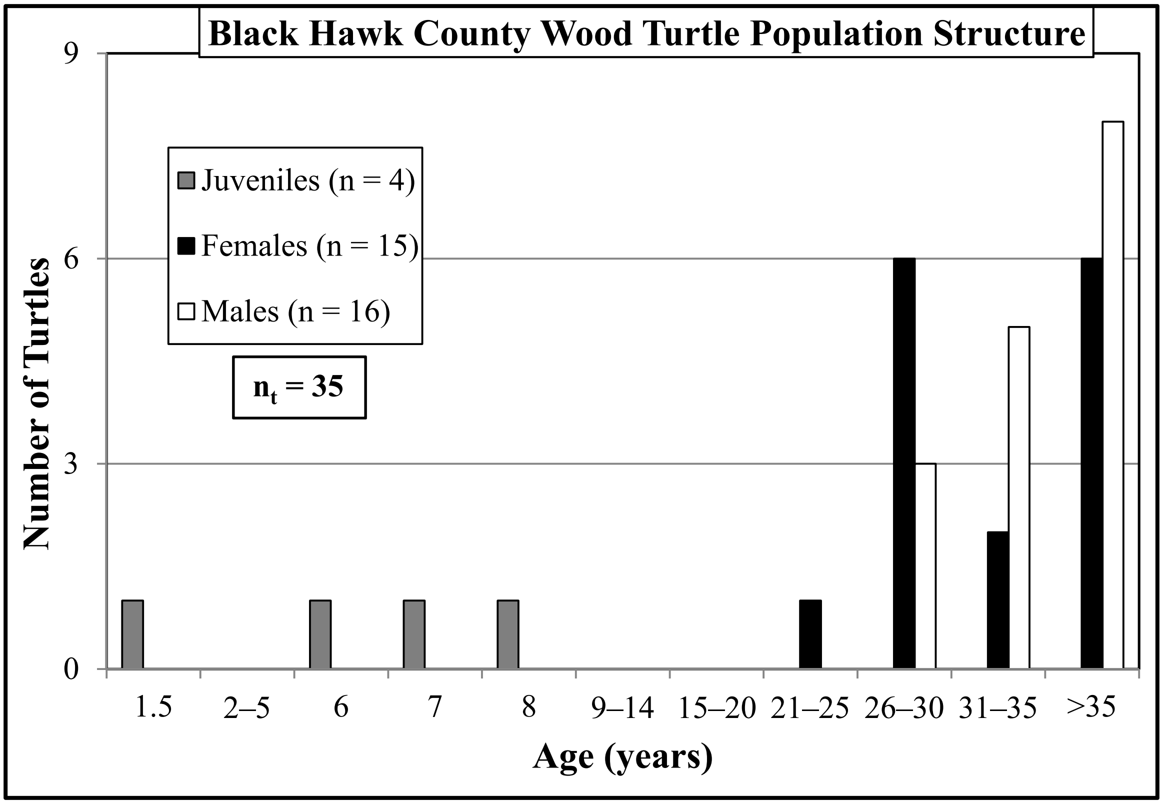

Figure 13. Age of each adult turtle upon initial encounter in BHC (n_t=35).

Butler County

A total of 61 turtles were captured and marked in BC from 2003 – 2009. Of the 61 captured turtles, 36 (59.0%) were female and 24 (39.3%) were male; only 1 (1.7%) juvenile was located. Fifteen adult turtles were equipped with a radio transmitter (9 females and 6 males) and the remaining 46 turtles were marked for future identification. The adult sex ratio of the BC population was 3:2 (60.0% female and 40.0% male) and the Lincoln-Petersen index total population size was estimated at 77 turtles (95% confidence interval = 61 – 110) (Spradling *et al.* 2010). Of the 61 turtles sampled, 11 (18.0%) were missing at least one limb and one > 35-year old male was missing both forelimbs.

The mean male CL was 192.7 mm (±8.1 SD; n=24) and the mean female CL was 181.7 mm (±6.9 SD; n=35). Carapace length of the only juvenile was 160.8 mm. The mean PL for males was 163.0 mm (± 6.1 SD; n=24) and the mean PL for females was 166.3 mm (±7.2 SD; n=35). The single juvenile PL was 138.6 mm. Males had a significantly larger CL than females (unpaired T-test, df = 57, t-value = -5.6, P-value < 0.0001); however, there was no significant difference in PL between males and females (unpaired T-test, df = 57, t-value = 1.8, P-value = 0.0817). Mean male mass was 985.2 g (± 288.6 SD; n=21) and mean female mass was 943.8 g (±105.2 SD; n=34), and there was no significant difference in mass between females and males females (unpaired T-test, df = 57, t-value = 0.624, P-value = 0.5351). Juvenile mass was 463.4 g.

Only 2 deaths were recorded over a 6-year period; a 21 – 25 year old female was killed in a flood event, and a second older female (> 35 years old) died of unknown causes. Adult survival rate was 96.7% and mortality was 3.3%. At the initial encounter, 63.9% of adult wood turtles in BC were recorded as 21 years or older in age, with 34 (55.7% of the population) turtles of both sexes being 21 – 30 years of age (Figure 14). Population structure for both study sites indicates that these populations consist of older adults with low numbers of juveniles (Figures 15 and 16).

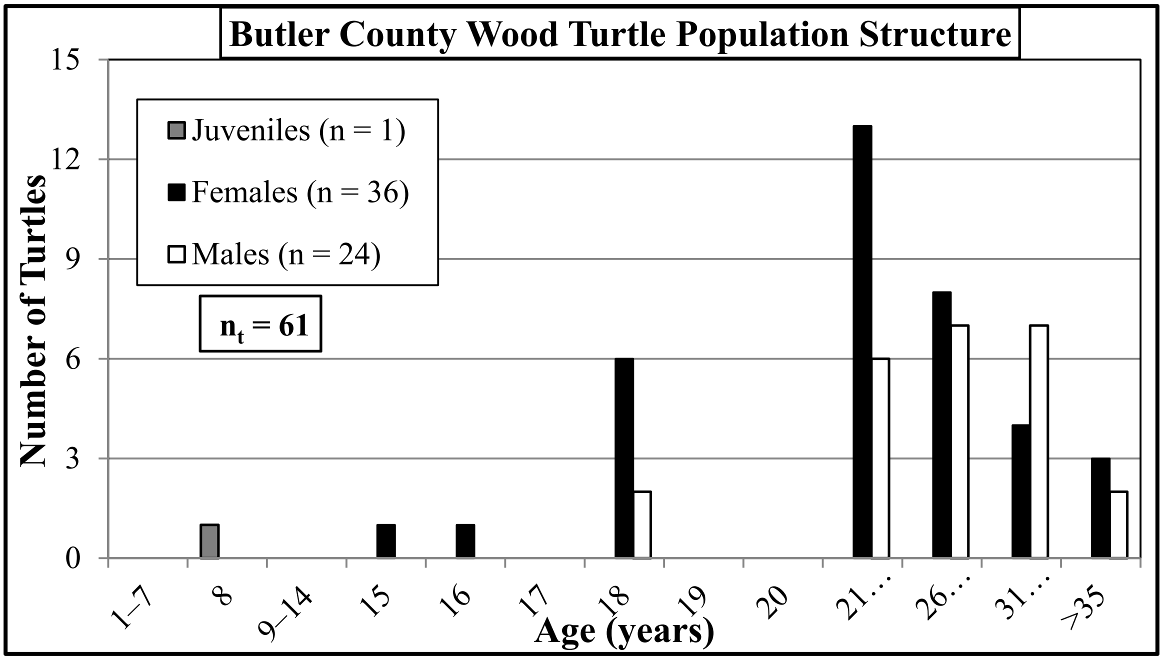

Figure 14. Age of each wood turtle upon first encounter in BC (n_t =61).

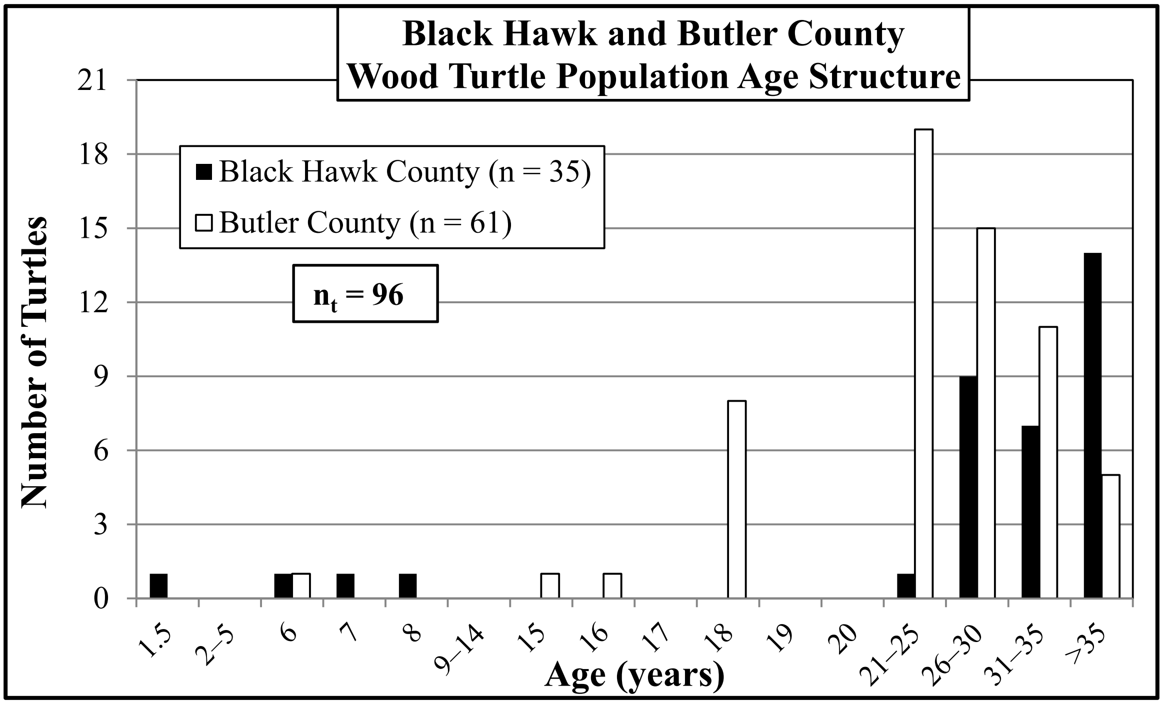

Figure 15. Comparison of wood turtle age structure in Black Hawk County (n=35) and Butler County (n=61).

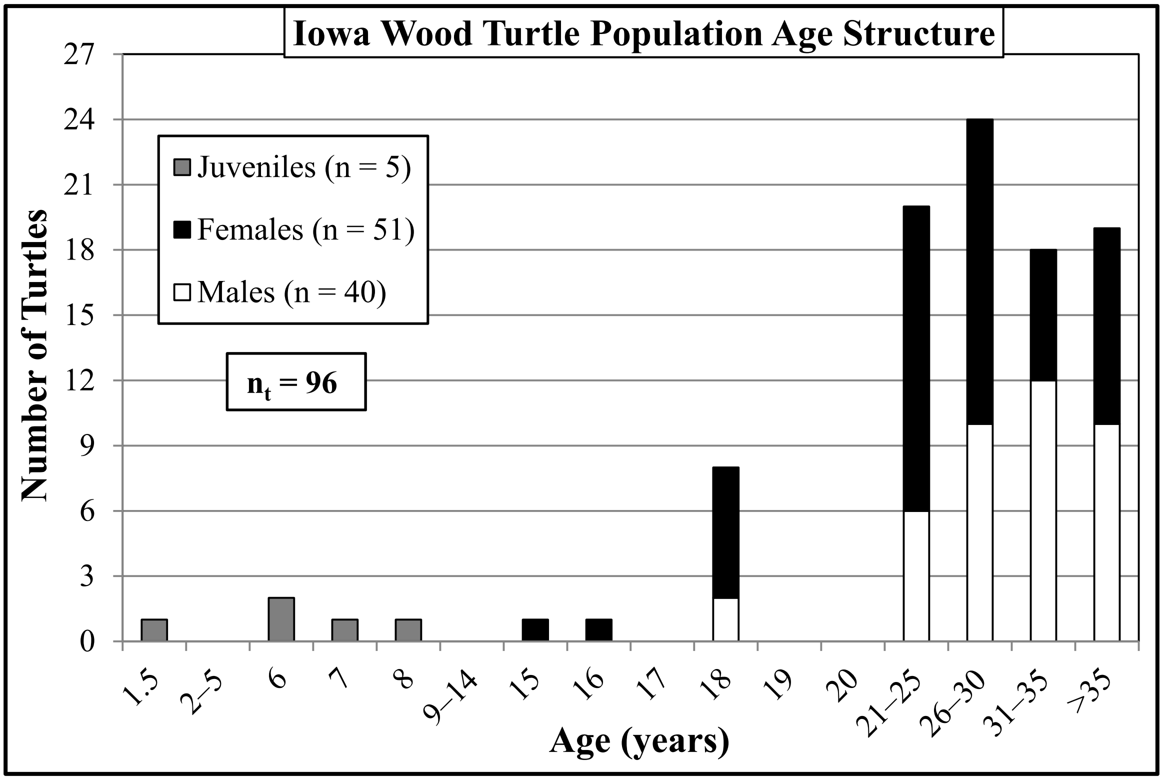

Figure 16. Sex and age of Iowa wood turtles upon first encounter; Juveniles: 5.2% (n=5), Females: 53.1% (n=51), and Males: 41.7% (n=40).

Temperature Data

Black Hawk County

Wood turtles in BHC were inactive during the Hibernation period and had a mean body temperature of 1.8 ˚C (±0.1 SE; n=606). Corresponding mean environmental temperatures during hibernation were: air = 2.6 ˚C (±0.3 SE), water = 1.8 ˚C (±0.1 SE), and soil = 0.9 ˚C (±0.1 SE). Females maintained a mean body temperature of 1.7 ˚C (±0.2 SE; n=316), and males maintained a mean body temperature of 1.9 ˚C (±0.2 SE; n=290) (Figure 17). Female and male wood turtles were not significantly different in body temperature during the 2012 Hibernation period (ANOVA: df = 1, F-value = 0.0153, P-value = 0.9027).

Turtles became active during Prenesting and maintained a mean body temperature [18.5 ˚C (±0.5 SE; n=324)] that was higher than the corresponding mean environmental values [air = 17.7 ˚C (±0.4 SE), water = 14.2 ˚C (±0.3 SE), and soil = 12.1 ˚C (±0.3 SE)]. Prenesting female mean body temperature was 18.5 ˚C (±0.6 SE; n=198), and male mean body temperature was 18.3 ˚C (±0.7 SE; n=124). During the 2012 Prenesting period in BHC, female and male turtles did not significantly differ in body temperature (ANOVA: df = 1, F-value = 0.2822, P-value = 0.6021). The 3 juvenile turtles documented at BHC were found during the Prenesting period and each was only encountered once; mean juvenile body temperature was 28.6 ˚C (±1.9 SE); corresponding environmental mean temperatures were: air = 25.0 ˚C (±4.2 SE), water = 19.3 ˚C (±1.4 SE), and soil = 18.9 ˚C (±1.6 SE).

During the Prenesting period, mating was observed 4 times in lotic water sources with a mean water temperature of 12.6 ˚C (±2.9 SE) (range = 12.5 – 12.6 ˚C). During mating events, turtle mean body temperature was 13.6 ˚C (±0.09 SE; n=2) in females and 12.6 ˚C (±0.01 SE; n=2) in males. The first terrestrial activity of both females and males in BHC was observed at a body temperature of 19.7 ˚C (Table 2). Feeding behavior began during Prenesting, and the lowest body temperature at which feeding was witnessed was 28.1 ˚C in a female and 26.4 ˚C in a male.

Table 2. Temperatures (˚C) associated with specific behaviors in BHC and BC. Other than mating (BHC, n=10; and BC, n=16), other behaviors solely reflect the individual highest, lowest, earliest, or latest recorded incidence of each behavior (e.g., terrestrial activity at the coldest temperature, n=1). Means are combined female and male wood turtle values.

BHC	**Male**	**Female**	**Mean**	**Air**	**Water**	**Soil**
First Aquatic Activity	10.3	10.0	10.2	11.8	10.2	7.3
First Terrestrial Activity	19.7	19.7	19.7	21.1	15.8	11.6
Mating	12.8	13.2	13.0	15.9	12.8	12.3
Feeding	26.4	28.1	27.2	22.6	15.2	15.1
Highest Temperature, Terrestrial Active	33.4	33.4	33.4	35.7	27.5	26.3
Lowest Temperature, Terrestrial Active	12.3	14.7	13.5	17.6	12.8	12.9
BC	**Male**	**Female**	**Mean**	**Air**	**Water**	**Soil**
First Aquatic Activity	12.6	11.6	12.1	18.4	12.1	9.2
First Terrestrial Activity	23.1	27.5	24.6	20.9	13	9.7
Mating	16.6	17.4	16.9	16.8	14.9	13
Feeding	13.9	20.1	17.0	19.1	15.8	14.1
Highest Temperature, Terrestrial Active	34.3	33.4	33.8	29.2	21.5	18.8
Lowest Temperature, Terrestrial Active	15.3	9.2	12.2	12.5	15.2	11.9

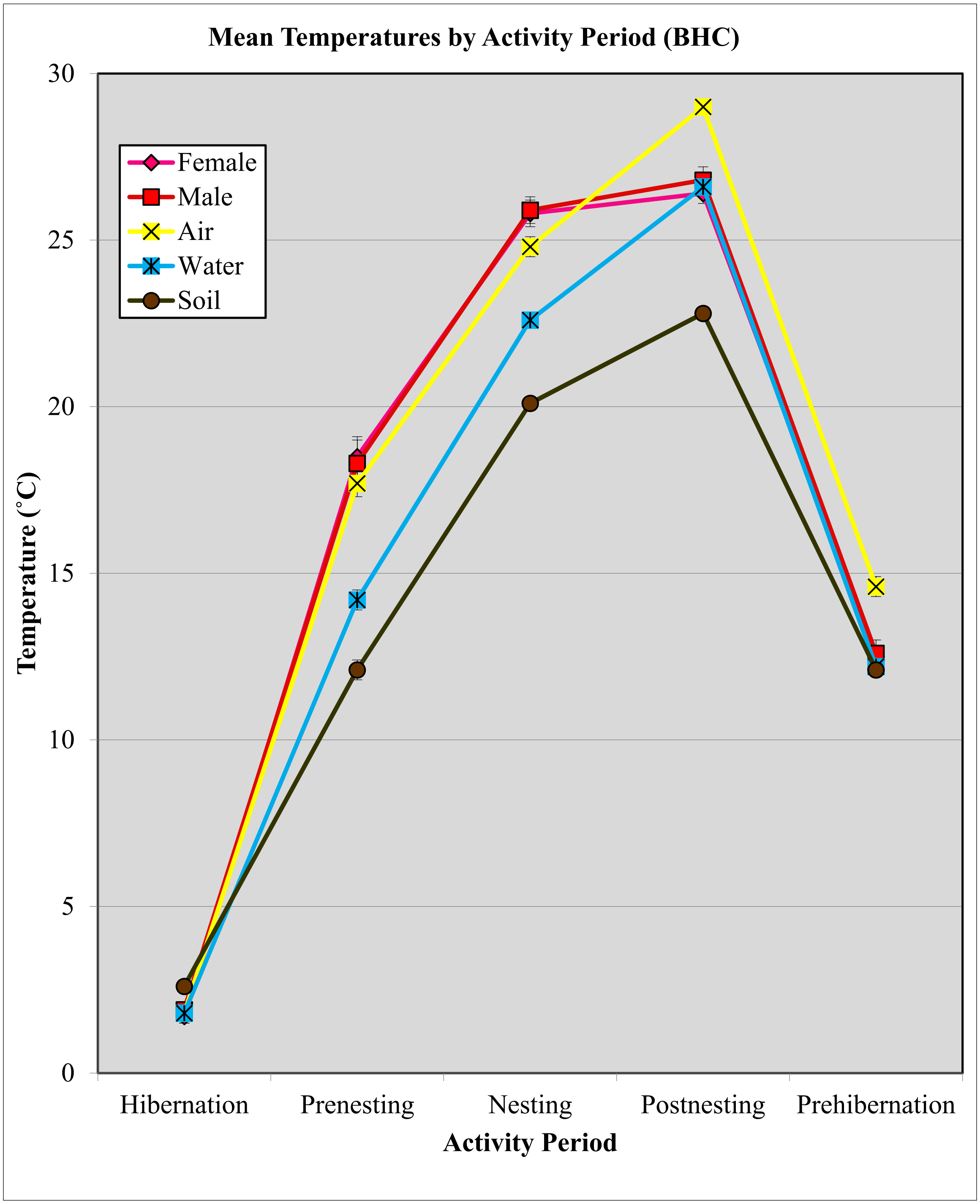

Figure 17. Turtle body and corresponding environmental temperatures recorded by activity period in BHC (n_t=1947); values are means ± SE.

During the Nesting period in BHC, turtles maintained a mean body temperature [25.9 ˚C (±0.3 SE; n=212)] that was higher than the corresponding mean environmental temperatures [air = 24.9 ˚C (±0.3 SE), water = 22.6 ˚C (±0.2 SE), and soil = 20.1 ˚C (±0.2 SE)]. Female [25.8 ˚C (±0.4 SE; n=99)] and male [25.9 ˚C (±0.4 SE; n=113)] mean body temperatures were similar and during the 2012 Nesting period, male and female turtle body temperatures were not significantly different (ANOVA: df = 1, F-value = 0.453, P-value = 0.5077).

For the Postnesting period, mean turtle body temperature [26.5 ˚C (±0.2 SE; n=381)] was maintained below the mean air temperature [29.0 ˚C (±0.2 SE)] and most similar to mean water temperature [26.6 ˚C (±0.2)]; mean soil temperature during this period was 12.5 ˚C (±0.2 SE). Postnesting mean body temperatures were similar for females [26.4 ˚C (±0.3 SE; n=267)] and males [26.8 ˚C (±0.4 SE; n=114)]. During the 2012 Postnesting period in BHC, male and female turtle body temperatures were marginally significantly different only when analyzed with I(day^2) (ANOVA: df = 1, F-value = 3.766, T-value = 1.9404, P-value = 0.0532); BHC male turtles had a 0.8 ˚C (±0.4 SE) higher mean body temperature than females. Environmental temperatures were highest throughout this study during the Postnesting period, and the highest body temperature at which turtles were observed as still active was 33.4 ˚C. At or above this temperature, 100% of surveyed turtles were inactive, and sought out shade or returned to water sources.

During the Prehibernation period, environmental temperatures decreased and turtles returned to lotic water sources. During this period, turtles became more aquatic and began to move towards their potential hibernation sites. During Prehibernation, mean turtle body temperature [12.6 ˚C (±0.3 SE; n=424)] was below the mean air temperature [14.6 ˚C (±0.3 SE)] and most similar to the mean water [12.2 ˚C (±0.2 SE)] and soil [12.1 ˚C (±0.2 SE)] temperatures. Female [12.5 ˚C (±0.3 SE; n=269)] and male [12.6 ˚C (±0.4; n=155)] mean body temperatures were nearly identical during Prehibernation across the entire study period. During the 2012 Prehibernation period, female and male turtles did not significantly differ in body temperature (ANOVA: df = 1, F-value = 0.429, P-value = 0.5132). The coldest body temperature at which turtles were still active terrestrially was 14.7 ˚C in females and 12.3 ˚C in males. During the fall Prehibernation period 3 mating events were observed in lotic habitats with a mean water temperature of 13.0 ˚C (±0.9 SE; range = 10.2 – 14.8 ˚C). Three female and 3 male turtles were recorded mating with mean body temperatures of 13.0 ˚C (±1.4 SE).

In Black Hawk County, across the entire study period of 2009 – 2012, mean turtle body temperatures were generally maintained at levels above mean environmental temperatures during the active portion of the activity cycle, except during the Postnesting and Prehibernation periods when air temperatures exceeded turtle body temperatures (Figure 18). Across the entire sampling period, female [15.1 ˚C (±0.5 SE)] and male [13.2 ˚C (±0.8 SE)] turtle mean body temperatures were slightly different. However, when the entire year of 2012 was analyzed statistically, there was no significant difference in body temperature between the sexes in BHC (ANOVA: df = 1, F-value = 1.936, P-value = 0.1643).

Butler County

During the Hibernation periods of 2003 – 2006, the BC population of wood turtles had a mean body temperature of 4.7 ˚C (±0.3 SE; n=89) when mean environmental temperatures were: air = 3.4 ˚C (±0.8 SE), water = 4.7 ˚C (±0.3 SE), and soil = 2.3 ˚C (±0.4 SE). Females exhibited a mean body temperature of 5.1 ˚C (±0.3 SE; n=49), and males sustained a mean body temperature of 4.3 ˚C (±0.4 SE; n=40) (Figure 19). When analyzed by year, there was no significant difference between female and male turtle body temperatures for the 2004 Hibernation period (ANOVA: df = 1, F-value = 0.0114, P-value = 0.9157), nor for the 2005 Hibernation period (ANOVA: df = 1, F-value = 0.5491, P-value = 0.4729).

In BC, the Prenesting period mean turtle body temperature [22.6 ˚C (±0.4 SE; n=246)] was higher than corresponding mean environmental temperatures: air = 20.6 ˚C (±0.3 SE), water = 15.9 ˚C (±0.2 SE), and soil = 13.7 ˚C (±0.2 SE). Turtles became active during this period; the earliest observed terrestrial activity occurred at a body temperature of 27.5 ˚C in females and 23.1 ˚C in males. Four terrestrial mating events were witnessed during Prenesting at a mean body temperature of 25.2 ˚C (±3.5 SE) in females (n=2) and 26.4 ˚C (±4.9 SE) in males (n=2). The coolest temperature at which feeding was observed during Prenesting was 20.1 ˚C by a female and 13.9 ˚C by a male (Table 2). Prenesting female mean body temperature was 23.6 ˚C (±0.6 SE; n=143), and male mean body temperature was 21.2 ˚C (±0.7 SE; n=102). During the Prenesting period, female and male turtle body temperatures were not significantly different in 2004 (ANOVA: df = 1, F-value = 0.0049, P-value = 0.9448) or in 2005 (ANOVA: df = 1, F-value = 0.6014, P-value = 0.4481). The only juvenile turtle observed at BC was located during the Prenesting period; juvenile body temperature was 23.9 ˚C (n=1) when the corresponding environmental temperatures were: air = 19.1 ˚C, water = 16.8 ˚C, and soil = 13.1 ˚C.

During the Nesting period, mean body temperature was also several degrees higher [26.5 ˚C (±0.4 SE; n=142)] than corresponding mean environmental temperatures [air = 24.3 ˚C (±0.4 SE), water = 20.7 ˚C (±0.3 SE), and soil = 18.4 ˚C (±0.3 SE). Female turtle mean body temperature was 27.2 ˚C (±0.5 SE; n=88) and male mean body temperature was 25.5 ˚C (±0.7 SE; n=54). During the Nesting period, females and males did not have statistically different body temperatures in 2004 (ANOVA: df = 1, F-value = 0.068, P-value = 0.7960) or 2005 (ANOVA: df = 1, F-value = 2.4488, P-value = 0.1372). The highest recorded body temperatures in BC occurred during the Nesting period; the highest body temperature at which a female was still active was 33.4 ˚C, and 34.3 ˚C in a male. In BC, activity was not observed above 34.3 ˚C.

Postnesting period mean turtle body temperature was 25.1 ˚C (±0.3 SE; n=268) when the corresponding mean environmental temperatures were: air = 24.6 ˚C (±0.3 SE), water = 22.4 ˚C (±0.2 SE), and soil = 19.8 ˚C (±0.1 SE). Female Postnesting mean body temperature was 25.5 ˚C (±0.3 SE; n=164) and the male mean was 24.6 ˚C (±0.4 SE; n=104). During Postnesting period, female and male body temperatures were not significantly different in 2004 (ANOVA: df = 1, F-value = 0.091, P-value = 0.7628) or during 2005 (ANOVA: df = 1, F-value = 0.210, P-value = 0.6554). One aquatic mating event was observed during the Postnesting period, the female body temperature was 18.5

˚C and the male body temperature was 18.9 ˚C at a water temperature 19.6 ˚C and an air temperature 15.6 ˚C.

During the Prehibernation period when wood turtles were primarily aquatic, mean turtle body temperature [13.9 ˚C (±0.4 SE; (n=148)] was similar to the mean water temperature [13.6 ˚C (±0.3 SE)], higher than the corresponding mean soil temperature [12.5 ˚C (±0.6 SE)] but slightly below the mean air temperature [15.5 ˚C (±0.5 SE)]. Prehibernation female mean body temperature was 13.8 ˚C (±0.5 SE; n=87) and male mean body temperature was 14.1 ˚C (±0.6 SE; n=61). During Prehibernation, female and male turtles were not significantly different in body temperature in 2004 (ANOVA: df = 1, F-value = 0.648, P-value = 0.4216) or in 2005 (ANOVA: df = 1, F-value = 0.5412, P-value = 0.4807). As seasonal ambient temperatures cooled, turtles returned to lotic water seeking out hibernacula. The coolest body temperature at which turtles were terrestrially active during the Prehibernation period was 9.2 ˚C in a female and 15.3 ˚C in a male. Aquatic mating was observed 10 times during the Prehibernation period at a mean water temperature of 13.1 ˚C (±1.3 SE) over a range of 6.7 – 18.8 ˚C; during mating events female mean body temperature was 13.2 ˚C (±2.5 SE; n=4) and male mean body temperature was 13.0 ˚C (±1.7 SE; n=6).

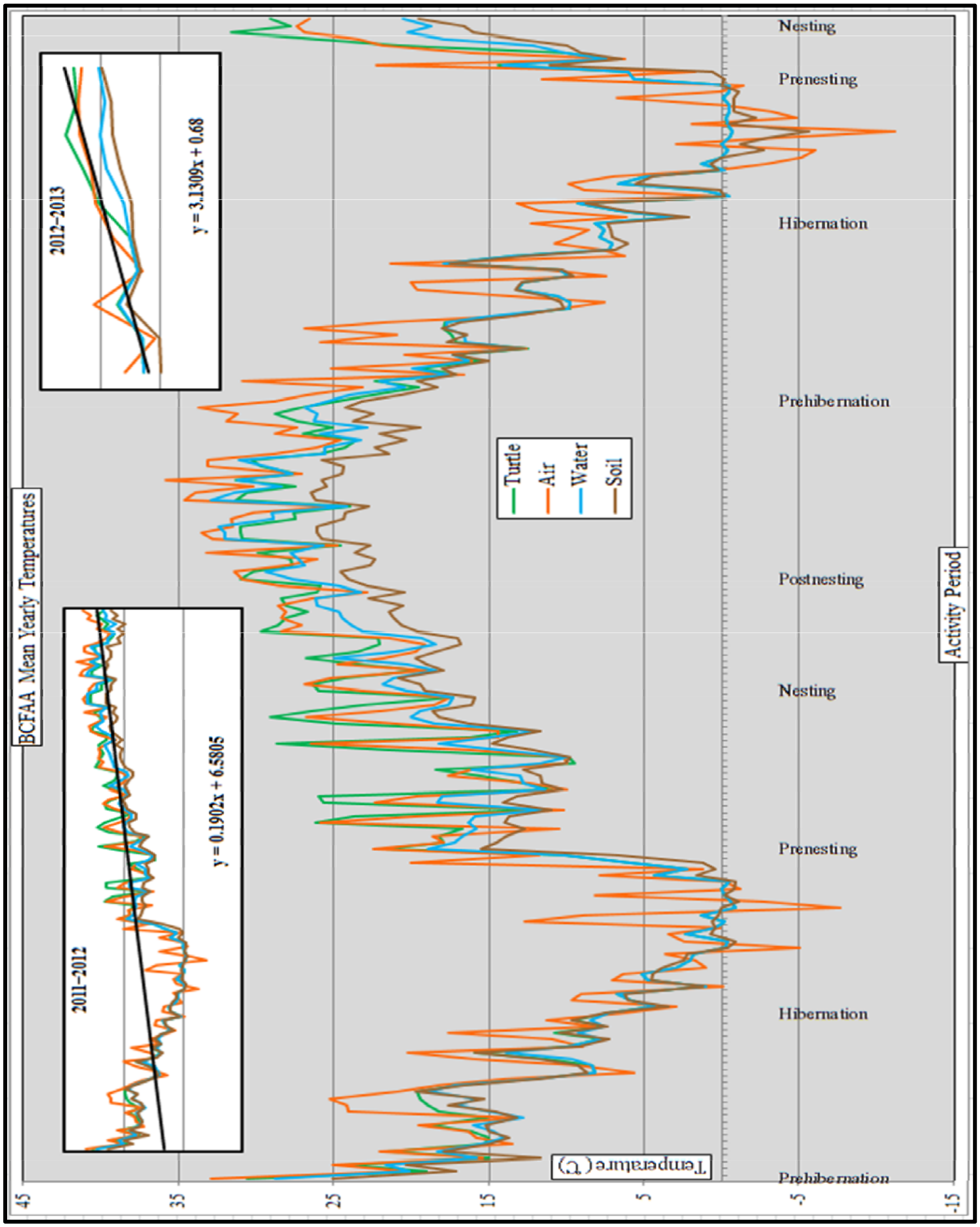

Figure 18. Mean turtle body and environmental temperatures across all days of data collection in BHC during 2011 – 2012 and 2012 – 2013; insert boxes show differences in regression line slope between the years analyzed.

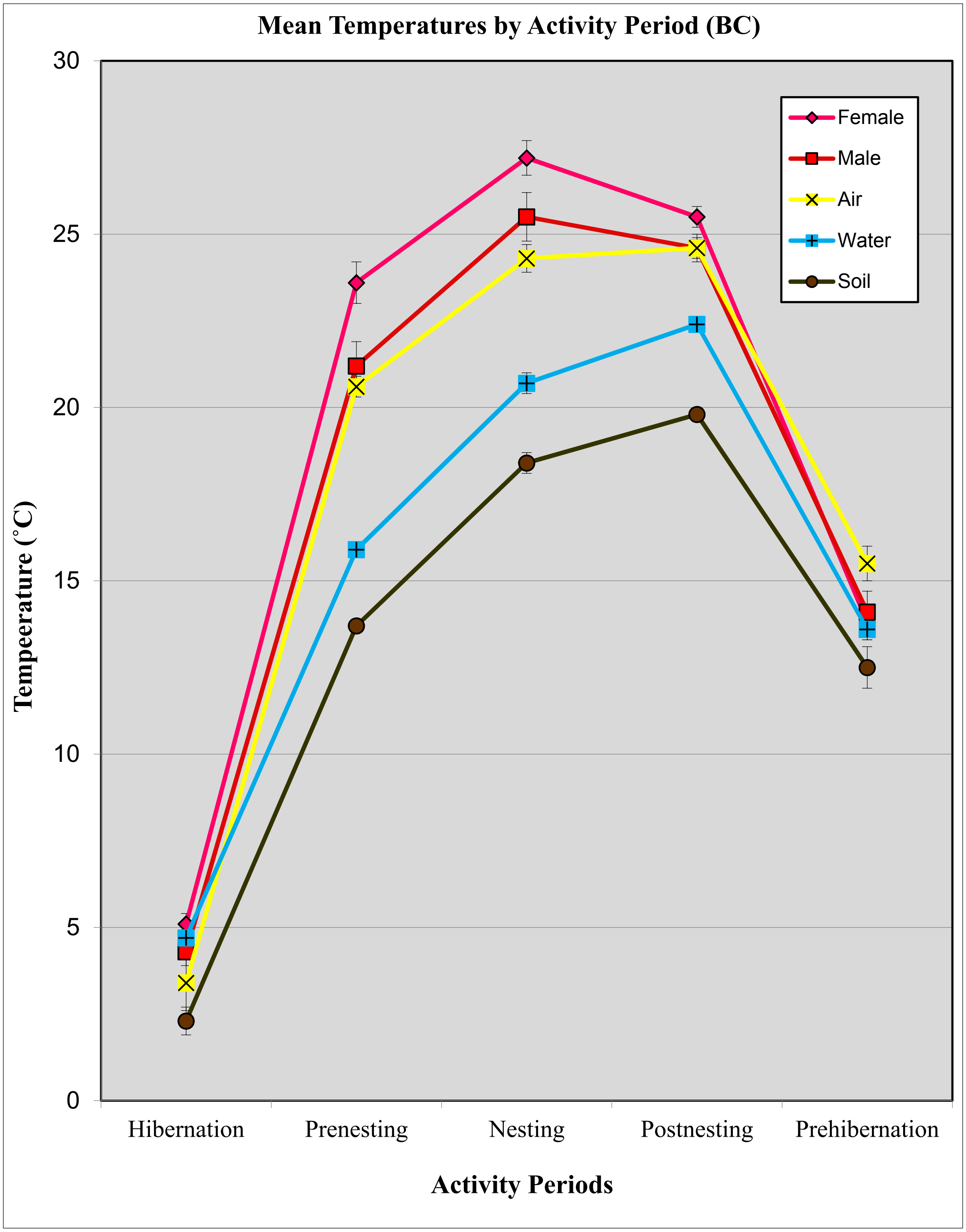

Figure 19. Turtle body and corresponding environmental temperatures recorded by activity period in BC (n_t=893); values are means ± SE.

When analyzed across the entire study, BC female mean body temperature [21.5 ˚C (±0.4 SE)] was higher than male mean body temperature [19.7 ˚C (±0.4 SE)] (ANOVA: df = 1, F-value = 4.080, T-value: -2.020, P-value = 0.0585); BC males were 0.9037 ˚C (±0.4474) cooler than BC females. However, this pattern was not evident during 2005 in BC (ANOVA: df = 1, F-value = 1.691, P-value = 0.2082). Across all dates in BC, mean turtle body temperatures were closest to mean air temperatures, and were generally maintained above the mean water and soil temperatures (Figure 20).

BC 2004 – BHC 2012

Females. Comparing BC 2004 data to BHC 2012 data, BC females across the entire year were significantly warmer than BHC females by 2.69 ˚C (±1.06 SE) when the day^2 value was removed (ANOVA: df = 1, F-value = 6.408, T-value = 2.531, P-value = 0.0175). When analyzed at the activity period level, BC 2004 females and BHC 2012 females were significantly different in mean body temperature during the Postnesting period (ANOVA: df = 1, F-value = 22.675, T-value = -4.762, P-value = 0.0204), BC females were 2.32 ˚C (±0.49 SE) cooler than BHC females. The Prehibernation period between BC 2004 and BHC 2012 females was the only other period that demonstrated a marginally significant difference between females in BC and BHC; BC females were 1.04 ˚C (±0.50 SE) warmer than BHC females (ANOVA: df = 1, F-value = 4.320, T-value = 2.0785, P-value = 0.0531) for this period.

Males. When BC male data from 2004 was compared with BHC male data from 2012 (across the whole year), BC males were 1.23 ˚C (±0.40 SE) cooler than BHC males (ANOVA: df = 1, F-value = 9.483, T-value = -3.08, P-value = 0.0055). When analyzed by activity period, Prenesting and Prehibernation were not significantly different in mean body temperature between BC 2004 males and BHC 2012 males. However, BC 2004 males were statistically different in mean body temperature from BHC 2012 males during the Nesting and Postnesting periods. Male wood turtles in BC during the 2004 Nesting period were 2.10 ˚C (±0.93 SE) cooler than the 2012 BHC Nesting period males (ANOVA: df = 1, F-value = 5.098, T-value = -2.258 P-value = 0.0383). During the Postnesting period, BC 2004 males were 3.52 ˚C (±0.62 SE) cooler than BHC 2012 males (ANOVA: df = 1, F-value = 32.6, T-value = -5.709, P-value = 0.0104).

BC 2005 – BHC 2012

Females. When data from 2005 BC females were compared with 2012 BHC females (across the entire year), there was no statistical difference in mean body temperature (ANOVA: df = 1, F-value = 1.073, P-value = 0.3091). Furthermore, when activity periods were compared between females in BC during 2005 and in BHC during 2012, only the Nesting period mean body temperature was significantly different. Nesting period females in BC during 2005 were 2.01 ˚C (±0.78 SE) warmer than BHC females during 2012 (ANOVA: df = 1, F-value = 6.697, T-value = 2.588, P-value = 0.0165).

Males. Comparing BC 2005 males to BHC 2012 males across the entire year revealed that BC 2005 males were 1.52 ˚C (±0.52 SE) cooler than BHC 2012 males in mean body temperature (ANOVA: df = 1, F-value = 8.635, T-value = -2.939, P-value = 0.0074). However, when statistically analyzed across the activity periods, there were no significant differences between BC 2005 males and BHC 2012 males during any individual activity period.

Effect of Air Temperature on the Selection of Aquatic or Terrestrial Habitats

Black Hawk county. During the 2012 Prenesting period, when air temperatures were cool and ranged from 7.1 – 14.9 ˚C, female wood turtles were 63.3% aquatic (n=19) and 36.7% terrestrial (n=11). When air temperatures were higher and ranged from 15.3 – 29.3 ˚C, female turtles were mostly terrestrial (84.7%; n=61). In this warmer temperature range, locations of females in aquatic habitats represented only 15.3% (n=11) of the observations. For the 2012 Prenesting period, at cool air temperatures ranging from 6.8 – 14.9 ˚C, male wood turtles were 84.6% aquatic (n=11) and 15.4% terrestrial (n=2); at warmer air temperatures ranging from 15.5 – 31.3 ˚C, male turtles were also mostly terrestrial (87.0%; n=47) with only a few observations (13.0%; n=7) occurring in aquatic habitats.

During the 2012 Nesting period, air temperatures were generally warm and ranged from 13.5 – 34.9 ˚C. Female wood turtles were 75.3% terrestrial (n=73) and 24.7% aquatic (n=24); similarly, male wood turtles were 73.5% terrestrial (n=83) and 26.6% aquatic (n=30).

For the 2012 Postnesting period, when air temperatures ranged from 14.3 – 39.0 ˚C, female wood turtles were 65.5% terrestrial (n=161) and 34.6% aquatic (n=85). During this same period, when air temperatures ranged from 16.2 – 37.2 ˚C, male wood turtles were located more frequently in aquatic habitats (47.7%; n=52) and observations in terrestrial habitats declined to 52.3% (n=57).

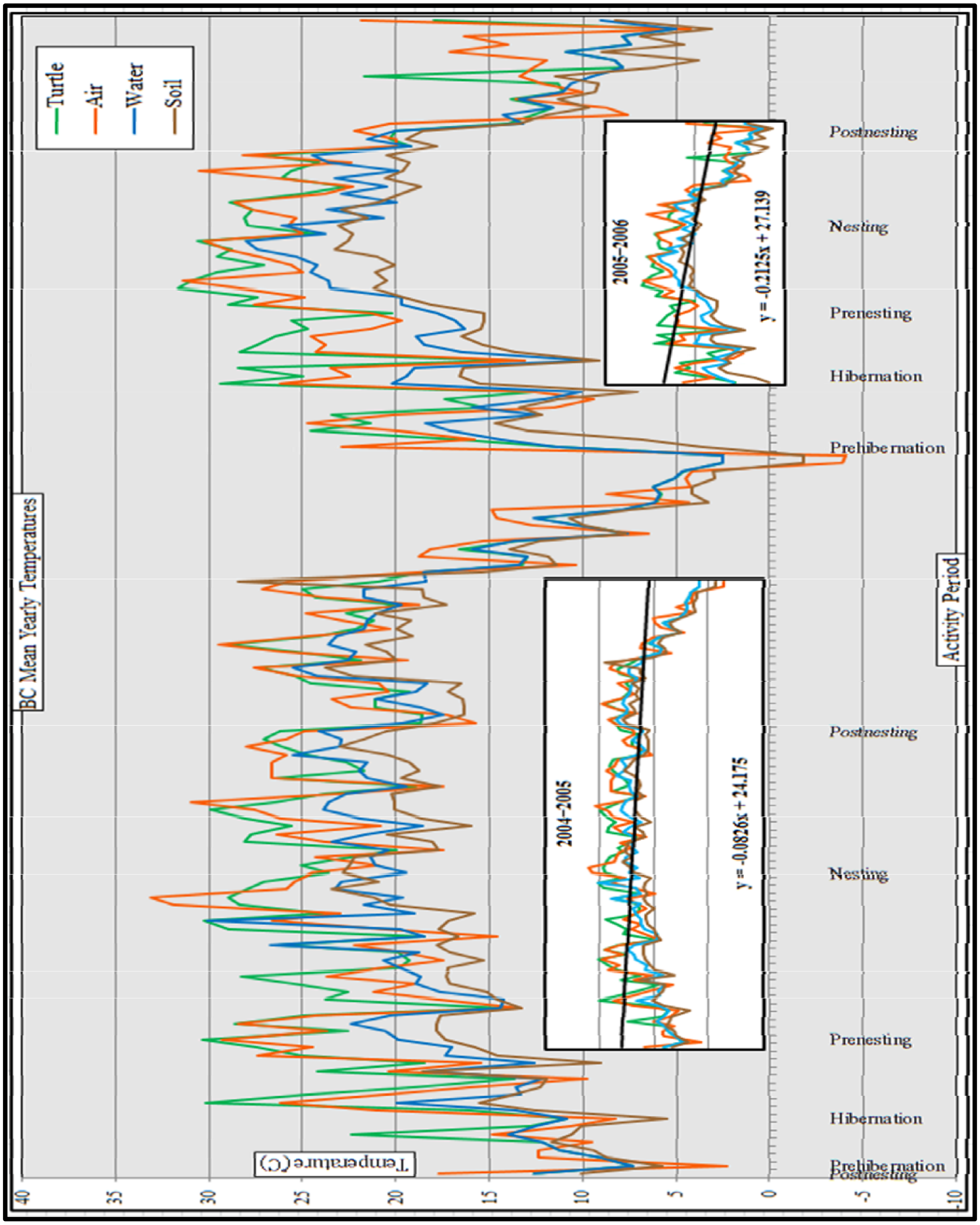

Figure 20. Mean turtle body and environmental temperatures across all days of data collection in BC during 2004 – 2005 and 2005 – 2006; insert boxes show differences in regression line slope between the years analyzed.

For the 2012 Prehibernation period, at cool air temperatures ranging from 6.0 – 14.5 ˚C female wood turtles were 98.3% aquatic (n=116) and 1.7% terrestrial (n=2); at warmer air temperatures ranging from 15.2 – 29.8 ˚C female turtles were still highly aquatic (84.6%; n=66) but terrestrial observations (15.4% n=12) increased. In this same cool air temperature range (6.0 – 14.5 ˚C), male wood turtles were 94.0% aquatic (n=63) and 6.0% terrestrial (n=4); at warmer air temperatures ranging from 15.3 – 29.0 ˚C, male turtles were 79.4% aquatic (n=27) and 20.6% terrestrial (n=7).

Butler county. During the 2004 Prenesting period, when air temperatures were cool and ranged from 9.6 – 15.1 ˚C, female wood turtles were 57.1% aquatic (n=4) and 42.9% terrestrial (n=3); when air temperatures were warmer and ranged from 15.3 – 33.4 ˚C female turtles became predominately terrestrial (93.5%; n=43) and only a few aquatic locations were observed (6.5%; n=3). During the 2004 Prenesting period, at cool air temperatures ranging from 8.3 – 14.8 ˚C, male wood turtles were 60.0% aquatic (n=3) and 40.0% terrestrial (n=2); at warmer air temperatures ranging from 15.5 – 30.5 ˚C, male turtles also became highly terrestrial (85.7% of observations; n=30). In this temperature range, only 14.3% (n=5) of male locations were in aquatic habitats.

For the 2005 Prenesting period, when air temperatures ranged from 7.5 – 14.9 ˚C, female wood turtles were 53.3% aquatic (n=8) and 46.7% terrestrial (n=7); at warmer air temperatures ranging from 15.7 – 27.9 ˚C, female turtles became primarily terrestrial (71.1%; n=27). Aquatic observations (n=11) represented only 29.0% of the total locations in this period. The pattern was similar for males in this period: at air temperatures ranging from 7.5 – 14.2 ˚C, male wood turtles were 75.0% aquatic (n=9) and 25.0% terrestrial (n=3). When air temperatures were warmer and ranged from 18.6 – 27.9 ˚C, male turtles were 75.0% terrestrial (n=15) and 25.0 % aquatic (n=5).

During the 2004 Nesting period both female and male wood turtles were predominantly terrestrial. At air temperatures ranging from 15.4 – 33.2 ˚C, female wood turtles were 79.2% terrestrial (n=19) and only 20.8% aquatic (n=5). At air temperatures ranging from 13.7 – 34.3 ˚C, male wood turtles were 68.2% terrestrial (n=15) and 31.8% aquatic (n=7). This pattern was even more pronounced during the 2005 Nesting period; even though maximum air temperatures were slightly lower than in 2004. In the 2005 the Nesting period, when air temperatures ranged from 17.8 – 31.8 ˚C, female wood turtles were 85.7% terrestrial (n=36) and only 14.3% aquatic (n=6); at air temperatures ranging from 17.5 – 31.3 ˚C, male wood turtles were 83.3% terrestrial (n=20) and 16.7% aquatic (n=4).

During the summer 2004 Postnesting period, when air temperatures ranged from 15.5 – 33.5 ˚C, female wood turtles were primarily terrestrial (86.4%; n=70). Only 11 observations (13.6%) were in aquatic habitats. During this period, males were located in aquatic habitats more often than females were; at air temperatures ranging from 15.1 – 32.8 ˚C, male wood turtles were 47.2% aquatic (n=34) and 52.8% terrestrial (n=38). During the 2005 Postnesting period, at air temperatures ranging from 14.5 – 33.0 ˚C, female wood turtles were 63.9% terrestrial (n=39) and 36.1% aquatic (n=22). At air temperatures ranging from 20.6 – 32.1 ˚C, male wood turtles were 55.6% aquatic (n=15) and 44.4% terrestrial (n=12).

Finally, during the 2004 Prehibernation period, when air temperatures were generally cool and ranged from 3.7 – 14.9 ˚C, female wood turtles were 100.0% aquatic (n=18). On warm days, when air temperatures ranged from 15.5 – 27.7 ˚C, some female turtles basked on land while others remained in lotic water sources [aquatic = 65.2% (n=15); terrestrial = 34.8% (n=8)]. During this period, on cool days when air temperatures ranged from 3.7 – 14.3 ˚C, male wood turtles were 100.0% aquatic (n=15). At warmer air temperatures ranging from 15.1 – 29.2 ˚C male turtles were 70.0% aquatic (n=14) and 30.0% terrestrial (n=6).

During the 2005 Prehibernation period, on cool days when air temperatures ranged from 6.7 – 14.3 ˚C, female wood turtles were 87.5% aquatic (n=21) and 12.5% terrestrial (n=3); on warm days when air temperatures ranged from 15.1 – 23.1 ˚C, more female turtles were observed on land [aquatic = 67.7% (n=12) and terrestrial = 33.3% (n=6)]. On cool days when air temperatures ranged from 7.8 – 13.4 ˚C, male wood turtles were exclusively aquatic (100.0%; n=7). On the few days when air temperatures were warm and ranged from 17.8 – 22.7 ˚C, a single male turtle was found on land [aquatic = 80.0% (n=4); terrestrial = 20.0% (n=1)].

Temperatures by Habitat

Black Hawk County

During Hibernation in BHC, turtles were 100% aquatic and located in lotic water with a mean temperature of 1.8 ˚C (±0.1 SE; n=606) (Figure 21). During Prenesting, turtles in BHC were found at the highest mean environmental temperatures in deciduous forest (23.0 ˚C ± 0.6 SE; n=50), emergent grasses and forbs (20.9 ˚C ± 0.5 SE; n=121), and grasses and willow saplings (20.9 ˚C ± 0.6 SE; n=3). Turtles located at the lowest mean environmental temperatures during Prenesting were found in lotic water (10.6 ˚C ± 0.3 SE; n=139) and lentic water (12.5 ˚C ± 0.1 SE; n=4).

During the Nesting period, a single turtle was located at the highest environmental mean air temperature (29.3 ˚C) on a riverbank. Habitats frequently used during Nesting with the warmest environmental temperatures were: deciduous forest (mean air temperature = 26.0 C ± 0.5 SE; n=65) and emergent grasses and forbs (mean air temperature = 25.1 ˚C ± 0.4 SE; n=88). Lower mean environmental temperatures during the Nesting period were recorded for open riverbank (23.9 ˚C ± 4.5 SE; n=3), lotic water (22.4 ˚C ± 0.4 SE; n=49), and lentic water (19.7 ˚C ± 0.5 SE; n=6).

For the Postnesting period, habitats used by wood turtles with the highest mean environmental temperatures were as follows: open riverbank (30.6 ˚C ± 2.1 SE; n=30), emergent grasses and forbs (29.7 ˚C ± 0.6 SE; n=80), and deciduous forest (29.3 ˚C ± 0.3 SE; n=154). The lowest mean environmental temperatures in habitats used by wood turtles during this period were recorded in non-cultivated fields (26.7 ˚C; n=1), and lentic (26.1 ˚C ± 0.9 SE; n=25) and lotic (26.0 ˚C ± 0.4 SE; n=121) water.

During the Prehibernation period, BHC turtles were located in the following habitats with the highest mean environmental temperatures open riverbank (20.9 ˚C ± 0.7 SE; n=3), emergent grasses and forbs (18.6 ˚C ± 0.7 SE; n=45), deciduous forests (18.6 ˚C ± 1.2 SE; n=17), and riverbank (17.8 ˚C ± 2.7 SE; n=6) habitats. The lowest mean environmental temperatures were recorded in aquatic habitats: lentic (15.0 ˚C ± 0.8 SE; n=17) and lotic (11.4 ˚C ± 0.2 SE; n=335) water.

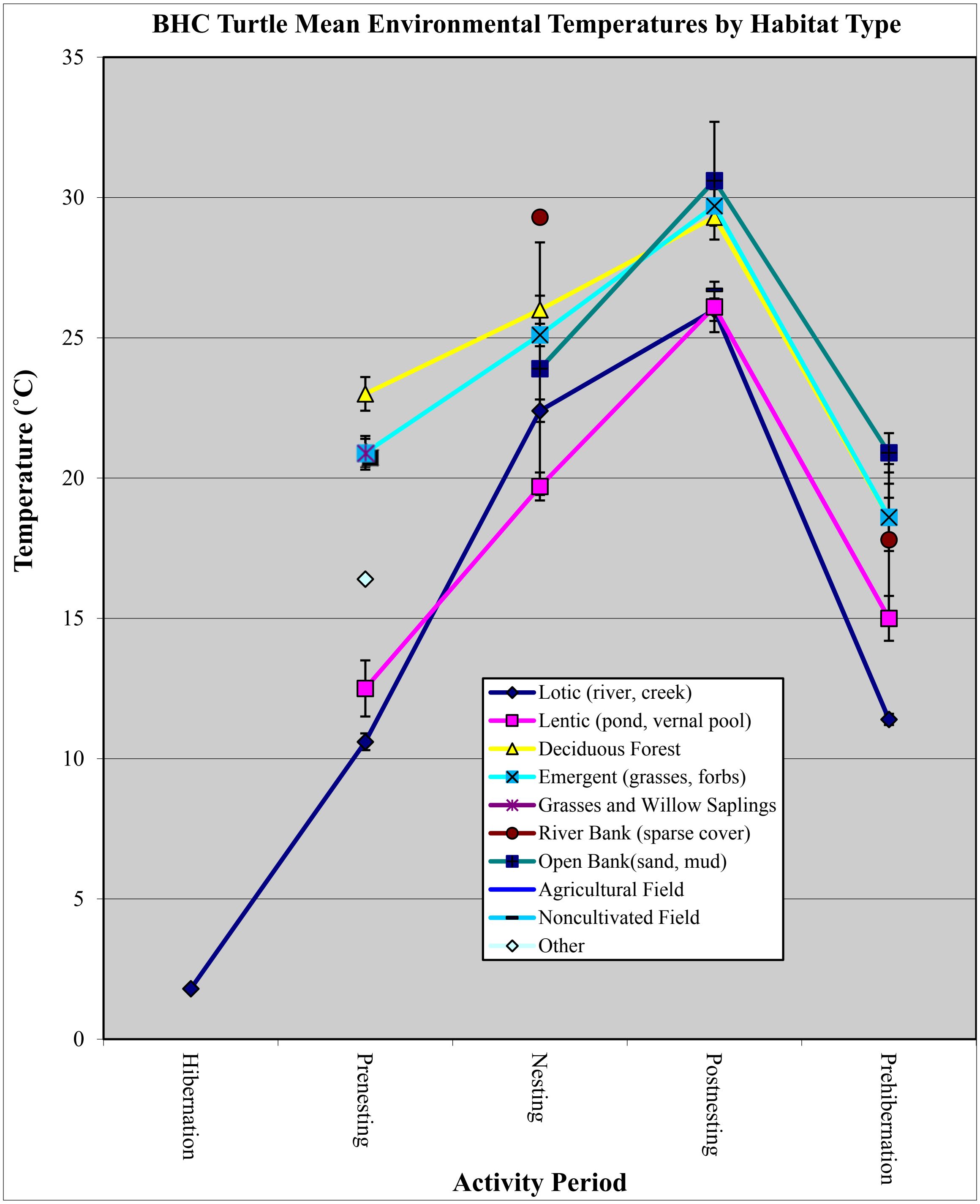

Figure 21. Environmental temperatures of habitats selected by wood turtles in BHC by activity period. Lotic and lentic habitat values are water temperatures, and all terrestrial values are air temperatures (n_t=1,959); values are means ± SE.

Black Hawk County females. BHC female turtles were 100% aquatic during the Hibernation period and were only located in lotic water (1.7 ˚C ± 0.2 SE; n=319) (Figure 22). During the Prenesting period, females were located at the warmest mean environmental temperatures in the following habitats: deciduous forest (23.2 ˚C ± 0.7 ˚SE; n=36), grasses and willows (21.4 ˚C ± 0.4 SE; n=2), and emergent grasses and forbs (20.3 ˚C ± 0.7 SE; n=71). When cool periods occurred in the Prenesting period, female turtles and were located at the lowest environmental temperature in lotic water (10.7 ˚C ± 0.4 SE; n=87).

In Black Hawk County, a female wood turtle on a riverbank was located at the highest mean environmental temperature (29.3 ˚C) recorded during the Nesting period. Other habitats that were frequently used by females and yielded warm temperatures during the Nesting period were: deciduous forests (26.3 ˚C ± 0.5 SE; n=38) and emergent grasses and forbs (24.6 ˚C ± 0.7 SE; n=34). During nesting, females were recorded at the lowest mean environmental temperatures in lotic water (21.9 ˚C ± 0.6 SE; n=23), on open banks (19.4 ˚C ± 0.5 SE; n=2), and in lentic water (18.5 ˚C; n=1).

During the Postnesting period, BHC female turtles were recorded at the highest mean environmental temperatures in deciduous forest (29.5 ˚C ± 0.4 SE; n=116), in emergent grasses and forbs (29.4 ˚C ± 0.8 SE; n=59), and on open banks (29.0 ˚C ± 2.5 SE; n=2). Females were located at the lowest mean environmental temperatures in lotic (25.6 ˚C ± 0.5 SE; n=68) and lentic water (26.3 ˚C ± 0.8 SE; n=23).

In Prehibernation, a female turtle was recorded at the highest mean environmental temperature observed on a riverbank (25.3). At lower mean environmental temperatures,

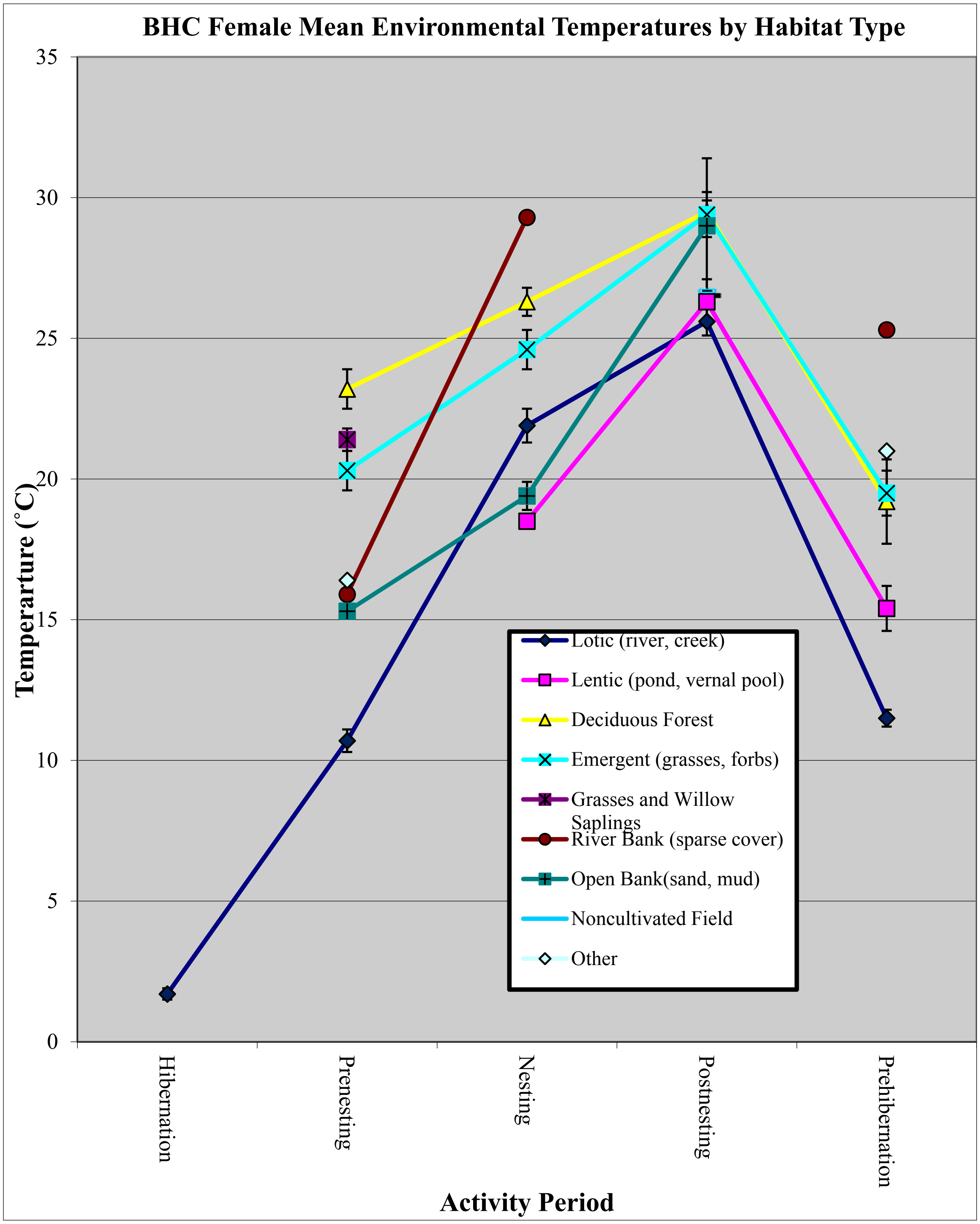

Figure 22. Environmental temperatures of habitats selected by female wood turtles in BHC by activity period. Lotic and lentic habitats display water temperatures, and all terrestrial habitats display air temperatures (n_t=1,155); values are means ± SE.

female turtles were documented in emergent grasses and forbs (19.5 ± 0.5 SE; n=26) and deciduous forest (19.2 ˚C ± 1.5 SE; n=11). Finally, at the lowest mean environmental temperatures observed, females were found in lotic (11.5 8 ˚C ± 0.3 SE; n=214) and lentic water (15.4 ˚C ± 0.8 SE; n=16).

Black Hawk County males. Male turtles in BHC were also 100% aquatic during the Hibernation period and located only in lotic habitats that averaged 1.9˚C (± 0.2 SE) over 297 observations (Figure 23). During the Prenesting period, male wood turtles were located at the warmest mean environmental temperatures in deciduous forest (22.5 ˚C ± 1.1 SE; n=14) and emergent grasses and forbs (21.7 ˚C ± 0.6 SE; n=50). During the Prenesting period, male turtles were located at the lowest environmental temperatures most frequently in lotic water (10.5 ˚C ± 0.6 SE; n=52) and occasionally in lentic water (12.5 ˚C ± 1.0 SE; n=4).

During the Nesting period, an active male wood turtle basking on an open riverbank was located at the highest mean environmental temperature observed (32.9 ˚C). Deciduous forest (25.7 ˚C ± 0.8 SE; n=27) and emergent grasses and forbs (25.4 ˚C ± 0.6 SE; n=54) were heavily used during this period to maintain warm body temperatures. Males were recorded at the lowest mean environmental temperatures in aquatic habitats [lotic water = 22.9 ˚C (± 0.5 SE; n=26) and lentic water = 20.0 ˚C (± 0.5 SE; n=5)].

During the Postnesting period in BHC, a male turtle was recorded at the highest mean environmental temperature on an open riverbank (33.9˚C). Emergent grasses and forbs (30.3 ˚C ± 0.9 SE; n=21) and deciduous forests (28.8 ˚C ± 0.7 SE; n=38) were the most frequently used habitats that yielded warm environmental temperatures during the summer. Males were located at the lowest mean environmental temperatures in lotic (26.6 ˚C ± 0.5 SE; n=53) and lentic water (23.6 ± 7.6 SE; n=2).

During Prehibernation, male wood turtles were recorded at the highest mean environmental temperatures on open riverbanks (20.9 ˚C ± 0.7 SE; n=3), emergent grasses and forbs (17.5 ˚C ± 1.1 SE; n=19), and deciduous forests (17.4 ˚C ± 1.9 SE; n=6). At lower mean environmental temperatures, male turtles were documented lotic (11.2 ˚C ± 0.3 SE; n=121) and lentic water (9.5 ˚C; n=1).

Butler County

Wood turtles at the two BC sites were also 100% aquatic during the Hibernation period, and the only habitat utilized was lotic water (4.7 ˚C ± 0.3 SE; n=90) (Figure 24). During the Prenesting period, turtles were located at the highest mean environmental temperatures on riverbanks (24.8 ˚C ± 1.8 SE; (n=4) and open riverbanks (24.1 ˚C ± 1.9 SE; n=3). Turtles were often located at more moderate mean environmental temperatures in grasses and willows (22.6 ˚C ± 0.5 SE; n=109), emergent grasses and forbs (21.1 ˚C ± 0.6 SE; n=47), and deciduous forests (21.0 ˚C ± 0.8 SE; n=17). The lowest mean environmental temperatures recorded for Prenesting were in lotic (13.5 ˚C ± 0.4 SE; n=63) and lentic (18.0 ˚C ± 2.1 SE; n=3) water habitats.

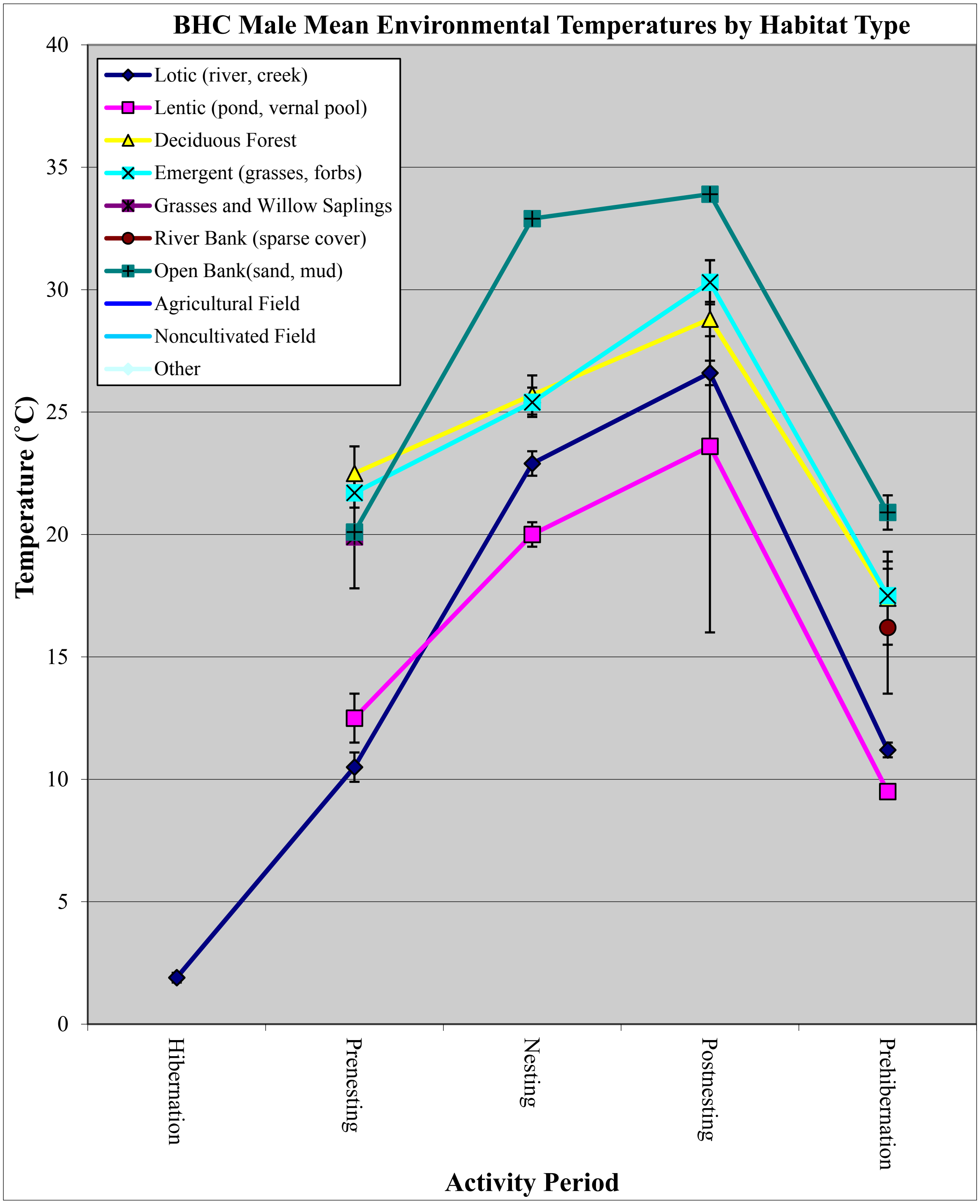

Figure 23. Environmental temperatures of habitats selected by male wood turtles in BHC by activity period. Lotic and lentic habitats display mean water temperatures, and all terrestrial habitats display mean air temperatures (n_t=804); values are means ± SE.

For the Nesting period, BC turtles were recorded at the highest mean environmental temperatures on riverbanks (29.6 ˚C ± 1.6 SE; n=3) and in a non-cultivated field (27.7 ˚C; n=1). Lower mean environmental temperatures were recorded in deciduous forests (25.6 ˚C ± 1.5 SE; n=10), emergent grasses and forbs (24.6 ˚C ± 0.6 SE; n=52), and grasses and willows (24.4 ˚C ± 0.5 SE; n=47). The lowest mean environmental temperatures were recorded on open riverbanks (21.2 ˚C ± 0.2 SE; n=4) and in lotic (21.1˚C ± 0.8 SE; n=16) and lentic water (19.2 ˚C ± 0.6 SE; n=7).

During Postnesting, riverbanks (27.4 ˚C ± 2.8 SE; n=5) and agricultural fields (26.6 ˚C ± 0.8 SE; n=5) were habitats used by wood turtles that yielded the highest mean environmental temperatures. Deciduous forest (25.7 ˚C ± 0.8 SE; n=12), non-cultivated fields (25.6 ˚C ± 1.9 SE; n=9), grasses and willows (25.3 ˚C ± 0.6 SE; n=44), emergent grasses and forbs (24.8 ˚C ± 0.4 SE; n=104), and lentic water (24.3 ˚C ± 1.1 SE; n=10) were all habitats with mean environmental temperatures that were within ≈ 1.5 ˚C of each other. Lotic water (22.7 ˚C ± 0.3 SE; n=74) represented the habitat with the lowest mean environmental temperatures selected by turtles during the Postnesting period.

The highest mean environmental temperature (24.0˚C) in a habitat used by wood turtles during the Prehibernation period was recorded in a non-cultivated field. At lower mean environmental temperatures was an open bank (21.7˚C; n=1), grasses and willows (20.9 ˚C ± 1.7 SE; n=7), deciduous forests (19.7 ˚C ± 3.1 SE; n=5), emergent grasses and forbs (19.3 ˚C ± 1.6 SE; n=11), and riverbanks (18.9 ˚C ± 2.4 SE; n=3). The lowest mean environmental temperatures were observed in lotic (12.6˚C ± 0.3 SE; n=119) and lentic (12.2 ˚C ± 0.0 SE; n=1) water.

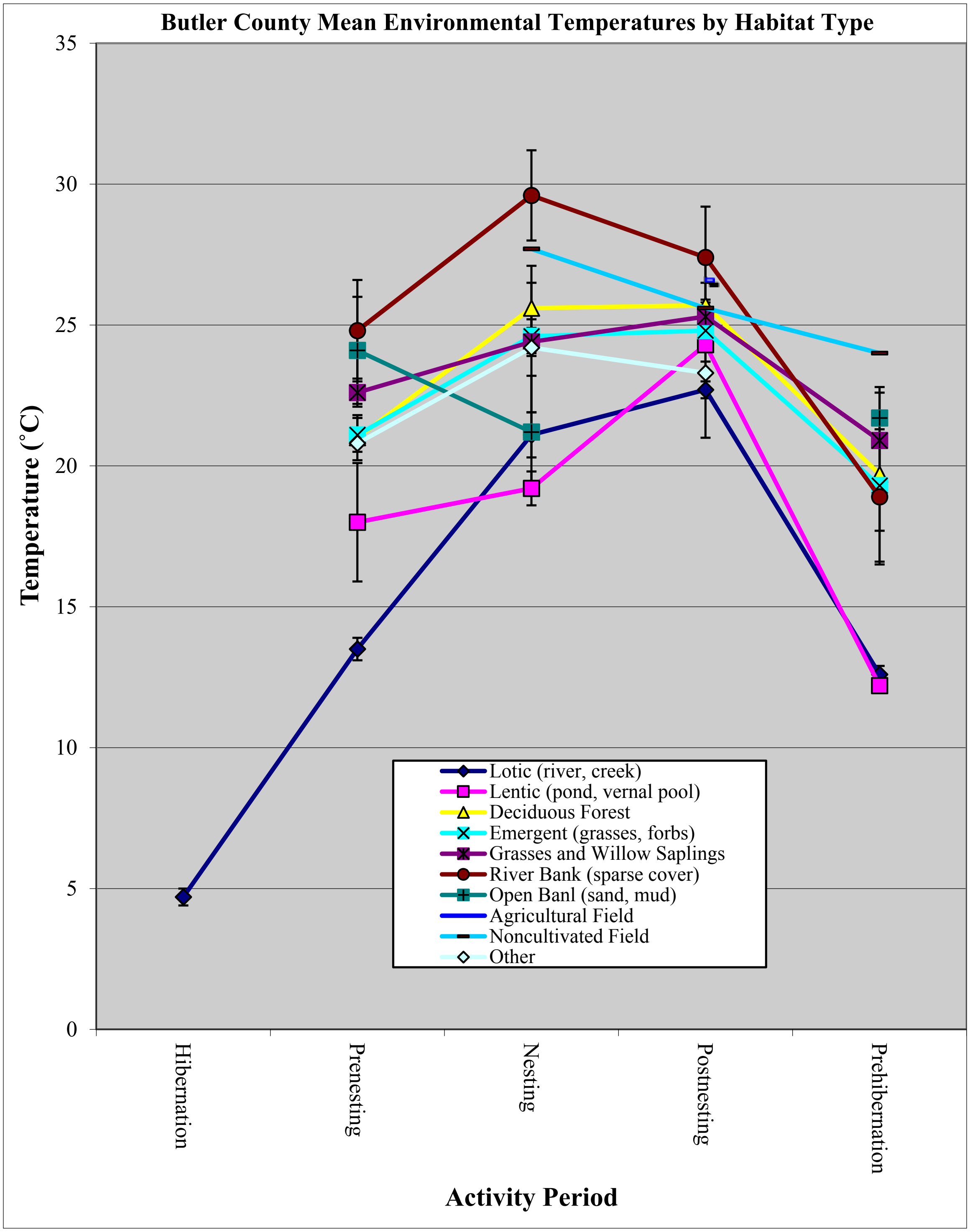

Figure 24. Environmental temperatures of habitats selected by wood turtles in BC by activity period. Lotic and lentic habitat values are water temperatures, and all terrestrial values are air temperatures (n_t=893); values are means ± SE.

Butler County females. Female wood turtles in BC were 100% aquatic during the Hibernation period, located only in lotic water (5.1 ˚C ± 0.3 SE; n=49) (Figure 25). During the Prenesting period, females were located at the warmest mean environmental temperatures in grasses and willows (22.6 ˚C ± 0.6 SE; n=62), on riverbanks (21.5 ˚C ± 0.4 SE; n=3), in emergent grasses and forbs (21.3 ˚C ± 0.7 SE; n=37), deciduous forest (21.3 ˚C ± 0.9 SE; n=11). When located in lotic water during Prenesting, BC female turtles were found at a much lower mean environmental temperature (13.4 ˚C ± 0.5 SE; n=30).

During the Nesting period in BC, a female wood turtle was located at the highest mean environmental temperature on a riverbank (32.7 ˚C). Females were recorded at slightly lower mean environmental temperatures in a non-cultivated field (27.7˚C; n=1), deciduous forest (27.2 ˚C ± 1.9 SE; n=5), grasses and willows (24.5 ˚C ± 0.6 SE; n=30), and emergent grasses and forbs (24.8 ˚C ± 0.7 SE; n=36). Females were recorded at the lowest mean environmental temperatures during the Nesting period in lotic water (21.4 ˚C ± 1.2 SE; n=9), on open banks (21.0 ˚C ± 4.8 SE; n=2), and in lentic water (18.8 ˚C ± 0.3 SE; n=4).

During the Postnesting period, BC female turtles were recorded at the highest mean environmental temperatures on a riverbank (28.2 ˚C; n=1), in agricultural fields (26.6 ˚C ± 0.8 SE; n=5), grasses and willows (26.0 ˚C ± 0.9 SE; n=21), and deciduous forests (25.5 ˚C ± 0.9 SE; n=10). Females were located at the lowest mean environmental temperatures in lentic water (23.5 ˚C ± 0.3 SE; n=6) and lotic water (23.7 ˚C ± 0.6 SE; n=25).

During the Prehibernation period, female turtles were recorded at the highest mean environmental temperature in a non-cultivated field (23.6 ˚C). Females also selected grasses and willows (21.6 ˚C; n=1), emergent grasses and forbs (20.2˚C ± 1.6 SE; n=11), and deciduous forest (19.9 ˚C ± 3.1 SE; n=5) as warm terrestrial habitats. Finally, at the lowest mean environmental temperature, a single female was found on an open bank at 13.4˚C. During Prehibernation, most females used lotic water with a mean temperature of 12.3 ˚C (± 0.5 SE; n=67).

Butler County males. Male turtles in BC used only lotic habitats for Hibernation; at turtle locations, mean water temperature was 4.3 ˚C (± 0.4 SE; n=41) (Figure 26). During the Prenesting period male wood turtles were located at the warmest mean environmental temperatures on open riverbanks (24.1 ˚C ± 1.9 SE; n=3), a vegetated riverbank (23.0˚C; n=1), and were frequently found in grasses and willows (22.5 ˚C ± 0.7 SE; n=47). Butler County male turtles were located at lower mean environmental temperatures in deciduous forest (20.9 ˚C ± 1.9 SE; n=6) and emergent grasses and forbs (20.4 ˚C ± 1.7 SE; n=10). During the Prenesting period, male turtles were located at the lowest environmental temperature in lotic water (13.5 ˚C ± 0.6 SE; n=33). Butler County male wood turtles during the Nesting period were located at the highest mean environmental temperatures on riverbanks (28.0 ˚C ± 0.9 SE; n=2), in grasses and willows (24.2 ˚C ± 0.8 SE; n=17), and in emergent grasses and forbs (24.0 ˚C ± 1.3 SE; n=16) and deciduous forest (24.0 ˚C ± 2.3 SE; n=5). Males were recorded at the lowest mean environmental temperatures in lotic (20.6 ˚C ± 1.1 SE; n=7) and lentic water (19.8 ˚C ± 1.5SE; n=3).

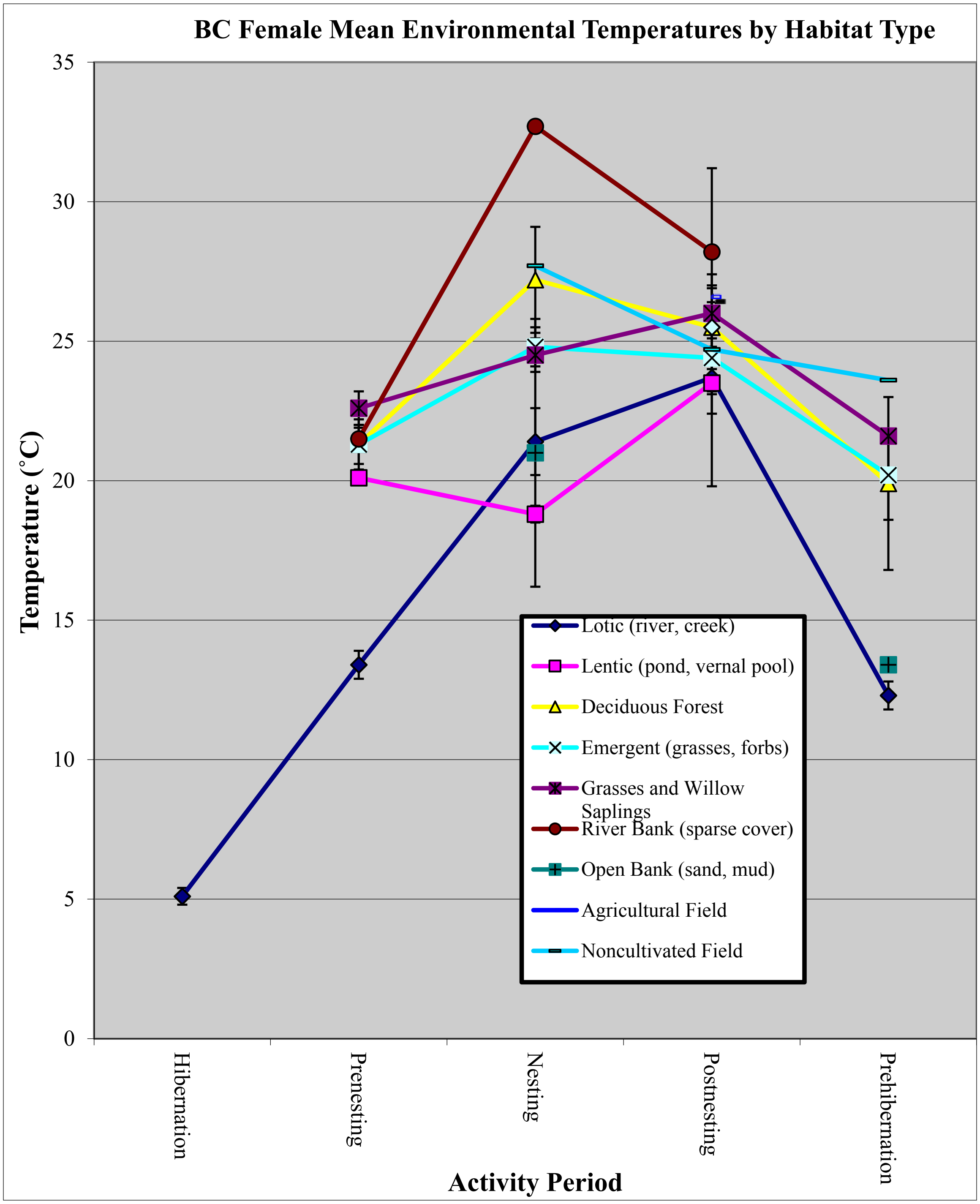

Figure 25. Environmental temperatures in locations selected by female turtles by activity period in BC. Lotic and lentic habitat values are water temperatures, and all terrestrial habitat values are air temperatures (n_t=529); values are means ± SE.

During the Postnesting period, BC turtles were recorded at the highest mean environmental temperatures in non-cultivated field (28.8 ˚C ± 0.9 SE; n=2), riverbank (27.2 ˚C ± 2.3 SE; n=4), emergent grasses and forbs (26.6 ˚C ± 0.7 SE; n=17), and deciduous forest (26.6 ˚C ± 2.0 SE; n=2) habitats. Males were most frequently found at the lowest mean environmental temperatures in lotic water (22.2 ˚C ± 0.4 SE; n=49).

For the Prehibernation period, male wood turtles in BC were recorded at the highest mean environmental temperatures in terrestrial habitats: grasses and willows = 17.8 ˚C (± 2.0 SE; n=6); and riverbank = 16.0 ˚C (± 1.2 SE; n=3). At lower mean environmental temperatures, male turtles were documented mostly in lotic water (13.0 ˚C ± 0.5 SE; n=52).

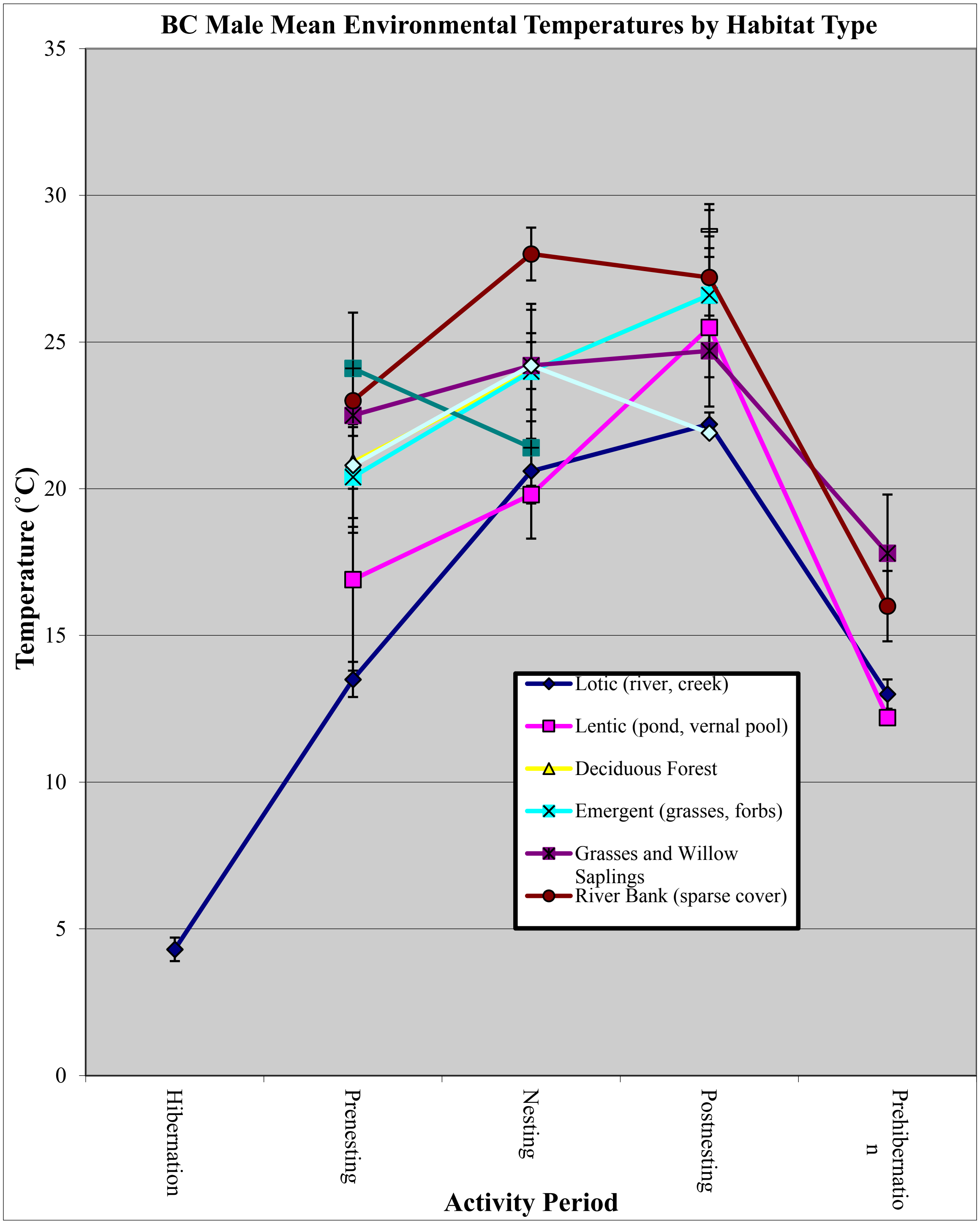

Figure 26. Environmental temperatures in locations selected by male wood turtles in BC by activity period. Lotic and lentic habitat values are water temperatures, and all terrestrial habitat values are air temperatures (n_t=364); values are means ± SE.

Sunlight Intensity

Black Hawk County

During the Hibernation period, wood turtles were largely inactive and were submerged in a lotic water source that was mostly covered by several inches of ice; although turtles were occasionally seen fully exposed in clear water and may have been experiencing limited solar heat gain during these events, they generally exhibited little or no exposure to direct sunlight throughout hibernation. In BHC during the Prenesting period, turtles became active during the day and were frequently found basking on land (usually located close to a lotic water source) to utilize solar radiation for thermoregulation. At terrestrial locations, the mean turtle sunlight intensity (SI_t) recorded for this period was 23,110 lux (±1,861 SE; n=326). This value was 47.1% of the maximum available sunlight intensity (SI_{max}) within 10 m of the turtle's location, but was 167.4% of sunlight intensity values recorded in the "average" habitat (SI_{avg}) within 10 m (i.e., the turtle's immediate vicinity).

During Prenesting, terrestrial locations that turtles selected displayed the following environmental sunlight values within 10 m of each turtle: a mean maximum sunlight (SI_{max}) available of 49,127 lux (±2,560 SE), average sunlight (SI_{avg}) available of 13,808 lux (±1,027 SE), and a mean minimum sunlight (SI_{min}) available of 306 lux (±28) (Figure 27). The mean female SI_t was 23,386 lux (±2,349 SE; n=199) (47.6% of SI_{max}, and 169.4% of SI_{avg}) and the mean male SI_t for Prenesting was 21,251 lux (±3,074 SE; n=124) (43.3% of SI_{max}, and 153.9% of SI_{avg}). When SI_t was analyzed for the 2012 Prenesting period, there was no significant difference between the sexes in mean SI_t

(ANOVA: df = 1, F-value = 0.3805, P-value = 0.5455). The 3 juvenile turtles observed during this period had a mean SI_t of 53,500 lux (±14,500 SE) (66.4% of SI_{max}, and 601.1% SI_{avg}); juveniles chose sites with an SI_{max} of 80,500 lux (±500 SE), a SI_{avg} of 8,900 lux (±7100 SE), and an SI_{min} of 796 lux (±106 SE).

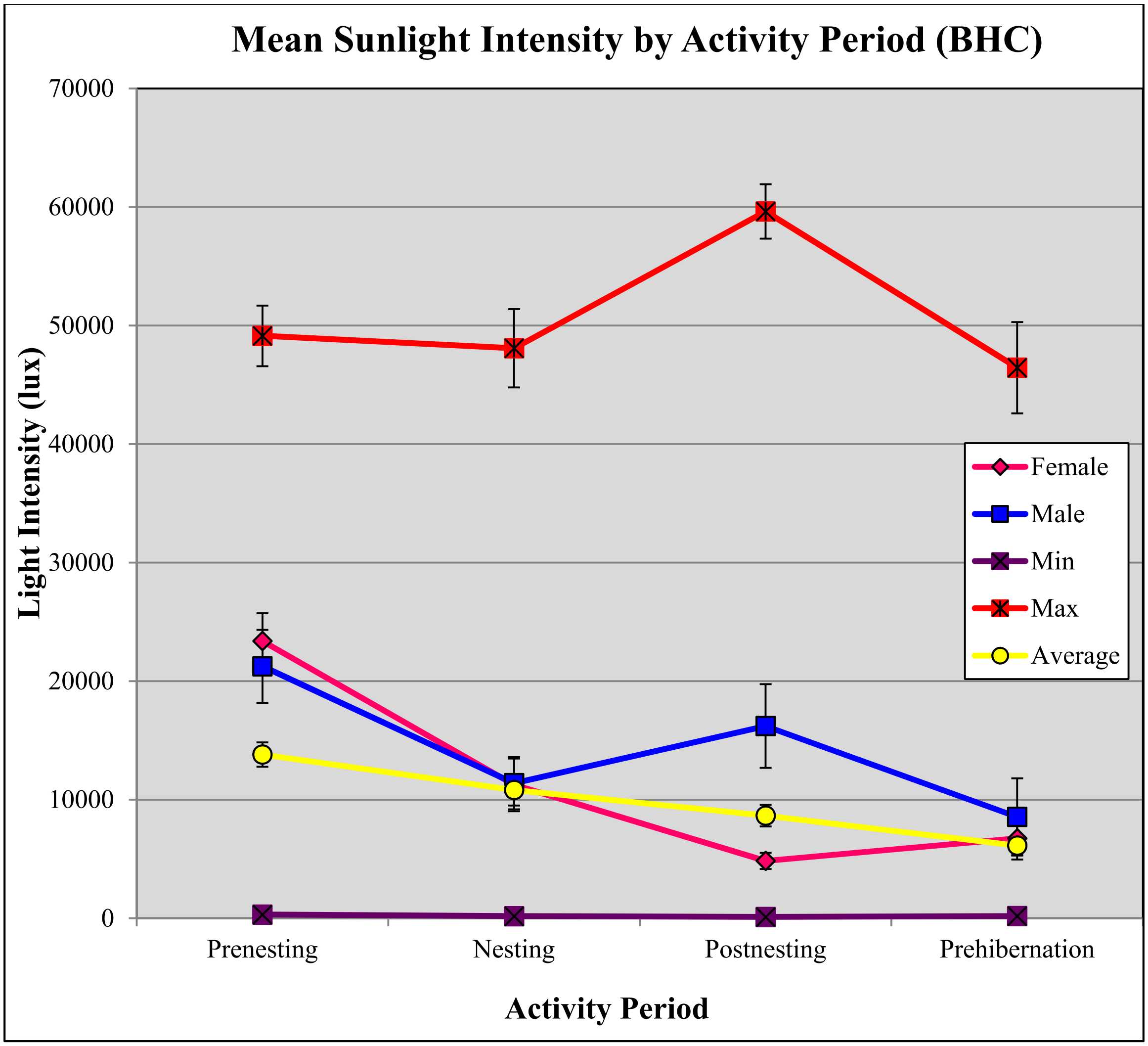

Figure 27. Sunlight intensity (lux) of specific turtle locations and corresponding environmental values within a 10 m radius by activity periods for BHC (n_t=1,964); values are means ± SE.

Through the Nesting period, the observed mean SI_t decreased by 51% to 11,326 lux (±1,562 SE; n=212) (23.56% of SI_{max}, and 104.65% of SI_{avg}), the mean SI_{max} was 48,084 lux (±3,299 SE), the mean SI_{avg} was 10,823 lux (±1,319 SE), and the mean SI_{min} was 171 lux (±14 SE). For the Nesting period, BHC female mean SI_t was 11,253 lux (±2,227 SE; n=99) (23.40% of SI_{max}, and 103.97% of SI_{avg}) and the mean male SI_t was 11,392 lux (±2,203 SE; n=113) (23.69% of SI_{max}, and 105.26% of SI_{avg}). The mean SI_t was analyzed for the 2012 Nesting period and there was no significant difference between the sexes (ANOVA: df = 1, F-value = 0.0056, P-value = 0.9410) in BHC.

For the Postnesting period as turtles moved deeper into woodlands, mean SI_t decreased to 7,708 lux (±1,070 SE; n=384) (12.9% of SI_{max}, and 89.1% of SI_{avg}) with corresponding environmental values of a mean SI_{max} of 59,625 lux (±2,296 SE), a mean SI_{avg} of 8,656 lux (±913 SE), and a mean SI_{min} of 105 lux (±8 SE). The mean female SI_t was well below the average at 4,840 lux (±680 SE; n=269) (8.1% of SI_{max}, and 55.5% of SI_{avg}), and the mean male SI_t 16,216 lux (±3,534 SE; n=115) (27.2% of SI_{max}, and 187.3% of SI_{avg}) was well above the SI_{avg} for the Postnesting Period. The mean SI_t for the 2012 Postnesting period was significantly different (ANOVA: df = 1, F-value = 21.8102, P-value < 0.0001) between the sexes in BHC. Male turtle mean SI_t during the 2012 Postnesting period was 11,679.85 lux (±2501 SE) greater than BHC female mean $SI_{t.}$

During the Prehibernation period, turtles began moving back to lotic water sources, but stayed in wooded areas with reduced sunlight exposure at ground level. The mean SI_t was 7,583 lux (±1,782 SE; n=424) (16.3% of SI_{max}, and 123.54% of SI_{avg}), the mean SI_{max} was 46,443 lux (±3,856 SE), the mean SI_{avg} was at 6,138 lux (±805 SE), and mean SI_{min} was 180 lux (±76 SE). The female mean SI_t was 6,743 lux (±1,788 SE; n=269) (14.5% of SI_{max}, and 109.9% of SI_{avg}) and the mean male SI_t was 8,549 lux (±3,261 SE; n=155) (18.4% of SI_{max}, and 139.3% of SI_{avg}). During the 2012 Prehibernation period in BHC, there was no statistical difference between the sexes in mean SI_t (ANOVA: df = 1, F-value = 0.9181, P-value = 0.3630).

In BHC, female wood turtles did not select SI that was significantly higher than males in any of the 4 active periods (Prenesting, Nesting, Postnesting, and Prehibernation). When analyzed across all active months for the year 2012, male and female wood turtles selected significantly different SI_t (ANOVA: df = 1, F-value = 7.5398, P-value = 0.0063), with male turtles selecting for a mean SI_t 4867.19 lux (±1773 SE) greater than BHC females. The 3 juvenile wood turtles (SI_t: 53,500 lux ±14,500 SE) selected sunlight exposure near mean SI_{max} (49,127 lux ±2,560 SE) for the Prenesting period.

Butler County

During the Prenesting period, BC turtles moved into riparian areas near lotic water. In terrestrial locations, the turtle mean SI_t was 22,994 lux (±1,951 SE; n=247) (42.6% of SI_{max}, and 162.9% of SI_{avg}). Locations chosen by turtles had an SI_{max} of 53,964 lux (±2,394 SE), an SI_{avg} of 14,114 lux (±943 SE), and a SI_{min} of 1,152 lux (±135 SE). The mean female SI_t was 23,055 lux (±2,414 SE; n=144) (42.7% of SI_{max}, and 163.4% of SI_{avg}) and the mean male SI_t was 23,153 lux (±3,346 SE; n=102) (42.9% of SI_{max}, and 164.1% of SI_{avg}) (Figure 28). The only juvenile turtle observed during the

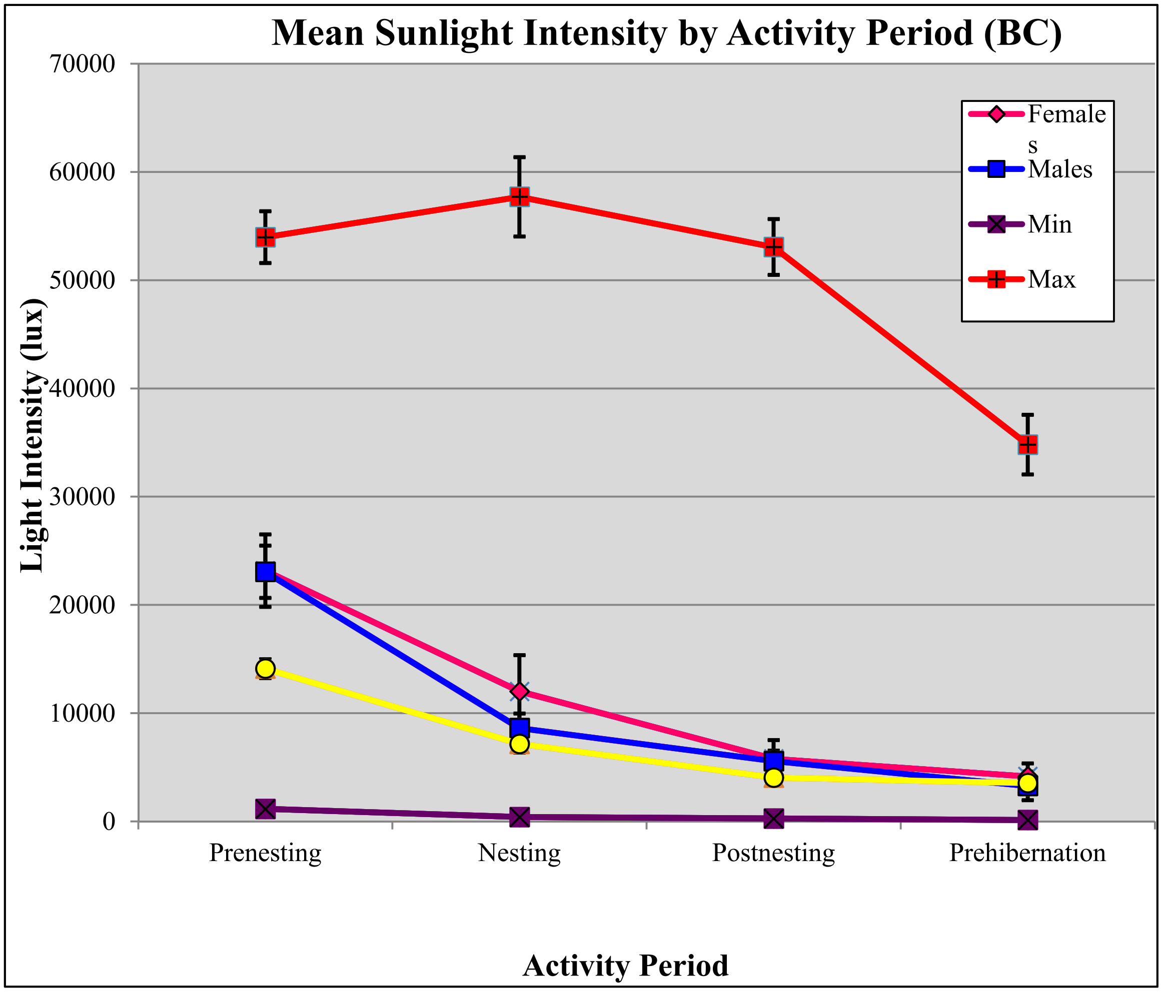

Figure 28. Sunlight intensity (lux) of specific turtle locations and corresponding environmental values within a 10 m radius by activity periods for BC (n_t=514), values are means ± SE.

Prenesting period was exposed to a SI_t of 5,010 lux (69.01% of SI_{max}, and 115.17% of SI_{avg}) in a location with corresponding environmental values of: SI_{max} = 7,260 lux; SI_{avg} = of 4,350 lux; and SI_{min} = 286 lux. For the 2004 and 2005 Prenesting period, there was no significant difference in mean SI_t between the sexes (2004 ANOVA:

df = 1, F-value = 0.0774, P-value = 0.7860; 2005 ANOVA: df = 1, F-value = 0.0888, P-value = 0.7691).

During the Nesting period, the mean SI_t was 9,869 lux (±1,495 SE; n=142) (17.11% of SI_{max}, and 137.72% of SI_{avg}), in areas that yielded a mean SI_{max} of 57,690 lux (±3,662 SE), a mean SI_{avg} of 7,166 lux (±885 SE), and with a mean SI_{min} of 397 lux (±41 SE). Mean female wood turtle SI_t was 8,617 lux (±1,344 SE; n=88) (14.94% of SI_{max}, and 120.25% of SI_{avg}) at terrestrial locations during the Nesting period, and male wood turtle mean SI_t was 12,012 lux (±3,339; n=54) (20.82% of SI_{max}, and 167.63% of SI_{avg}). For the 2004 and 2005 Nesting period, there was no significant difference in mean SI_t between the sexes (2004 ANOVA: df = 1, F-value = 1.2558, P-value = 0.2950; 2005 ANOVA: df = 1, F-value = 1.2411, P-value = 0.2817).

For the Postnesting period the mean SI_t was 5,632 lux (±844 SE; n=265) (10.6% of SI_{max}, and 139.0% of SI_{avg}), at a mean SI_{max} of 53,054 lux (±2,575 SE), a mean SI_{avg} of 4,052 lux (±298 SE), with a mean SI_{min} of 267 lux (±30 SE). Mean female SI_t was 5,572 lux (±964 SE; n=162) (10.5% of SI_{max}, and 137.5% of SI_{avg}) and mean male SI_t was observed at 5,783 lux (±1,730 SE; n=103) (10.9% of SI_{max}, and 142.7% of SI_{avg}). For the 2004 and 2005 Postnesting period, there was no significant difference in mean SI_t between the sexes (2004 ANOVA: df = 1, F-value = 0.1885, P-value = 0.6734; 2005 ANOVA: df = 1, F-value = 3.010, P-value = 0.1134).

During Prehibernation, turtles remained near lotic water sources and reduced the amount of sunlight they were exposed to in terrestrial locations. Mean SI_t was 3,550 lux (±973 SE; n=137) (10.2% of SI_{max}, and 100.3% of SI_{avg}), in areas that produced environmental values of mean SI_{max} of 34,802 lux (±2,758 SE), mean SI_{avg} of 3,541 lux (±454 SE), and a mean SI_{min} of 128 lux (±10 SE). The Prehibernation period mean female SI_t was 3,276 lux (±1,318; n=87) (9.4% of SI_{max}, and 92.5% of SI_{avg}), and mean male SI_t was 4,158 lux (±1,194 SE; n=50) (12.0% of SI_{max}, and 120.5% of SI_{avg}). For the 2004 and 2005 Prehibernation period, there was no significant difference in mean SI_t between the sexes (2004 ANOVA: df = 1, F-value = 1.9990, P-value = 0.1911; 2005 ANOVA: df = 1, F-value = 0.1330, P-value = 0.7304). Across all active months in BC for both 2004 and 2005, female and male wood turtles did not select significantly different mean SI_t (2004 ANOVA: df = 1, F-value = 0.0531, P-value = 0.8207; 2005 ANOVA: df = 1, F-value = 0.2881, P-value = 0.5974) (Figure 30).

BC 2004, 2005 – BHC 2012

Females. There was no significant difference in mean SI_t between BHC females in 2012 and BC females in 2004 and 2005 during any portions of the annual cycle: Prenesting 2004 ANOVA: df = 1, F-value = 0.4839, P-value = 0.49661; Prenesting 2005 ANOVA: df = 1, F-value = 2.010, P-value = 0.1721; Nesting 2004 ANOVA: df = 1, F-value = 0.2999, P-value = 0.5920; Nesting 2005 ANOVA: df = 1, F-value = 2.5273, P-value = 0.1255; Postnesting 2004 ANOVA: df = 1, F-value = 0.1358, P-value = 0.7171; Postnesting 2005 ANOVA: df = 1, F-value = 1.0735, P-value = 0.3139; Prehibernation 2004 ANOVA: df = 1, F-value = 1.532, P-value = 0.2416; Prehibernation 2005 ANOVA: df = 1, F-value = 0.4731, P-value = 0.5072.

Males. During the Prenesting and Nesting periods, there was no statistical difference in mean SI_t between male wood turtles in BHC during 2012 and males in BC during 2004 and 2005 (Prenesting 2004 ANOVA: df = 1, F-value = 0.0825, P-value = 0.7788; Prenesting 2005 ANOVA: df = 1, F-value = 0.1284, P-value = 0.7250; Nesting 2004 ANOVA: df = 1, F-value = 1.1940, P-value = 0.2918; Nesting 2005 ANOVA: df = 1, F-value = 0.0482, P-value = 0.8291. However, there was a marginal statistical difference in mean SI_t during the Postnesting period between male wood turtles in BHC during 2012 and those in BC 2004 and 2005 (2004 ANOVA: df = 1, F-value = 4.556, T-value = -2.134, P-value = 0.0541; 2005 ANOVA: df = 1, F-value = 4.462, T-value = -2.112, P-value = 0.0583). Mean SI_t of 2012 BHC males was 10,434 lux (±4,888 SE) more than BC 2004 males, and 17,412 lux (±8,242) more than BC 2005 males. For the Prehibernation period, there was no statistical difference in mean SI_t among male wood turtles in BHC during 2012 and males in BC during 2004 and 2005 (2004 ANOVA: df = 1, F-value = 0.9017, P-value = 0.3740; 2005 ANOVA: df = 1, F-value = 0.2222, P-value = 0.6619).

April and May were when females in both BC and BHC populations sought specific terrestrial locations with the highest levels of SI. Female turtles in BHC were exposed to the highest levels of SI in May (Figure A3), while BC females were exposed to the highest SI during April (Figure A4). This may be directly related to emergence from the Hibernation period, when maximizing thermal gain (via sunlight exposure) is crucial to begin feeding and egg development (Dubois *et al.* 2008, 2009). In June and July, female SI_t in was less than the mean SI_{avg}, while in BC, female's SI exposure was comparable to the mean SI_{avg}. In April, BC males were exposed to the highest SI_t, and in August, BHC males exposed to the highest SI_t. For all active months (March – November), in both BC and BHC wood turtle populations, mean SI_t was above the mean SI_{min}, and below the mean SI_{max}.

Distance to Water

Black Hawk County

During the Hibernation period, the BHC wood turtle population was mostly inactive and strictly aquatic; the distance from water was 0.0 m for all surveyed turtles. During Prenesting, turtles moved out of their lotic aquatic hibernation spots and frequently utilized riparian areas near the water. The mean distance to water (DTW) for both sexes during Prenesting was 28.6 m (±2.5 SE; n=183) (Figure 29). For 2012, females were not located significantly (ANOVA: df = 1, F-value = 0.8448, P-value = 0.3709) further from water [mean = 35.6 m (±3.5 SE; n=112)] than males [mean = 17.9 (±3.1 SE; n=68)]. The DTW for the 3 juvenile turtles was 12 m (±1.0 SE) during Prenesting.

During the 2012 Nesting period in BHC, females [mean = 22.6 (±2.0 SE; n=75)] were not located significantly (ANOVA: df = 1, F-value = 0.8610, P-value = 0.3635) closer to lotic water sources than males [mean = 30.9 (±3.2 SE; n=83)]. The mean DTW for turtles during this period was 27.0 m (±2.0 SE; n=158). During the Postnesting period, both sexes moved further away from lotic water sources into terrestrial habitats. The mean DTW for turtles during this period was 43.1 m (±2.3 SE; n=238). Females in BHC were located further away from water than were males; female mean DTW during

Postnesting was 47.0 m (±2.7 SE; n=178) and male mean DTW for males was 31.6 m (±3.9 SE; n=60). Female and male DTW during the 2012 Postnesting period were not significantly different (ANOVA: df = 1, F-value = 0.6939, P-value = 0.4059).

During the Prehibernation period, both male and female turtles moved back to riparian habitats near lotic water sources as they prepared to seek out hibernation sites. The mean turtle DTW for Prehibernation was 10.5 m (±4.0 SE; n=72), the mean female DTW was 6.3 m (±1.2 SE; n=37), and the mean DTW for males was 14.6 m (±3.9 SE; n=35); however, there was no significant difference in DTW for the 2012 Prehibernation period (ANOVA: df = 1, F-value = 2.544, P-value = 0.1452). When analyzed across the whole 2012 year, female and male BHC wood turtles were not significantly different in DTW during active periods (ANOVA: df = 1, F-value = 1.513, P-value = 0.2194).

Butler County

In BC, the population of wood turtles was inactive and entirely aquatic during the Hibernation period and the mean DTW was 0.0 m. During Prenesting, turtles moved out of their winter hibernacula into riparian areas and were located at a mean DTW of 17.9 m (±2.0 SE; n=184) (Figure 29). For the Prenesting period, mean DTW for BC females was 18.0 m (±2.7 SE; n=114) and male mean DTW was 17.9 m (±2.9 SE; n=69). As these values were similar, there was no significant difference in mean DTW between the sexes for Prenesting during 2004 or 2005 (2004: ANOVA: df = 1, F-value = 0.9623, P-value = 0.3477; 2005: ANOVA: df = 1, F-value = 1.147, P-value = 0.2983). The only juvenile turtle observed in BC was located during the Prenesting period at a DTW of 9.0 m. Through the Nesting period, the mean turtle DTW was 28.8 m (±0.4 SE; n=119); females remained closer to water and exhibited a mean DTW of 24 m (±4.4 SE; n=76) while male mean DTW was 37.1 m (±7.8 SE; n=43); however, there was no statistical difference in DTW between the sexes for both Nesting 2004 and 2005 (2004: ANOVA: df = 1, F-value = 0.3753, P-value = 0.5571; 2005: ANOVA: df = 1, F-value = 0.9763, P-value = 0.3378).

During the Postnesting period, turtles in the BC were located the furthest from water during their annual cycle. The mean turtle DTW was 75.5 m (±6.4 SE; n=187); the mean female DTW during Postnesting was 93.4 m (±8.2 SE; n=133), and male mean DTW was 31.6 m (±5.3 SE; n=54). For both the Postnesting period 2004 and 2005, female and male DTW were not significantly different in BC (2004: ANOVA: df = 1, F-value = 2.876, P-value = 0.1208; 2005: ANOVA: df = 1, F-value = 0.000001, P-value = 0.9991).

During the Prehibernation period, turtles moved closer to lotic water sources and the mean DTW for BC turtles decreased to 42.1 m (±8.5 SE; n=29). The mean female DTW was 52.3 m (±11.5 SE; n=20) and the mean male DTW was 19.4 m (±5.1 SE; n=9), there was no significant difference in DTW between the sexes for Prehibernation 2004 and 2005 (2004: ANOVA: df = 1, F-value = 0.2702, P-value = 0.6157; 2005: ANOVA: df = 1, F-value = 0.4057, P-value = 0.5522). Overall, across their active yearly cycle, wood turtles in the BC did not differ significantly between the sexes in mean DTW for both 2004 and 2005 years (2004: ANOVA: df = 1, F-value = 1.379, P-value = 0.2574; 2005: ANOVA: df = 1, F-value = 0.5050, P-value = 0.4855).

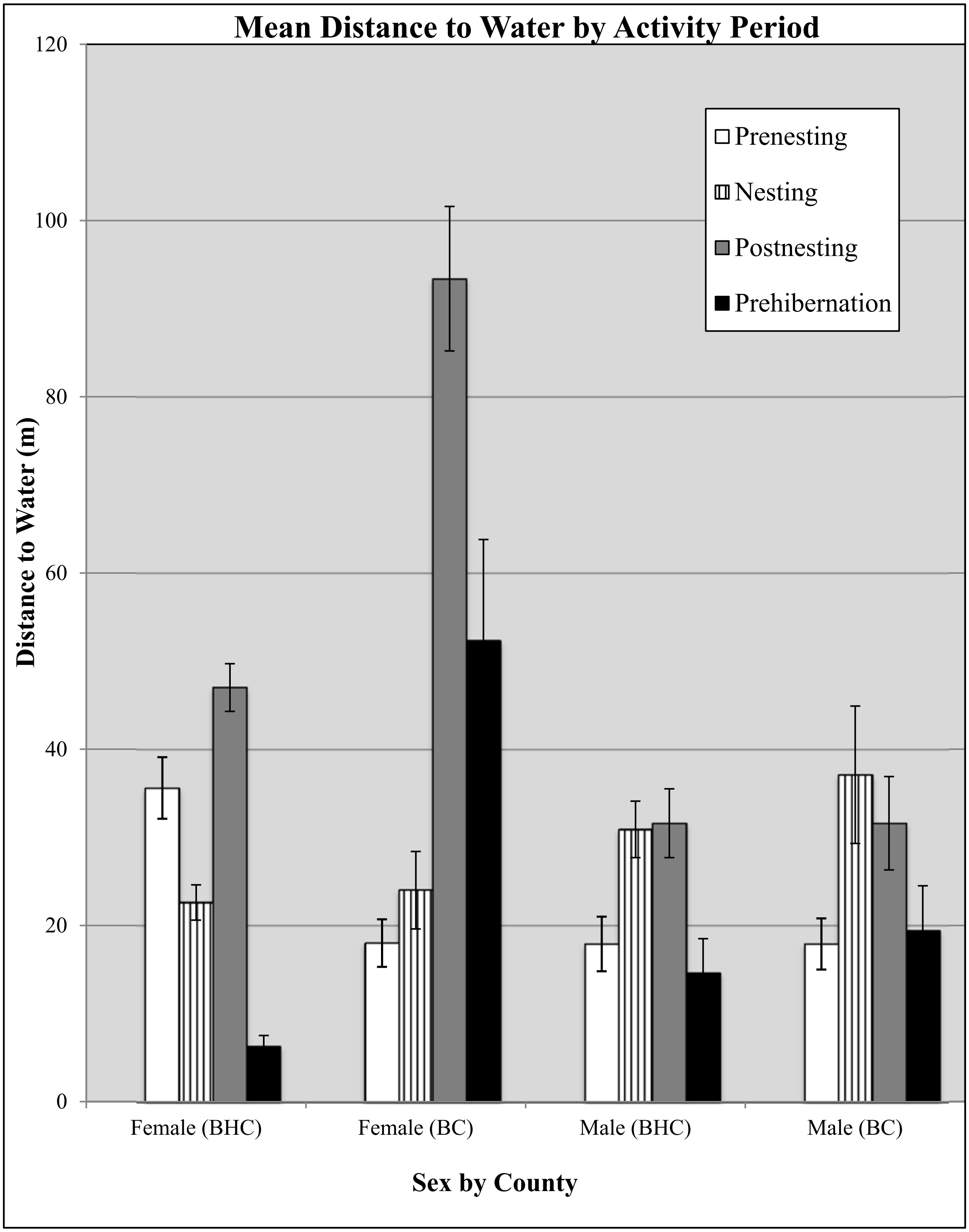

Figure 29. Distance to water for wood turtles at terrestrial locations in BHC (n_t=1,269) and BC (n_t=609) populations by activity period; values are means ± SE.

Water Depth

Black Hawk County

Wood turtles were exclusively aquatic during Hibernation. The mean water depth (WD) for turtles in BHC during the Hibernation period was 82 cm (±2.0 SE; n=378) [76.6% of mean maximum WD (WD_{max}), and 215.8% of mean channel WD ($WD_{channel}$)] (Figure 30). Within 10 m of these locations, mean $WD_{channel}$ was 38 cm (±1.0 SE), mean minimum WD (WD_{min}), was 22 cm (±1.0 SE), and WD_{max} was 107 cm (±2.0 SE). Female mean WD was 81 cm (±2.0 SE; n=191) (75.7% of mean WD_{max}, and 213.2% of mean $WD_{channel}$) and male mean WD was 82 cm (±3.0; n=187) (76.6% of mean WD_{max}, and 215.8% of mean $WD_{channel}$). Water depth used by female and male turtles were similar, and no significant difference in turtle WD existed between the sexes in BHC during the Hibernation period of 2012 (ANOVA: df = 1, F-value = 0.0516, P-value = 0.8225).

Wood turtles became noticeably less aquatic during the Prenesting period; however, at 109 aquatic locations, mean turtle WD was 86 cm (±4.0 SE) (83.5% of mean WD_{max}, and 130.3% of mean $WD_{channel}$). At these locations, mean $WD_{channel}$ was 66 cm (±5.0 SE), mean WD_{min} available was 25 cm (±1.0 SE), and mean WD_{max} was 103 cm (±1.0 SE). During Prenesting, BHC females selected mean WD of 85 cm (± 4.0 SE; n=68) (82.5% of WD_{max}, and 128.8% of mean $WD_{channel}$), and male mean WD was 88 cm (±6.0 SE; n=41) (85.4% of mean WD_{max}, and 133.3% of mean $WD_{channel}$); there was no statistical difference between female and male turtle WD during the 2012 Prenesting period (ANOVA: df = 1, F-value = 0.301, P-value = 0.5936).

During the Nesting period, lotic water depth utilized decreased; turtle mean WD was 69 cm (±3.0 SE; n=52) (79.3% of mean WD_{max}, and 125.5% of mean $WD_{channel}$), at locations with a mean channel WD of 55 cm (±3.0 SE), a mean min WD of 23 cm (±1.0 SE), and a mean maximum available WD of 87 cm (±3.0 SE). Females were located at a mean WD of 67 cm (± 5.0 SE; n=23) (77.0% of mean WD_{max}, and 121.8% of mean $WD_{channel}$) and male turtles were located at a mean WD of 70 cm (± 5.0 SE; n=29) (80.5% of mean WD_{max}, and 127.3% of mean $WD_{channel}$). During the 2012 Nesting period there was no significant difference in turtle WD between the sexes (ANOVA: df = 1, F-value = 0.1172, P-value = 0.7363).

During the Postnesting period in BHC, water levels dropped even further, and the mean turtle WD utilized was 57 cm (±2.0 SE; n=142) (83.8% of mean WD_{max}, and 203.6% of mean $WD_{channel}$). At these locations, mean $WD_{channel}$ was 28 cm (±1.0 SE), mean WD_{min} was 22 cm (±5.0 SE), and a mean WD_{max} of 68 cm (±2.0 SE). Female mean WD was 57 cm (±2.0 SE; n=68) (83.8% of mean WD_{max}, and 203.6% of mean $WD_{channel}$) and male mean WD was 56 cm (±3.0 SE; n=53) (82.4% of mean WD_{max}, and 200.0% of mean $WD_{channel}$); there was no statistical difference in turtle WD between the sexes during 2012 Postnesting (ANOVA: df = 1, F-value = 0.6596, P-value = 0.4279).

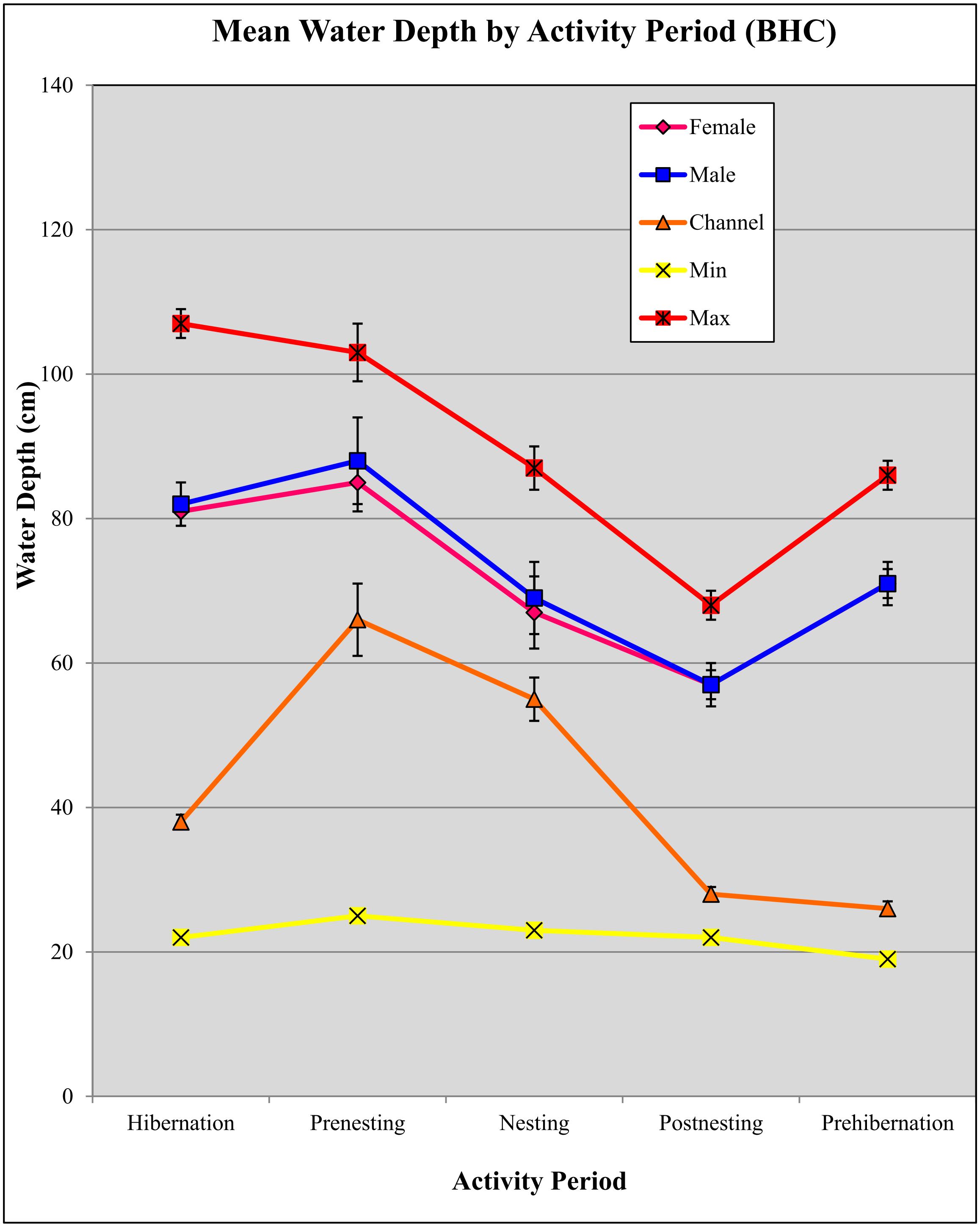

Figure 30. Water depth utilized by turtles and corresponding environmental values within 10 m of each turtle location by activity period in BHC (n_t=1,020); values are mean ± SE.

During the Prehibernation period, water levels increased and BHC turtles were located more frequently in lotic water sources in preparation for the Hibernation period. The mean turtle WD during Prehibernation was 71 cm (±1.0 SE; n=339) (82.6% of mean WD_{max}, and 273.1% of mean $WD_{channel}$), in habitats with a mean available $WD_{channel}$ of 26 cm (±1.0 SE), a mean WD_{min} of 19 cm (±4.0 SE), and a mean maximum available WD of 86 cm (±2.0 SE). During Prehibernation, female mean WD was 71 cm (±2.0 SE; n=226) (82.6% of mean WD_{max}, and 273.1% of mean $WD_{channel}$) and male mean WD was 71 cm (±3.0 SE; n=113) (82.6% of mean WD_{max}, and 273.1% of mean $WD_{channel}$). Finally, for the 2012 Prehibernation period, turtle WD was not significantly different between the sexes in BHC (ANOVA: df = 1, F-value =0.1173, P-value = 0.7322).

<u>Butler County</u>

In BC during the Hibernation period, mean turtle WD was 69 cm (±3.0 SE; n=90) (61.6% of mean WD_{max}, and 153.3% of mean $WD_{channel}$), at a mean $WD_{channel}$ of 45 cm (±1.0 SE), a mean minimum available WD of 20 cm (±1.0 SE), and mean maximum available WD of 112 cm (±3.0 SE) (Figure 31). During Hibernation, the mean female WD was 80 cm (±3.0 SE; n=49) (71.4% of mean WD_{max}, and 177.8% of mean $WD_{channel}$) and male mean WD was 56 cm (±3.0 SE; n=41) (50.0% of mean WD_{max}, and 124.4% of mean $WD_{channel}$). Turtle WD during Hibernation in BC 2004 was significantly different between the sexes (ANOVA: df = 1, F-value = 7.891, P-value = 0.0158), however during Hibernation 2005, turtle WD was not significantly different between the sexes in BC (ANOVA: df = 1, F-value = 1.744, P-value = 0.2113).

As temperatures increased during the Prenesting period, turtles became less aquatic and more terrestrial. The mean turtle WD in BC during Prenesting was 63 cm (±4.0 SE; n=66) (55.8% of mean WD_{max}, and 80.8% of mean $WD_{channel}$), mean $WD_{channel}$ was 78 cm (±7.0 SE), mean WD_{min} was 24 cm (±2.0 SE), and mean maximum available WD was 113 cm (±7.0 SE). Prenesting female turtle mean WD was 63 cm (±6.0 SE; n=32) (55.8% of mean WD_{max}, and 80.8% of mean $WD_{channel}$) and male mean WD was 59 cm (±5.0 SE; n=34) (52.2% of mean WD_{max}, and 75.6% of mean $WD_{channel}$); turtle WD between sexes was not significantly different during the Prenesting 2004 or 2005 activity period (2004: ANOVA: df = 1, F-value = 0.00056, P-value = 0.9820; 2005: ANOVA: df = 1, F-value = 0.3715, P-value = 0.5536).

Through the Nesting period in BC, the mean turtle WD was 52 cm (±6.0 SE; n=21) (47.3% of mean WD_{max}, and 61.2% of mean $WD_{channel}$), mean $WD_{channel}$ was 85 cm (±10.0 SE), mean WD_{min} was 22 cm (±4.0 SE), and mean WD_{max} was 110 cm (±10.0 SE). Nesting period female mean WD was 57 cm (±10.0 SE; n=11) (51.8% of mean WD_{max}, and 67.1% of mean $WD_{channel}$), and male mean WD was 44 cm (±7.0 SE; n=10) (40.0% of mean WD_{max}, and 51.8% of mean $WD_{channel}$). Turtle WD during the Nesting period did not statistically differ between the sexes in both 2004 and 2005 (2004: ANOVA: df = 1, F-value = 0.676, P-value = 0.4424; 2005: ANOVA: df = 1, F-value = 0.3645, P-value = 0.5886).

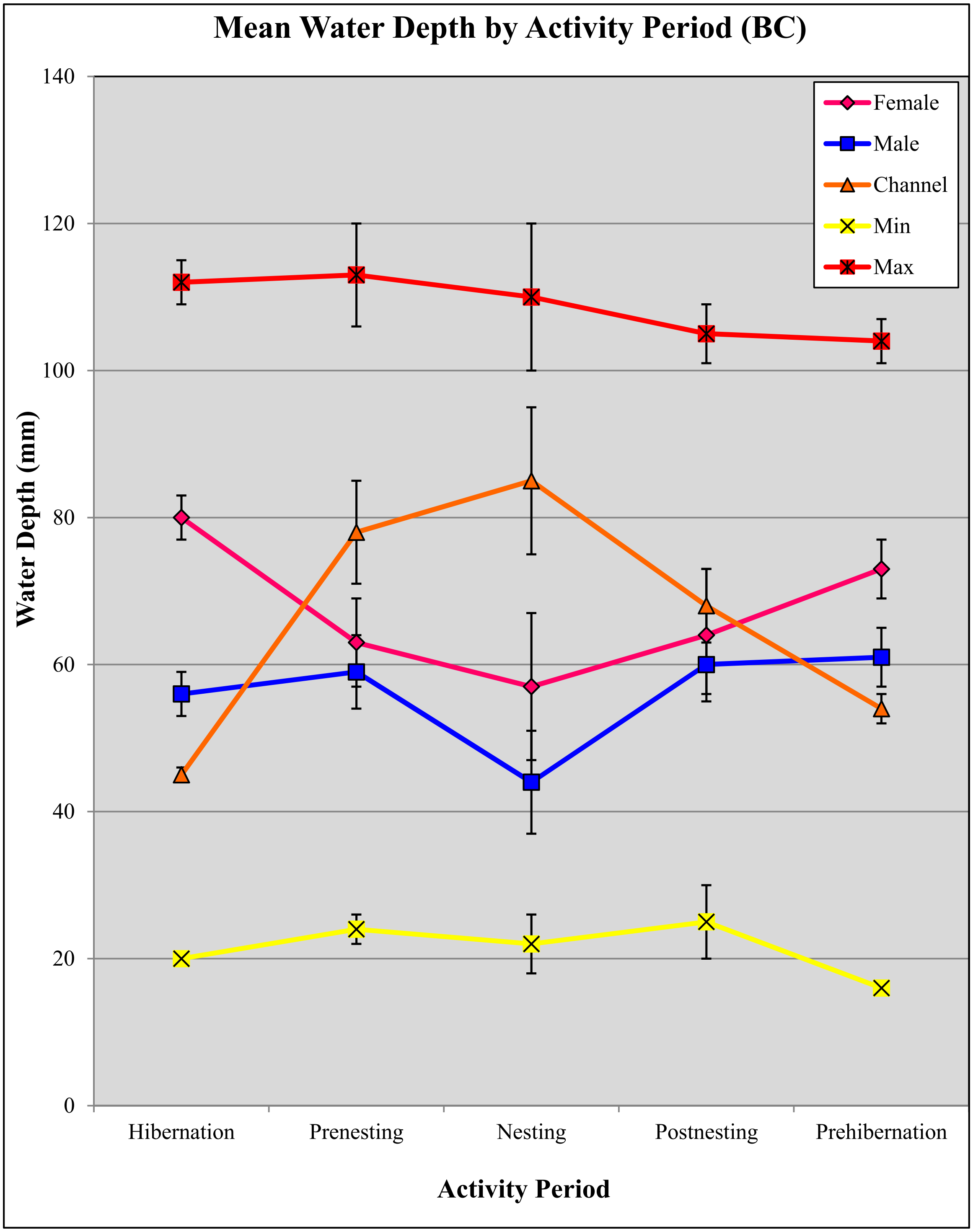

Figure 31. Water depth utilized by turtles and corresponding environmental values within 10 m of each turtle location by activity period in BC (n_t=381); values are means ± SE.

During the Postnesting period, turtles were mostly terrestrial, but were still occasionally located in lotic water sources. The mean turtle WD was 63 cm (±4.0 SE; n=84) (60.0% of mean WD_{max}, and 92.7% of mean $WD_{channel}$); mean $WD_{channel}$ was 68 cm (±5.0 SE), mean WD_{min} 25 cm (±5.0 SE), and mean WD_{max} was 105 cm (±4.0 SE). For BC females, mean WD was 64 cm (±9.0 SE; n=31) (61.0% of mean WD_{max}, and 94.12% of mean $WD_{channel}$) and male mean WD was 60 cm (±4.0 SE; n=53) (57.1% of mean WD_{max}, and 88.2% of mean channel WD); for the Postnesting period, turtle WD did not significantly differ between the sexes in 2004 or 2005 (2004: ANOVA: df = 1, F-value = 0.7346, P-value = 0.4136; 2005: ANOVA: df = 1, F-value = 0.2988, P-value = 0.5966).

In the Prehibernation period, BC wood turtles became more aquatic. The mean turtle WD was 68 cm (±3 SE; n=120) (65.4% of mean WD_{max}, and 125.83% of mean $WD_{channel}$), at a mean $WD_{channel}$ 54 cm (±2.0 SE), a mean WD_{min} 16 cm (±1.0 SE), and a mean maximum available WD 104 cm (±3.0 SE). Prehibernation female mean WD was at 73 cm (±4.0 SE; n=67) (70.2% of mean WD_{max}, and 135.2% of mean $WD_{channel}$) and male mean WD was 61 cm (±4.0 SE; n=53) (58.7% of mean WD_{max}, and 113.0% of mean $WD_{channel}$). During the Prehibernation period, turtle WD was not significantly different between the sexes for 2004 or 2005 (2004: ANOVA: df = 1, F-value = 0.4808, P-value = 0.5039; 2005: ANOVA: df = 1, F-value = 1.314, P-value = 0.2812).

Percent Exposure

Black Hawk County

Among BHC wood turtles, percent exposure (PE) of each turtle was not significantly different between the sexes in 4 out of 5 activity periods (Figure 32). The

2012 Prehibernation period was the only period in which BHC wood turtles displayed a significant difference in mean PE, females [5.0% (±1.0 SE)] were less exposed than male turtles [17.0% (± 3.0)] (ANOVA: df = 1, F-value = 5.66, T-value = 2.380, P-value = 0.0180). During the 2012 Prehibernation period, BHC males were 10.2% (±4.3 SE) more exposed than females. The juvenile mean PE of 85.0% (±15.0 SE) was larger than both female (51.0% ± 5.0 SE) and male (55.0% ± 5.0 SE) turtle PE during May (Figure A9a).

Butler County

The BC population of turtles showed no differences in mean PE between females and males in any of the activity periods (Figure 32); for both 2004 and 2005, across all activity periods, there were no statistical differences in mean PE between the sexes. The single juvenile account occurred during the Prenesting period (in the month of May) and displayed a higher PE at 85.0% when compared with female [May mean = 71.0% (±3.0 SE)] and male [May mean = 72.0% (±4.0 SE)] mean PE for the Prenesting period (Figure A9b).

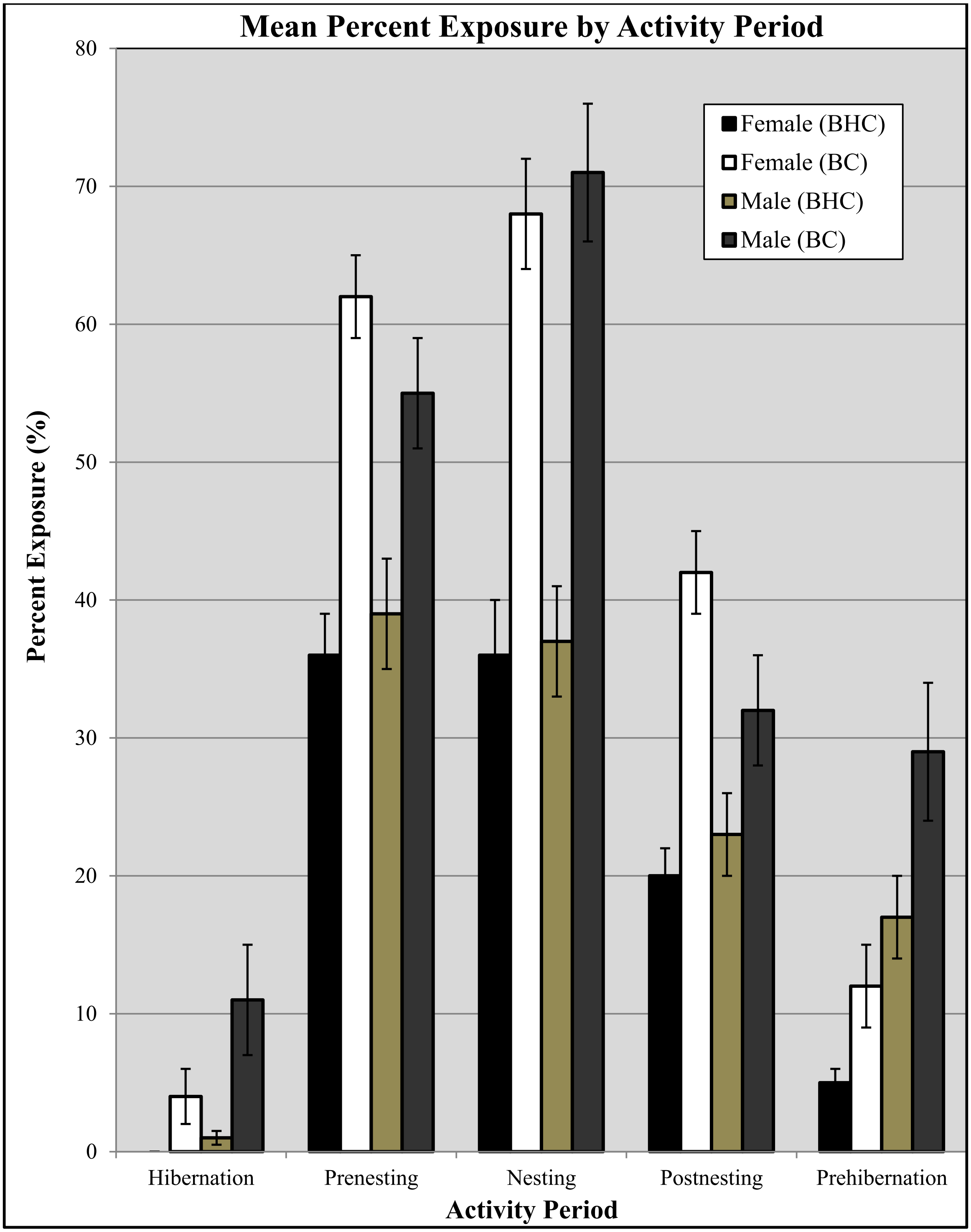

Figure 32. Percent exposure by activity period for wood turtles in BHC (n=1,961) and BC (n=898); values are means ± SE.

Behavior

Black Hawk County

By annual cycle. Across all 5 activity periods in the BHC population, females were observed hiding in water during 47.8% of the observed locations, while male turtles were hiding in water during 64.2% of all observations. Female turtles were hiding on land 14.5% out of all observations, and males were hiding on land during 12.6% of all observations. Out of all recorded BHC female observations, basking on land represented 11.0%, while male basking on land was 16.0% of observations. Female turtles were observed feeding on land 4.2% of the total study observations, and males were observed feeding on land during 5.4% of the study observations. Mating behavior was exclusively aquatic and witnessed in the Prenesting and Prehibernation periods. Female mating observations represented 0.03%, and male mating observations 0.05%, of the total study observations. Several times throughout the study turtles were witnessed locomoting in the water; females were observed moving in water 0.02% and males 0.08% of the total study observations.

Basking in shallow lotic water sources was witnessed very rarely in this study; only 2 females were witnessed basking in water, once during Postnesting and once during Prehibernation. Two males were basking in water during the Prehibernation period. The most pronounced difference occurred during the Postnesting period: during the summer, males were more aquatic and females were more terrestrial. This trend carried across the entire year, male turtles were more aquatic while females were more terrestrial. When analyzed across the entire study, male and female BHC wood turtles displayed significant difference in activities recorded (Chi square 60.172, P-value: < 0.0001).

By activity period (females). For the Hibernation period, both female and male BHC turtles were 100.0% aquatic, and were most frequently found hiding in water (n=617). During the Prenesting period, females were recorded as 40% hiding in water, 36.0% basking on land, 14.8% hiding on land, 9.0% feeding on land, and 0.01% mating in water. For the Nesting period, females were recorded hiding in water during 19.5% of the observations, hiding on land represented 33.3%, basking on land equaled 27.6%, and feeding on land represented 19.5% of observations during the study period (Figure 33).

During Postnesting, females in BHC were observed hiding on land during 45.8% of the observations, with 31.4% hiding in water, 15.7% basking on land, 6.3% feeding on land, 0.4% moving in water, and 0.4% basking in water. For the Prehibernation period, females were 83.5% hiding in water, 8.5% hiding on land, 4.7% basking on land, 1.1% feeding on land, 1.1% mating in water, 0.7% moving in water, and 0.4% basking in water.

By activity period (males). For the Prenesting period, BHC male turtles were observed hiding in water during 40.2% of the observations; 11.2% were hiding on land, 39.6% were basking on land, 7.5% were feeding on land, and mating in water represented 1.5%. During the Nesting period, males were observed hiding in water during 20.7% of the observations, 32.2% were hiding on land, 27.1% were basking on land, 19.3% were feeding on land, and 0.7% were moving in water. During Postnesting, males were 43.1% hiding in water, 30.1% hiding on land, 17.9% basking on land, 6.5% feeding on land, 1.6% moving in water, and one specimen was found dead (0.1%). For the Prehibernation period, males were recorded as 72.4% hiding in water, 6.4% hiding on land, 14.7% basking on land, 1.3% basking in water, 2.6% moving in water, 1.9% mating in water and 0.7% feeding on land (Figure 33).

Butler County

By annual cycle. In the BC population of turtles, females were observed hiding in water 19.7% of the time (including winter hibernation), while male turtles were observed hiding in water during 16.0% of the study observations (including winter hibernation). Female turtles were hiding on land 7.0% out of all observations, and males were observed as hiding on land 2.5% of all observations. Out of all recorded BC female observations, basking on land represented 27.2%, while basking on land was 15.1% of the male observations. Female turtles were observed feeding on land during 1.3% of the study, and males were observed as feeding on land 0.6% of the study. Mating behavior was witnessed aquatically and terrestrially in the Prenesting and Prehibernation periods; records of females mating in water and on land represented 0.5% and 0.3%, respectively. Males were observed mating in water 0.7% of the study and mating on land during 0.2% of the study observations.

Several times throughout the study turtles were witnessed locomoting in the water: females were observed moving in water during 1.1% and males 3.6% of the study observations. Basking in shallow lotic water sources was witnessed very rarely during the study; no females were witnessed exhibiting this behavior, and only 3 males were witnessed basking in water, once during Nesting and twice during Postnesting. Female and male turtles in BC were not drastically different in their observed behaviors across the 5 activity periods. The most pronounced difference was that during the Postnesting period males were more aquatic than females, and for the Prehibernation period females were more aquatic and males were more terrestrial. Additionally, throughout the entire year, female turtles were slightly more terrestrial while males were slightly more aquatic.

By activity period (females). For the duration of the Hibernation period, female BC turtles were 100.0% aquatic, and were always located hiding in water. As turtles became active during the Prenesting period, females were recorded as basking on land during 67.8% of the study observations; the remaining were: 19.5% hiding in water, 5.6% hiding on land, 5.6% moving on land, 1.4% mating on land, 0.7% feeding on land, 0.7% moving in water, and 0.7% found dead. During the Nesting period, females were mostly recorded basking on land (68.5% of the study observations). Other behaviors were as follows: hiding in water = 12.4%, hiding on land = 7.9%, moving on land = 7.9%, feeding on land = 4.5%, moving in water = 2.3%, and nesting on land = 2.3%. During Postnesting, females were basking on land during 43.9% of the observations and hiding on land during 23.8%; the remaining behavioral percentages were: 15.9% hiding in water, 3.1% feeding on land, 2.4% moving in water, 0.6% mating on land, and 0.4% basking in water. During the Prehibernation period, females were most frequently hiding in water (68.6% of the study observations); the remaining behavioral percentages were: 11.6% basking on land, 9.3% hiding on land, 4.7% mating in water, 3.5% were moving in water, 1.2% were feeding on land, and 1.2% of the observations were of turtles moving on land (Figure 34).

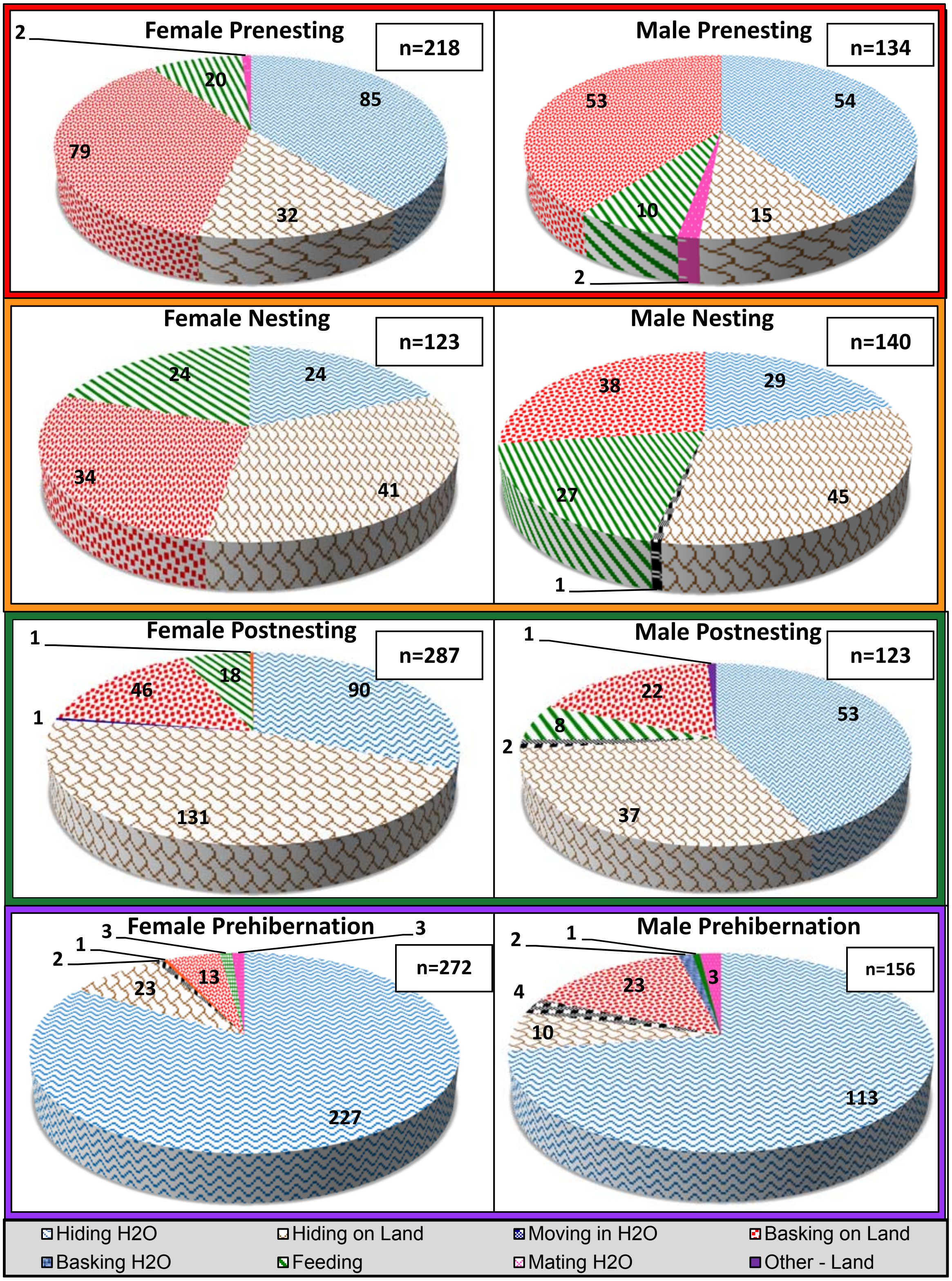

Figure 33. Wood turtle behavior by activity period for the BHC population (n_t=2,070).

By activity period (males). As with females, male BC turtles were 100.0% aquatic during hibernation, and were always located hiding in water. During the Prenesting period, BC male turtles were basking on land during 52.1% of the observations; the remaining behavioral observations were as follows: 20.8% hiding in water, 10.4% hiding on land, 10.4% moving on land, 8.3% moving in water, 3.1% feeding on land, 2.1% mating on land, and 1.1% feeding in water. During the Nesting period, males were basking on land frequently (69.8% of observations), and the remaining behaviors cumulatively represented ≈ 30.0% of all observations: 17.0% hiding in water, 3.8% moving in water, 3.8% moving on land, 1.9% hiding on land, 1.9% feeding on land, and 1.9% basking in water.

During Postnesting, males were 38.0% hiding in water, 38.0% basking on land, 10.0% hiding on land, 10.0% moving in water, 2.0% basking in water, 1.0% feeding on land, and 1.0% moving on land. For the Prehibernation period, as turtles moved back to lotic water sources, males became more aquatic and were recorded as 54.1% hiding in water, 19.7% moving in water, 13.1% basking on land, 9.8% mating in water, 1.6% hiding on land, 1.6% other behavior in water, and 0.7% feeding on land (Figure 34).

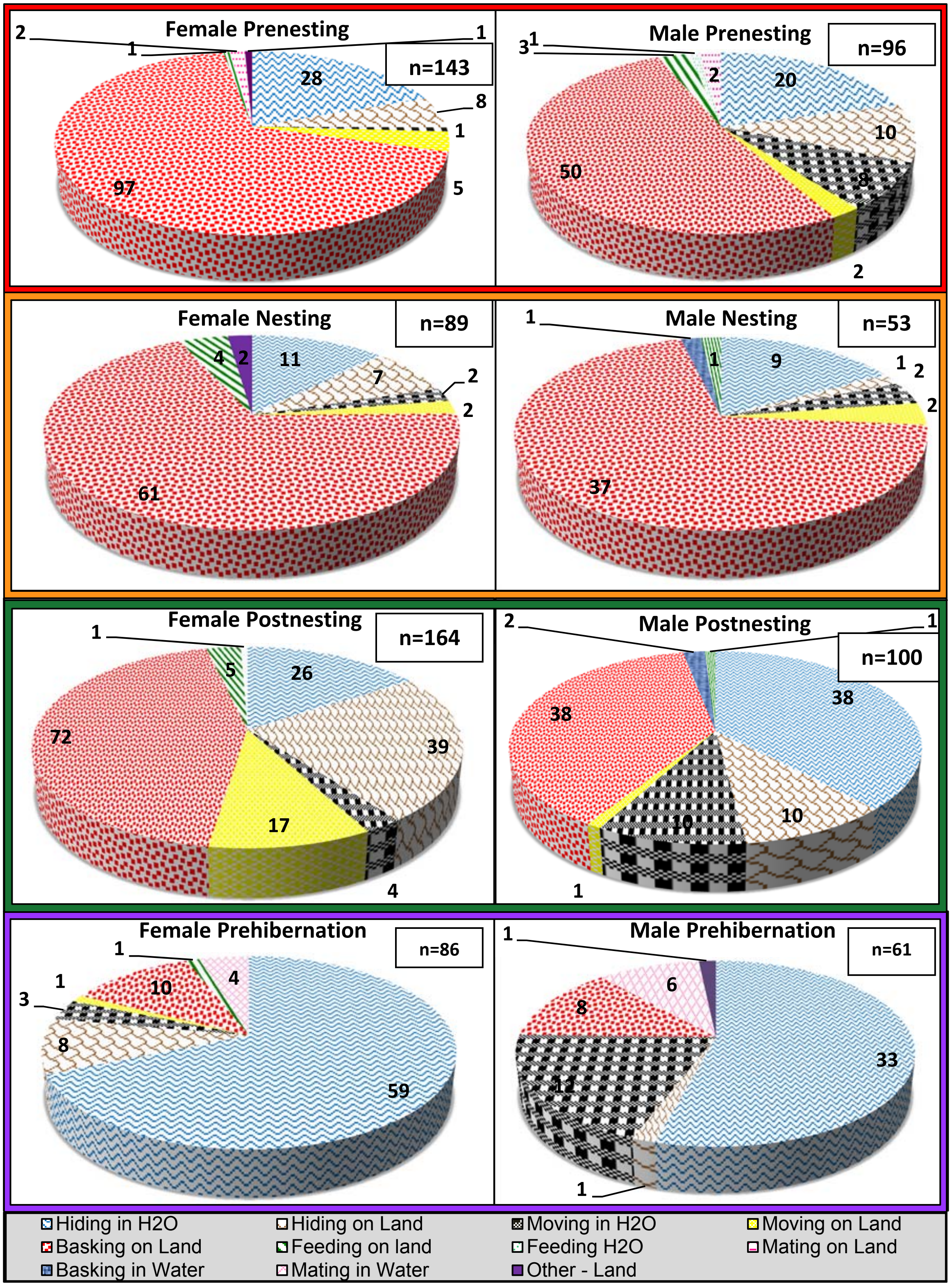

Figure 34. Wood turtle behavior by activity period for the BC population (n_t=883).

CHAPTER 4

DISCUSSION

Morphometrics, Population Size and Structure

Morphometrics

Comparing body size between both Iowa populations of wood turtles, female turtles in BHC did not differ significantly in mass from females in BC (df = 50, t-value = 1.6, P-value = 0.09); male turtles from BHC and BC also showed no significant difference in mass (df = 37, t-value = 0.1, P-value = 0.8). Females from BHC have larger CL and PL when compared to BC female turtles (CL: df = 50, t-value = 2.9, P-value = 0.005; PL: df =50, t-value = 5.7, P-value = <0.0001). BHC males were not significantly longer in CL, but were significantly longer in PL when compared with BC male turtles (CL: df = 37, t-value = 1.5, P-value = 0.1; PL: df = 37, t-value = 2.5, P-value = 0.01). Because reptiles show indeterminate growth, the larger body size of BHC turtles may reflect their slightly older age composition in comparison to the BC population.

Compared to populations of wood turtles in other regions, BHC females (989.1 g ± 112.2 SD) and BC females (943.8 g ± 105.2 SD) have larger mean body mass compared to females in a Quebec, Canada population (880 g ± 20 SD) (Daigle 1997) and females in a New Hampshire population (711.4 g ± 85.9 SD) (Tuttle and Carroll 1997). However, compared with an Ontario, Canada, population located at the northern edge of their range (mean female body mass = 1,170 g ± 50 SD; Brooks *et al.* 1992), the BHC and BC female mean body masses are smaller. This may be a function of selection for larger body size and lower SA:V ratio in extreme northern populations. Mean body mass of BHC males (998.3 g ± 309.5 SD) and BC males (985.2 g ± 254.6 SD) was less than the mean male body mass of two populations of wood turtles in Canada (Ontario: 1,280 ± 170 g, Brooks *et al.* 1992; Quebec: 1,050 g ± 30 SD, Daigle 1997). However, Iowa male turtles had a larger mean body mass than males in a New Hampshire population (mean body mass: 750.3 g ± 134.0 SD) (Tuttle and Carroll 1997). Additionally, wood turtles in BHC, BC, Ontario (Canada), Michigan, and Virginia have a larger mean CL than turtles from two different populations sampled in New Jersey (Table 3).

The BHC sex ratio was 1:1 female to male, while the BC sex ratio was 3:2 female to male (0.68 males for each female) (Tamplin in press). The 1:1 sex ratio of the BHC population is similar to the sex ratios reported throughout their range (Ross *et al.* 1991, Brooks *et al.* 1992, Tuttle and Carroll 1997, Remsberg *et al*. 2006); however, sex ratios have been reported to vary between 1.0:0.38 – 1.0:1.6 (females:males) in some populations (Farrell and Graham 1991, Ross *et al.* 1991, Brooks *et al.* 1992).

Mortality

The mortality rate in BC was lower than that observed in the BHC population; two turtles died over a 6-year period in BC while 5 turtles died over a 2.5-year period in BHC. One of the two deaths in BC was directly attributed to a flood event, while the other was undetermined and may have been due to natural causes (an older female who was found undisturbed in her normal Postnesting period location with no evidence of predation).

Table 3. Female and male CL compared across different wood turtle populations (adapted from Brooks *et al*. 1992).

Population	Sex	N	Mean CL	CL Range	Source
Algonquin Park, Ontario	F	57	202	185 – 225	Brooks *et al*., 1992
	M	21	219	199 – 244	
Michigan	F	105	182	158 – 218	Harding and Bloomer, 1979
	M	86	200	169 – 228	
Black Hawk County, IA	**F**	**16**	**186.0**	**178.0 – 196.7**	**Present study**
	M	**16**	**198.2**	**182.5 – 212.2**	
Butler County, IA	**F**	**36**	**181.7**	**168.4 – 195.8**	**Present study**
	M	**24**	**192.7**	**180.5 – 208.2**	
Virginia	F	14	183	181 – 185	Lovich *et al*., 1990
	M	11	196	193 – 199	
New Jersey	F	49	171	158 – 200	Farrell and Graham, 1991
	M	69	177	161 – 201	
New Jersey	F	464	165	160 – 188	Harding and Bloomer, 1979
	M	311	178	160 – 206	

Although it is clear that flooding is a primary factor in the high levels of wood turtle nest destruction in Iowa (Spradling *et al*., 2010), flooding events may also be a leading cause of adult death. Wood turtles in Iowa respond to heavy flooding by leaving the river channel and inhabiting slow moving backwater areas until the floods subside (Jeffrey W. Tamplin, personal observations 2003 – 2009); however, in extreme flash flood events wood turtles may be overwhelmed by the river current, or trapped and buried while hiding under creek and river banks, and unable to survive these conditions. Given that 4 of the 7 (57.1%) observed adult deaths were directly due to flooding, and that adult wood turtles frequently survive attacks by predators, changed patterns of flooding in Iowa over the past 50 – 100 years (see Spradling *et al.* 2010) may be the leading cause of population decline. Although flood-related deaths were observed at both sites, a greater number of these deaths in the Beaver Creek BHC wood turtle population suggests that this population may be more heavily impacted by flooding than the BC population, partly due to the Beaver Creek watershed's decreased flow capacity compared to the West Fork Cedar River, or possibly due to lower flood mitigation capability by the surrounding property. If the latter, this may be an indicator of poor habitat quality in this population.

Recruitment

Both BHC and BC populations demonstrate low annual recruitment rates. In BHC only 8.6% of the population were identified as juveniles, and in BC only 1.6% of the population were juveniles. No subadults (turtles ages 9 – 14) were observed in either study location. Studies in other Midwestern states have noted similar low levels of recruitment in woods turtle populations: in Wisconsin, Ross *et al.* (1991) reported only 8.6% juveniles; and in Michigan, Remsberg *et al.* (2006) reported only 14.7% juveniles. In Eastern regions, other populations of wood turtles are noted to have high recruitment rates: in New Jersey, 66.0% juveniles/subadults were reported by Tuttle and Carroll (1997); and in West Virginia, Niederberger and Seidel (1999) identified 46.0% of the population as juveniles. The paucity of recruitment to Iowa wood turtle populations may be directly related to the shift in flooding events. Historically, seasonal flooding occurred in April and has recently shifted to June and July during the egg gestation period (Spradling *et al.* 2010). This causes 100% nest lost in areas with flooding as wood turtle eggs cannot survive aquatic submersion any longer than approximately 24 hours.

Furthermore, high presence of mesopredators throughout North America, and typically throughout the wood turtle range, may cause high rates of nest failure as the eggs are predated well before hatching.

Injuries

In the BHC population, 17.1% of wood turtles were missing at least one limb, and 37.1% of turtles were missing an extensive portion of their tail. With respect to the BC population, 18.0% of the population has at least 1 limb amputated (Tamplin in press.). Other populations of wood turtles throughout their range are documented as missing limbs, possibly due to predator activity. Brooks *et al.* (1992) found 60% of adults and 28.6% of juveniles showed evidence of predatory attack. In a New Jersey population of 316 marked turtles, 8.5% were missing a limb and 16.8% displayed visible injuries (Farrell and Graham 1991). In northern Michigan, 12.5% of adult wood turtles had amputated limbs and 2% were missing 2 limbs; the recapture rate was significantly lower for injured turtles, suggesting that limb loss may affect survival, but several mutilated females were recaptured multiple years in a row (Harding and Bloomer 1979, Ernst and Lovich 2009). In BC, Iowa, a single older male (1.6% of population) was found missing both forelimbs; this male was recaptured several times over a 6-year period (Jeffrey W. Tamplin, personal observations 2007 – 2013). Additionally, one female turtle (2.9% of population) in the BHC population was missing one eye. Carroll and Ehrenfeld (1978) reported that a blind wood turtle (≈ 18 years of age) was able to find her way back to her home site after release from capture. These data indicate that wood turtles are well adapted to function even when physically deformed.

Population Summary

In BHC, the Lincoln Peterson estimated population size is 39 turtles in 469 ha of land; the resulting population density (0.08 turtles/ha) is one of the lowest reported across their range (Williams 2013); this population is noticeably smaller when compared with the BC population of wood turtles (Lincoln Peterson Index = 77 turtles). The population of wood turtles in BHC exists in a disturbed suburban habitat; this land is impacted by high traffic roads, human housing and recreational development, isolated houses, and agricultural landscapes. The BC population of wood turtles exists on larger, non-suburban, and relatively undisturbed land that is marginally impacted by agriculture and low density rural development. Additionally, BC wood turtles have multiple areas of open grassy clearings that are ideal for wood turtle thermoregulation. The BHC wood turtles have limited areas with open grassland habitat that may be affecting their behavior patterns, their home range size, and their abilities to effectively thermoregulate.

Similarly, wood turtle populations living in an agriculturally disturbed landscape in Canada, turtles displayed an increased risk of injury, slowed growth rates, and a decrease in annual recruitment when compared with turtles inhabiting a heavily forested and less disturbed landscape (Saumure and Bider 1998, Saumure *et al.* 2007). Two populations of turtles in disturbed Michigan habitats displayed a slow, but evident, decline in numbers, most likely in response to the degradation of their once undisturbed habitat (Willoughby *et al.* 2013). This difference in habitat quality (suburban vs. non-suburban) may account for the lower number of turtles observed in the BHC population. Although all human development that results in habitat loss, habitat alteration, or habitat fragmentation may negatively impact wild animal populations, specialist species like the wood turtle, a species that prefers habitat edges and requires a varied habit, may be more heavily impacted by suburban development than rural development.

Temperature Comparisons

Black Hawk County – Butler County

Activity range. Turtles in the BHC population were active terrestrially within a body temperature range of 12.3 – 33.4 ˚C (based on observed first and last days of terrestrial activity), while turtles in the BC population were active within a body temperature range of 9.2 – 34.3 ˚C. In a Pennsylvania population, turtles were active within a similar body temperature range of 7.5 – 30.0 ˚C (Ernst 1986). The warmest temperature that a turtle in BHC was observed as still active was at a body temperature of 33.4 ˚C, at a corresponding air temperature of 35.7 ˚C; in BC, the warmest a turtle was observed as active was at a body temperature of 34.3 ˚C and a corresponding air temperature of 29.2 ˚C. Ernst (1986) determined that wood turtles in a Pennsylvania population remained active until they reached a body temperature of ≈ 30.0 ˚C, and became mostly inactive at temperatures exceeding 30.0 ˚C.

Individual turtles surveyed from both populations in Iowa presented a preference for terrestrial activity at a temperature range from ≈ 20 – 30˚C; at air temperatures well above 30 ˚C, wood turtles in both Iowa populations mitigated additional heat gain by retreating to the cooler thermal refuges offered by lotic water sources and shaded woodlands. Across their entire range, wood turtles may have the ability to maintain physiological function at temperatures well above 30.0 ˚C, as the CTM for wood turtles in laboratory studies is 41.3 ˚C (Cloudsley-Thompson 1971, Harless and Morlock 1979); however, several field studies and laboratory preference studies suggest that 30 ˚C is the near upper end of T_{set} (i.e., the approximate value of T_{upper}) for this species (Dubois et al. 2008, 2009; Tamplin 2006, 2009), and the field observations reported here support these observations.

Feeding. Terrestrial feeding events were not observed until body temperatures reached 26.4 ˚C in BHC, but were recorded at a much lower temperature (13.9 ˚C) in the BC population; however, this latter temperature is similar to the value that Ernst (1986) observed (15 ˚C) in a Pennsylvania population of wood turtles, so it is likely that 26.4 ˚C was not the lowest temperature at which wood turtles fed at the BHC site. The higher initial feeding temperature recorded in BHC is most likely due to a sampling gap, where the first days of terrestrial activity were missed in BHC.

Mating. Mating was witnessed during the Prenesting and Prehibernation activity periods in both BHC and BC wood turtle populations; this is congruent with other studies of this species showing two distinct mating periods in their yearly cycle (Harding and Bloomer 1979, Ernst 1986, Ernst and Lovich 2009). In BHC, mating was only witnessed aquatically at a mean body temperature of 13.0 ˚C, a mean water temperature of 12.8 ˚C, and a mean air temperature of 15.9 ˚C; in the BC population, mating was witnessed mostly aquatically, and twice terrestrially, at a mean body temperature of 16.9 ˚C, a mean water temperature of 14.9 ˚C, and mean air temperature of 16.8 ˚C. These results are consistent with those observed by Ernst (1986) in a Pennsylvania wood turtle population, where mating was observed at a temperature range of 10 – 20 ˚C in water and 11 – 23 ˚C in non-aquatic habitats.

Female and male body temperatures. BHC females were only significantly different from BHC males in mean body temperature during the 2012 Postnesting period, a timeframe characterized by a drought and an extended heat wave across the Midwest. A possible explanation may be that, out of all observations, female turtles had a body temperature at or above 30.0 ˚C for 99 days (8.6% of the study), while male turtles were at or above 30.0 ˚C for only 62 days (7.8% of the study); the greatest number of days at or above 30.0 ˚C occurred during the Postnesting period 2012 and may have played a factor in the significant difference between the sexes during Postnesting in BHC. In a Pennsylvania population, female turtles basked more frequently during April and May, presumably to augment egg development (Ernst 1986). Furthermore, Dubois *et al.* (2009) surmised that population spatial distribution of wood turtles is constrained by thermoregulatory requirements, and that turtles selected terrestrial habitats to take advantage of positive thermal gain. In BC, there was no significant difference between the sexes in mean body temperature across either year or within any activity period. Mostly likely, any differences observed between 2004 and 2005 thermal data from BC and 2012 data from BHC are tied to the unusually warm temperatures that occurred from mid-March through the end of the Summer 2012.

Because wood turtles do not select specific environmental temperatures during their inactive (Hibernation) period (Greaves and Litzgus 2007), it is not surprising that there was no statistical difference in body temperature between the sexes during Hibernation in either population.

Temperatures by Habitat

By activity period. Environmental temperatures measured in habitats frequently used by wood turtles were similar in both populations. During hibernation, wood turtles sought refuge from subzero air and surface soil temperatures by remaining in lotic habitats with mean water temperatures that were above 0 ˚C (1.8 ˚C and in BHC and 4.7 ˚C in BC). Even during time periods when daily water temperatures dropped below 0 ˚C, hibernation sites were not subject to freezing due to current flow and these sites were thermally stable compared the extremely low air temperatures associated with seasonal arctic fronts.

During active periods wood turtles chose habitats that generally facilitated maintaining body temperatures between 20 – 30 ˚C. During Prenesting and Nesting, these habitats were most often open canopy habitats such as emergent grasses and forbs and grasses and willow saplings in BC; in BHC, habitats chosen that facilitated these body temperatures were more likely to be deciduous forest and emergent grasses and forbs, but this is most likely due to the prevalence of deciduous forest and the lack of open canopy at the study site. During Postnesting, these habitat choices expanded to include deciduous forest and lotic and lentic water sources that remained seasonally warm at both study sites. During Prehibernation, wood turtles at both study sites were often found close to lotic water sources and were primarily aquatic; in the fall, they were rarely found on land, even when thermal conditions would have prompted it earlier in the year. Wood turtles in Iowa seem to invest less time and effort in thermoregulation during the Fall; it may be that to fully acclimate to winter temperatures requires increased exposure to cool water temperatures in the fall, or it may be a response to increased activity by terrestrial mammalian predators during cool weather.

Wood turtles occupying the BHC study site lack abundant openings in the forest canopy that produce naturally warm terrestrial microhabitats. The study site is 60.4% deciduous forest (which represents 72.8% of wood turtle home ranges), 8.9% grasses and forbs (9.0% of turtle home ranges) and only 2.1% grasses and willows habitat (2.4% of turtle home ranges) (Williams 2013); therefore, only 11% of the study site represents terrestrial habitat that is productive for heat gain during typical Prenesting and Nesting temperature cycles.

The limited variability in BHC habitat may also affect the DTW, PE, and % of behavior exhibited between the study sites as effectiveness of thermoregulation may be different between study sites. Previous research has demonstrated that wood turtles shuttle about seeking sun to bask in and alter their thermoregulatory behavior based on the amount of cloud cover (Dubois *et al.* 2009). Habitat constraints limiting the amount of sunlight available to BHC wood turtles may play a role in the alteration of daily and seasonal thermoregulation behavior and habitat usage that is evident when compared with the BC population.

Sunlight Intensity

The selection of microhabitats that are below the SI_{max} of an immediate location likely reflects balancing the benefits of thermoregulation with predator avoidance behavior. There was no significant difference in sunlight exposure between the sexes within or between counties, except for the Postnesting periods where BHC males were exposed to significantly more sunlight than BC male wood turtles. This difference was most likely a result of the effects of the 2012 drought; male turtles tend to select habitats close to lotic water sources, because of the drought at the study site in BHC the vegetation died back especially in open sunlit areas (e.g., creek banks, riparian areas). Therefore, BHC males appeared to have greater sunlight exposure during the Postnesting period when compared to BC males in non-drought years. Overall, BHC turtles did not differ from BC turtles in mean sunlight exposure; this may indicate that basking preferences are similar both intrasexually and intersexually.

Distance to Water

Females

Because the study sites have different boundaries associated with different levels of human development, there are a few significant differences in the DTW that wood turtles were found during the active portion of the annual cycle. Female turtles only differed significantly between counties in mean DTW when comparing the BHC 2012 Postnesting period to the BC 2004 Postnesting period (ANOVA: df = 1, F-value = 5.558, T-value = 2.358, P-value = 0.0306); BC females had a mean DTW of 54.0 m (±22.9 SE) greater than BHC females for the 2012 Postnesting period. However, all other comparisons in mean DTW by activity periods and years (e.g., 2004 – 2012 and 2005 – 2012) between females in both counties were not significantly different.

This result indicates that female turtles in BHC have smaller mean DTW than BC females, particularly during the Postnesting (BHC = 47.0 m; BC = 93.4 m) and Prehibernation periods (BHC = 6.3 m; BC = 52.3 m). This is possibly due to the compression of available habitat by human development in BHC, and the extent of relatively undisturbed habitat available in BC. Turtles in BHC are confined by suburban development, roadways, and the surrounding agricultural land. Wood turtles seek out areas near forest edges and open clearings in order to reduce predation risk while at the same time maximizing thermal gain (Compton *et al.* 2002). Even though turtles in BHC have a much smaller DTW compared with BC turtles, turtles in BHC were continually observed at "pseudoedge" habitats. Pseudoedge habitats in BHC are those that are not distinct forest edges bordered by large tracts of open areas, rather they are locations that offer small clearings and reduced tree canopy, such as small openings in the tree canopy with in dense woodlands, areas with small forbs near the border of the railroad and the forest, and near roadway ditches bordered by forested areas.

Males

Male turtles in both BC and BHC populations maintained DTW that were similar across all observed activity periods and years. This is a consequence of male wood turtle behavior; males maintain linear home ranges close to lotic waterways during active months, while females move away from water sources and live mostly terrestrially after the Nesting period.

Water Depth

Females

Depth of water used by female wood turtles in BHC and BC differed slightly between the study sites. Yearly mean WD used by females in BHC during 2012 and WD used by BC females in 2004 was not significantly different (ANOVA: df = 1 , F-value = .6838 , P-value = 0.4185); nor were BC 2004 females significantly different in WD from BHC 2012 females across any of the individual activity periods. When comparing BHC 2012 to BC 2005, the yearly mean WD used by BC females was significantly deeper than that used by BHC females (ANOVA: df = 1 , F-value = 5.166, T-value = 2.273, P-value = 0.0355); this may be a function of flow rate differences between the years and two watersheds. Only during the Prehibernation period of 2004 were BC females located in significantly deeper water than BHC Prehibernation females in 2012 (ANOVA: df = 1 , F-value = 7.611, T-value = 2.759, P-value = 0.0134).

Males

Comparing males from the same years revealed that BC males [-13.93 cm (±5.16)] have significantly lower yearly mean turtle WD than BHC males only when the day^2 was removed (ANOVA without day^2: df = 1, F-value = 7.277, T-value = -2.698, P-value = 0.0143); and only during the Nesting period did BHC males have significantly deeper mean turtle WD than BC males [-31.56 cm (±9.88)] (ANOVA: df = 1, F-value = 10.198, T-value = -3.194, P-value = 0.0071). Comparing BC 2005 males and BHC 2012 males did not differ in mean yearly turtle WD (ANOVA: df = 1, F-value = 0.0580, P-value = 0.8123), nor did male turtles in BC and BHC significantly differ across any individual activity period for mean turtle WD. The significant difference in turtle water depth between BC 2004 males and BHC 2012 males may have been caused by drought-like conditions during 2012. BC 2004 males mean water depth was shallower compared with BHC 2012 males possibly because the BHC 2012 males sought out unusually deep aquatic locations for 2012; these locations in BHC 2012 were the only spots aquatically with enough water depth to provide cover.

Percent Exposure

Females

When comparing BHC 2012 data to BC 2004 data, the yearly mean PE in BC females was significantly greater [18.9% (±3.9 SE)] than BHC females (ANOVA: df = 1, F-value = 23.79, T-value = 4.877, P-value < 0.0001); also BC 2004 females were significantly more exposed [30.5% (±11.6 SE)] than BHC females during the Nesting (ANOVA: df = 1, F-value = 6.93, T-value = 2.632, P-value = 0.0189) and Postnesting [22.8% (±5.2 SE)] (ANOVA: df = 1, F-value = 19.03, T-value = -0.6481, P-value = 0.0004) activity periods. When comparing BHC 2012 data to BC 2005 data, the yearly mean PE in BC females was significantly greater [17.1% (±4.0 SE)] than BHC females (ANOVA: df = 1, F-value = 18.59, T-value = 4.311, P-value = 0.0002); also BC 2005 females were significantly more exposed than BHC females during the Nesting [33.29% (±8.4 SE)] (ANOVA: df = 1, F-value = 15.71, T-value = 3.963, P-value = 0.0006) and Postnesting [22.43% (±5.8 SE)] (ANOVA: df = 1, F-value = 15.17, T-value = 3.894, P-value = 0.0011) activity periods.

Males

Comparing the PE of males revealed that BC 2004 males had significantly higher [13.34% (±6.0 SE)] yearly mean PE than BHC 2012 males (ANOVA: df = 1, F-value = 4.96, T-value = 2.226, P-value = 0.0366). However, when analyzed by activity period, no single period yielded significant differences in PE between males from the two study sites. Butler county 2005 males had significantly higher [18.4% (±5.4 SE)] yearly mean PE than BHC 2012 males only when day^2 is removed as a factor (ANOVA without day ^2: df = 1, F-value = 11.55, T-value = 3.399, P-value = 0.0025). The Nesting period is the only activity period where mean PE was significantly greater in BC 2005 males [40.4% (±14.2 SE)] when compared to BHC 2012 males (df = 1, F-value = 8.16, T-value = 2.856, P-value = 0.0114).

These results suggest several things: turtles in BC may bask more frequently than BHC turtles, and/or the study site in BC has a greater percentage of ideal basking locations in comparison to the BHC site. Both of these conclusions are supported by behavioral category and study site analysis, so both observations may be in effect. In addition, the suburban BHC site may have a greater number of subsidized predators and therefore wood turtles hide more or expose themselves less as an adaptive strategy to avoid predation at the BHC site. Alternatively, the poor habitat quality of the BHC site may limit turtles in this population to bask in terrestrial locations that are not as highly exposed to sunlight. Furthermore, wood turtles are known to seek out open grassy areas to maintain optimal body temperatures (Dubois *et al.* 2008, 2009; Ernst and Lovich 2009); however, this behavior was not obvious in the BHC population. This further supports that the poor habitat quality at this suburban site may not offer habitat with ideal terrestrial habitats for thermoregulation.

Behavior by Activity Period

Midwestern populations of wood turtles are noted to be more aquatic than Eastern populations (Ernst and Lovich 2009), and Arvisais *et al.* (2004) reported that a Canadian population utilized aquatic habitats (59.1%) more frequently than terrestrial habitats (40.9%) during the active season. However, another Canadian population in Algonquin Park utilized aquatic habitats only 14.0% of the time during the spring and summer (Quinn and Tate 1991); and Compton *et al.* (2002) recorded only 16.0% of all turtle observations from May – September (excluding females during the nesting season) in lotic water sources in Maine; perhaps these infrequent observations occurred because aquatic habitats are colder in the summer at these northern locations.

Data from Williams (2013) indicates that BHC wood turtles are more aquatic throughout year (49.8% aquatic; 50.2% terrestrial) compared with BC turtles (36.3% aquatic; 63.7% terrestrial). This increased aquatic preference of BHC turtles compared to BC turtles may be due to the effects of high air temperatures during the summer of 2012, or it may indicate that BHC wood turtles are utilizing aquatic habitats in lieu of terrestrial habitats due to the reduced availability of ideal terrestrial habitat in BHC. Furthermore, other studies on wood turtles have concluded that turtles stay near aquatic habitats as a thermal refuge from inconsistent terrestrial habitats, returning to water at night, and returning to water at extremes of high and low temperatures (Dubois *et al.* 2008, 2009). In BHC, this may indicate that the deciduous forest that dominates the available habitat is of poor quality for thermoregulation, forcing turtles to seek out alternative habitats to mitigate this effect. Across all activity periods, BC turtles basked on land frequently, while BHC turtles were observed more frequently hiding on land. This may also be due to the increased availability of ideal thermoregulatory habitat in BC relative to the study site in BHC.

Conclusions

Overall, the thermal ecology of wood turtles in BHC was similar to that of the BC population. However, there were several dissimilarities between the study sites with respect to the hypotheses tested in this study. The first hypothesis, that males will emerge from winter hibernation earlier and at lower ambient temperatures than females, was not supported by data from both the suburban BHC and the rural BC populations. Because ectothermic species rely on heat gain from environmental conduction or convection, sexually dimorphic ectothermic species may express differences in the timing of emergence from hibernation between the sexes. Adult male wood turtles are of larger body size than adult female wood turtles and have smaller SA:V; this observation was consistent in both populations, and hence male wood turtles should become active at slightly lower environmental temperatures, and earlier, than females. Therefore, this conclusion may represent a gap in data sampling.

The second hypothesis was not supported by the results of this study: male wood turtles are active and move more frequently at cooler temperatures than females. Males were active in terrestrial and aquatic habitats later in the year but not earlier in the year when compared to female wood turtles. The larger volume of male wood turtles reduces conductive heat loss and facilitates activity at temperatures that may force female turtles into inactivity in aquatic habitats. Furthermore, males utilized the early Prenesting period and late Prehibernation periods to seek out females and carry out social interactions that establish and maintain their mating hierarchy. Male wood turtles may display mate-seeking behavior during cool temperature periods because finding females is most efficient when they are relatively inactive in or near water. Perhaps this conclusion also represents a gap in the data sampling, where the first male activity was not witnessed or was not documented accurately.

The third hypothesis tested was: females maintain higher internal body temperatures than males during the Prenesting and Nesting (egg development) period. This was rejected in both the BHC population and the BC wood turtle population. Female turtles in BHC were significantly different in mean body temperature from male turtles only during the Postnesting period 2012. This was well after the egg development period, and it was most likely an effect of a prolonged heat wave and the increased terrestrial habitat usage of females compared to males. Additionally, female turtles in the BC population displayed no significant difference in mean body temperature from males during any activity period, and therefore this hypothesis was not supported for the BC population either. Additionally, the BHC 2012 female turtles were significantly different in their mean temperature from BC 2004 female turtles when comparing the entire year(s); female turtles in BC 2004 were 2.69 ˚C (±1.06) warmer than BHC 2012 females, despite the summer 2012 heat wave. These results could further indicate that BHC turtles lack optimal thermoregulatory habitat, and hence females are unable to elevate their body temperature significantly above male turtles without excessive predation risk in exposed areas.

The final hypothesis tested was: turtles of both sexes will maximize optimal thermal gain by differentially utilizing available habitats based on current ambient environmental temperatures. The suburban habitat of BHC is distinctly different from the rural habitat in BC. Turtles in BHC lack abundant inland grassy clearings that are heavily utilized by the BC population of turtles. Therefore, turtles in BHC thermoregulate in deciduous woods and in small isolated patches of emergent grasses and forbs; wood turtles in BC thermoregulate in large expanses emergent grasses and forbs and in long stretches of grasses and willows that line the riverbanks. Aside from the disparity in habitat types between BC and BHC, the fourth hypothesis is supported in both wood turtle populations. As temperatures increased, post-Hibernation turtles in both counties sought out terrestrial habitats with positive thermal gain. During the peak temperature months in the Postnesting period, turtles sought out shady wooded refuges or aquatic environments to avoid reaching their CTM. As temperatures cooled during the Prehibernation period, in both counties turtles moved closer to potential hibernation sites and began heavily utilizing thermally stable lotic water sources. Collectively, these results support that both BHC and BC wood turtles seek out different habitats depending on the environmental temperatures in order to mediate thermal gain.

Management Recommendations

Both Iowa populations of wood turtles in the present study may be defined as “ghost populations” (Compton 1999); i.e., they represent populations of older adults that have low rates of mortality, but little or no recruitment and experience high rates of egg and juvenile mortality, either due to the effects of flooding events or nest predators (Spradling *et al.* 2010). The BC population of wood turtles has fewer juveniles, but a higher population density, a lower mortality rate, and individuals with larger home ranges (Williams 2013); this population may be more stable than the BHC population, but the adults do not appear to be replacing themselves at rates that will sustain the population.

The BHC population of wood turtles may be in potential danger of extirpation. Although there are more adults at the study site than were expected, frequent flooding events have destroyed nesting sites and killed adult turtles. In addition, human disturbance is increasing as development of the West section of the study site continues, and the population of Cedar Falls is progressively shifting to the Western edge of the city limits. Unfortunately, over the summers of 2012 and 2013 a total of 5 adult turtles were found dead. This loss of reproductively capable turtles in an already disturbed suburban landscape does not bode well for the population as a whole. Already low annual recruitment to the population is evident, and with the loss of 5 breeding adults it is difficult to say how this BHC population will respond. Studies have demonstrated that loss of even a few adult turtles leads to highly negative consequences for the population as a whole; additionally this loss in adults must be balanced by high survivorship and recruitment of juvenile turtles to sustain individual turtle populations (Garber and Burger 1995, Brooks *et al.* 1991, Congdon *et al.* 1993, Saumure *et al.* 2007). However, declines in turtle populations within other studies were directly related to anthropogenic activity (e.g., haying and other agricultural practices, canoeing, and illegal collection of specimens); in BHC the wood turtle population is most drastically affected by the indirect effects of anthropogenic suburbanization. Of the 5 known dead BHC wood turtles, 3 out of 5 were most likely killed by the ever-increasing cyclical flooding events, and two were most likely predated by a predator such as a raccoons, skunk, possum, or feral house cat. The increased occurrence of flooding events in the wood turtle's Iowa range in is a consequence of changing agricultural practices and suburban land development. Not only do these drastic flooding events pose a threat to adult wood turtles, they pose a mortal risk to all wood turtle nest sites.

In BHC, three individual wood turtle nesting sites were identified. During flood events, these nesting sites remained submerged underwater for weeks at a time, killing 100% of wood turtle eggs, and resulting in 0% annual recruitment to the BHC wood turtle population. With respect to the subsidized predator issue, it may be of significance for local conservation board individuals to institute annual trapping of these mesopredators. Not only would this reduce adult turtle predation, but it would also decrease the frequent levels of nest predation witnessed across multiple turtle species at the study sites. A further option to reduce egg predation would be to erect electric fencing around identified nesting sites during the Nesting period. Bennett *et al.* (2009) and Geller (2012) have demonstrated at least a 20 – 30% reduction in egg predation after fencing was in place.

The present study demonstrated that female wood turtles in BHC may be having difficulty raising their internal temperatures during the Prenesting and Nesting season due to a lack of optimal open grassy habitat found at BHC study site. This inability to optimally thermoregulate during the egg development period may affect female turtle health and vigor as well as negatively affect recruitment numbers in the development and hatching of new wood turtles.

In order to offset the potential “ghost population” effect that is occurring with the BHC wood turtle population, certain habitat modification and local law changes may be required. Several studies have demonstrated that stream bank erosion rates and run-off pollutant level may be significantly decreased when appropriate riparian buffers are created around all nearby agricultural fields (Schultz *et al.* 2004, Zaimes *et al.* 2004). Perhaps similar restoration practices may positively impact the BHC site, mediating extreme flooding events when applied to the surrounding agricultural, recreational, and other suburbanized landscapes. Importantly, if water runoff levels could be decreased during flooding events, perhaps some of the nesting sites would remain dry and be successful in hatching, thus increasing annual recruitment rates of wood turtles in the BHC population. Furthermore, adult wood turtles may not be as at risk to mortality during periods of high water flow if some areas remain dry and available for turtles to escape flood waters.

The BHC study site is a combined private property and public recreational area exposed to high levels of human activity on a daily basis. For the benefit of this state endangered species, local government should consider amending the public portion of the BHC study site to protected status, rendering it inaccessible to human recreation to offer at least some respite to the declining wood turtle numbers found in this area. Furthermore, modifying the habitat by removing sections of trees and allowing grassy clearings to develop may offer BHC wood turtles the habitat required to optimally thermoregulate. As wood turtles in the BHC are located far from water within dense deciduous woods, offering alternative inland habitats may positively affect this population. Finally, if future research on the BHC wood turtle population reveals continued little to no annual recruitment and a continual decline in adult wood turtle numbers is observed, then more drastic measures may be in order: head starting eggs and juveniles, nest caging, or artificial nest mount construction.

REFERENCES

Arvisais M, Bourgeois JC, Daigle C, Masse D, Jutras J. 2004. Habitat selection by the wood turtle (*Clemmys insculpta*) at the northern limit of its range. Canadian Journal of Zoology 82(3):391–398.

Arvisais M, Bourgeois JC, Levesque E, Daigle C, Masse D, Jutras J. 2002. Home range and movements of a wood turtle (*Clemmys insculpta*) population at the northern limit of its range. Canadian Journal of Zoology 80:402–408.

Baldwin EA, Marchand MN, Litvaitis JA. 2004. Terrestrial habitat use by nesting painted turtles in landscapes with different levels of fragmentation. Northeastern Naturalist 11(1):41–48.

Bennett C, Chaudhry S, Clemens M, Gilmer L, Lee S, Parker T, Peterson E, Rajkowski, J, Shih K, Subramaniam S, Wells R, White J. 2009. Excluding mammalian predators from diamondback terrapin nesting beaches with an electric fence. [master’s thesis]. [College Park, MD] University of Maryland.

Bernstein NP, Black RW. 2005. Thermal environment of overwintering ornate box turtles, *Terrapene ornata ornata*, in Iowa. American Midland Naturalist 153(2):370–377.

Big Marsh Wildlife Management Area. 2013. [cited: 2013, Jan 23]. Available from http://www.iowadnr.gov/portals/idnr/uploads/wildlife/wmamaps/bigmarsh.pdf

Blair RB. 1996. Land use and avian species diversity along an urban gradient. Ecological Applications 6:506–519.

Bonin F, Devaux B, Dupré A. 2006. Turtles of the World. Baltimore, MD: Johns Hopkins University Press.

Brooks RJ, Brown GP, Galbraith DA. 1991. Effects of a sudden increase in natural mortality of adults on a population of the common snapping turtle (*Chelydra serpentina*). Canadian Journal of Zoology 69:1314–1320.

Brooks RJ, Shilton CM, Brown GP, Quinn NW. 1992. Body size, age distribution, and reproduction in a northern population of wood turtles (*Clemmys insculpta*). Canadian Journal of Zoology 70 (3):462–469.

Brown GP, Brooks RJ. 1991. Thermal and behavioral responses to feeding in free-ranging turtles, *Chelydra serpentina*. Journal of Herpetology 25(3):273–278.

Buhlmann KA. 1993. Legislation and conservation alert. Herpetological Review 24:125.

Buhlmann K, Tuberville T, Gibbons W. 2008. Turtles of the Southeast. A Wormsloe Foundation Nature Book. Athens, GA: University of Georgia Press.

Bull JJ, Legler JM, Vogt RC. 1985. Non-temperature dependent sex determination in two suborders of turtles. Copeia 1985:784–786.

Cagle FR. 1939. A system of marking turtles for future identification. Copeia 1939:170–173.

Carroll TE, Ehrenfeld DW. 1978. Intermediate-range homing in the wood turtle, *Clemmys insculpta*. Copeia 1978:117–126.

Chessman BC. 1987. Atmospheric and aquatic basking of the Australian freshwater turtle *Emydura macquarii.* Herpetologica 43(3):301–306.

Christiansen JL, Bailey RM. 1997. The lizards and turtles of Iowa. Iowa Department of Natural Resources, Nongame Technical Series No. 3. Des Moines, IA.

Cloudsley-Thompson JL. 1971. The temperature and water relation in reptiles. Walford Herts, England: Merrow Publ. Co. Ltd.

Compton BW. 1999. Ecology and conservation of the wood turtle (*Clemmys insculpta*) in Maine. [master's thesis]. [Orono, ME]: University of Maine.

Compton BW, Rhymer JM, McCollough M. 2002. Habitat selection by Wood Turtles (*Clemmys insculpta*): An application of paired logistic regression. Ecology 83(3):833–843.

Conant R, Collins JT. 1998. A Field Guide to Reptiles and Amphibians of Eastern and Central North America, 3rd Ed., Expanded. Boston, MA: Houghton Mifflin Co.

Congdon JD, Dunham AE, van Loben Sels RC. 1993. Delayed sexual maturity and demographics of Blanding's Turtles (*Emydoidea blandingii*): Implications for conservation and management of long-lived organisms. Conservation Biology 7(4):826–833.

Congdon JD, Graham TE, Herman TB, Lang JW, Pappas MJ, Brecke BJ. 2008. *Emydoidea blandingii* (Holbrook 1838) – Blanding's turtle. In: Rhodin AGJ, Pritchard PCH, van Dijk PP, Saumure RA, Buhlmann KA, Iverson, JB. (Eds.). Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group. Chelonian Research Monographs No. 5.

Congdon JD, Keinath DA. 2006. Blanding's Turtle (*Emydoidea blandingii*): a technical conservation assessment. USDA Forest Service, Rocky Mountain Region. [cited:2013, Feb 6] Available from http://www.fs.fed.us/r2/projects/scp/assessments/blandingsturtle.pdf

Costanzo JP, Lee RE, Wright MF. 1993. Physiological responses to freezing in the turtle *Terrapene carolina*. Journal of Herpetology 27:117–120.

Curtin CG. 1995. Latitudinal gradients in biophysical constraints: Implication for species response to shifting land-use and climate. [Ph.D. Dissertation]. [Madison, WI]: University of Wisconsin.

Daigle C. 1997. Size and characteristics of a wood turtle, *Clemmys insculpta*, population in southern Quebec. Canadian Field Naturalist 111(3):440–444.

DeStefano S, DeGraaf RM. 2003. Exploring the ecology of suburban wildlife. Frontiers in Ecology and the Environment 1(2):95–101.

Dodd KC. 1990. Effects of habitat fragmentation on a stream-dwelling species, the flattened musk turtle, *Sternotherus depressus*. Biological Conservation 54(1):33–45.

Dubois Y, Blouin-Demers G, Thomas D. 2008. Temperature selection in wood turtles (*Glyptemys insculpta*) and its implications for energetics. Ecoscience 15(3):398–406.

Dubois Y, Blouin-Demers G, Shipley B, Thomas D. 2009. Thermoregulation and habitat selection in wood turtles *Glyptemys insculpta*: chasing the sun slowly. Journal of Animal Ecology 78(5):1023–1032.

Eckler JT, Breisch AR, Behler JL. 1990. Radio telemetry techniques applied to the bog turtle (*Clemmys muhlenbergii*). New York State Museum Bulletin 471:69–70.

Edwards AL, Blouin-Demers G. 2007. Thermoregulation as a function of thermal quality in a Northern population of Painted Turtles, *Chrysemys picta*. Canadian Journal of Zoology 85(4):526–535.

Ernst CH. 1968. Evaporative water-loss relationships of turtles. Journal of Herpetology 2(3/4): 159–161.

Ernst CH. 1972. Temperature activity relationships in the painted turtle, *Chrysemys picta*. Copeia 1972:217−222.

Ernst CH. 1977. Biological notes on the bog turtle, *Clemmys muhlenbergii*. Herpetologica 1977(33):241–246.

Ernst CH. 1982. Environmental temperatures and activities in wild spotted turtle, *Clemmys guttata*. Journal of Herpetology 16(2):112–120.

Ernst CH. 1986. Environmental temperatures and activities in the wood turtle, *Clemmys insculpta*. Journal of Herpetology 20(2):222–229.

Ernst CH, Lovich JE. 2009. Turtles of the United States and Canada. Second Edition. Baltimore (MD): Johns Hopkins University Press.

Ernst CH, Lovich JE., Barbour RW. 1994. Turtles of the United States and Canada. Washington (DC): Smithsonian Institution Press.

Ewert MA, Nelson CE. 1991. Sex determination in turtles: Diverse patterns and some possible adaptive values. Copeia 1991:50–69.

Fahrig L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics 34:487–515.

Farrell RF, Graham TE. 1991. Ecological notes on the turtle *Clemmys insculpta* in northwestern New Jersey. Journal of Herpetology 25(1):1–9.

Feldman CR., Parham JF. 2001. Molecular systematics of emydine turtles. Linnaeus Fund Research Report. Chelonian Conservation and Biology 4(1):224–228.

Feldman CR, Parham JF. 2002. Molecular phylogenetics of emydine turtles: Taxonomic revision and the evolution of shell kinesis. Molecular Phylogenetic Evolution 22:388–398.

Frair W, Ackman RG, Mrosovsky N. 1972. Body temperature of *Dermochelys coriacea*: warm turtle from cold water. Science 177(4051):791–793.

Galbraith DA. 1991. Studies of mating systems in wood turtles (*Clemmys insculpta*) and snapping turtles (*Chelydra serpentina*) using DNA fingerprinting. [Ph.D. Dissertation]. [Kingston, Ontario (Canada)]: Queen's University.

Garber SD, Burger J. 1995. A 20 year study documenting the relationship between turtle decline and human recreation. Ecological Applications 5(4):1151–1162.

Geller GA. 2012. Reducing predation of freshwater turtle nests with a simple electric fence. Herpetological Review 43(3):398.

Gibbons JW. 1968. Population structure and survivorship in the painted turtle, *Chrysemys picta.* Copeia 1968:260–268.

Gibbs JP. 1998. Distribution of woodland amphibians along a forest fragmentation gradient. Landscape Ecology 13(4):263–268.

Gibbs JP, Shriver WG. 2002. Estimating the effects of road mortality on turtle populations. Conservation Biology 16(6):1647–1652.

Graham TE, Forsberg JE. 1991. Aquatic oxygen uptake by naturally wintering wood Turtles, *Clemmys insculpta*. Copeia 1991:836–838.

Greaves WF, Litzgus JD. 2007. Overwintering ecology of wood turtles (*Glyptemys insculpta*) at the species' northern range limit. Journal of Herpetology 41(1):32–40.

Harding JH. 1997. Amphibians and reptiles of the Great Lakes Region. University of Michigan Press. Ann Arbor, MI.

Harding JH., Bloomer TJ. 1979. The wood turtle, *Clemmys insculpta* . . . a natural history. HERP, Bulletin of the New York Herpetological Society 15:9–26.

Harding JH., Davis SK. 1999. *Clemmys insculpta* (wood turtle*)* and *Emydoidea blandingii* (Blanding's turtle): Hybridization. Herpetological Review 30(4): 225–226.

Harless M, Morlock H. (Eds.). 1979. Turtles: perspectives and research. New York (NY): John Wiley and Sons.

Herman D. 1981. Status of the bog turtle in the southern Appalachians. Proceedings of the Non-game/Endangered Wildlife Symposium, Technical Bulletin WL-5, Georgia Department of Natural Resources, Game and Fish Division.

Hertz PE, Huey RB, Stevenson RD. 1993. Evaluating temperature regulation by field-active ectotherms: The fallacy of the inappropriate question. American Naturalist 142:796–818.

Hoffmann CO, Gottschang JL. 1977. Numbers, distribution, and movements of a raccoon population in a suburban residential community. Journal of Mammalogy 58:623–636.

Holman JA, Fritz, U. 2001. A new emydine species from the Middle Miocene (Barstovian) of Nebraska, USA with a new generic arrangement for the species of *Clemmys* sensu McDowell (1964) (Reptilia: Testudines: Emydidae). Zoologische Abhandlungen Staatliches Museum für Tierkunde Dresden 51:331–354.

Holt SM. 2000. Development and evaluation of a model for turtle embryonic growth. [master's thesis]. [Guelph, Ontario (Canada)]: University of Guelph.

Hutchison VH, Maness JD. 1979. The role of behavior in temperature acclimation and tolerance in ectotherms. American Zoologist 19(1):367–384.

Hutchison VH, Vinegar A, Kosh RJ. 1966. Critical thermal maxima in turtles. Herpetologica 22(1):32–41.

Iowa-Cedar Rivers UNESCO-HELP Basin. 2013. [cited: 2013, Jan 23] Available from http://iowacedarbasin.org/cedar/watershed

Iowa Department of Natural Resources (IA DNR). Iowa Natural Areas Inventory. 2013. [cited: 2013, Jan 23] Available from https://programs.iowadnr.gov/naturalareasinventory/pages/RepSpeciesByCounty.aspx?elementID=560&type=County

Iowa Natural Resource Commission. 2009. Chapter 77: Endangered and Threatened Plant and Animal Species. [cited: 2013, Jan 16] Available from https://www.legis.iowa.gov/DOCS/ACO/IAC/LINC/Chapter.571.77.pdf

Kaufmann JH. 1992a. Habitat use by wood turtles in central Pennsylvania. Journal of Herpetology 26(3):315–321.

Kaufmann JH. 1992b. The social behavior of wood turtles, *Clemmys insculpta*, in central Pennsylvania. Herpetological Monographs 6:1–25.

Knight TW, Layfield, JA, Brooks RJ. 1990. Nutritional status and mean selected temperature of hatchling snapping turtles (*Chelydra serpentina*): Is there a thermophilic response to feeding? Copeia 1990:1067–1072.

Lamberson RH, McKelvey R, Noon BR, Voss C. 2002. A dynamic analysis of northern spotted owl viability in a fragmented forest landscape. Conservation Biology 6(4):505–512.

LeClere JB. 2013. A Field Guide to the Reptiles and Amphibians of Iowa. Rodeo (NM): ECO Publishing & Distribution.

Legler JM. 1960. Natural history of the ornate Box Turtle, *Terrapene ornata ornata* Agassiz. University of Kansas, Publ. Museum of Natural History 11:527–669.

Lenk P, Fritz U, Joger U, Wink M. 1999. Mitochondrial phylogeography of the European pond turtle, *Emys orbicularis* (Linnaeus 1758). Molecular Ecology 8:1911–1922.

Levell JP. 2000. Commercial exploitation of Blanding's turtles, *Emydoidea blandingii*, and the wood turtle, *Clemmys insculpta*, for the live animal trade. Chelonian Conservation and Biology 3(4):665–674.

Litzgus JD, Brooks RJ. 2000. Habitat and temperature selection of *Clemmys guttata* in a northern population. Journal of Herpetology 34(2):178–185.

Litzgus JD, Costanzo JP, Brooks RJ, Lee Jr RE. 1999. Phenology and ecology of hibernation in spotted turtles (*Clemmys guttata*) near the northern limit of their range. Canadian Journal of Zoology 77(9):1348–1357.

Lovich JE, Ernst CH, McBreen JF. 1990. Growth, maturity, and sexual dimorphism in the wood turtle, *Clemmys insculpta*. Canadian Journal of Zoology 68(4):672–677.

Manning B, Grigg GC. 1997. Basking is not of thermoregulatory significance in the "basking" freshwater turtle *Emydura signata*. Copeia 1997(3):579–584.

Marchand MN, Litvaitis JA. 2004. Effects of landscape composition, habitat features, and nest distribution on predation rates of simulated turtle nests. Biological Conservation 117(3):243–251.

Marzluff JM. 2001. Worldwide urbanization and its effects on birds. Avian ecology and conservation in an urbanizing world. Kluwer Academic, Norwell, MA.

Mitchell TS, Warner DA, Janzen FJ. 2013. Phenotypic and fitness consequences of maternal nest-site choice across multiple early life stages. Ecology 94(2):336–345.

My County Parks: Beaver Creek Access. 2013. [cited: 2013, Jan 23] Available from http://www.mycountyparks.com/county/Black-Hawk/Park/Beaver-Creek-Access.aspx

National Audubon Society. 2013. [cited: 2013, Jun 26] Available from http://web4.audubon.org/bird/at_home/Backyard.html

Newton EJ, Herman TB. 2009. Habitat, movements, and behavior of overwintering Blanding's turtles (*Emydoidea blandingii*) in Nova Scotia. Canadian Journal of Zoology 87(4):299–309.

Niederberger AJ, Seidel ME. 1999. Ecology and status of a wood turtle (*Clemmys insculpta*) population in West Virginia. Chelonian Conservation and Biology 3(3):414–418.

Nutting WL, Graham TE. 1993. Preferred body temperatures in five Nearctic freshwater turtles: A preliminary study. Comparative Biochemistry and Physiology 104A:243–246.

Oldfield B, Moriarty JJ. 1994. Amphibians and Reptiles Native to Minnesota. Minneapolis (MN): University of Minnesota Press.

O'Steen SO. 1998. Embryonic temperature influences juvenile temperature choice and growth rate in snapping turtles *Chelydra serpentina*. Journal of Experimental Biology 201:439–449.

Parham JF, Feldman CR. 2002. Generic revisions of emydine turtles. Turtle and Tortoise Newsletter 6:28–30.

Parmenter RR. 1980. Effects of food availability and water temperature on the feeding ecology of pond sliders (*Chrysemys s. scripta*). Copeia 1980:503–514.

Parren SG, Rice MA. 2004. Terrestrial overwintering of hatchling turtles in Vermont nests. Northeastern Naturalist 11:229–233.

Pearse DE, Avise JC. 2001. Turtle mating systems: behavior, sperm storage, and genetic paternity. Journal of Heredity 92:206–211.

Pittman SE, Dorcas ME. 2009. Movements, habitat use, and thermal ecology of an isolated population of Bog Turtles (*Glyptemys muhlenbergii*). Copeia (4):781–790.

Plummer MV. 2003. Activity and thermal ecology of the box turtle, *Terrapene ornata*, at its southwestern range limit in Arizona. Chelonian Conservation and Biology 4(3):569–577.

Plummer MV, Krementz DG, Powell LA, Mills NE. 2008. Effects of habitat disturbance on survival rates of softshell turtles (*Apalone spinifera*) in an urban stream. Journal of Herpetology 42(3):555–563.

Plummer MV, Williams BK, Skiver MM, Carlyle JC. 2003. Effects of dehydration on the critical thermal maximum of the desert box turtle (*Terrapene ornata luteola*). Journal of Herpetology 37:747–750.

Pough FH, Gans C. 1982. The vocabulary of reptilian thermoregulation. In: Gans C. (Ed.), Biology of the Reptilia. New York (NY): Academic Press.

Profitt K, Chance B. 2004. Status of the wood turtle (*Clemmys insculpta*) on the coastal plain of Harford County, Maryland. In: Swarth CW, Roosenburg WM, Kiviat E. (Eds.), Conservation and Ecology of Turtles of the Mid-Atlantic Region: A Symposium. Bibliomania, Salt Lake City, UT.

Quinn NWS., DP Tate. 1991. Seasonal movement and habitat of wood turtles (*Clemmys insculpta*) in Algonquin Park, Journal of Herpetology 25:220–222.

Rafferty AR., Reina RD. 2014. The influence of temperature on embryonic developmental arrest in marine and freshwater turtles. Journal of Experimental Marine Biology and Ecology 450:91–97.

Remsberg AJ, Lewis TL, Huber PW, Asmus KA. 2006. Home ranges of wood turtles (*Glyptemys insculpta*) in northern Michigan. Chelonian Conservation and Biology 5(1):42–47.

Rhodin AG, van Dijk PP, Iverson JB, Shaffer HB. 2010. Turtles of the World, 2010 Update: Annotated checklist of taxonomy, synonymy, distribution, and conservation status. Chelonian Research Monographs 5:1–80.

Ropert-Coudert Y, Wilson RP. 2004. Subjectivity in bio-logging science: Do logged data mislead? Memorial National Institute for Polar Research, Special Issue 58:23–33.

Ross DA, Anderson RK. 1990. Habitat use, movements, and nesting of *Emydoidea blandingii* in central Wisconsin. Journal of Herpetology 24:6–12.

Ross DA, Brewster KN, Anderson RK, Ratner N, Brewster CM. 1991. Aspects of the ecology of wood turtles, *Clemmys insculpta*, in Wisconsin. Canadian Field Naturalist. 105(3):363–367.

Rowe JW, Moll EO. 1991. A radiotelemetric study of activity and movements of the Blanding's turtle (*Emydoidea blandingii*) in Northeastern Illinois. Journal of Herpetology 25:178–185.

Saumure RA. 2010. Wood turtle distribution. [cited: 2013, Jun 26] Available from https://www.woodturtle.com/Distribution.html

Saumure RA, Bider JR. 1998. Impacts of agricultural development on a population of wood turtles (*Clemmys insculpta*) in Southern Quebec, Canada. Chelonian Conservation and Biology 3:37–45.

Saumure RA, Herman TB, Titman RD. 2007. Effects of haying and agricultural practices on a declining species: The North American wood turtle, (*Glyptemys insculpta*). Biological Conservation 135(4):565–575.

Schultz RC, Isenhart TM, Simpkins WW, Colletti JP. 2004. Riparian forest buffers in agroecosystems—lessons learned from the Bear Creek Watershed, Central Iowa, USA. Agroforestry Systems 61(1–3):35–50.

Seymour RS. 1982. Physiological adaptations to aquatic life. Biology of the Reptilia 13:1–51.

Snyder DM. 1994. Iowa's Trees. Iowa Association of Naturalists, Ames, IA.

Souza FL, Martins FI. 2006. Body temperature of free-living freshwater turtles, *Hydromedusa maximiliani*. Amphibia-Reptilia 27(3):464–468.

Spradling TA, Tamplin JW, Dow SS, Meyer KJ. 2010. Conservation genetics of a peripherally isolated population of the Wood Turtle (*Glyptemys insculpta*) in Iowa. Conservation Genetics 11(5):1667–1677.

Stephens PR, Wiens JJ. 2003. Ecological diversification and phylogeny of emydid turtles. Biological Journal of the Linnean Society 79:577–610.

Strang CA. 1983. Spatial and temporal activity patterns in two terrestrial turtles. Journal of Herpetology 17(1):43–47.

Tamplin JW. 2006a. *Glyptemys insculpta* (wood turtle). Diet. Herpetological Review 37:456–457.

Tamplin JW. 2006b. Response of hatchling wood turtles (*Glyptemys insculpta*) to an aquatic thermal gradient. Journal of Thermal Biology 31:400–405.

Tamplin J. 2009. Effect of age and body size on selected temperature by juvenile wood turtles (*Glyptemys insculpta*). Journal of Thermal Biology 34:41–48.

Tamplin JW. In Press. *Glyptemys insculpta* (LeConte, 1830). In: Bernstein N, Christiansen J, VanDeWalle T. (Eds.). Natural History of the Amphibians and Reptiles of Iowa. Iowa City (IA): University of Iowa Press.

Telemeco RS, Warner DA, Reida MK, Janzen FJ. 2012. Extreme developmental temperatures result in morphological abnormalities in painted turtles (*Chrysemys picta*): A climate change perspective. Integrative Zoology 8(2):197–208.

Tuttle SE. 1996. Ecology and natural history of the wood turtle (*Clemmys insculpta*) in southern New Hampshire. [master's thesis]. [Keene (NH)]: Antioch University.

Tuttle SE, Carroll DM. 1997. Ecology and natural history of the wood turtle (*Clemmys insculpta*) in southern New Hampshire. Chelonian Conservation and Biology 2:447–449.

Van Dijk PP, Harding JH. 2012. *Glyptemys insculpta*. In: IUCN 2012. IUCN Red List of Threatened Species. Version 2012.2. [cited: 2013, Nov 2013] Available from www.iucnredlist.org. Retrieved: 22 November 2013.

Walde AD. 1998. Ecology of the wood turtle, *Clemmys insculpta*, Quebec, Canada. [master's thesis]. [Montreal (Canada)]: McGill University.

Walde AD, Bider JR, Daigle C, Masse D, Bourgeois JC, Jutras J, Titman RD. 2003. Ecological aspects of a wood turtle, *Glyptemys insculpta*, population at the northern limits of its range in Quebec. Canadian Field Naturalist 117(3):377–388.

Wiens JJ, Kuczynski CA, Stephens PR. 2010. Discordant mitochondrial and nuclear gene phylogenies in emydid turtles: implications for speciation and conservation. Biological Journal of the Linnean Society 99:445–461.

Williams JJ. 2013. Habitat usage, movement patterns, and home range size of wood turtles (*Glyptemys insculpta)* in a suburban habitat. [master's thesis]. [Cedar Falls (IA)]:University of Northern Iowa.

Williamson LU, Spotila JR, Standora EA. 1989. Growth, selected temperature and the CTM of young snapping turtles, *Chelydra serpentina*.. Journal of Thermal Biology 14:33–39.

Willoughby JR, Sundaram M, Lewis TL, Swanson BJ. 2013. Population decline in a long-lived species: The wood turtle in Michigan. Herpetologica, 69(2):186–198.

Yagi KT, Litzgus JD. 2013. Thermoregulation of spotted turtles (*Clemmys guatta*) in a beaver-flooded bog in southern Ontario, Canada. Journal of Thermal Biology (38):205–213.

Zaimes GN, Schultz RC, Isenhart TM. 2004. Stream bank erosion adjacent to riparian forest buffers, row-crop fields, and continuously-grazed pastures along Bear Creek in central Iowa. Journal of Soil and Water Conservation 59(1):19–27.

APPENDIX A

ECOLOGICAL DATA GRAPHS BY MONTH

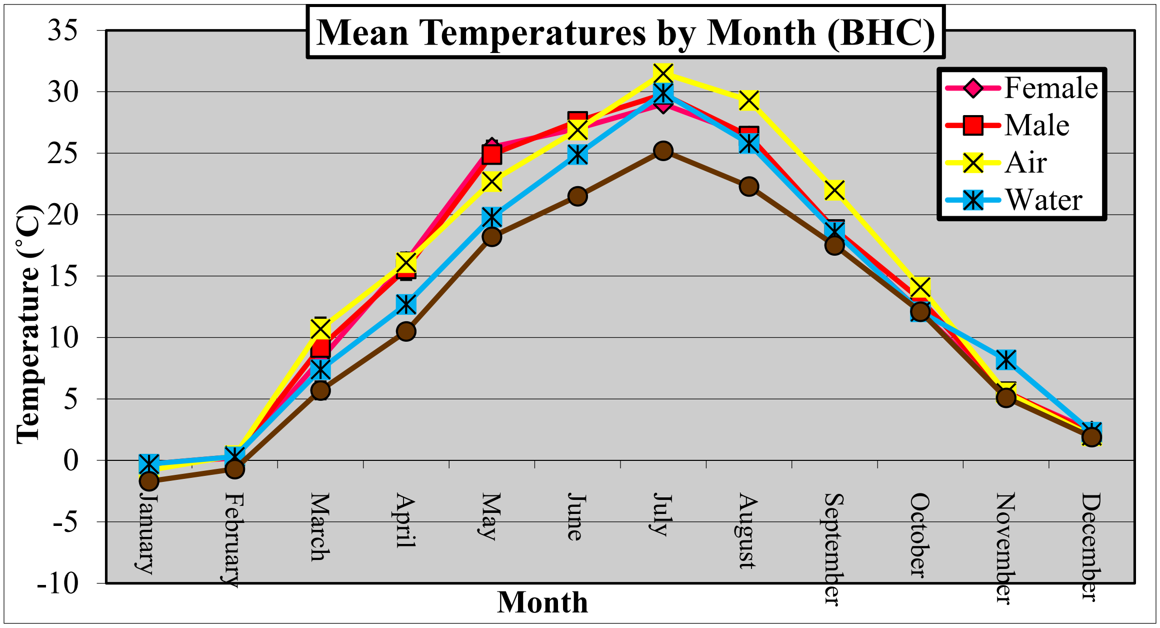

Figure A1. Turtle body and environmental temperatures recorded by month for BHC(n_t=1947); values are means ± SE.

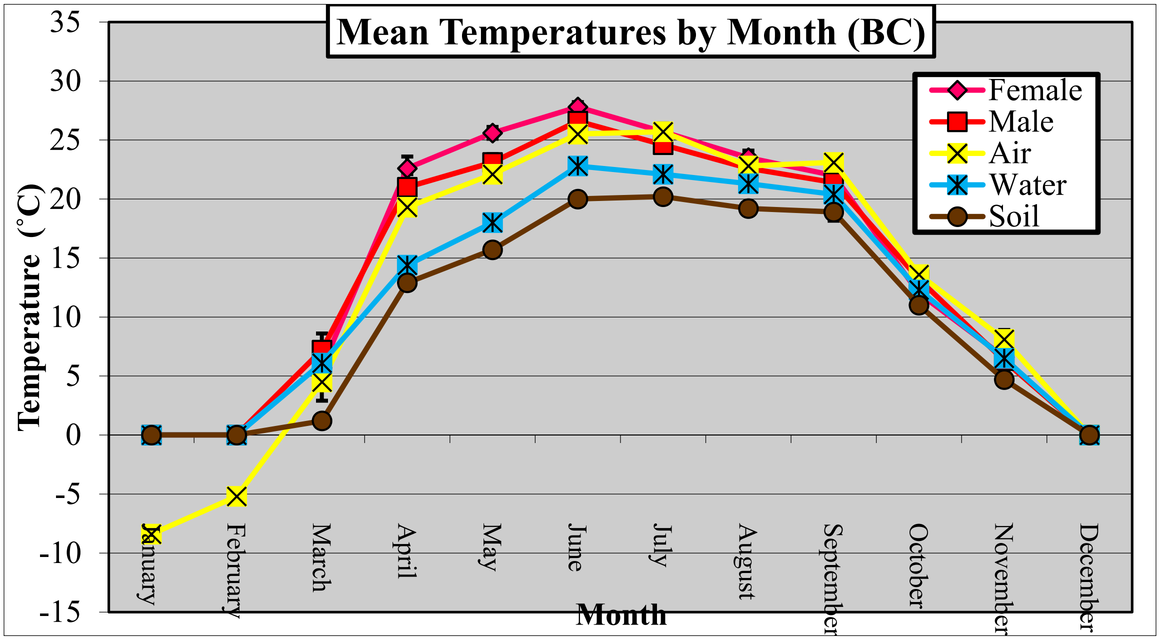

Figure A2. Turtle and environmental temperatures recorded by month for BC (n_t=893); values are means ± SE.

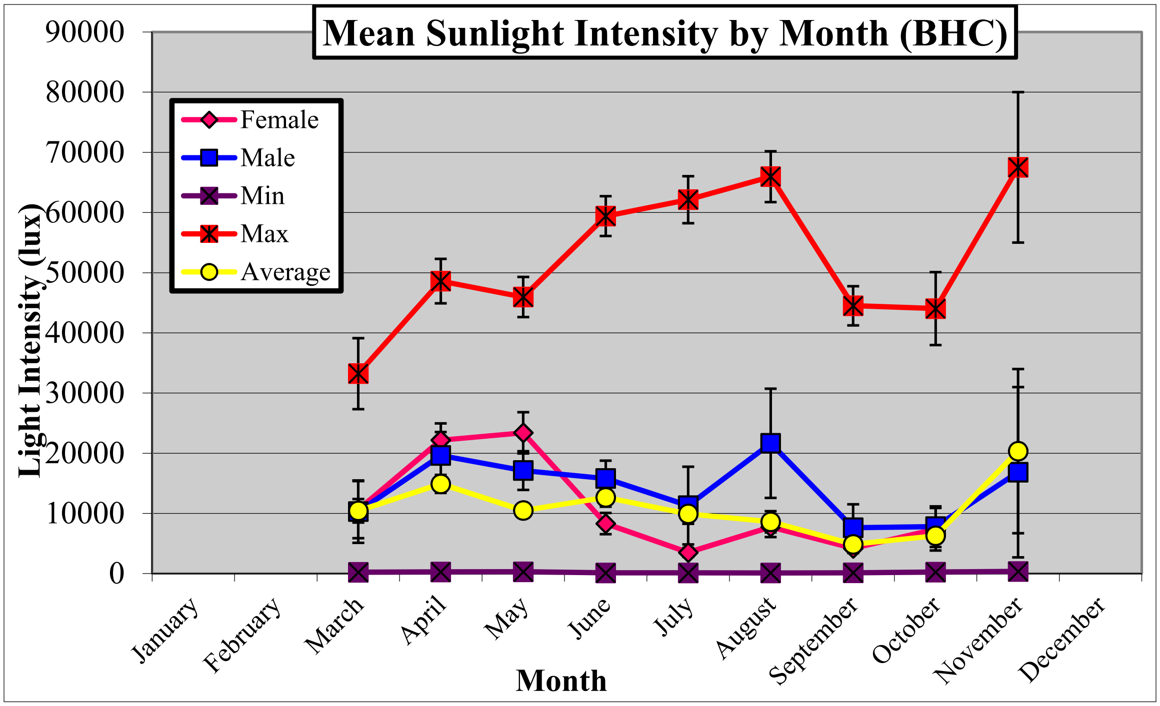

Figure A3. Sunlight intensity selected by turtles and corresponding environmental values by month for BHC (n_t=1157); values are means ± SE.

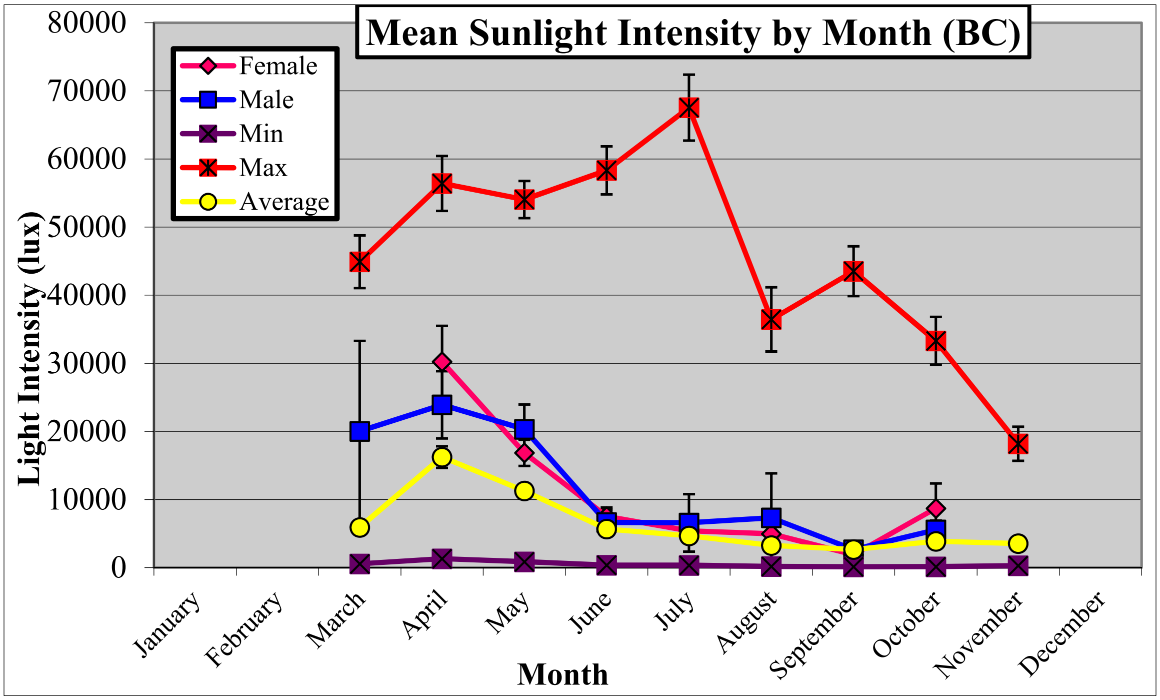

Figure A4. Sunlight intensity selected by turtles and corresponding environmental values by month for BC (n_t=514); values are means ± SE.

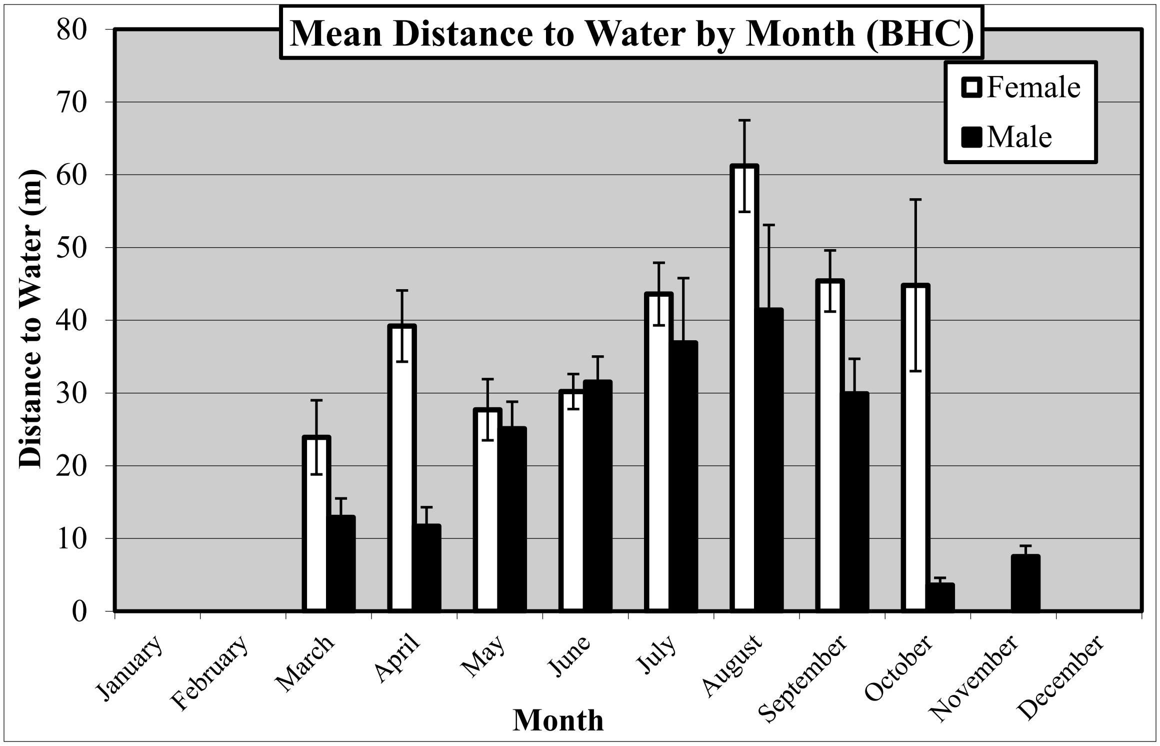

Figure A5. Distance to water by month for BHC (n_t=1,269); values are means ± SE.

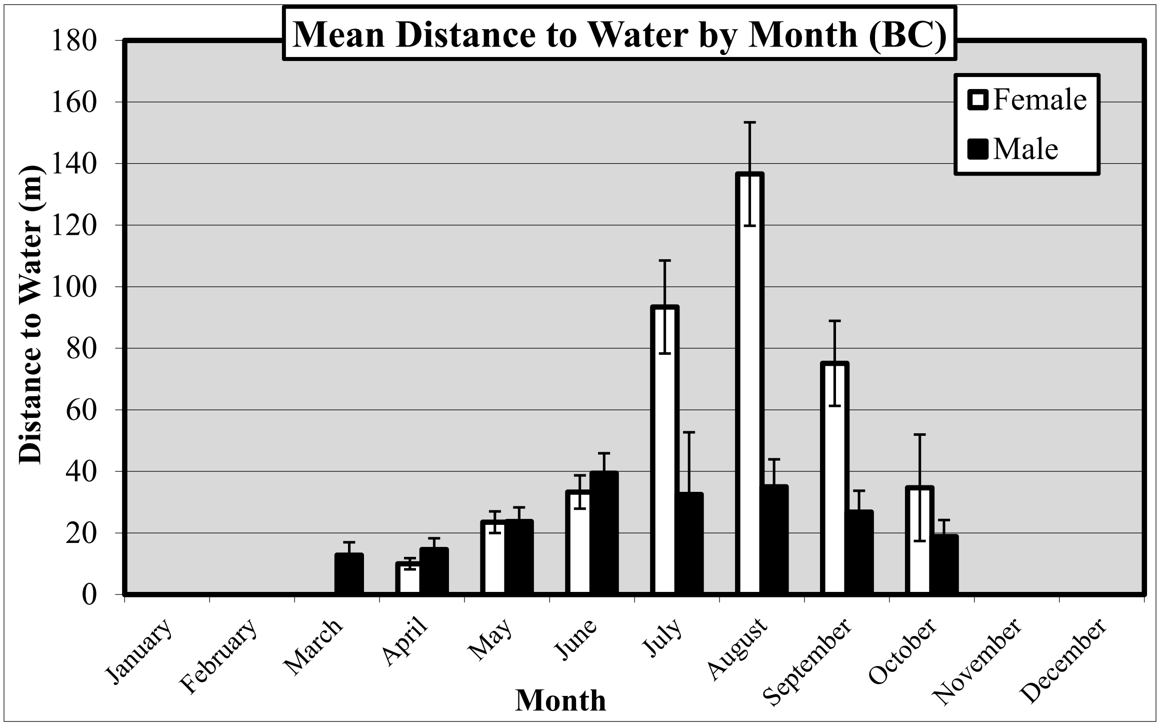

Figure A6. Distance to water by month for BC (n_t=609); values are means ± SE.

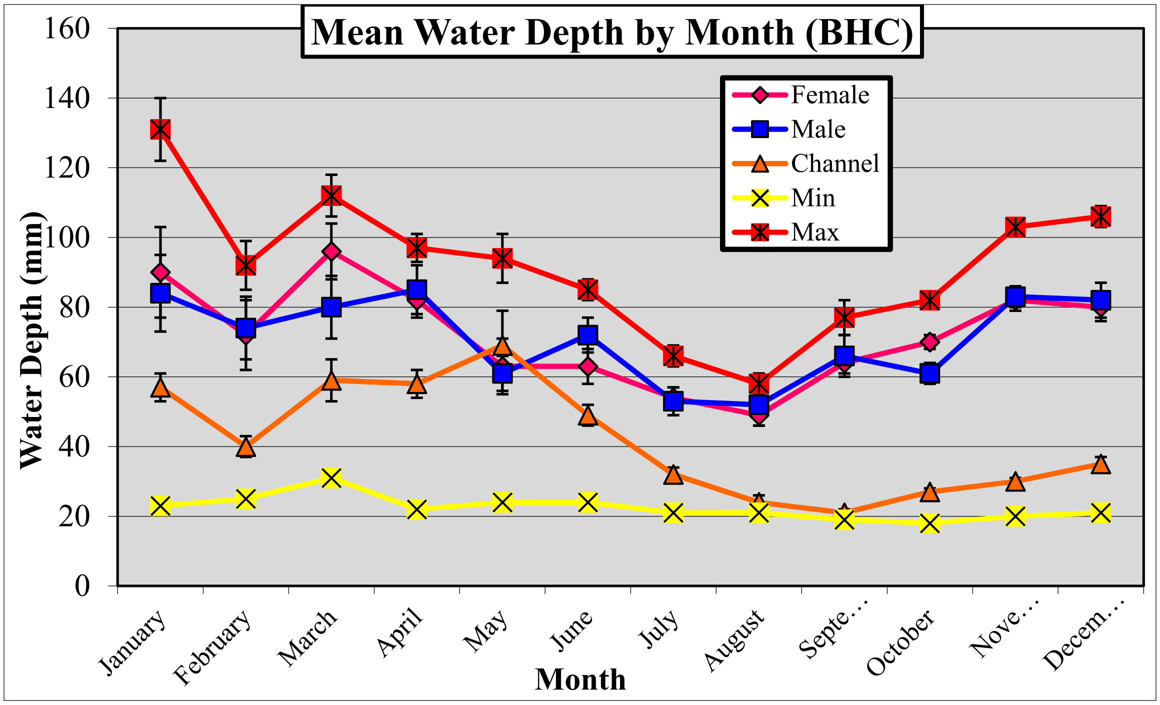

Figure A7. Water depth used by turtles and corresponding environmental values by month for BHC (n_t=1,020); values are means ± SE.

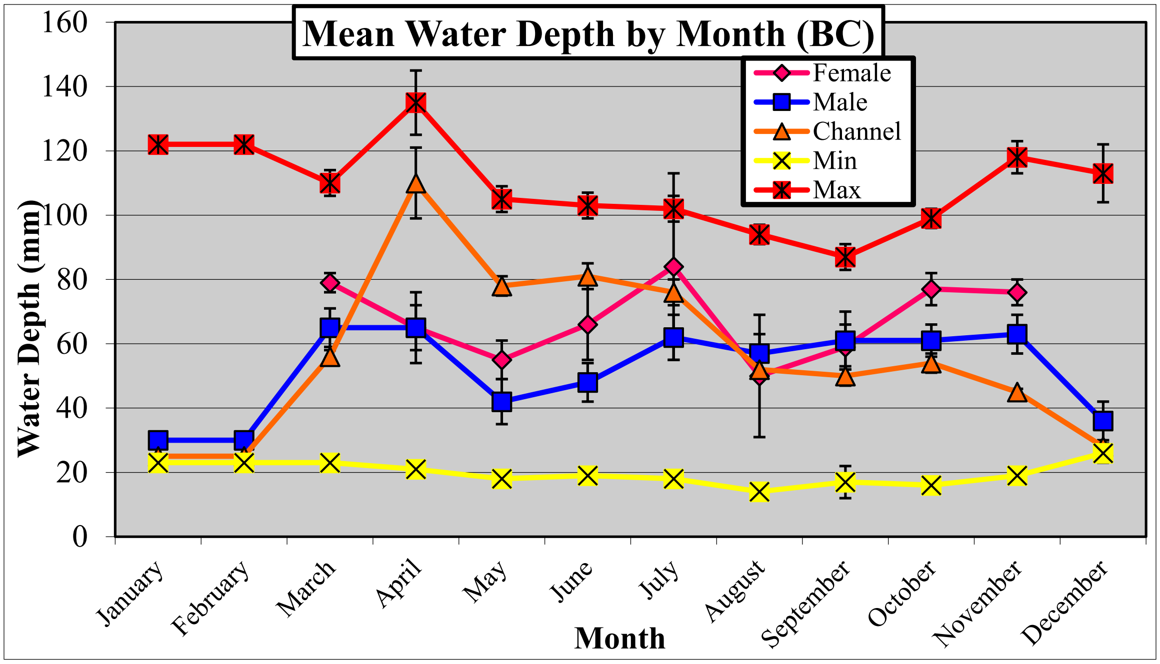

Figure A8. Water depth used by turtles and corresponding environmental values by month for BC (n_t=381); values are means ± SE.

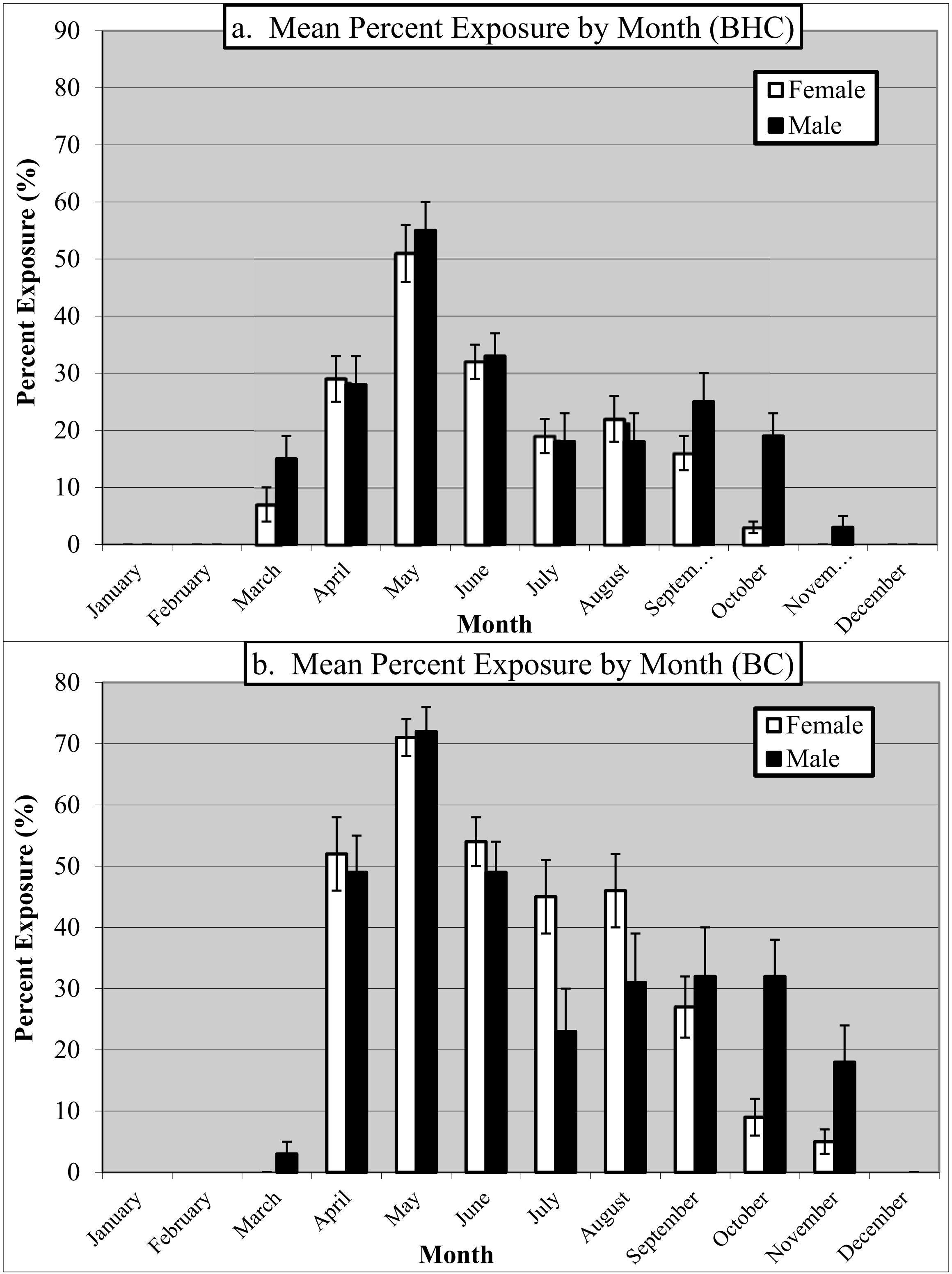

Figure A9. Percent exposure by month for: a) BHC (n=1,961), and b) BC (n=898); values are means ± SE.

APPENDIX B

LIST OF ABBREVIATIONS

Item	Term
ANOVA	analysis of variance
ATS	Advanced Telemetry Systems
ATV	all terrain vehicle
BC	Butler county
BCFA	Beaver Creek Falls Access Area
BHC	Black Hawk County
BMWMA	Big Marsh Wildlife Management Area
˚C	degrees Celsius
CITES	Convention on the International Trade of Endangered Species
CL	carapace length
cm	centimeter(s)
CW	carapace width
df	degrees of freedom
DNR	Department of Natural Resources
DTW	distance to water
e.g.	“for example”
f	f value
g	gram
GIS	geographic information system

GPS	global positioning system
h	hour(s)
ha	hectare
HW	head width
IA	Iowa
IUCN	International Union for Conservation of Nature
kg	kilogram(s)
km	kilometer(s)
lat	latitude
long	longitude
m	meter(s)
M	mass
min	minute(s)
mm	millimeter(s)
n	number
N	North
na	not available
nt	total number
P	probability value
PE	percent exposure
PL	plastron length
pp	pages

PV	plastron to vent length
rd	road
SA	surface area
SD	standard deviation
SE	standard error
SH	shell height
SI	sunlight intensity
SI_{avg}	average sunlight intensity
SI_{max}	maxiumum sunlight intensity
SI_{min}	minimum sunlight intensity
SI_t	turtle sunlight intensity
sp(p)	species
t	t value
T	temperature
T_a	air temperature
T_b	body (cloacal) temperature
T_o	optimum temperature
T_s	soil temperature
T_{set}	thermoregulatory set point range
T_{upper}	95th percentile of the thermoregulatory set point
T_w	water temperature
V	volume

VTL	vent to end of tail length
W	West
$WD_{channel}$	channel water depth
WD_{max}	maximum water depth
WD_{min}	minimum water depth
WD_t	turtle water depth
WFAA/PP	West Fork Access Area/Private Property