SPATIAL ECOLOGY, HABITAT USE, GENETIC DIVERSITY, AND REPRODUCTIVE SUCCESS: MEASURES OF CONNECTIVITY OF A SYMPATRIC FRESHWATER TURTLE ASSEMBLAGE IN A FRAGMENTED LANDSCAPE

BY

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DISSERTATION

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ABSTRACT

Habitat fragmentation can have serious conservation implications for long-lived species such as freshwater turtles. Using integrative radio-telemetry and molecular methods, I examined characteristics in five species of turtles that should influence connectivity and long-term persistence of populations among remnant preserves within the Lower Des Plaines River Valley, a fragmented landscape in northeastern Illinois. Comparisons of movement and habitat use among Blanding's turtle (*Emydoidea blandingii*), spotted turtle (*Clemmys guttata*), painted turtle (*Chrysemys picta*), common snapping turtle (*Chelydra serpentina*), and eastern musk turtle (*Sternotherus odoratus*) revealed that *E. blandingii* made long distance movements and readily moved between wetlands, whereas the other species were more restricted to aquatic movements. However, *S. odoratus*, *C. serpentina*, and *C. picta* were also capable of making long distance aquatic movements (≥ 1 km) via the Des Plaines River. Conversely, *C. guttata* exhibited the shortest movements and smallest home range. Patterns of macro- and micro-habitat use demonstrated strong partitioning between *C. guttata* and *C. picta*, *C. serpentina*, *S. odoratus* as well as broad measures of niche breadth and niche overlap for *E. blandingii* and *C. serpentina*. These results suggest that *E. blandingii* and *C. serpentina* are habitat generalists whereas *C. guttata* is a habitat specialist. Differences in movement and habitat use were likely caused by species-specific traits and requirements and can impact levels of gene flow within species in fragmented landscapes. Using microsatellite DNA markers, I examined population genetic structure in *E. blandingii*, *C. picta*, and *C. serpentina*. I observed moderate to high levels of genetic diversity in all three species. I detected significant pairwise F_{ST} divergence in *E. blandingii* between an intact site and three fragmented sites as well as between two fragmented sites and in *C. serpentina* between two fragmented sites. Gene flow was male-biased in *E. blandingii* across the fragmented sites but differences in patterns of dispersal between males and

females in *C. picta* and *C. serpentina* were weak. I found no evidence of genetic population bottlenecks in any species, but simulations of future genetic diversity suggest that *E. blandingii* is more vulnerable to loss of genetic diversity than *C. picta* or *C. serpentina*. Finally, I evaluated the mating system of *E. blandingii* by corroborating field observations of mating attempts during radio-telemetry surveys with genetic parentage analysis. I observed promiscuous mating behavior in *E. blandingii* as males and females engaged in mounting behaviors with multiple individuals. Males and females mated successfully with multiple individuals, but successful matings did not always correspond with observed mating attempts and parentage was strongly skewed in males. For males, the number of successful mates was positively correlated with total number of offspring sired. Correlation between relatedness of male-female pairs and reproductive success was not evident. Repeat paternity in clutches among years was common but I only documented one confirmed instance of across-season sperm storage. I also only detected 8% multiple paternity in 28 clutches. High variation in reproductive success and low levels of multiple paternity may be attributed to small population size. During this study, I detected differences among species in traits such as vagility, niche breadth, and future levels of genetic diversity. These differences are likely related to species-specific life history traits and should differentially influence how each of these species responds to fragmentation.

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CHAPTER 1

SPATIAL ECOLOGY OF A FRESHWATER TURTLE ASSEMBLAGE IN A FRAGMENTED LANDSCAPE

INTRODUCTION

Understanding the consequences of habitat fragmentation requires knowledge about an organism's life history and ecological traits (e.g. reproductive effort, generation time, body size, dispersal ability, habitat specialization; Henle et al., 2004; Ewers and Didham, 2006). Sensitivity to fragmentation depends on a species' vagility, the ability to move through a landscape, with less mobile species often suffering more negative effects than more mobile species in fragmented landscapes (Lens et al., 2002; Öckinger et al., 2009; Öckinger et al., 2010). Thus, this chapter will focus on vagility as a determinant of species' responses to fragmentation.

Reptiles have restricted mobility compared to most other vertebrate taxa. Although some species of freshwater turtles are known to move several kilometers during nesting forays and among wetlands (Ernst and Lovich, 2009), such movements are often prevented by anthropogenic barriers such as roads and railroad tracks (Aresco, 2005; Kornilev et al., 2006; Shepard et al., 2008). Many turtle species are imperiled because of fragmentation (Mitchell and Klemens, 2000), and persistence of species depends on the ability of individuals to move both within populations (e.g. among habitat types) and among populations (immigration-emigration processes).

Using radio-telemetry methods, I examined the spatial ecology for two locally rare and three common sympatric turtle species occurring in a fragmented landscape. My objectives were to 1) compile home range and movement parameters for each species, 2) test for differences in these spatial metrics among sex and stage class within species, 3) test for differences in spatial

metrics among populations within species, 4) test for correlation between body size and home range size within each species, and 5) test for differences in spatial metrics among species. Specifically, I was interested in addressing the following questions about spatial ecology within and among species: 1) Does home range and movement differ among stage/sex classes within each species? 2) Do these spatial metrics differ among sites within species? 3) Does body size within stage/sex groups influence home range size? and 4) Does home range and movement differ among species?

I expected that spatial metrics would differ among stage/sex class within species because life history strategies vary between adults and juveniles between males and females. For example, life history strategies of juvenile *E. blandingii* are concentrated on growth and overcoming low survival rates (Congdon et al., 1993), and most activity appears to be limited to specific habitat areas that provide better foraging opportunities and refugia (Pappas and Brecke, 1992). Thus, I predicted adults to have larger movements and home range areas than juvenile *E. blandingii*. Further, because differences in reproductive strategies (mate searching vs. nesting) between males and females are predicted to influence movement and activity (Morreale et al., 1984), with the exception of *E. blandingii*, I predicted that males in the remaining species to have larger movements and home range areas than females. Both male and female *E. blandingii* are known to make long-distance movements (Rowe and Moll, 1991, Sexton, 1995; Piepgras and Lang, 2000; Joyal et al., 2001), thus I predicted no differences in spatial metrics between males and females in *E. blandingii*. In addition, because *E. blandingii* are considerably vagile (Rowe and Moll, 1991, Sexton, 1995; Piepgras and Lang, 2000; Joyal et al., 2001), use multiple habitat types, and have a larger estimate of niche breadth (Chapter Two), I also expected *E. blandingii* to

have larger estimates of home range size and movement than *C. guttata*, *S. odoratus*, *C. picta*, and *C. serpentina*.

METHODS

Study Site

The Lower Des Plaines river valley (LDPRV) was once a prairie-dominated landscape (Bowles and McBride, 2001) composed of semi-contiguous, prairie-wetland matrices that would have allowed turtles to disperse along the river corridor without anthropogenic impediment. Since the early 1800's there have been drastic changes (e.g. agriculture, roadways, industrial parks, quarries, shipping canals) to the LDPRV landscape. Remaining natural areas are effectively isolated from one another except for their connection along the usually very narrow Des Plaines River and its riparian zone. This study took place at three of these remnant areas in Will County, Illinois; Will 1 (95 ha), Will 2 (188 ha), and Will 3 (124 ha). Each of these preserves was inhabited by an abundant turtle fauna including state-listed species such as the Blanding's turtle (*Emydoidea blandingii*) and spotted turtle (*Clemmys guttata*) as well as three common species, the common snapping turtle (*Chelydra serpentina*), painted turtle (*Chrysemys picta*), and common musk turtle (*Sternotherus odoratus*).

Radio-telemetry

Selected numbers of turtles were radio-tagged and tracked for varying lengths of time (depending on species and location) during 2005-2010. Radio-tagged turtles were located during at least two months of one active season (April-October). I radio-located *C. serpentina*, *C. picta*, and *S. odoratus* at the Will 3 site, *C. guttata* at the Will 2 and Will 3 sites, and *E. blandingii* at

Will 1, Will 2, and Will 3 sites. I outfitted transmitters (Holohil Systems Ltd., Carp, ON, Canada; Wildlife Materials International Inc., Murphysboro, IL, USA; and L.L. Electronics, Mahomet, IL, USA) to the right or left posterior portion of the carapace. For individuals < 175 g, I adhered transmitters by gently abrading the shell with sand paper, applying a small amount of quick drying epoxy (Marine Power PC·11) around the transmitter, and then molding it firmly to the shell with masking tape (which was removed after the epoxy dried). For individuals >175 g, I used either the epoxy method or I drilled 1-2 holes in the marginal scutes and securely bolted a transmitter package constructed of aluminum flashing, plasti-dip, and epoxy. Transmitter package weight did not exceed 10% of the individual's mass. Stage/sex class (adult male, adult female, and juvenile) was assigned based on the presence or absence of secondary sexual characteristics (e.g. concavity of plastron, elongated foreclaws, position of cloaca relative to the posterior edge of carapace) and sizes of maturation based on previous studies (Ernst and Lovich, 2009). I tracked turtles approximately 3-7 times per week during the active season (April – October) and reduced the frequency of locations to1-2 times per month during over-wintering (November-March). At each location, I recorded GPS coordinates (UTM-NAD 83 CONUS).

Estimation of spatial parameters

I plotted all turtle location coordinates on an aerial photograph of the preserves using ArcView 3.2. I included nesting movements of gravid females because these movements and locations represent areas critical for reproduction. Using the Spatial Analyst and Animal Movement extensions, I generated movement paths, location statistics, and home ranges for each individual (Hooge and Eichenlaub, 1997). I calculated mean daily distance (MDD) using only

locations collected one or two days apart from each other during the active season to reduce under-estimation of actual movements

I estimated home range size in ArcView using multiple methods: minimum convex polygon (MCP), home range length (HRL), 95% fixed kernel density isopleths (95K), and 50% fixed kernel density isopleths (50K). I counted the number of 50% isopleth activity centers (core activity centers, #C) for each individual. Multiple methods were used so that comparisons could be made easily to other studies. In addition, providing different estimates of home range methods alleviate criticisms associated with approaches. For example, multiple convex polygons (MCP) tend to over-estimate home range use by including areas not used by an individual and size is often correlated with number of locations (Worton, 1987). Because kernel density estimates are a function of the time an organism spends in an area, they are often better predictors of actual area use than MCP (Worton, 1987; Seaman and Powell, 1996). However, kernel density estimates can exclude important areas that are infrequently used, such as overland corridors among wetlands or critical habitats (i.e. nesting areas) that are important for conservation planning. Home range length (HRL) was measured as the distance between the two farthest locations and used to indicate how far an individual was able to transverse during the study; this information was not always conveyed by home range area estimates. Number (#C) and size of core area use (50K) was used to evaluate differences in routine area use (e.g. daily foraging).

Frequent radio-locations can lead to non-independence among locations within individuals. However, autocorrelation has little effect on accuracy of kernel density estimates and subsampling locations to reduce autocorrelation decreases sample size and accuracy of home range estimates (De Solla et al., 1999). Thus, all radio-locations were included when estimating home range parameters.

For kernel estimates, I calculated the smoothing factor (h-values) by averaging the ad hoc default generated via least squares cross validation (LSCV) for each turtle over the study duration (Seaman and Powell, 1996). I constructed area curves by plotting MCP size of sequential samples and MCP size of random samples. I generated sequential MCP areas in Biotas 1.03a (Ecological Software Solutions LLC) and random MCP areas from bootstrapping (100 samples) using the Animal Movement Extension. I determined that a sufficient number of locations had been obtained to represent home range for each turtle when area curve plots were asymptotic.

Within-species comparisons

Because, *E. blandingii* and *C. guttata* were monitored across multiple sites and multiple stage/sex classes, I used a two-way ANOVA to compare MCP, 95K, 50K, MDD, and HRL among sites, between stage/sex class, and stage/sex class*site. For significant effects within *E. blandingii*, I followed the ANOVA with Gabriel's multiple comparison for unequal sample sizes. Because *S. odoratus*, *C. serpentina*, and *C. picta* were only tracked at one site, I used a Student's t-test to test for differences in all spatial variables only between stage/sex class. Number of core areas (#C) did not meet the assumptions of normality, thus, I used non-parametric tests to compare #C among and between sites and stage/sex class. For *E. blandingii*, I used Kruskal-Wallis tests to compare #C by stage/sex class and by site. For *C. guttata*, *S. odoratus*, *C. serpentina*, and *C. picta*, I used a Mann-Whitney U-test to compare #C by stage/sex class and by site when applicable. Finally, I tested for correlations between carapace length (CL) and home range (MCP and 95K) to determine if body size influences home range size.

Among-species comparisons

To compare home range and movement among species, I pooled males and females from the Will 3 site and recalculated MCP, MDD, and HRL to include only locations collected from May-September 2006. I excluded 2005 data to control for between-year variation because 2005 was a drought year (Anthonysamy et al. in review) and most of my telemetry subjects were *E. blandingii* in 2005. In addition, I excluded *E. blandingii* and *C. guttata* from the Will 1 and Will 2 sites from this analysis because not all species were tracked at all sites and site-effect differences could bias results. Because I sampled only adult individuals in the other species, I also excluded juvenile *E. blandingii* from this analysis. Kernel estimates (95K, 50K, and #C) were not used in this analysis because smoothing factors generated for kernel estimates were species-specific and invalidated statistical comparisons among species. I used a one-way ANOVA followed with a Gabriel's multiple comparison for unequal sample sizes to compare MCP, MDD, and HRL among species.

For all statistical tests, I tested the assumptions of normality and homogeneity of variables using the Shapiro-Wilk test and Levene's test, respectively. Variables were $Log_{10}+1$ (MCP, 95K, 50K), Log_{10} (HRL), or Ln (MDD) transformed for parametric tests when necessary to meet the assumptions. I conducted statistical analyses in SPSS 17.0 (SPSS Inc. Chicago, Illinois) and accepted significance at the 95% level except for post hoc comparisons. Significance levels for post hoc tests were adjusted with Bonferroni correction and are reported in the results. Home range and movement parameters are reported as mean ± 1 S.E.

RESULTS

Within-species comparisons – rare species

Emydoidea blandingii

I was unable to obtain a sufficient number of locations for area curves to asymptote in 11 individuals. For the remaining 69 *E. blandingii*, I collected 7210 locations (277.3 ± 23.8) for seven males, 15 females, and four juveniles at the Will 1 site from 2006-2009; 3013 locations (215.2 ± 33.4) for three males, six females, and five juveniles at the Will 2 site from 2007-2009; and 5390 locations (185.9 ± 13.4) for five males, 14 females, and ten juveniles at the Will 3 site from 2005-2007 (Appendix A). Turtles were assigned as residents to the site of their original capture. During this study, two resident turtles (one male and one female) from the Will 2 site moved to the Will 1 site and back and one resident male from Will 1 moved to the Will 2 site and back.

Mean values for home range and movement parameters by site and stage/sex class are shown in Table 1.1 and illustrated Fig(s) 1.1A-E. For males at all sites, minimum convex polygon home range estimates (MCP) averaged 48.1 ± 10.0 ha, 95% fixed kernel home range estimates (95K) averaged 14.4 ± 1.4 ha, 50% fixed kernel density isopleths (50K) averaged 1.5 ± 0.1 ha, mean daily distance (MDD) averaged 47.8 ± 5.6 m, and home range length (HRL) averaged 1507.4 ± 240.5 m. For females at all sites, MCP averaged 26.6 ± 2.8 ha, 95K averaged 13.3 ± 1.0 ha, 50K averaged 1.8 ± 0.2 ha, MDD averaged 34.5 ± 2.7 m, and HRL averaged 1087.9 ± 82.4 m. For juveniles at all sites, minimum convex polygon home range estimates (MCP) averaged 11.8 ± 3.3 ha, 95K averaged 7.1 ± 0.7 ha, 50K averaged 1.4 ± 0.1 ha, MDD averaged 20.8 ± 2.2 m, and HRL averaged 721.1 ± 111.6 m.

Two-way ANOVA results are provided in Table 1.2. Minimum convex polygons (MCP) varied among stage/sex class ($F_{2,60} = 11.52$, $P \leq 0.0001$) and site ($F_{2,60} = 5.3$, $P = 0.008$) but not by the stage/sex*site interaction term. Post-hoc comparisons (adjusted $\alpha = 0.0167$) revealed that adult females had larger MCP estimates than juveniles ($P \leq 0.0001$) and adult males had larger MCP estimates than juveniles ($P \leq 0.0001$). No difference in MCP was detected between males and females. Among sites, turtles at the Will 1 and Will 2 sites had larger MCP estimates than those at the Will 3 site before Bonferroni correction ($P = 0.003$ and $P = 0.029$, respectively). No difference in MCP was detected between the Will 1 and Will 2 sites.

Ninety-five percent fixed kernel density isopleths (95K) varied among stage/sex class ($F_{2,60} = 11.38$, $P \leq 0.0001$) but not site. The stage/sex class*site interaction term was not significant. Post-hoc comparisons revealed that adult females had larger 95K estimates than juveniles ($P \leq 0.0001$) and adult males had larger 95K estimates than juveniles ($P \leq 0.0001$). No difference in 95K was detected between adult males and adult females. Fifty percent fixed kernel density isopleths (50K) did not differ among stage/sex class or site.

Mean daily distance (MDD) varied among stage/sex class ($F_{2,60} = 6.60$, $P = 0.003$) and site ($F_{2,60} = 15.12$, $P \leq 0.0001$) but the stage/sex class*site interaction term was not significant. Post-hoc comparisons revealed that adult females had significantly greater MDD than juveniles ($P = 0.003$) and adult males had greater MDD than juveniles ($P \leq 0.0001$). No difference in MDD was detected between adult males and adult females. Among sites, turtles at the Will 1 and Will 2 sites had greater MDD than those at the Will 3 site ($P \leq 0.0001$, $P = 0.002$, respectively). No difference in MDD was detected between Will 1 and Will 2 sites.

Home range length (HRL) varied among stage/sex class ($F_{2,60} = 5.96$, $P = 0.004$) and site ($F_{2,60} = 6.04$, $P = 0.004$) but the stage/sex class*site interaction term was not significant. Post-

hoc comparisons revealed that adult females had greater HRL than juveniles ($P = 0.004$) and that adult males had greater HRL than juveniles ($P \leq 0.0001$). No difference in HRL was detected between adult males and adult females. Among sites, turtles at the Will 1 site had greater HRL than those at the Will 3 site ($P = 0.001$). No difference in HRL was detected between Will 1 and Will 2 or Will 2 and Will 3.

The number of core activity centers (#C) averaged 1.4 ± 0.2 m, 1.4 ± 0.1 m, and 1.2 ± 0.1 m for males, females, and juveniles, respectively. There was no difference among #C for sex/stage class ($X^2 = 2.577$, df = 2, $P = 0.276$) or site ($X^2 = 5.817$, df = 2, $P = 0.055$). Carapace length was positively correlated with MCP ($r^2 = 0.547$, $P \leq 0.0001$) and with 95K ($r^2 = 0.566$, $P \leq 0.0001$). Within sex/stage class, carapace length was only correlated with 95K ($r^2 = 0.606$, $P = 0.013$).

Clemmys guttata

I was unable to obtain a sufficient number of locations for area curves to asymptote in two individuals. For the remaining 34 *C. guttata*, I collected 1186 locations (mean = 107.8 ± 16.2) for six males and five females at the Will 3 site during 2005-2006, and 3729 locations (mean = 162.1 ± 17.3) for 12 males and 11 females at the Will 2 site from 2007-2008 (Appendix B).

Mean values for home range and movement parameters by site and stage/sex class are shown in Table 1.3 and illustrated in Fig(s) 1.2A-E. For males at both sites, minimum convex polygon home range estimates (MCP) averaged 2.2 ± 0.5 ha, 95% fixed kernel home range estimates (95K) averaged 1.2 ± 0.1 ha, 50% fixed kernel home range estimates (50K) averaged 0.2 ± 0.02 ha, mean daily distance (MDD) averaged 12.2 ± 1.3 m, and home range length (HRL)

averaged 261.7 ± 37.7 m. For females at both sites, MCP averaged 3.0 ± 0.8 ha, 95K averaged 1.3 ± 0.1 ha, 50K averaged 0.2 ± 0.0 ha, MDD averaged 14.7 ± 1.7 m, and HRL averaged 328.8 ± 57.9 m.

Two-way ANOVA results are provided in Table 1.2. Minimum convex polygons (MCP) did not vary among stage/sex class or site. Ninety-five percent fixed kernel density isopleths (95K) and 50K varied between sites ($F_{1,30} = 7.85$, $P = 0.009$; $F_{1,30} = 6.13$, $P = 0.019$, respectively) but not between stage/sex class or for the stage/sex*site interaction terms. Mean daily distance (MDD) was greater for females than males ($F_{1,30} = 40.27$, $P \leq 0.0001$) and greater in the Will 2 than Will 3 site ($F_{1,30} = 40.27$, $P \leq 0.0001$) but not for the stage/sex*site interaction term. Home range length (HRL) did not differ among stage/sex class or site.

The number of core activity centers (#C) averaged 1.4 ± 0.2 m and 2.0 ± 0.2 m for males and females, respectively. Females had a significantly greater #C than males ($U = 74.0$, $P = 0.008$) but there were no differences between the Will 2 and Will 3 sites ($U = 94.0$, $P = 0.191$). I found a nearly significant correlation between carapace length and MCP ($r^2 = 0.332$, $P = 0.055$). Within stage/sex class, I found a significant correlation between carapace length and MCP ($r^2 = 0.583$, $P = 0.018$) and a nearly significant correlation between carapace length and 95K ($r^2 = 0.484$, $P = 0.058$) only in females.

Within-species comparisons – common species

Sternotherus odoratus

I was unable to obtain a sufficient number of locations for area curves to asymptote in three individuals and thus excluded them from analyses. For the remaining 12 *S. odoratus*, I

collected 708 (mean = 59.0 ± 5.0) locations for six males and six females at the Will 3 site from 2005-2006 (Appendix C).

Mean values for home range and movement parameters by site and stage/sex class are shown in Table 1.4 and illustrated in Fig(s) 1.3A-E. For males, minimum convex polygon home range estimates (MCP) averaged 11.6 ± 9.3 ha, 95% fixed kernel home range estimates (95K) averaged 5.0 ± 0.8 ha, 50% fixed kernel home range estimates (50K) averaged 0.9 ± 0.1 ha, mean daily distance (MDD) averaged 36.3 ± 11.6 m, and home range length (HRL) averaged 585.4 ± 278.1 m. For females, MCP averaged 8.2 ± 4.7 ha, 95K averaged 5.3 ± 1.2 ha, 50K averaged 1.0 ± 0.2 ha, MDD averaged 30.0 ± 5.6 m, and HRL averaged 589.8 ± 222.3 m. No difference in MCP, 95K, 50K, MDD, or HRL was detected between males and females (Table 1.5).

The number of core activity centers (#C) averaged 1.3 ± 0.2 m and 1.2 ± 0.2 m for males and females, respectively. There was no statistically significant difference between #C for stage/sex class (U = 15.0, $P = 0.523$). I found no correlation between carapace length and home range size estimates.

Chelydra serpentina

I was unable to obtain a sufficient number of locations for area curves to asymptote in two individuals and thus excluded them from analyses. For the remaining nine *C. serpentina*, I collected 597 locations (mean = 66.3 ± 6.8) for five males and four females at the Will 3 site in 2006 (Appendix D).

Mean values for home range and movement parameters by site and stage/sex class are shown in Table 1.4 and illustrated in Fig(s) 1.3A-E. For males, minimum convex polygon home

range estimates (MCP) averaged 3.9 ± 1.9 ha, 95% fixed kernel home range estimates (95K) averaged 2.8 ± 0.9 ha, 50% fixed kernel home range estimates (50K) averaged 0.6 ± 0.1 ha, mean daily distance (MDD) averaged 28.3± 10.8 m, and home range length (HRL) averaged 434.5 ± 147.2 m. For females, MCP averaged 8.1 ± 2.1 ha, 95K averaged 5.6 ± 1.3 ha, 50K averaged 0.5 ± 0.1 ha, MDD averaged 42.3 ± 10.3 m, and HRL averaged 647.0 ± 169.2 m. No difference in MCP, 95K, 50K, MDD, or HRL was detected between males and females (Table 1.5).

The number of core activity centers (#C) averaged 1.0 ± 0.0 m and 1.3 ± 0.3 m for males and females, respectively. There was no statistically significant difference between #C for stage/sex class (U = 7.5, $P = 0.264$). I found no correlation between carapace length and home range size estimates.

Chrysemys picta

I was unable to obtain a sufficient number of locations for area curves to asymptote in one individual and thus excluded her from analyses. For the remaining eight *C. picta*, I collected 379 locations (mean = 47.4 ± 6.6) for five males and three females at the Will 3 site in 2006 (Appendix E).

Mean values for home range and movement parameters by site and stage/sex class are shown in Table 1.4 and illustrated in Fig(s) 1.3A-E. For males, minimum convex polygon home range estimates (MCP) averaged 7.5 ± 2.7 ha, 95% fixed kernel home range estimates (95K) averaged 11.1 ± 1.2 ha, 50% fixed kernel home range estimates (50K) averaged 2.3 ± 0.3 ha, mean daily distance (MDD) averaged 70.8 ± 34.4 m, and home range length (HRL) averaged 663.3 ± 269.4 m. For females, MCP averaged 3.9 ± 2.1 ha, 95K averaged 7.5 ± 1.4 ha, 50K

averaged 1.9 ± 0.1 ha, MDD averaged 24.0 ± 6.2 m, and HRL averaged 762.4 ± 424.2 m. No difference in MCP, 95K, 50K, MDD, or HRL was detected between males and females (Table 1.5).

The number of core activity centers (#C) averaged 1.0 ± 0.0 m for both, males and females. There was no statistically significant difference between #C for stage/sex class ($U = 7.5$, $P = 1.00$). I found no correlation between carapace length and home range size estimates.

Among-species comparison

A total of 17 *E. blandingii*, ten *C. guttata*, nine *S. odoratus*, nine *C. serpentina*, and eight *C. picta* were included in the among species comparison. Mean MCP for *E. blandingii*, *C. guttata*, *S. odoratus*, *C. serpentina*, and *C. picta* was 8.8 ± 2.0 ha, 1.6 ± 0.6 ha, 3.2 ± 0.9 ha, 5.8 ± 1.5 ha, and 6.2 ± 1.9 ha, respectively. Mean MDD for *E. blandingii*, *C. guttata*, *S. odoratus*, *C. serpentina*, and *C. picta* was 39.0 ± 5.1 m, 9.0 ± 1.9 m, 25.9 ± 1.8 m, 35.5 ± 7.5 m, and 53.2 ± 22.4 m, respectively. Mean HRL for *E. blandingii*, *C. guttata*, *S. odoratus*, *C. serpentina*, and *C. picta* was 545.2 ± 81.4 m, 238.1 ± 60.1 m, 360.7 ± 52.5 m, 528.9 ± 110.4 m, and 700.5 ± 213.4 m, respectively.

Significant differences in MCP, MDD, and HRL were detected among species of adult individuals at the Will 3 site ($F_{4,48} = 3.951$, $P = 0.008$; $F_{4,48} = 11.139$, $P \leq 0.0001$; $F_{4,48} = 3.606$, $P = 0.012$, respectively). Post-hoc comparisons (adjusted $\alpha = 0.0125$) revealed that *E. blandingii* had significantly greater MCP estimates than *C. guttata* ($P = 0.005$; Fig. 1.4A). No difference in MCP was detected between *E. blandingii* and the remaining species. *Emydoidea blandingii*, *S. odoratus*, *C. serpentina*, and *C. picta* had significantly greater MDD estimates than *C. guttata* ($P \leq 0.001$; Fig. 1.4B). No differences in MDD comparisons were detected between

the other species. *Emydoidea blandingii* and *C. picta* had significantly greater HRL than *C. guttata* before but not after Bonferroni correction ($P = 0.019$ and $P = 0.021$; Fig. 1.4C). No differences in HRL comparisons were detected between the other species.

DISCUSSION

Within-species comparisons – rare species

Many radio-telemetry studies report on the spatial ecology of *E. blandingii* and *C. guttata* because of the elevated conservation status of these species throughout their ranges (Ernst and Lovich, 2009). However, my radio-telemetry studies of *E. blandingii* and *C. guttata* in a fragmented landscape provide extensive data sets with robust estimates of the movement and home range of these two species. For example, I collected numerous radio-locations for several individuals of different stage/sex classes during periods of ≥ 1 active season across multiple sites. In comparison, many other studies located far fewer turtles and located individuals less frequently or over a shorter time period, precluding their ability to estimate a rigorous home range size for some individuals (Ernst, 1970; McNeil, 2002), statistically compare stage/sex classes (Graham, 1995; Rubin et al., 2001; Innes et al., 2008), or test independent data (i.e. pooling multiple observations for single individuals; Ross and Anderson, 1990; Rowe and Moll, 1991). My data sets can be used to establish a firm foundation of spatial ecology on which to further develop ideas and hypotheses about additional issues of turtle spatial ecology (e.g. connectivity in a fragmented landscape).

Emydoidea blandingii

Adult *E. blandingii* populations within the LDPRV averaged larger 95% fixed kernel home range estimates, mean daily movement distances, and home range length distances than juveniles. Piepgras and Lang (2000), also reported smaller juvenile home range sizes compared to adults but found that females and juveniles travel greater straight-line daily distances than males. Adult *E. blandingii* are known to make long (> 1 km) inter-wetland forays (Piepgras and Lang, 2000; Rowe and Moll, 1991) and when traveling to nesting locations (Sexton, 1995; Piepgras and Lang, 2000; Joyal et al., 2001). In my study, I observed three adult individuals to move from their resident site to a different adjacent site and then move back to their resident site. Conversely, because the life history strategies of juvenile *E. blandingii* are concentrated on growth and overcoming low survival rates (Congdon et al., 1993), most activity appears to be limited to specific habitat areas that provide better foraging opportunities and refugia (Pappas and Brecke, 1992). The inclusion of post-nesting locations in one radio-telemetry study were thought to be responsible for larger female movements compared to males (Ross and Anderson, 1990) and reproductive class had an effect on home range size in an Ontario population (Millar and Blouin-Demers, 2011). Although I included nesting locations in estimates of movement and home range, I found no difference in these parameters between male and female *E. blandingii* within the LDPRV. Similar findings were reported for suburban *E. blandingii* populations in Massachusetts (252-1246 ha; Grgurovic and Sievert, 2005), an intact population in Ontario (3400 ha; Edge et al., 2010), and a large but historically disturbed site in Wisconsin (3884 ha; Schuler and Thiel, 2008). In my study, larger males tended to have larger home range sizes than smaller males.

Effects of site location were also important in this study as individuals from the Will 1 site averaged greater movement and home range length distances than individuals from the Will 3 site. Site resource differences, such as the size, type, and distribution of wetland areas and the proximity of these areas to the Des Plaines River, likely accounted for some of this variation. In addition, tracking was conducted at different years among sites and differences in habitat availability among years, could account for site differences. For example, *E. blandingii* at a preserve in Will County moved shorter mean daily distances during a drought year compared to a wet year (Anthonysamy et al. in review). Core area (50% kernel estimate size and number) use was similar among all individuals within LDPRV regardless of stage/sex class or site and primarily represented intra-marsh foraging movements. Many *E. blandingii* spatial ecology studies report on the number of activity centers and differences in number of activity centers among stage/sex classes (Ross and Anderson 1990; Rowe and Moll, 1991; Piepgras and Lang, 2000; Innes et al., 2008) but wide variation in core area (i.e. activity center) definition and estimation exists among these studies. Thus, it is difficult to make comparisons of core area use between other studies and LDPRV.

Average MCP areas for adult LDPRV turtles (males = 48.1 ha; females = 26.6 ha) fell within the range of estimates reported for other studies (Ernst and Lovich, 2009) but were large compared to seasonal MCP estimates reported for populations in another urban Illinois landscape of similar size (Rubin et al., 2001) and comparable to MCP estimates for a large Minnesota population (Piepgras and Lang, 2000). The relatively large MCP estimates for LDPRV turtles may be a result of multi-year radio-tracking for some individuals. Schuler and Thiel (2008) showed that *E. blandingii* home range size increases linearly with monitoring duration over multiple years. However, comparisons of my LDPRV 95% fixed kernel home range estimates

were smaller than kernel estimations for the Ontario and Massachusetts studies (Grgurovic and Sievert, 2005; Edge et al., 2010) suggesting that kernel estimators may serve as better home range comparisons among studies than MCP. Only two previous studies documented home range for juvenile *E. blandingii* (Piepgras and Lang, 2000; Innes et al., 2008). Average juvenile MCP and 95K size (11.8 ha and 7.1 ha, respectively) for LDPRV was comparable to Minnesota MCP size (12.8 ha) and larger than a single juvenile 95% MCP home range size (3.3 ha) in New Hampshire (Innes et al., 2008).

Clemmys guttata

Female *C. guttata* populations within the LDPRV averaged greater mean daily movement distances than males but this did not produce significant differences in home range estimates or home range length between the sexes. Similarly, no differences in MCP home range were found between males and females in Pennsylvania (Ernst, 1970) and Ontario (Rasmussen and Litzgus, 2010) or in MCP and home range length in Massachusetts (Milam and Melvin, 2001). However, differences in MCP home range between males and females were previously detected at the Will 3 site and South Carolina populations when including locations of gravid females (Wilson, 1994; Litzgus and Mousseau, 2004). Thus, differences in movement and numbers of core home range areas between male and female *C. guttata* in the LDPRV is likely attributed to nesting forays of gravid females. Other studies have reported movement differences among seasons (Litzgus and Mousseau, 2004; Rasmussen and Litzgus, 2010) but I did not test for seasonal effects in the LDPRV populations. The positive correlation between body size and home range size in females may have resulted from the lack of nesting migrations in smaller, immature individuals.

The effect of site was also important for *C. guttata* within LPDRV as individuals from the Will 2 site averaged greater home range estimates (95K and 50K) and mean daily distance than individuals from the Will 3 site. As noted above for *E. blandingii*, differences in resource distribution between sites or year effects, and tracking duration (one year at Will 3 vs. two years at Will 2) could have accounted for some of this variation. Core area (50K) was similar between stage/sex classes but was greater for individuals at the Will 2 than Will 3 site. The number of core areas used was greater for females than males, and possibly accounts inter-wetland use for nesting forays, but differences were not evident between sites.

Home range estimates and home range length for *C. guttata* within the LDPRV fell within ranges reported in most other studies (Ernst and Lovich, 2009) but were smaller than those estimated for one study in Ontario (6.5-7.9 ha; Rasmussen and Litzgus, 2010). Besides the previous study in Will County by Wilson (1994; males = 0.7 ha; females = 1.8 ha; 1994), the MCP home range size and length of the LDPRV populations most closely resembled those of *C. guttata* populations in central Massachusetts (males = 1.9 ha, 261 m; females = 4.6 ha, 345 m; Milam and Melvin, 2001) and Victoria County, Ontario (males = 3.6 ha; females = 4.7 ha; Haxton and Berrill, 1999).

Within-species comparisons – common species

Although they are more abundant and widely distributed, common species are often less studied than rare species. Only a few radio-telemetry studies have assessed aspects of spatial ecology for common species such as *C. picta* (Rowe, 2003; Rowe and Dalgarn, 2010), *S. odoratus* (Rowe et al., 2009), and *C. serpentina* (Obbard and Brooks, 1980; Obbard and Brooks, 1981; Brown and Brooks, 1993). Previous studies examining home range and movement have

also been geographically limited and may not represent the complete range of spatial metrics for a particular species throughout its distribution. Also, inconsistencies in home range estimates and movement distances reported among the few studies may result from the use of different field techniques (trapping vs. radio-telemetry) and not necessarily from variation in spatial metrics among turtles. For example, many movements go undetected during trapping surveys compared to radio-telemetry surveys and this disparity makes generalizations between such studies problematic.

For common species, loss of habitat and increased isolation also has detrimental impacts including increased road mortality and skewed sex ratios (Aresco, 2005). Further, small decreases in survival rates of adults are predicted to cause drastic population declines, even in a common turtle species (Congdon et al., 1994). Yet the impacts of fragmentation on populations of common turtle species have not been well documented.

Sternotherus odoratus

I detected no differences between male and female *S. odoratus* for any home range or movement parameters at the Will 3 site. Rowe et al. (2009), the only other radio-telemetry study on *S. odoratus*, also found no differences in home range estimates between sexes. However, trapping studies documented that male *S. odoratus* moved longer distances and more frequently between recaptures than females (Mahmoud, 1969; Ernst, 1986; Smar and Chambers, 2005). In the present study, small sample sizes of male (N=6) and female (N=6) *S. odoratus* as well as individual variation may have prevented the detection of significant differences in home range and movement estimates between sexes.

The 95% fixed kernel density isopleth home range estimate for a population in Michigan (2.8 ha) was smaller compared to *S. odoratus* at the Will 3 site (5.1 ha) but 50% fixed kernel density isopleths (core areas) were similar between the studies, 1.5 ha and 1.0 ha, respectively (Rowe et al., 2009). Turtles in both studies used 1-2 core areas (Rowe et al., 2009). Average home range size, estimated from trapping data, for a population in Pennsylvania was also smaller (males = 1.8 ha; females = 0.9 ha; Ernst, 1986) than in *S. odoratus* at Will 3 site, but these estimates were derived from recapture locations and likely underestimated home range size.

In Virginia, *S. odoratus* displayed site fidelity to ponds suggesting movement was limited and home ranges were small (Holinka et al., 2003). Yet I documented long-distance movements of *S. odoratus* at the Will 3 site as individuals made inter-wetland movements between ponds and river habitat and completed long forays > 1 km within the Des Plaines River. Other studies, including displacement studies, have also reported long-distance movements for *S. odoratus* (Ernst, 1986; Holinka et al., 2003; Smar and Chambers, 2005; Andres and Chambers, 2006; Rowe et al., 2009).

Chelydra serpentina

Previous thorough studies on the movement and home range of *C. serpentina* (Obbard and Brooks, 1980; Obbard and Brooks, 1981; Brown and Brooks, 1993; Pettit et al., 1995) are geographically limited (restricted to Ontario, Canada) considering the widespread distribution of this species in North America. In previous radio telemetry studies, no difference in home range size was found between males and females at Algonquin Park, Ontario (Obbard and Brooks, 1981) but differences in seasonal movement between the sexes were observed at the same location (Brown and Brooks, 1993). At Hamilton Harbor, Ontario, female *C. serpentina* were

observed to have larger home ranges and move longer distances than males (Pettit et al., 1995). I observed marked variation in home range or movement estimates among individuals but failed to detect differences between male and female *C. serpentina* at Will 3 site. Average MCP home range estimates for male *C. serpentina* in Ontario (3.2 ha) were comparable to males at the Will 3 site (3.9 ha) but estimates for females at the Will 3 site (8.1 ha) were larger than females at Ontario (3.8 ha; Obbard and Brooks, 1981). Small sample size of males (N=5) and females (N=4) may have prevented the detection of significant differences in home range and movement estimates between sexes in my study.

Chelydra serpentina has been reported as being sedentary and inactive (Ernst and Lovich, 2009). However, mean daily distance of *C. serpentina* in my study averaged 34.5 m and home range length for two individuals approached 1 km suggesting that this species is moderately active and capable of long distance movements at the Will 3 site. Radio-telemetered turtles were typically re-located in the same area for several days at a time but individuals would occasionally make inter-wetland movements or long forays within the Des Plaines River. I did not assess the reproductive status nor did I observe nesting of radio-telemetered *C. serpentina* in my study but nesting females are capable of moving multiple kilometers over a few days (Obbard and Brooks 1980; Pettit et al., 1995). Reports of inactivity in *C. serpentina* could be a result of the misclassification of inactive turtles (e.g. inactive turtle moved when approached and vice versa) or a bias in the ability to observe active turtles versus inactive turtles (Obbard and Brooks, 1981).

Chrysemys picta

I failed to detect significant differences in home range or movement parameters between males (N=5) and females (N=3) but this could be attributed to small sample size. However, in

previous radio telemetry studies, no differences were observed in home range or movement parameters among male, female, and juvenile *C. picta* in Michigan (Rowe, 2003; Rowe and Dalgarn, 2010). The average mean daily distance (MDD) of 47.4 m/day in my study was shorter than estimates (68.1- 96.5 m/day) for *C. picta* in Michigan (Rowe, 2003; Rowe and Dalgarn, 2010). The turtles in my study were radio-located less frequently (once per day) than the Michigan studies (three times per day) which likely underestimated total daily movement and accounted for the shorter movement distances in the Will 3 site turtles. However, average MCP home range estimates for *C. picta* in Michigan (males = 2.9 ha; females = 1.8 ha) (Rowe and Dalgarn, 2010) were smaller in comparison to estimations for turtles at the Will 3 site (males = 7.5 ha; females = 3.9 ha). This could be because the *C. picta* in my study were radio-located at a wetland complex consisting of marsh, pond, and river habitats whereas the Michigan study occurred at a small marsh system (Rowe, 2003; Rowe and Dalgarn, 2010).

Considering the widespread abundance of *C. picta*, few other studies have examined the spatial ecology for this common species (Pearse, 1923; Sexton, 1959; Gibbons, 1968; McAuliffe, 1978; MacCulloch and Secoy 1983; House et al. 2010). Reported movement distances vary widely and are dependent on the type of habitat system where the turtles are studied. For example, distances transversed by *C. picta bellii* from a river system in Saskatchewan during trapping studies (MacCulloch and Secoy, 1983) were greater than distances reported for the same sub-species at a pond complex in a trapping study conducted in Kansas (House et al., 2010). Additionally, variation in movement among individuals at the Will 3 site tended to correspond with habitat use. For example, individuals that used the Des Plaines River traveled longer distances and had larger home range estimates than individuals solely occupying marsh or pond habitats. Inconsistencies in reported movement distances are also likely a result of the use of

different field techniques (trapping vs. radio-telemetry). As stated above, many movements go undetected during trapping surveys compared to radio-telemetry surveys and this disparity makes comparisons between the few studies problematic.

Among-species comparison

Common and rare reptile species demonstrate different sensitivities to fragmentation (Attum et al., 2008). Although turtles are classified as long-lived organisms with low juvenile recruitment and high adult survival, variation in life history and ecology traits (i.e. ecological tolerance, vagility, generation time, clutch size, diet, etc.) exists among turtle species (Ernst and Lovich, 2009) that should impact how they respond to fragmentation. For example, generalist (common) species are suggested to be more tolerant of fragmentation than specialist (rare) species (Henle et al., 2004; Ewers and Didham, 2006).

Species included in my study (*E. blandingii*, *C. guttata*, *S. odoratus*, *C. serpentina*, and *C. picta*) exhibit variation in their vagility and habitat specialization (Chapter Two), and I expected differences in home range size and movement. Within the LDPRV, *E. blandingii* had significantly larger MCP home range estimates than *C. guttata*. Because they are capable of making long overland forays between wetlands and to nesting sites, *E. blandingii* are considerably vagile (Ernst and Lovich, 2009). The ability to transverse the preserve as well as use a number of different habitat types (Chapter Two) likely contributed to the larger home range estimates for this species. However, *E. blandingii* home range length (HRL) was only significantly larger than *C. guttata*, indicating that *S. odoratus*, *C. picta*, and *C. serpentina* are also capable of making long-distance movements. The primary difference in mobility patterns between *E. blandingii* and the common species was that long distance movements by *S.*

odoratus, *C. serpentina*, and *C. picta* were mostly restricted to within wetlands (i.e. the Des Plaines River) whereas *E. blandingii* moved among wetlands.

Clemmys guttata made smaller daily movement distances compared to all other species. This is likely because *C. guttata* at the Will 3 site are restricted to concentrated areas of the preserve that predominantly consist of shallow, sedge-marsh habitat (Chapter Two). Except for *S. odoratus*, *C. guttata* is also the smallest of the five species and may have lower energy requirements. The other species typically use deeper and more open-water habitats (i.e. ponds, river) that are conducive to larger movements (Chapter Two). Failure to detect further differences in some parameters between species could be attributed to small samples sizes in the common species.

LITERATURE CITED

Andres, K.M., and R.M. Chambers. 2006. A test of philopatry by common musk turtles. American Midland Naturalist 156:45-51.

Aresco, M.J. 2005. The effect of sex-specific terrestrial movements and roads on the sex ratio of freshwater turtles. Biological Conservation 123:37-44.

Attum, O., Y.M. Lee, J.H. Roe, and B.A. Kingsbury. 2008. Wetland complexes and upland-wetland linkages: landscape effects on the distribution of rare and common wetland reptiles. Journal of Zoology 275:245-251.

Bowles, M.L., and J. McBride. 2001. Historical landscape vegetation pattern, composition, and structure of Will County, Illinois, as recorded by the U.S. Public Land Survey (1821-1838). http://www.greenmapping.org

Brown, G.P., and R.J. Brooks. 1993. Sexual and seasonal differences in activity in a northern population of snapping turtles, *Chelydra serpentina*. Herpetologica 49: 311-318.

Congdon, J.D., A.E. Dunham, and R.C. van Loben Sels. 1993. Delayed sexual maturity and demographics of Blanding's turtles (*Emydoidea blandingii*): Implications for conservation and management of long-lived organisms. Conservation Biology 7:826-833.

Congdon, J.D., A.E. Dunham, and R.C. van Loben Sels. 1994. Demographics of common snapping turtles *(Chelydra serpentina)*: Implications for conservation and management of long-lived organisms. American Zoologist 34:397-408.

De Solla, S.R, R. Bonduriansky, and R.J. Brooks. 1999. Eliminating autocorrelation reduces biological relevance of home range estimates. Journal of Animal Ecology 68:221-234.

Edge, C.B., B.D., Steinberg, R.J., Brooks, and J.D. Litzgus. 2010. Habitat selection by Blanding's turtles (*Emydoidea blandingii*) in a relatively pristine landscape. Ecoscience 17:90-99.

Ernst, C.H. 1970. Home range of the spotted turtle, *Clemmys guttata* (Schneider). Copeia 1970: 391-393.

Ernst, C.H. 1986. Ecology of the turtle, *Sternotherus odoratus*, in southeastern Pennsylvania. Journal of Herpetology 20:341-352.

Ernst, C.H. and J.E., Lovich. 2009. Turtles of the United States and Canada. 2nd edition. John Hopkins University Press, Baltimore.

Ewers, R.M., and R.K. Didham. 2006. Confounding factors in the detection of species responses to habitat fragmentation. Biological Review 81:117-142.

Gibbons, J.W. 1968. Reproductive potential, activity, and cycles in the painted turtle, *Chrysemys picta*. Ecology 49:399-409.

Graham, T.E. 1995. Habitat use and population parameters of the spotted turtle, *Clemmys guttata*, a species of special concern in Massachusetts. Chelonian Conservation Biology 1:207-214.

Grgurovic, M., and P.R. Sievert. 2005. Movement patterns of Blanding's turtles (*Emydoidea blandingii*) in the suburban landscape of eastern Massachusetts. Urban Ecosystems 8:203-213.

Haxton, T., and M. Berrill. 1999. Seasonal activity of spotted turtles (*Clemmys guttata*) at the northern limit of their range. Journal of Herpetology 35:606-614.

Henle, K., D.B. Lindenmayer, C.R. Margules, D.A. Saunders, and C. Wissel. 2004. Species survival in fragmented landscapes: Where are we now? Biodiversity and Conservation 13:1-8.

Holinka, A.M., R., Dave, and R.M. Chambers. 2003. Population ecology of musk turtles (*Sternotherus odoratus*) in a lake in Virginia. Chelonian Conservation and Biology 4:721-725.

Hooge, P.N., and B., Eichenlaub. 1997. Animal movement extension to ArcView: version 1.1. Anchorage, Alaska, Alaska Biological Science Center, United States Geological Survey.

House, W.J., I.M. Nall, and R.B. Thomas. 2010. Interpond movements of western painted turtles (*Chrysemys picta*) in east-central Kansas. The Southwestern Naturalist 55:403-410.

Innes, R.J., K.J. Babbitt, and J.J. Kanter. 2008. Home range of Blanding's turtles (*Emydoidea blandingii*) in New Hampshire. Northeastern Naturalist 15:431-444.

Joyal, L.A., M. McCollough, and M.L. Hunter Jr. 2001. Landscape ecology approaches to wetland species conservation: a case study of two turtle species in southern Maine. Conservation Biology 15:1755-1762.

Kornilev, Y.V., S.J. Price, M.E. Dorcas. 2006. Between a rock and a hard place: Responses of eastern box turtles (*Terrapene carolina*) when trapped between railroad tracks. Herpetological Review 37:145-148.

Lens, L., S. Van Dongen, K. Norris, M. Githiru, E. Matthysen. 2002. Avian persistence in fragmented rainforest. Science 298:1236-1238.

Litzgus, J.D., and T.A. Mousseau. 2004. Home range and seasonal activity of southern spotted turtles (*Clemmys guttata*): Implications for management. Copeia 2004:804-817.

MacCulloch, R.D., and D.M. Secoy. 1983. Movement in a river population of *Chrysemys picta bellii* in southern Saskatchewan. Journal of Herpetology 17:283-285.

Mahmoud, I.Y. 1969. Comparative ecology of the kinosternid turtles of Oklahoma. Southwest Naturalist 14:31-66.

McAuliffe, J.R. 1978. Seasonal migrational movements of a population of the western painted turtle, *Chrysemys picta bellii* (Reptilia, Testudines, Testudinidae). Journal of Herpetology 12:143-149.

McNeil, J.A. 2002. Distribution, movements, morphology, and reproduction in a population of Blanding's turtle (*Emydoidea blandingii*) in an unprotected landscape in southwestern Nova Scotia. Masters Thesis, Acadia University, Wolfville, Nova Scotia. 236 pp.

Milam, J.C., and S.M. Melvin. 2001. Density, habitat use, movements, and conservation of spotted turtles (*Clemmys guttata*) in Massachusetts. Journal of Herpetology 35:418-427.

Millar, C.S., and G. Blouin-Demers. 2011. Spatial ecology and seasonal activity of Blanding's turtles (*Emydoidea blandingii*) in Ontario, Canada. Journal of Herpetology 45:370-378.

Mitchell, J.C., and M.W. Klemens. 2000. Primary and secondary effects of habitat alteration. Pp. 5–32. *In*: M.W. Klemens (ed.). Turtle Conservation. Smithsonian Institution Press, Washington.

Morreale, S.J., J.W. Gibbons, and J.D. Congdon. 1984. Significance of activity and movement in the yellow-bellied slider turtle (*Pseudemys scripta*). Canadian Journal of Zoology 42:1038-1042.

Obbard, M.E., and R.J. Brooks. 1980. Nesting migrations of the snapping turtles (*Chelydra serpentina*). Herpetologica 36:158-162.

Obbard, M.E., and R.J. Brooks. 1981. A radio-telemetry and mark-recapture study of activity in the common snapping turtle, *Chelydra serpentina*. Copeia 1981:630-637.

Öckinger, E., M. Franzén, M. Rundlöf, H.G. Smith. 2009. Mobility-dependent effects on species richness in fragmented landscapes. Basic and Applied Ecology 10:573-578.

Öckinger, E., O. Schweiger, T.O. Crist, D.M. Debinski, J. Krauss, M. Kuussaari, J.D. Petersen, J. Pöyry, J. Settele, K.S. Summerville, and R. Bommarco. 2010. Life-history traits predict species responses to habitat area and isolation: a cross-continental synthesis. Ecology Letters 13:969-979.

Pappas, M.J., and B.J. Brecke. 1992. Habitat selection of juvenile Blanding's turtles, *Emydoidea blandingii*. Journal of Herpetology 26:233-234.

Pearse, A.S. 1923. The abundance and migration of turtles. Ecology 4:24-28.

Pettit, K.E., C.A. Bishop, and R.J. Brooks. 1995. Home range and movements of the common snapping turtle, *Chelydra serpentina serpentina*, in a coastal wetland of Hamilton Harbour, Lake Ontario, Canada. Canadian Field-Naturalist 109:192-200.

Piepgras, S.A., and J.W. Lang. 2000. Spatial ecology of Blanding's turtle in central Minnesota. Chelonian Conservation and Biology 3:589-601.

Rasmussen, M.L., and J.D. Litzgus. 2010. Habitat selection and movement patterns of spotted turtles (*Clemmys guttata*): Effects of spatial and temporal scales of analyses. Copeia 2010:86-96.

Ross, D.A., and R.K., Anderson. 1990. Habitat use, movement, and nesting of *Emydoidea blandingii* in central Wisconsin. Journal of Herpetology 24:6-12.

Rowe, J.W. 2003. Activity and movements of midland painted turtles (*Chrysemys picta marginata*) living in a small marsh system on Beaver Island, Michigan. Journal of Herpetology 37:342-353.

Rowe, J.W., E.O. Moll. 1991. A radiotelemetric study of activity and movements of the Blanding's turtle (*Emydoidea blandingii*) in northeastern Illinois. Journal of Herpetology 25: 178-185.

Rowe, J.W., G.C. Lehr, P.M. McCarthy, and P.M. Converse. 2009. Activity, movements, and activity area size in stinkpot turtles (*Sternotherus odoratus*) in a southwestern Michigan Lake. American Midland Naturalist. 162:266-275.

Rowe, J.W., and S.F. Dalgarn. 2010. Home range size and daily movements of midland painted turtles (*Chrysemys picta marginata*) in relation to body size, sex, and weather patterns. Herpetological Conservation and Biology 5:461-473.

Rubin, C.S., R.E. Warner, and D.R. Ludwig. 2001. Habitat use and movements of radiotagged Blanding's turtles (*Emydoidea blandingii*) in a suburban landscape. Chelonian Conservation and Biology 4:136-141.

Schuler, M., and R.P. Thiel. 2008. Annual vs. multiple-year home range sizes of individual Blanding's turtles, *Emydoidea blandingii*, in Central Wisconsin. Canadian Field-Naturalist 122:61-64.

Seaman, D.E., and R.A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77:2075-2085.

Sexton, O.J. 1959. Spatial and temporal movements of a population of the painted turtle, *Chrysemys picta marginata* (Agassiz). Ecological Monographs 29:113-140.

Sexton, O. J. 1995. Miscellaneous comments on the natural history of Blanding's turtle (*Emydoidea blandingii*). Transactions of the Missouri Academy Science 29:1-13.

Shepard, D.B, M.J. Dreslik, B.C. Jellen, and C.A. Phillips. 2008. Reptile road mortality around an oasis in the Illinois corn desert with emphasis on the endangered eastern massasauga. Copeia 2008:350-359.

Smar, C.M., and R.M. Chambers. 2005. Homing behavior of musk turtles in a Virginia lake. Southeastern Naturalist 4:527-532.

Wilson, T.P. 1994. Ecology of the spotted turtles, *Clemmys guttata*, at the western range limit. Masters Thesis, Eastern Illinois University, Charleston, Illinois. 97 pp.

Worton, B.J. 1987. A review of models of home range for animal movement. Ecological Modelling 38:277-298.

TABLES

Table 1.1 Spatial statistics for 69 *E. blandingii* radio-tracked at three sites (Will 1-3) in Will County, Illinois from 2005-2010. Individuals were allocated to three different stage/sex categories; males (M), females (F) and juveniles (J). Listed for each site and stage/sex are means ± 1SE for: carapace length (CL), number of radio-locations (#Loc), minimum convex polygon (MCP), mean daily distance moved (MDD), 95% fixed kernel density isopleth (95K), 50% fixed kernel density isopleth (50K), number of 50% fixed kernel density isopleths (#C), and home range length (HRL).

Will 1	**CL (mm)**	**# Loc**	**MCP (ha)**	**MDD (m)**	**95K (ha)**	**50K (ha)**	**#C**	**HRL (m)**
M	219.0 ± 6.9	276.3 ± 36.2	56.6 ± 13.6	63.4 ± 7.2	18.2 ± 2.2	1.6 ± 0.2	1.4 ± 0.2	1903.8 ± 454.7
F	205.0 ± 3.1	270.0 ± 35.8	25.6 ± 3.0	37.8 ± 2.7	13.7 ± 1.2	1.5 ± 0.2	1.3 ± 0.2	1143.8 ± 85.9
J	147.3 ± 6.5	306.5 ± 57.7	21.3 ± 13.9	32.2 ± 2.5	6.8 ± 1.8	1.4 ± 0.1	1.0 ± 0.0	1102.9 ± 375.1
Will 2	**CL (mm)**	**# Loc**	**MCP (ha)**	**MDD (m)**	**95K (ha)**	**50K (ha)**	**#C**	**HRL (m)**
M	203.7 ± 13.5	287.3 ± 12.4	75.8 ± 39.1	50.0 ± 6.9	13.0 ± 2.2	1.3 ± 0.2	1.0 ± 0.0	1844.3 ± 494.6
F	200.2 ± 3.0	216.8 ± 56.7	33.9 ± 9.6	42.3 ± 6.4	12.6 ± 1.5	2.4 ± 0.4	1.0 ± 0.0	1271.2 ± 341.9
J	118.0 ± 10.5	170.0 ± 63.2	13.6 ± 3.6	22.3 ± 4.0	9.1 ± 1.7	1.8 ± 0.2	1.2 ± 0.2	720.7 ± 163.9
Will 3	**CL (mm)**	**# Loc**	**MCP (ha)**	**MDD (m)**	**95K (ha)**	**50K (ha)**	**#C**	**HRL (m)**
M	213.4 ± 6.2	167.6 ± 25.8	23.4 ± 6.6	24.3 ± 5.8	10.2 ± 1.2	1.4 ± 0.3	1.8 ± 0.4	841.3 ± 168.5
F	199.5 ± 3.3	210.5 ± 21.9	24.9 ± 4.6	28.8 ± 5.1	13.2 ± 2.0	1.9 ± 0.2	1.7 ± 0.2	946.8 ± 105.6
J	125.3 ± 5.8	160.5 ± 18.1	7.0 ± 2.7	15.5 ± 2.3	6.2 ± 0.8	1.2 ± 0.1	1.2 ± 0.1	568.6 ± 116.4

Table 1.2 Two-way ANOVA results for comparisons of spatial statistics among stage/sex class and site for 69 *E. Blandingii* and 34 *C. guttata* radio-tracked at three sites (Will 1-3) in Will County, Illinois from 2005-2010. Listed are: minimum convex polygon home range area (MCP), 95% fixed kernel density isopleth (95K), 50% fixed kernel density isopleth (50K), mean daily distance moved (MDD), and home range length (HRL) among stage/sex class and site.

.

		E. blandingii			***C. guttata***		
Variable	**Effect**	**F**	**df**	***p***	**F**	**df**	***p***
MCP	Stage/sex	11.520	2,60	**<0.0001**	1.246	1,30	0.273
	Site	5.300	2,60	**0.008**	0.101	1,30	0.752
	Stage/sex * Site	0.496	4,60	0.739	0.875	1,30	0.357
95K	Stage/sex	11.380	2,60	**<0.0001**	1.233	1,30	0.276
	Site	2.281	2,60	0.111	7.852	1,30	**0.009**
	Stage/sex * Site	1.004	4,60	0.413	2.514	1,30	0.123
50K	Stage/sex	2.875	2,60	0.064	1.251	1,30	0.272
	Site	1.527	2,60	0.225	6.129	1,30	**0.019**
	Stage/sex * Site	1.551	4,60	0.199	0.235	1,30	0.632
MDD	Stage/sex	6.706	2,60	**0.002**	4.522	1,30	**0.042**
	Site	15.365	2,60	**<0.0001**	40.274	1,30	**<0.0001**
	Stage/sex * Site	1.106	4,60	0.362	2.446	1,30	0.128
HRL	Stage/sex	6.219	2,60	**0.004**	1.102	1,30	0.302
	Site	6.335	2,60	**0.003**	0.014	1,30	0.908
	Stage/sex * Site	0.700	4,60	0.595	0.261	1,30	0.613

Table 1.3 Spatial statistics for 34 *C. guttata* radio-tracked at two sites (Will 1-2) in Will County, Illinois from 2005-2009. Individuals were allocated to two different stage/sex categories; males (M) and females (F). Listed for each site and stage/sex are means ± 1SE for: mean carapace length (CL), number of radio-locations (#Loc), minimum convex polygon (MCP), mean daily distance moved (MDD), 95% fixed kernel density isopleth (95K), 50% fixed kernel density isopleth (50K), number of 50% fixed kernel density isopleths (#C), and home range length (HRL).

Will 2	**CL (mm)**	**# Loc**	**MCP (ha)**	**MDD (m)**	**95K (ha)**	**50K (ha)**	**#C**	**HRL (m)**
M	97.1 ± 2.1	146.6 ± 21.9	2.5 ± 0.7	15.3 ± 1.1	1.4 ± 0.1	0.2 ± 0.0	1.7 ± 0.3	269.5 ± 49.1
F	99.5 ± 1.8	179.1 ± 27.3	2.7 ± 0.8	17.2 ± 1.9	1.3 ± 0.1	0.2 ± 0.0	2.0 ± 0.2	296.0 ± 50.2
Will 3	**CL (mm)**	**# Loc**	**MCP (ha)**	**MDD (m)**	**95K (ha)**	**50K (ha)**	**#C**	**HRL (m)**
M	110.7 ± 5.5	82.7 ± 3.6	1.7 ± 0.8	5.8 ± 0.9	0.8 ± 0.1	0.1± 0.0	1.0 ± 0.0	246.0 ± 61.6
F	107.6 ± 1.4	138.0 ± 31.6	3.8 ± 1.8	9.1 ± 1.3	1.1 ± 0.2	0.1 ± 0.0	2.0 ± 0.3	400.7 ± 156.7

Table 1.4 Spatial statistics for 12 *S. odoratus*, nine *C. serpentina*, and eight *C. picta* radio-tracked in Will County, Illinois from 2005-2006. Individuals were allocated to two different stage/sex categories; males (M) and females (F). Listed for each site and stage/sex are means ± 1SE for: mean carapace length (CL), number of radio-locations (#Loc), minimum convex polygon (MCP), mean daily distance moved (MDD), 95% fixed kernel density isopleth (95K), 50% fixed kernel density isopleth (50K), number of 50% fixed kernel density isopleths (#C), and home range length (HRL).

	CL (mm)	# Loc	MCP (ha)	MDD (m)	95K (ha)	50K (ha)	#C	HRL (m)
S. odoratus								
M	105.7 ± 3.6	49.0 ± 6.9	11.6 ± 9.3	36.3 ± 11.6	5.0 ± 0.8	0.9 ± 0.1	1.3 ± 0.2	585.4 ± 278.1
F	114.0 ± 2.2	69.0 ± 5.0	8.2 ± 4.7	30.0 ± 5.6	5.3 ± 1.2	1.1 ± 0.2	1.2 ± 0.2	589.8 ± 222.3
	CL (mm)	**# Loc**	**MCP (ha)**	**MDD (m)**	**95K (ha)**	**50K (ha)**	**#C**	**HRL (m)**
C. serpentina								
M	275.8 ± 12.8	71.4 ± 7.5	3.9 ± 1.9	28.3 ± 10.8	2.8 ± 0.9	0.6 ± 0.1	1.0 ± 0.0	434.5 ± 147.2
F	253.0 ± 14.0	60.0 ± 12.7	8.1 ± 2.1	42.3 ± 10.3	5.6 ± 1.3	0.5 ± 0.1	1.3 ± 0.3	647.0 ± 169.2
	CL (mm)	**# Loc**	**MCP (ha)**	**MDD (m)**	**95K (ha)**	**50K (ha)**	**#C**	**HRL (m)**
C. picta								
M	141.0 ± 4.2	53.2 ± 8.2	7.5 ± 2.7	70.8 ± 34.4	11.1 ± 1.2	2.3 ± 0.3	1.0 ± 0.0	663.3 ± 269.4
F	141.7 ± 8.8	37.7 ± 10.4	3.9 ± 2.1	24.0 ± 6.2	7.5 ± 1.4	1.9 ± 0.1	1.0 ± 0.0	762.4 ± 424.2

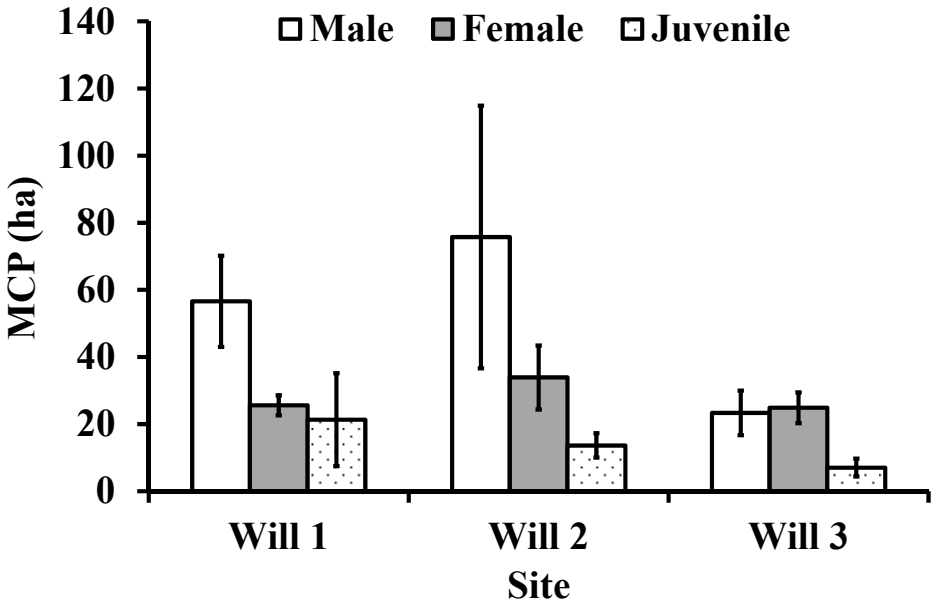
Table 1.5 Student's t-test results for comparisons of spatial statistics between stage/sex class for 12 *S. odoratus*, nine *C. serpentina*, and eight *C. picta* radio-tracked at Will County, Illinois from 2005-2006. Listed are: minimum convex polygon home range (MCP), 95% fixed kernel density isopleth (95K), 50% fixed kernel density isopleth (50K), mean daily distance moved (MDD), and home range length (HRL).

	S. odoratus			***C. serpentina***			***C. picta***		
Variable	**t**	**df**	***p***	**t**	**df**	***p***	**t**	**df**	***p***
MCP	-0.075	10	0.942	-1.491	7	0.180	1.132	6	0.780
95K	-0.174	10	0.865	-1.998	7	0.086	1.982	6	0.095
50K	-0.672	10	0.517	0.044	7	0.966	0.881	6	0.412
MDD	0.324	10	0.753	-1.099	7	0.308	1.395	6	0.213
HRL	-0.101	10	0.922	-0.999	7	0.351	-0.119	6	0.909

FIGURES

Fig. 1.1 Comparisons of spatial statistics between stage/sex class for 69 *E. blandingii* radio-tracked at three preserves in Will County, Illinois from 2005-2010. Listed are: mean estimates (± 1SE) of A) Minimum convex polygon (MCP), B) 95% fixed kernel density isopleth (95K), C) 50% fixed kernel density isopleth (50K), D) mean daily distance moved (MDD), and E) home range length (HRL).

A)



B)

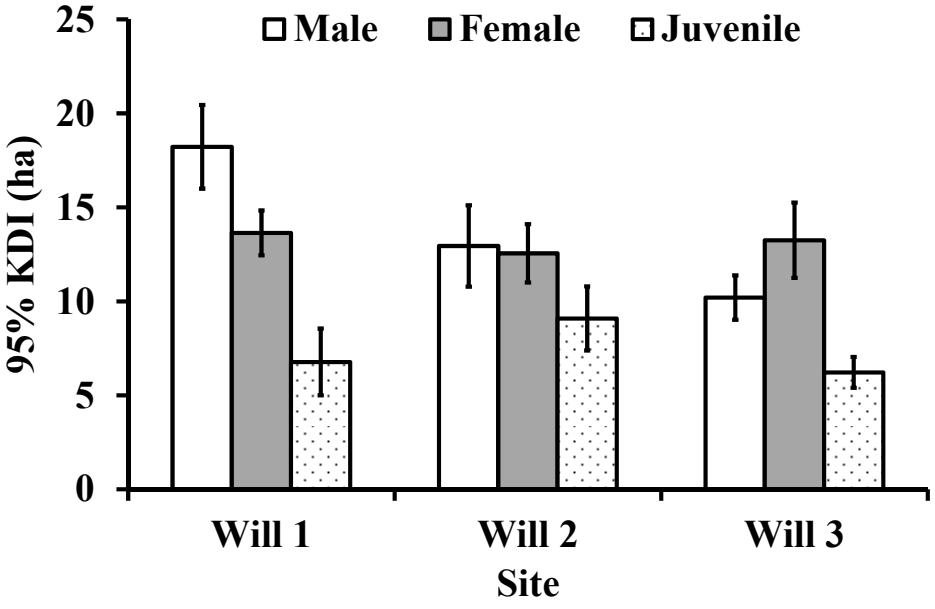
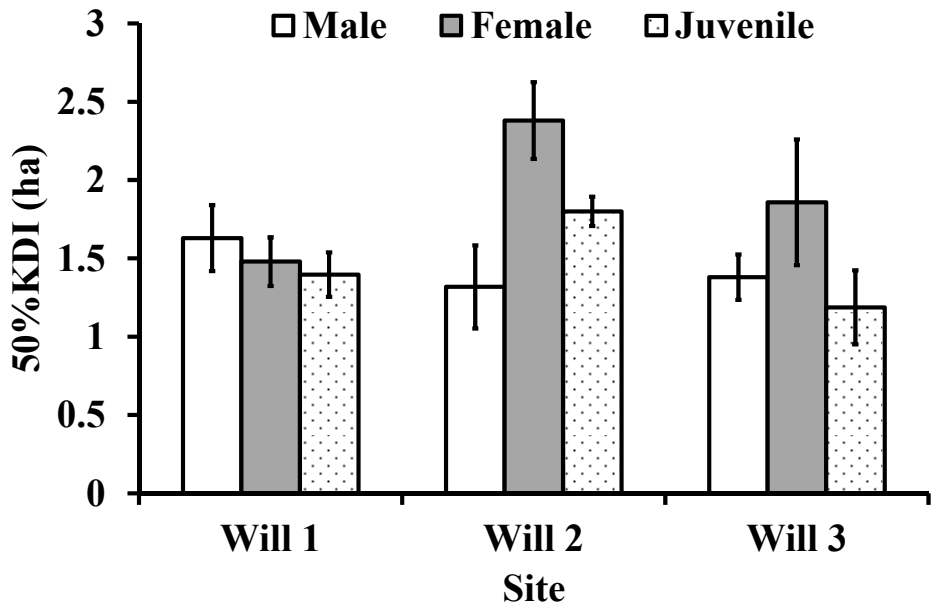


Fig. 1.1 (cont.)

C)



D)

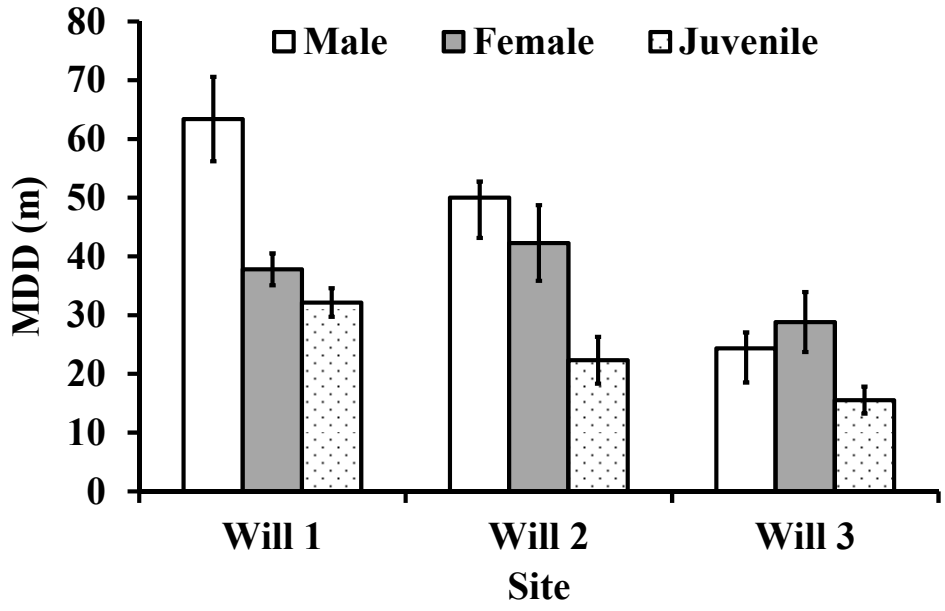


Fig. 1.1 (cont.)

E)

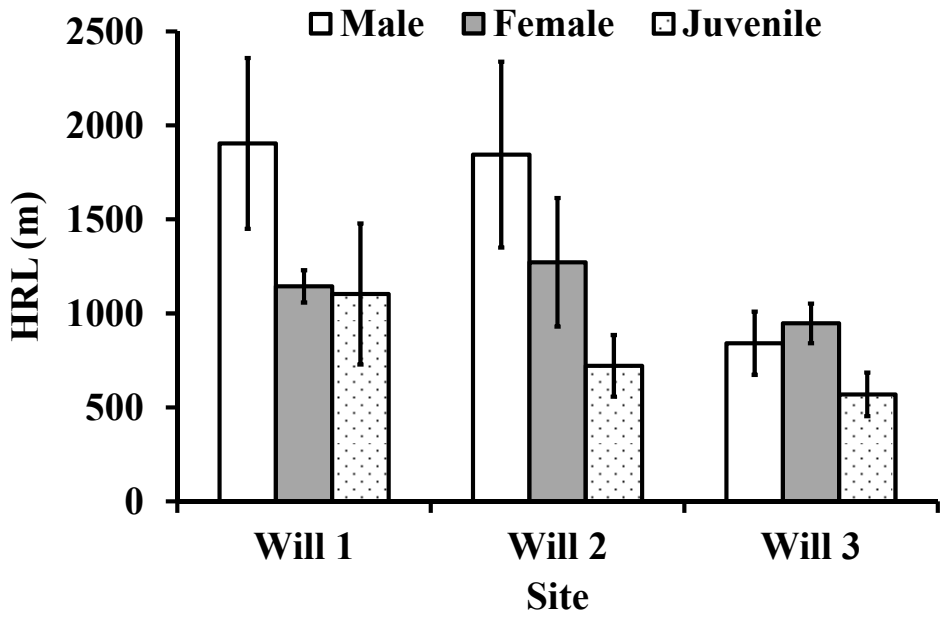
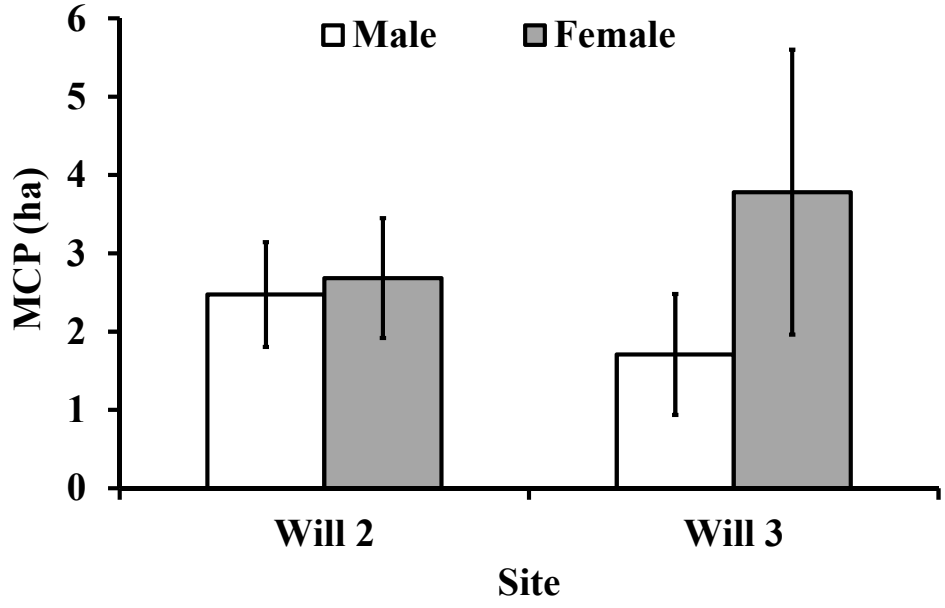

Male
Female
Juvenile
2500
2000
1500
1000
500
0
HRL (m)
Will 1
Will 2
Will 3
Site

Fig. 1.2 Comparisons of spatial statistics between stage/sex class for 34 *C. guttata* radio-tracked at two preserves in Will County, Illinois from 2005-2008. Listed are: mean estimates (± 1SE) of A) Minimum convex polygon (MCP), B) 95% fixed kernel density isopleth (95K), C) 50% fixed kernel density isopleth (50K), D) mean daily distance moved (MDD), E) and home range length (HRL).

A)



B)

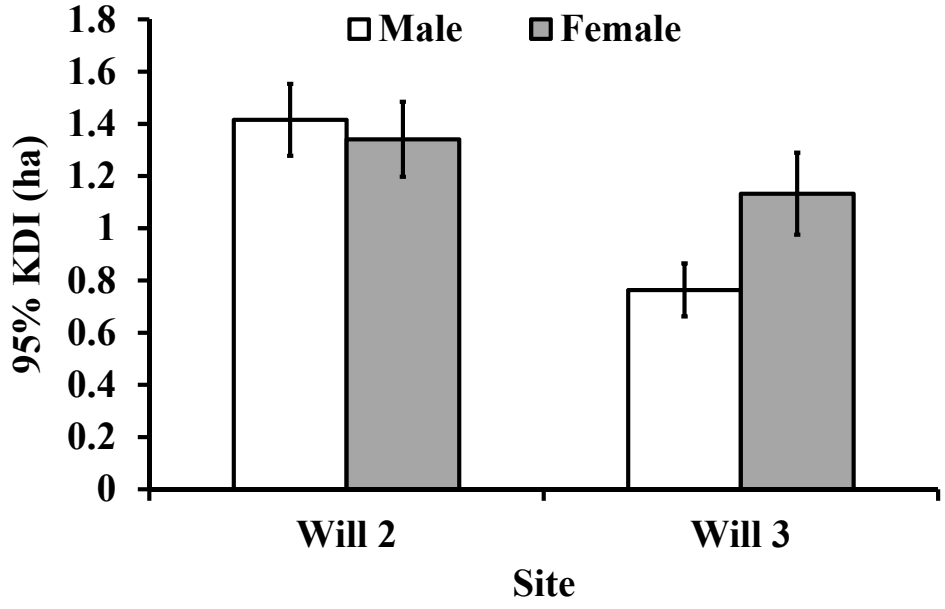
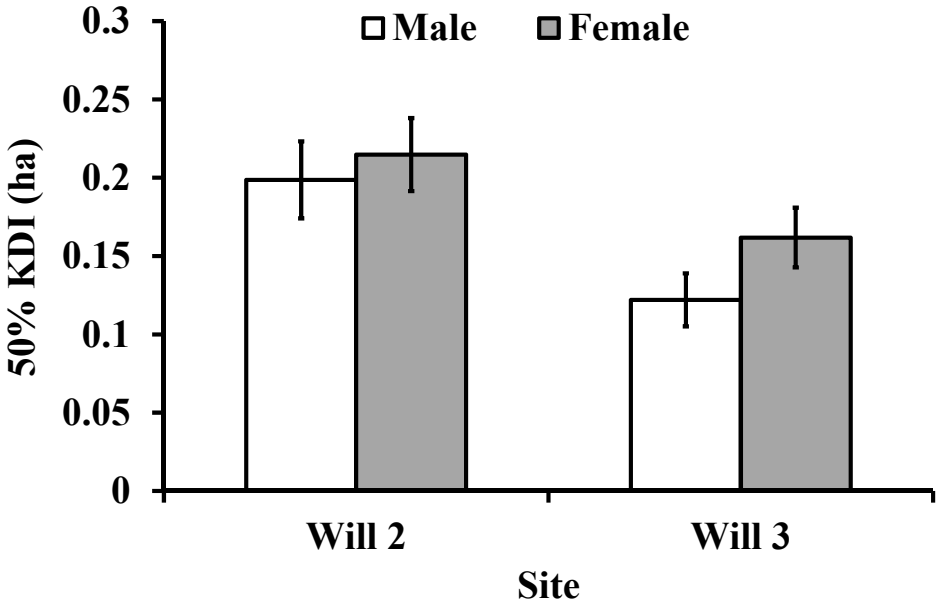


Fig. 1.2 (cont.)

C)



D)

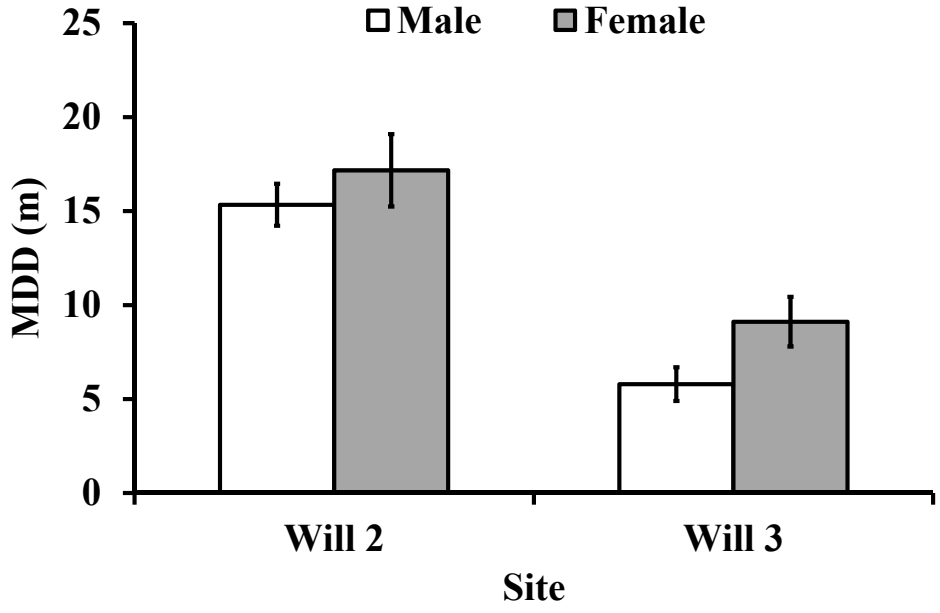


Fig. 1.2 (cont.)

E)

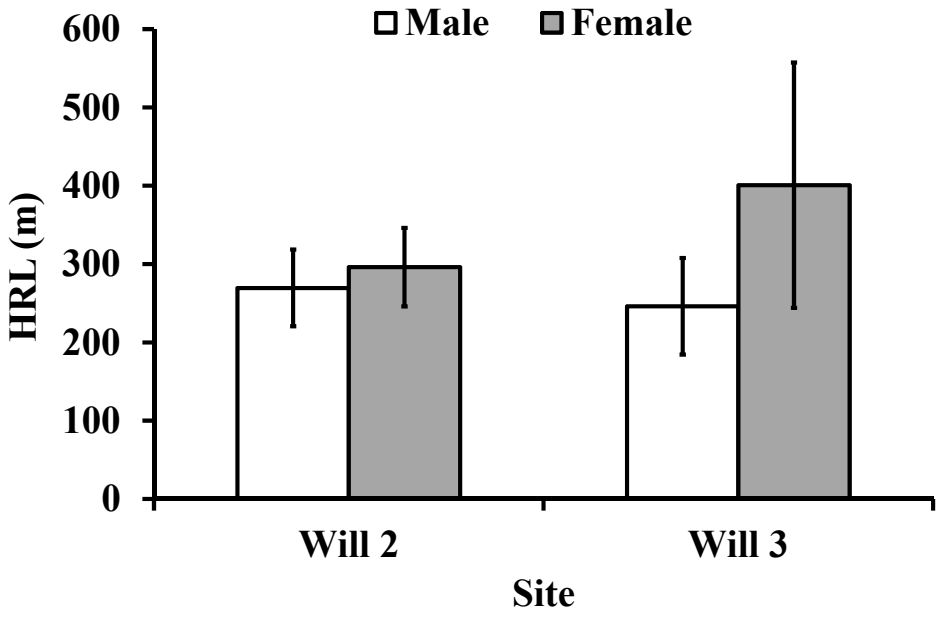
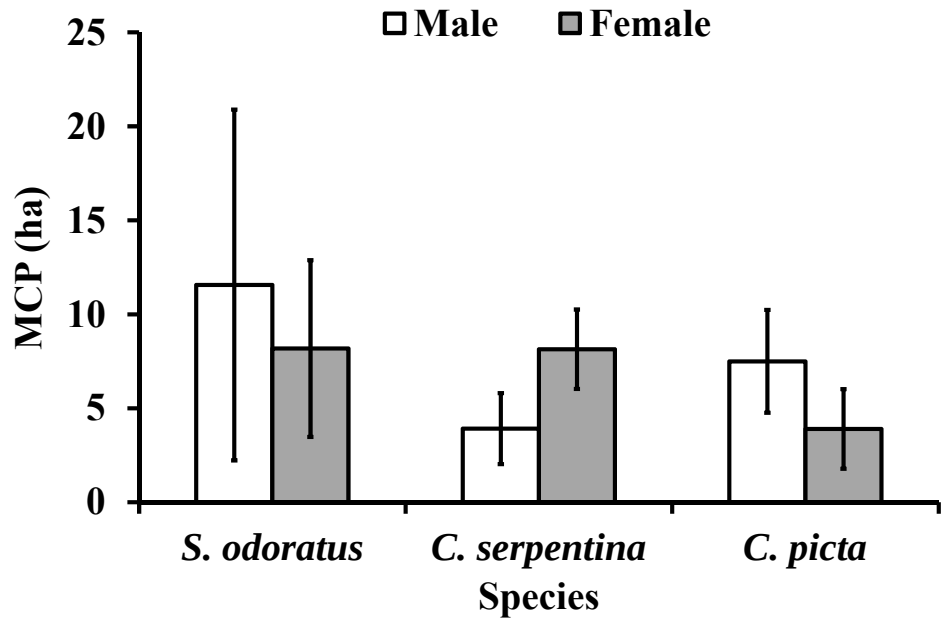


Fig. 1.3 Comparisons of spatial statistics between stage/sex class for 12 *S. odoratus*, nine *C. serpentina*, and eight *C. picta* radio-tracked at a preserve in Will County, Illinois from 2005-2006. Listed are: mean estimates (± 1SE) of A) Minimum convex polygon (MCP), B) 95% fixed kernel density isopleth (95K), C) 50% fixed kernel density isopleth (50K), D) mean daily distance moved (MDD), E) and home range length (HRL).

A)



B)

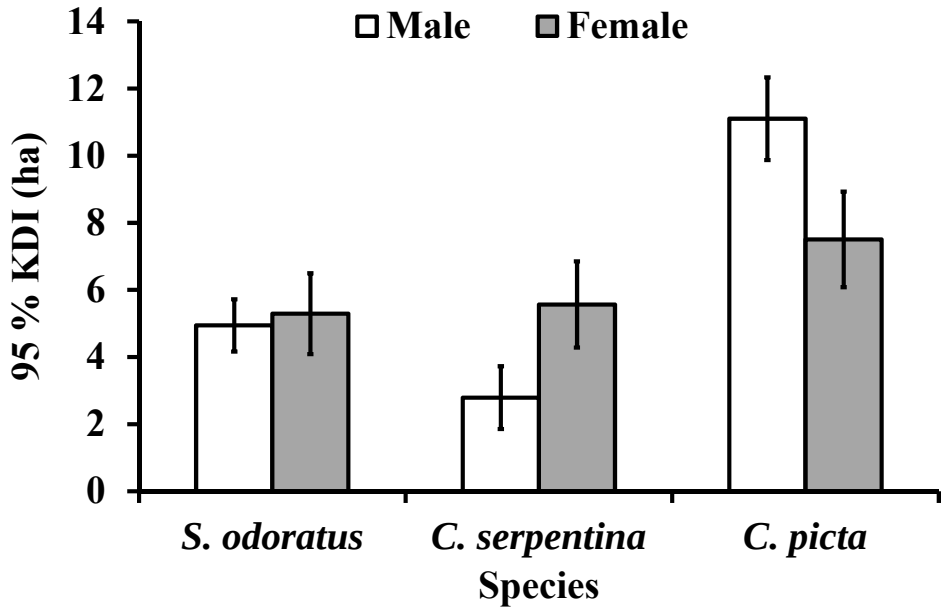
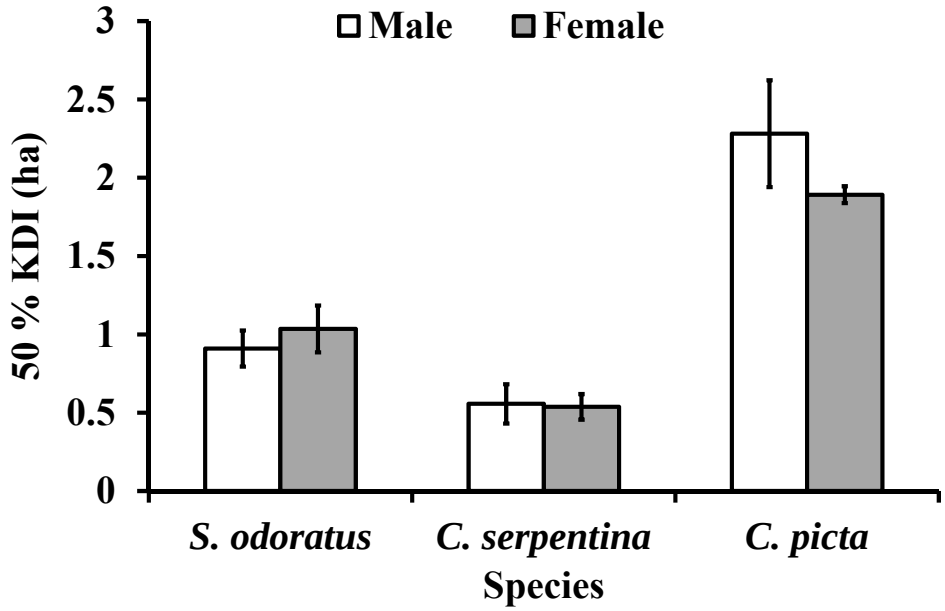


Fig. 1.3 (cont.)

C)



D)

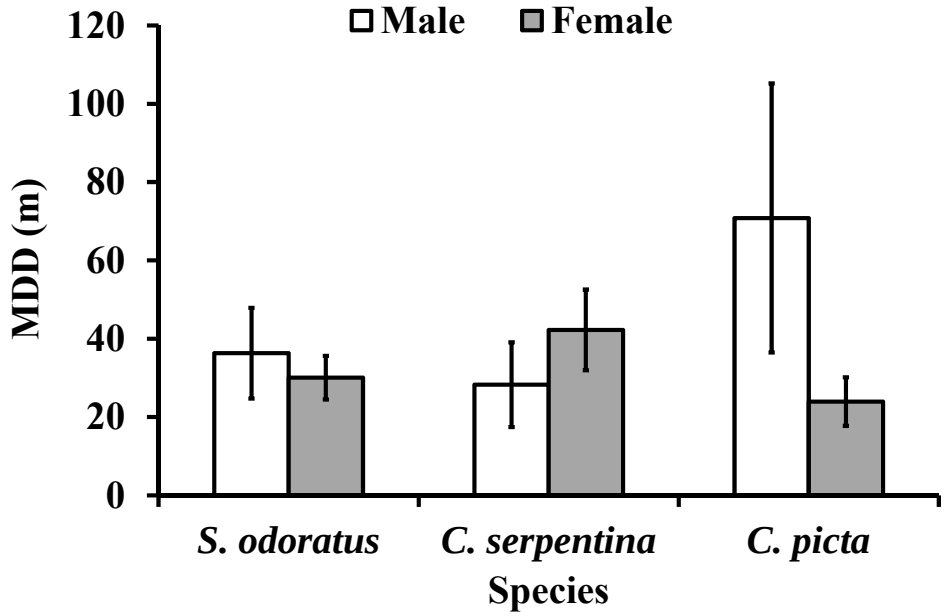


Fig. 1.3 (cont.)

E)

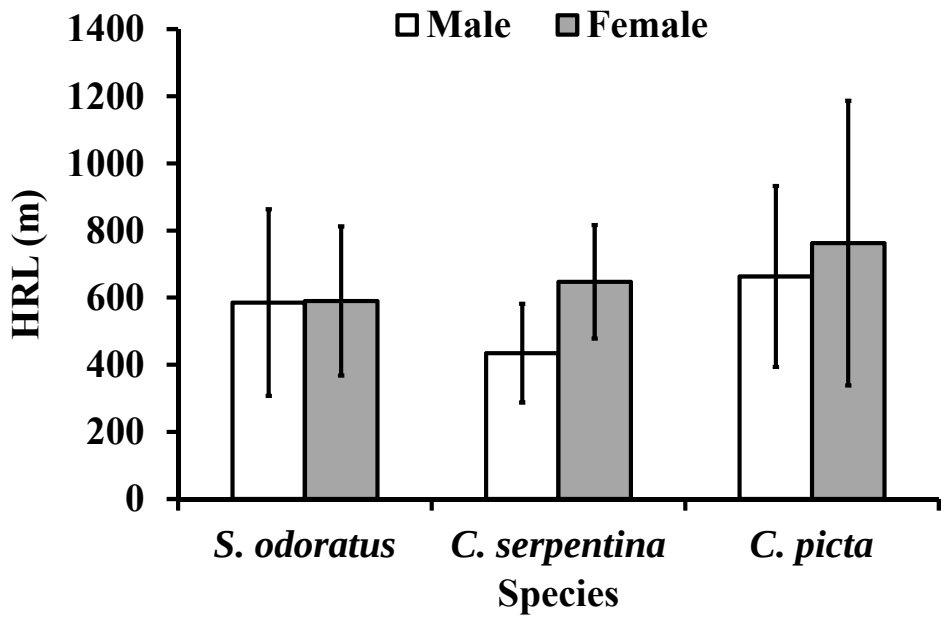
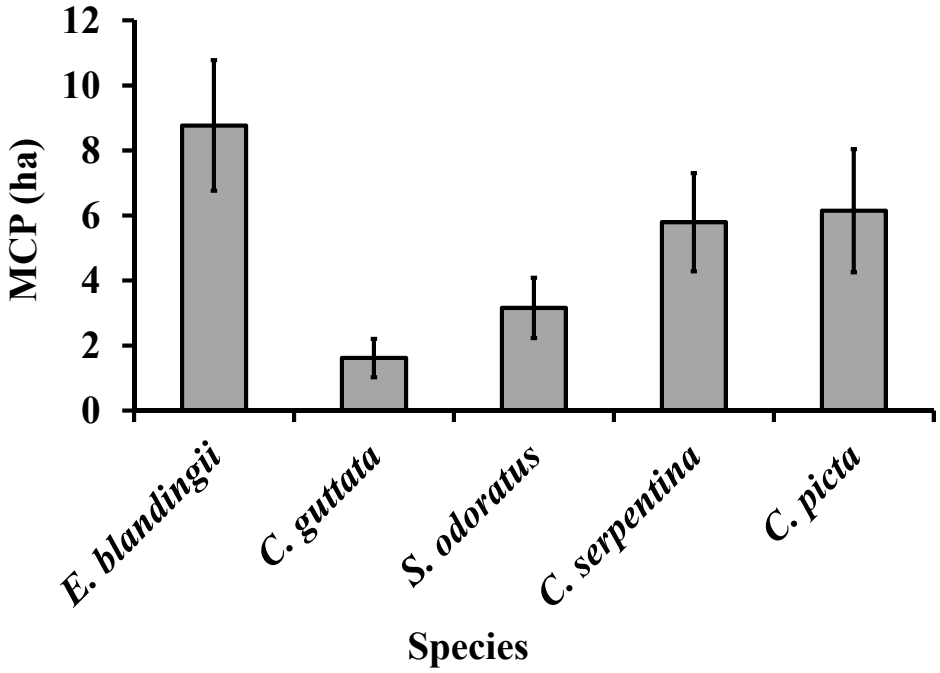

Male
Female
1400
1200
1000
800
600
400
200
0
HRL (m)
S. odoratus
C. serpentina
C. picta
Species

Fig. 1.4 Comparisons of spatial statistics between 17 *E. blandingii*, ten *C. guttata*, nine *S. odoratus*, nine *C. serpentina*, and eight *C. picta* radio-tracked at a preserve in Will County, Illinois during 2006. Listed are: mean estimates (± 1SE) of A) Minimum convex polygon (MCP), B) mean daily distance moved (MDD), and C) home range length (HRL).

A)



B)

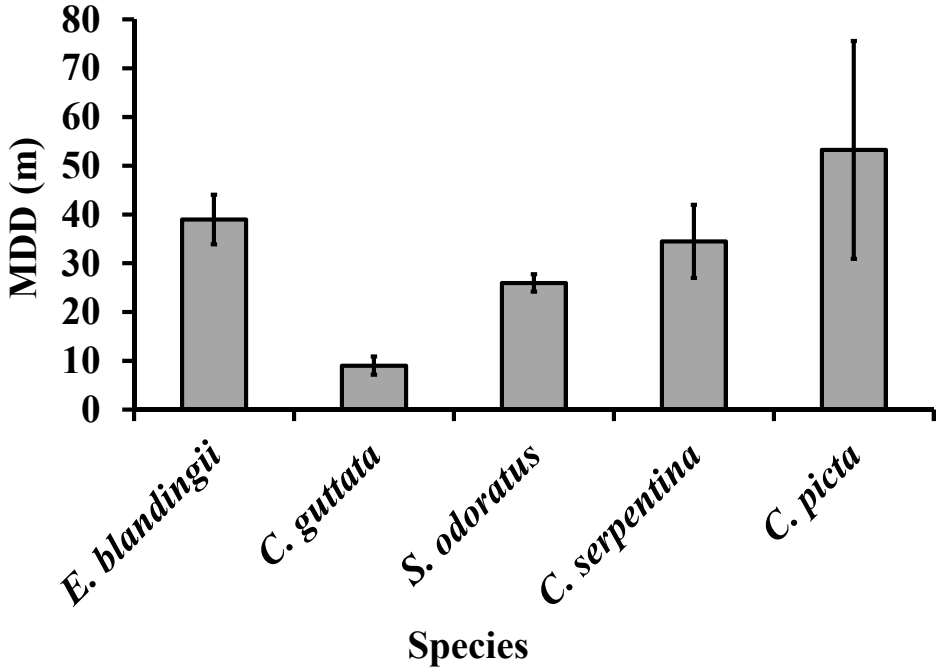
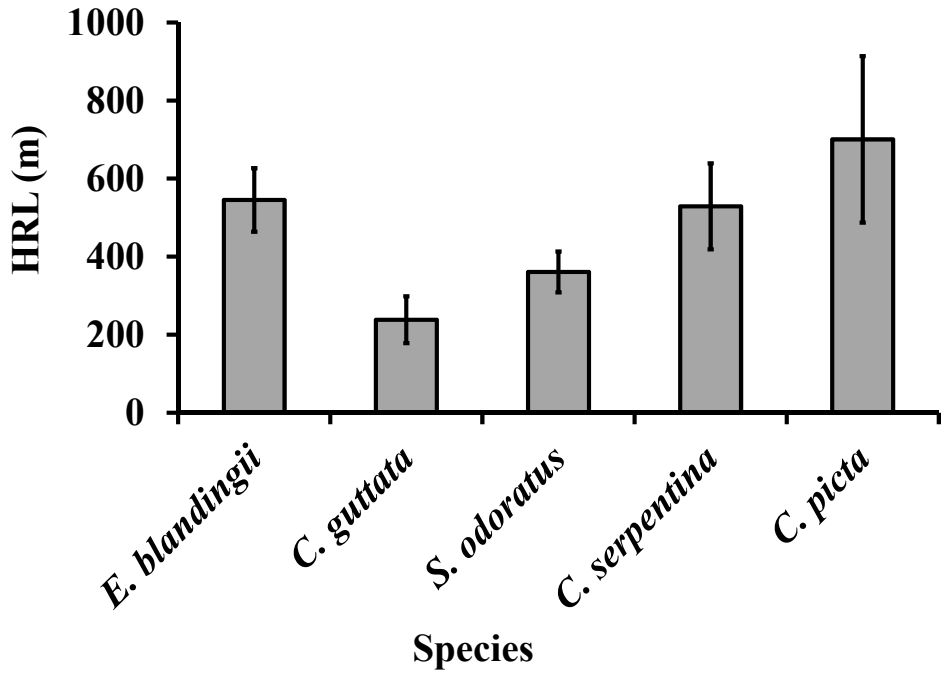


Fig. 1.4 (cont.)

C)


1000
800
600
400
200
0
HRL (m)
E. blandingii
C. guttata
S. odoratus
C. serpentina
C. picta
Species

CHAPTER 2

HABITAT PARTITIONING IN FIVE SYMPATRIC FRESHWATER TURTLE SPECIES AT AN ISOLATED PRESERVE

INTRODUCTION

Resource partitioning is fundamental to community structuring (Schoener, 1974). Empirical studies demonstrate that species coexist by partitioning resources along multiple gradients such as food, habitat, time, and space (Luiselli, 2006; Luiselli, 2008; Robertson et al., 2008). Niche breadth and amount of niche overlap among co-existing species varies depending on phenotypic and ecological similarities (Pacala and Roughgarden, 1982; Cromsigt and Olff, 2006) as well as abiotic factors such as the availability of limiting resources (Sebastiá, 2004). In a review of resource partitioning studies in freshwater turtles, habitat was a resource dimension often partitioned (Luiselli, 2008).

Habitat loss and fragmentation have caused drastic declines in freshwater turtles (Mitchell and Klemens, 2000). Because habitat quality is vital for population persistence and important in structuring turtle communities, understanding species-habitat relationships will aid in assessing fitness and long-term population persistence, criteria essential for conservation practices (Morrison et al., 2006). To evaluate species-habitat relationships in a sympatric freshwater turtle community, I assessed habitat partitioning using radio-telemetry data collected at an isolated preserve within a highly disturbed landscape in northeastern Illinois. The goal of this project was to determine macro- and micro-habitat use and estimate habitat partitioning and overlap at both habitat levels among three common and two rare species. My objectives were to 1) evaluate macro- and micro-habitat use for each species 2) compare macro- and micro-habitat

use among species 3) measure niche breadth and niche overlap for species at both habitat use levels and 4) identify partitioning strength of micro-habitat variables among species.

METHODS

Study Site and Species.—The study was conducted from May – September 2006 at a 124 ha preserve located in Will County, Illinois and is situated in a matrix of urbanization and industrial development. The preserve is a prairie-wetland mosaic consisting of various wetland macro-habitats that can be broadly classified as cattail (*Typha*) marsh, sedge meadow, and pond. The preserve also lies adjacent to the Des Plaines River and associated riparian macro-habitats such as scoured backwater ponds and floodplain forest. Micro-habitat characteristics such as vegetation structure and composition, water depth, canopy cover, and substrate vary substantially among habitat types and aid in defining the broader habitat categories. For example, presence and height of emergent vegetation is considerably greater in marsh habitats than in pond or riparian habitats. Within the preserve boundary, much of the wetland substrate is characterized as organic; however, substrate within the Des Plaines River and backwater areas is predominantly characterized as silt. Many transitional areas between habitat types also exist resulting in micro-habitat variation within macro-habitat types. During high water events, the river and backwater pools carry silt into adjacent wetlands within the preserve, altering the substrate composition. Additionally, within interior wetlands, cattail marsh bordering a sedge meadow typically has shallower water depths than cattail marsh bordering a pond.

An abundant turtle fauna inhabits the wetland areas within the preserve and the adjacent riparian habitats (Anthonysamy et al. unpubl.). Common turtle species include the painted turtle (*Chrysemys picta*), snapping turtle (*Chelydra serpentina*), and eastern musk turtle (*Sternotherus*

odoratus); however, two rare turtle species, the Blanding's turtle (*Emydoidea blandingii*) and spotted turtle (*Clemmys guttata*) also occur at the preserve. *Chelydra serpentina*, *S. odoratus*, and *C. picta* are widely distributed and abundant throughout much the United States whereas *E. blandingii* and *C. guttata* have more restricted distributions, are found at lower population densities, and are considered to be species of conservation concern throughout their range, mainly because of habitat loss (Ernst and Lovich, 2009).

Field methods.—I radio-tracked 61 adult turtles: five male and 15 female *E. blandingii*, five male and seven female *C. guttata*, four male and five female *S. odoratus*, five male and four female *C. picta*, and six male and five female *C. serpentina*. I affixed radio-transmitters to the rear marginals of turtles using transmitters and methods as described in Anthonysamy et al. (*in review*) and radio-located turtles from three to seven times a week. At each radio-location I attempted to visually or tactilely confirm presence of the turtle and recorded GPS coordinates (UTM-NAD 83 CONUS) and a suite of habitat variables.

Macro-habitat use.—I plotted turtle location coordinates onto a vegetation community map provided by the Forest Preserve District of Will County that was field-checked during the study. Coordinates were assigned to seven macro-habitat categories: cattail marsh, pond, sedge meadow, river, floodplain (forested and open riparian areas), mesic dolomite prairie, and dry dolomite prairie. Using the habitat assignments, I calculated the proportion of locations for each turtle in each habitat and the proportion of available habitat types in the study area. I then used compositional analysis to assess macro-habitat use vs. availability for each species (Aebischer et al., 1993). For each turtle, I used the proportion of available and the proportion of used macro-

habitats to calculate the difference in log ratios for each macro-habitat pair. To qualitatively assess macro-habitat use within and among species, differences in log ratios of use vs. availability between macro-habitat pairs were used to establish rankings in macro-habitat use for each individual turtle (Aebischer et al., 1993). Rankings ranged from zero to seven (number of habitat types) with larger ranks representing higher use than smaller ranks. Mean habitat rankings (± 1 SE) were calculated for each species for each habitat type. To quantitatively assess differential habitat use among species, I used a multivariate analysis of variance (MANOVA) to test for differences in log ratio values of use vs. availability among species. Because species sample size was unequal, I used Gabriel's multiple comparison post hoc tests to compare differences in macro-habitat use between species.

Using macro-habitat proportions, I estimated niche breadth for each species as well as niche overlap between species. To account for variation in macro-habitat availability, I used the Proportional Similarity Index (Feinsinger et al. 1981),:

$$PS = 1 - 0.5 \sum_i |p_i - q_i|$$

where PS = Proportional Similarity Index

p_i = Proportion of radio-locations in macro-habitat *i*

q_i = Proportion of available macro-habitat *i*

For broad niche breadths or those where habitats are used in proportion to availability, PS = 1.0. Conversely, $PS = [\min q_i]$ when habitat used is specialized.

Niche overlap in macro-habitat use was calculated between each species pair using the percentage overlap measure proposed by Renkonen (1938) and given in Krebs (1989) by:

$$P_{jk} = \left[\sum^{n} \left(minimum\ p_{ij}, p_{ik}\right)\right] 100$$

where P_{jk} = Percentage macro-habitat use overlap between species *j* and species *k*

p_{ij}, p_{ik} = Proportion of macro-habitat used *i* of the total macro-habitat proportions used by species *j* and species *k*

n = Total number of macro-habitats

The percentage overlap measure is interpreted as the area of overlap of resource use between two species (Krebs, 1989).

Micro-habitat use.— I quantified the following micro-habitat structural variables at each radio-location: structure and type of vegetation, water depth, amount of open water, and substrate type. I measured water depth at the location of the turtle and height of the tallest plant within 0.5 m of the turtle. I determined proportion of open water vs. vegetation at the surface by holding a spherical densiometer upside down above head height (~1.5-2.0 m) and counting the number of grid dots obscured by water or vegetation to the nearest 1%. I also measured understory canopy cover (*i.e.* emergent vegetation, grasses) and overstory canopy cover (*i.e.* trees) by holding the densiometer at waist (~ 1.0 m) and at chest height (~ 1.3 m), respectively. Densiometer measurements were taken within 0.5 m of the turtle in each cardinal direction and then averaged across directions. I classified substrate at turtle locations as organic (i.e., unconsolidated with non-woody debris and a dark color), inorganic (*i.e*. containing silt, sand, or rock, usually consolidated and light in color), or mixed and calculated the proportion of locations having entirely organic substrates for each turtle. Based on published accounts of turtle habitat associations, I considered organic substrates to indicate higher quality wetlands for the turtle species in my study (Ross and Anderson, 1990; Kiviat, 1997; Marchand and Litvaitis, 2004).

To avoid correlation among micro-habitat variables, I conducted a principle components analysis (PCA) using the continuous variables from the radio-locations to create new orthogonally independent variables. Because substrate was categorical variable, it was not included in the PCA. I chose to include only individuals having at least 20 locations with complete habitat data in the analyses to ensure adequate sampling and retained components with eigenvalues > 0.9. For each turtle, I plotted mean component scores against each other to examine relative micro-habitat niche breadth and niche overlap among species. To identify patterns of micro-habitat partitioning among species, mean PCA component values and proportion of locations with organic substrates for each turtle were used in a one-way analysis of variance (ANOVA) to test for differences in micro-habitat use among species. Proportions were arcsine-square root transformed prior to analysis. I used Gabriel's multiple comparison post hoc tests to compare differences in micro-habitat use between species. Analyses were conducted in SPSS 17.0 (SPSS Inc. Chicago, Illinois). Averages are reported as mean ± 1 S.E and all significance levels were set at $\alpha = 0.05$.

I used the classification-tree analysis package "tree", implemented in R software 2.13.2 (R Development Core Team 2011) to determine how effectively the micro-habitat variables partitioned the species. Classification trees are non-parametric methods useful for revealing complex ecological patterns (De'ath and Fabricius, 2000). The tree was constructed from principal component scores and proportion of locations with organic substrates of individual turtles with species as the response variable. Optimal tree size range was identified by using the cross-validation (cv.tree) code to plot the change in deviance against tree size. I simplified the tree using the pruning (prune.tree) code to find the tree size closest to five (number of species) with the lowest misclassification rate. After optimal tree size was determined, I calculated a *K*

statistic to assess tree performance. I calculated *K* using the method employed by Dellinger et al. (2007) as follows:

$$K = \frac{(A - B)}{(C - B)} \qquad B = \frac{\#\ observations}{\#\ classification\ categories}$$

where K = Ratio of the improvement of the optimal tree classification from chance classification and a tree with perfect classification

A = # actual observations correctly classified by tree

B = # observations correctly classified by chance on average

C = # observations correctly classified by a perfect tree

I used the benchmark ranges for values of *K* created by Landis and Koch (1977) to evaluate strength of the optimal tree: < 0.00 poor, 0.00-0.20 slight, 0.21-0.40 fair, 0.41-0.60 moderate, 0.61-0.80 substantial, and 0.81-1.00 almost perfect.

RESULTS

Fifty turtles had at least 20 radio-locations with complete habitat data and were included in the analyses: five male and 13 female *E. blandingii*, five male and five female *C. guttata*, four male and five female *S. odoratus*, four male and two female *C. picta*, and four male and three female *C. serpentina* (Appendix F). Average number of radio-locations for individuals used in analyses was 75.5 ± 5.55 for *E. blandingii*, 69.0 ± 2.56 for *C. guttata*, 41.8 ± 4.83 for *C. picta*, 66.4 ± 4.25 for *C. serpentina*, and 50.7 ± 5.52 for *S. odoratus*. Of the 50 turtles retained for analysis, one male *E. blandingii*, one male *C. guttata* and one female *C. picta*, were depredated during the study. Use of dry dolomite prairie was minimal for all species and will not be considered further.

Macro-habitat use.—Qualitative assessments of wetland macro-habitat use vs. availability differed substantially resulting in variation in mean macro-habitat ranks among species (Table 2.1, Fig. 2.1). In relation to availability, *E. blandingii* and *C. guttata* most often used marshes, whereas *C. picta*, *C. serpentina*, and *S. odoratus* most often use ponds. Among wetland macro-habitats, floodplain was used the least among all species. The most notable differences in mean rankings were between *C. guttata* and the common species; *C. guttata* used mesic dolomite prairie, marsh, and sedge meadow to a greater extent whereas *C. picta*, *C. serpentina*, and *S. odoratus* used river and pond to a greater extent (Fig. 2.1). For mesic dolomite prairie, river, marsh, sedge meadow, and pond macro-habitats, *E. blandingii* ranked intermediately between *C. guttata* and the common species.

The results of the MANOVA also showed that proportional use of macro-habitats differed among species (Wilks' $\lambda = 0.163$, $F_{24, 140} = 3.996$, $P < 0.001$). Post-hoc tests were consistent with qualitative measures of the macro-habitat rankings (Appendix G). Mesic prairie was used more by *C. guttata* than *C. picta*, *C. serpentina*, and *S. odoratus* ($P < 0.012$). Further, *C. guttata* also used sedge meadow more than *S. odoratus* ($P = 0.007$). Both *C. serpentina* and *S. odoratus* used river more than *C. guttata* ($P < 0.045$). Finally, *C. picta*, *C. serpentina*, and *S. odoratus* used pond to a greater extent than *E. blandingii* and *C. guttata* ($P < 0.008$). No significant differences in macro-habitat use were detected between the two rare species or among the three common species.

Macro-habitat niche breadth was broadest for *E. blandingii* (0.56) followed by *C. serpentina* (0.52), *C. guttata* (0.34), *C. picta* (0.32), and *S. odoratus* (0.20). Niche overlap of macro-habitat use was greatest among the common species and lowest between *C. guttata* and

the common species (Table 2.2). *Emydoidea blandingii* shared intermediate levels of overlap with *C. guttata* and *C. serpentina* and lower levels of overlap with *C. picta* and *S. odoratus*.

Micro-habitat use.—Two components were retained from the PCA analysis of micro-habitat variables recorded at turtle radio-locations. The first component (PC1) explained 58% of the variance. The variables loading high on PC1 were vegetation surface cover, vegetation height, and understory canopy cover (positive) and water depth and water surface cover (negative; Table 2.3). The second component (PC2) explained 18% of the variance. Overstory canopy cover (negative) was the only variable to load high on PC2 (Table 2.3). Plots of mean component scores illustrated narrower dimensions of micro-habitat use for *C. guttata*, *C. picta*, and *S. odoratus* compared to *E. blandingii* and *C. serpentina* (Fig. 2.2). Further, separation of *C. guttata* from *C. picta* and *S. odoratus* along gradients of vegetation and water characteristics (PC1 axis) was apparent, whereas micro-habitat use of *E. blandingii* and *C. serpentina* overlapped with multiple other species (Fig. 2.2).

For the ANOVA, PC1, water and vegetation characteristics ($F_{4, 45} = 29.40$, $P < 0.001$), PC2, overstory canopy cover ($F_{4, 45} = 3.93$, $P = 0.008$), and substrate ($F_{4, 45} = 17.14$, $P < 0.001$) differed significantly among species. Post hoc tests revealed that micro-habitat use of *C. guttata* was characterized by shallower water depths, taller vegetation heights, higher vegetation surface cover, greater amount of understory cover, and more organic substrates than all other species ($P \leq 0.016$; Fig. 2.3; see Appendix G). Similarly, micro-habitat use of *E. blandingii* was characterized by shallower water depths, and greater vegetation structure and organic substrates than *C. picta* and *S. odoratus* ($P < 0.001$) but not *C. serpentina*. No differences in water and vegetation or substrate micro-habitat characteristics were detected among the common species.

Micro-habitat use of shoreline tree cover was greater for *S. odoratus* than *E. blandingii* and *C. picta* ($P \leq 0.032$).

The classification tree analysis most strongly differentiated species by PC1 (water and vegetation characteristics) followed by PC2 (shoreline tree cover; Fig. 2.4). Optimal tree size derived from cross-validation and pruning consisted of four terminal nodes, one for each species except *C. serpentina*. Higher PC1 values (≥ 0.39), or use of more highly vegetated micro-habitats with less water (*i.e.* shallow cattail marsh), most strongly differentiated *C. guttata* from all other species. Further, moderate use of micro-habitats with more vegetation and less water (≥ -0.58) differentiated *E. blandingii* from *S. odoratus* and *C. picta*. Lastly, use of micro-habitats with greater shoreline tree cover separated *S. odoratus* from *C. picta*. Substrate was not selected by the "tree" package for tree construction presumably because substrate use was correlated with PC1 and rendered no additional information. The optimal tree had an overall correct classification rate of 0.70 and correctly classified 100% of *C. guttata*, 83% of *E. blandingii*, 0% of *C. serpentina*, 83% of *S. odoratus*, and 83% of *C. picta*. Three *E. blandingii* were misclassified as *C. guttata*. One *S. odoratus* was misclassified as *C. picta* and vice versa. One *C. serpentina* was misclassified as an *S. odoratus* and the remaining six individuals were misclassified as *E. blandingii*. The classification tree demonstrated substantial agreement (*K* statistic = 0.62) of the tree model based on the benchmark range of Landis and Koch (1977).

DISCUSSION

Macro-habitat analysis was useful for identifying coarse patterns of habitat use and partitioning in my study. *Emydoidea blandingii*, *C. guttata*, *C. serpentina*, *S. odoratus*, and *C. picta* are known to inhabit a variety of wetland habitats throughout their ranges but *E. blandingii* and *C.*

guttata are less tolerant of habitat degradation (Ernst and Lovich, 2009). In this study, all species used multiple macro-habitat types, but the rare turtle species, *E. blandingii* and *C. guttata*, most frequently used cattail marsh macro-habitats whereas the common species (*C. picta*, *C. serpentina*, and *S. odoratus*) most frequently used pond macro-habitats. *Emydoidea blandingii* used the highest number of macro-habitat types (N = 7) followed by *C. serpentina* (N = 5) and *C. guttata* (N = 4) whereas *S. odoratus* and *C. picta* used the fewest number of macro-habitats (N = 3). Use of multiple habitat types at a study site has also been documented for other populations of *E. blandingii* and *C. guttata* (Joyal et al., 2001; Edge et al., 2010). In my study, cattail marsh was the most available wetland habitat and was the only macro-habitat used by all species.

The quantitative comparison of macro-habitat use between species revealed that use of mesic prairie, sedge meadow, river, and pond macro-habitats differed between *C. guttata* and common species while only use of pond macro-habitats differed between *E. blandingii* and two common species, *S. odoratus*, and *C. picta*. Similarly, Bury and Germano (2003) found that within turtle communities in Nebraska, *E. blandingii* occurred most often in marshes and small ponds whereas more *C. picta* occurred in lakes and open waters. Although I failed to detect differences in macro-habitat use between *E. blandingii* and *C. guttata*, differences in seasonal patterns of macro-habitat use between these species have been observed in Maine (Joyal et al., 2001). Joyal et al. (2001) reported that use of permanent pools was greater in *E. blandingii* and *C. guttata* used wet meadows whereas *E. blandingii* did not.

I found that species most strongly partitioned micro-habitat along an axis comprised of water depth, water and vegetative surface cover, vegetation height, and understory canopy cover. *Clemmys guttata* and *S. odoratus* displayed a narrower range of use of vegetative and water characteristics compared to the other species; however, differentiation in water and vegetation

micro-habitat use was greatest between *C. guttata* and all common species. Separation of *C. guttata* in micro-habitat use from the other species was also supported by the classification tree analysis. Similarly, water depth and vegetation characteristics were also partitioned in different size classes of juvenile *E. blandingii* in Minnesota (Pappas and Brecke, 1992) and vegetation structure and open water affected habitat selection of adult *E. blandingii* in Ontario (Millar and Blouin-Demers, 2011). Water characteristics such as depth, open water, and velocity have been key determinants of habitat use in other freshwater turtles (Plummer, 1977; Souza and Abe, 1998). Proportion of organic substrates at radio-locations also differentiated habitat use among species in this study; use of organic substrates was highest among *C. guttata* and *E. blandingii*. Similarly, substrate characteristics were shown to be important for differentiating habitat use among species of map turtles, *Graptemys sp*. (Fuselier and Edds, 1994).

Micro-habitat use differentiated species to a greater extent than macro-habitat use indicating that species were using distinct micro-habitats within macro-habitats. For example, no difference in macro-habitat use was detected between the two rare species (both highly used cattail marsh) yet *C. guttata* used shallower wetlands with more vegetation structure and organic substrates than *E. blandingii*. The interior wetlands at my study site contained more organic substrates and likely provided higher quality habitat compared to the peripheral preserve areas that are subjected to flooding and silt deposition by the Des Plaines River. I observed that *C. guttata* and *E. blandingii* most often used these higher quality interior cattail marsh habitats; however, some *E. blandingii* occasionally used peripheral wetlands and shallow areas of the Des Plaines River. For example, three *E. blandingii* (EMBL 7, EMBL 22, & EMBL 36) used the river > 50% of the time whereas *C. guttata* almost never used silted peripheral wetlands and were never observed in the river. Further, *E. blandingii* are obligated to seek refuge and use the

river and surrounding riparian habitats more extensively during years of drought when interior marsh habitat becomes dry (Anthonysamy et al. in review). Similarly, Fuselier and Edds (1994) found that finer scale environmental variables differentiated three *Graptemys* species even though overlap in habitat use was high.

Although *C. picta* and *S. odoratus* exhibited high overlap in macro-habitat use and similar micro-habitat use of vegetation and water characteristics, *S. odoratus* were more apt to use micro-habitats near the shore as they occasionally used mammal excavations and undercuts within the bank. Use of muskrat burrows by *S. odoratus* has also been documented by Ernst (1986). Thus, greater use of shoreline tree cover by *S. odoratus* than *C. picta* is not necessarily a preference for shaded habitats but more likely a preference for a different resource characteristic (*e.g*. foraging, basking, dietary) that is coincidently associated with floodplain habitat such as riparian forest that often bordered macro-habitats used by these species.

Measures of niche breadth and niche overlap also varied among species. Among all species, *E. blandingii* and *C. serpentina* most broadly and similarly used macro- and micro-habitats and maintained a relatively large measure of niche breadth. Further, these two species also demonstrated a considerable amount of niche overlap with the other species in their respective rare and common species groups; *E. blandingii* with *C. guttata* and *C. serpentina* with *C. picta* and *S. odoratus*. Hence, these findings indicated that *E. blandingii* and *C. serpentina* were functioning as habitat generalists. Swihart et al. (2006) also found that *C. serpentina* in Indiana had the greatest niche breadth among a group of eight turtle species including *E. blandingii*, *S. odoratus*, and *C. picta*. Interestingly, in my study, *C. picta* and *S. odoratus* exhibited the narrowest measures of macro-habitat niche breadth, but attained the highest measure of niche overlap (82.9; Table 2.2) and used the most silted and peripheral habitats.

Further, micro-habitat use of water and vegetation structure of these species overlapped substantially with *C. serpentina*. Finally, *C. guttata* demonstrated a narrower but intermediate range of macro-habitat niche breadth compared to the other species; however use of micro-habitat was most divergent for this species and was also restricted to the higher quality, interior wetlands, with organic substrates. These findings suggest that *C. guttata* is a micro-habitat specialist. Nevertheless, my estimates of macro-habitat use and niche breadth measures should be interpreted with caution as these measurements were calculated based on the proportion of available macro-habitats as delineated by me and sample size was limited for some species.

Resource partitioning may result from competition, predation, and physiological constraints, as well as complex interactions among these biological mechanisms (Toft, 1985). In a review of resource partitioning among freshwater turtles, Luiselli (2008) concluded that partitioning was most likely a result of interspecific competition. Competition and aggressive behavior have been documented among emydid turtle species for basking sites (Lovich, 1988; Lindeman, 1999; Cadi and Joly, 2003). In addition, differential survival (Cadi and Joly, 2004) and differential growth in low resource conditions (Aresco, 2010) have been observed between species. In my study, interspecific competition for resources should be greatest among the species with the greatest niche overlap, *C. serpentina*, *S. odoratus*, and *C. picta*; however, I did not observe competitive interactions or aggressive behaviors among turtle species.

Predation is a critical threat to turtles at my study site as one male *E. blandingii*, one male *C. guttata* and one female *C. picta*, were depredated during this study. Turtles exhibit patterns of size-dependent predation with smaller body sizes being more susceptible to predators (Janzen, 1993; Congdon et al., 1993; 1994; Tucker et al., 1999; Janzen et al., 2000). My findings supported this idea in that the second smallest species, *C. guttata*, was the least aquatic and

strictly used micro-habitats with higher amounts of vegetation structure that afforded more protection from predation than more open water habitats. However, the smallest species in this study, and possibly the most aquatic, *S. odoratus*, used deeper wetlands with little to no vegetation cover and overlapped in habitat use with the largest species, *C. serpentina*. Hence, the predation risk/body size association may be influencing habitat use in turtle species at my study site but other factors are probably also contributing to differential habitat use among species.

Habitat partitioning observed in this study is likely related to species-specific traits. The species in this study exhibit variation in traits such as morphometrics, foraging strategies, dietary preferences, and basking habits (see Ernst and Lovich, 2009) that have been shown to influence habitat partitioning in turtles (Plummer, 1977; Vogt, 1981; Williams and Christiansen, 1981; Hart, 1983; Vogt and Guzman, 1988; Lindeman, 2000). Because different habitat types likely vary in food availability, thermal properties, and ease of maneuverability, use of habitat types that optimize fitness should also be expected to differ among species. Compared to *C. guttata*, *S. odoratus* and *C. picta* have evolved morphological characteristics such as extensive toe-webbing that improve aquatic locomotion in deeper, more open water habitats with less vegetation (Ludwig et al., 2007) that helps to explain the strong divergence in habitat use observed between these species. In another scenario, dense cattail stands and shallow wetlands may inhibit foraging in larger species with higher energetic demands (i.e. *C. serpentina*) but may provide optimal refugia and foraging opportunities for small species (i.e. *C. guttata*). *Emydoidea blandingii* and *C. serpentina* tended to use a greater range of habitats than smaller species, and presumably because of their larger body size, likely exploited larger-sized dietary items compared to the smaller species (Costa et al., 2008). In addition, frequency and method (e.g. aerial, surface, land) of basking varies for the species in this study (Ernst and Lovich, 2009; pers. obs.); therefore

species may have also used micro-habitat features that were conducive for species-specific basking habits.

Conservation Implications.—Species-habitat relationships and dimensions of habitat partitioning in sympatric turtle communities are important components for the conservation and management of freshwater turtles. I emphasize the need to assess fine-scale micro-habitat use because species with high overlap in macro-habitat use showed distinct differences when micro-habitat variables were included. Additionally, management efforts for sympatric species of conservation concern should be considered for each species independently. For example, the two rare species demonstrated different overall patterns of habitat use; *C. guttata* was more of a habitat specialist whereas *E. blandingii* was more of a habitat generalist. Species that are habitat specialists are predicted be less tolerant of wetland loss and degradation than those that are habitat generalists (Henle et al., 2004; Ewers and Didham, 2006). Compared to the other turtle species *C. guttata* is most vulnerable to degradation of high quality interior shallow cattail marsh, sedge meadow, and mesic dolomite prairie from siltation caused by flooding of the Des Plaines River. Illinois populations of *C. guttata* represent the western-most periphery of this species' distribution which further increases these populations' vulnerability to habitat fragmentation (Swihart et al., 2006). For *E. blandingii*, these findings are surprising as this species is threatened throughout its range due to habitat loss (Ernst and Lovich, 2009); however, *E. blandingii* is highly vagile and capable of long-distance movements (Rowe and Moll, 1991; Sexton, 1995; Piepgras and Lang, 2000; Joyal et al., 2001, Chapter One) that allow it to access a greater number of wetlands such as the river and peripheral pond habitats in my study. These

findings suggest that multiple macro-habitat types and wide variation in water and vegetation micro-habitat characteristics are necessary to support a diverse freshwater turtle community.

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LITERATURE CITED (Formatted for the Journal Copeia)

Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74:1313-1325.

Aresco, M. J. 2010. Competitive interactions of two species of freshwater turtles, a generalist omnivore and an herbivore, under low resource conditions. Herpetologica 66:259-268.

Bury, R. B., and D. J. Germano. 2003. Differences in habitat use by Blanding's turtles, *Emydoidea blandingii*, and painted turtles, *Chrysemys picta*, in the Nebraska Sandhills. American Midland Naturalist 149:241-244.

Cadi, A., and R. Joly. 2003. Competition for basking places between the endangered European pond turtle (*Emys orbicularis galloitalica*) and the introduced red-eared slider (*Trachemys scripta elegans*). Canadian Journal of Zoology 81:1392-1398.

Cadi, A., and R. Joly. 2004. Impact of the introduction of the red-eared slider (*Trachemys scripta elegans*) on survival rates of the European pond turtle (*Emys orbicularis*). Biodiversity and Conservation 13:2511-2518.

Congdon, J. D., A. E. Dunham, and R. C. van Loben Sels. 1993. Delayed sexual maturity and demographics of Blanding's turtles (*Emydoidea blandingii*): Implications for conservation and management of long-lived organisms. Conservation Biology 7:826-833.

Congdon, J. D., A. E. Dunham, and R. C. van Loben Sels. 1994. Demographics of common snapping turtles *(Chelydra serpentina)*: Implications for conservation and management of long-lived organisms. American Zoologist 34:397-408.

Costa, G. C., L. J. Vitt, E. R. Pianka, D. O. Mesquita, and G. R. Colli. 2008. Optimal foraging constrains macroecology patterns: body size and dietary niche breadth in lizards. Global Ecology and Biogeography 17:670-677.

Cromsigt, J. P. G. M., and H. Olff. 2006. Resource partitioning among savanna grazers mediated by local heterogeneity: An experimental approach. Ecology 87:1532-1541.

De'ath, G., and K. E. Fabricius. 2000. Classification and regression trees: A powerful yet simple technique for ecological data analysis. Ecology 81:3178-3192.

Dellinger, R. L., P. Bohall Wood, P. D. Keyser, and G. Seidel. 2007. Habitat partitioning of four sympatric thrush species at three spatial scales on a managed forest in West Virginia. The Auk 124:1425-1438.

Edge, C. B., B. D. Steinberg, R. J. Brooks, and J. D. Litzgus. 2010. Habitat selection by Blanding's turtles (*Emydoidea blandingii*) in a relatively pristine landscape. Ecoscience 17:90-99.

Ernst, C. H. 1986. Ecology of the turtle, *Sternotherus odoratus*, in southeastern Pennsylvania. Journal of Herpetology 20:341-352.

Ernst, C. H., and J. E. Lovich. 2009. Turtles of the United States and Canada. 2nd edition. John Hopkins University Press, Baltimore, Maryland, USA.

Ewers, R. M., and R. K. Didham. 2006. Confounding factors in the detection of species responses to habitat fragmentation. Biological Review 81:117-142.

Feinsinger, P., and E. E. Spears. 1981. A simple measure of niche breadth. Ecology 62:27-32.

Fuselier, L., and D. Edds. 1994. Habitat partitioning among three sympatric species of map turtles, genus *Graptemys*. Journal of Herpetology 28:154-158.

Hart, D. R. 1983. Dietary and habitat shift with size of red-eared turtles (*Pseudemys scripta*) in a southern Louisiana population. Herpetologica 39:285-290.

Henle, K., D. B. Lindenmayer, C. R. Margules, D. A. Saunders, and C. Wissel. 2004. Species survival in fragmented landscapes: Where are we now? Biodiversity and Conservation 13:1-8.

Janzen, F. J. 1993. An experimental analysis of natural selection on body size of hatchling turtles. Ecology 74:332-341.

Janzen, F. J., J. K. Tucker, and G. L. Paukstis. 2000. Experimental analysis of an early life-history stage: Selection on size of hatchling turtles. Ecology 81:2290-2304.

Joyal, L. A., M. McCollough, and M. L. Hunter Jr. 2001. Landscape ecology approaches to wetland species conservation: a case study of two turtle species in southern Maine. Conservation Biology 15:1755-1762.

Kiviat, E. 1997. Blanding's turtle habitat requirements and implications for conservation in Dutchess County, New York, p. 377-382. *In*: Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles—An International Conference. J. van Abbema (ed.). New York Turtle and Tortoise Society, New York, USA.

Krebs, C. J. 1989. Ecological Methodology. Harper Collins Publishers Inc., New York, New York, USA.

Landis, J. R., and G. G. Koch. 1977. The measurement of observer agreement for categorical data. Biometrics 33:159-174.

Lindeman, P. V. 1999. Aggressive interactions during basking among four species of emydid turtles. Journal of Herpetology 33:214-219.

Lindeman, P. V. 2000. Resource use of five sympatric turtle species: effects of competition, phylogeny, and morphology. Canadian Journal of Zoology 78:992-1008.

Lovich, J. 1988. Aggressive basking behavior in eastern painted turtles (*Chrysemys picta picta*). Herpetologica 44:197-202.

Ludwig, M., M. Auer, and U. Fritz. 2007. Phalangeal formulae of geoemydid terrapins (*Batagur*, *Callagur*, *Hardella*, *Heosemys*, *Kachuga*, *Orlitia*, *Pangshura*, *Rhinoclemmys*) reflect distinct modes of life. Amphibia-Reptilia 28:574-576.

Luiselli, L. 2006. Resource partitioning and interspecific competition in snakes: the search for general geographical and guild patterns. Oikos 114:193-211.

Luiselli, L. 2008. Resource partitioning in freshwater turtle communities: A null model meta-analysis of available data. Acta Oecologica 34:80-88.

Marchand, M. N., and J. A. Litvaitis. 2004. Effects of habitat features and landscape composition on the population structure of a common aquatic turtle in a region undergoing rapid development. Conservation Biology 18:758-767.

Millar, C.S., and G. Blouin-Demers. 2011. Spatial ecology and seasonal activity of Blanding's turtles (*Emydoidea blandingii*) in Ontario, Canada. Journal of Herpetology 45:370-378.

Mitchell, J. C., and M. W. Klemens. 2000. Primary and secondary effects of habitat alteration, p. 5–32. *In*: Turtle Conservation. M. W. Klemens (ed.). Smithsonian Institution Press, Washington D.C., USA.

Morrison, M. L., B. G. Marcot, and R. W. Mannan. 2006. Wildlife-Habitat Relationships: Concepts and Applications 3rd Edition. Island Press, Washington D.C., USA.

Pacala, S., and J. Roughgarden. 1982. Resource partitioning and interspecific competition in two two-species insular *Anolis* lizard communities. Science 217:444-446.

Pappas, M. J. and B. J. Brecke. 1992. Habitat selection of juvenile Blanding's turtles, *Emydoidea blandingii*. Journal of Herpetology 26:233-23.

Piepgras, S. A., and J. W. Lang. 2000. Spatial ecology of Blanding's turtle in central Minnesota. Chelonian Conservation and Biology 3:589-601.

Plummer, M. V. 1977. Activity, habitat, and population structure in the turtle, *Trionyx muticus*. Copeia 1977:431-440.

Renkonen, O. 1938. Statistisch-ökologische Untersuchungen über die terrestrische käferwelt der finnischen bruchmoore. Annales Botanici Societatis Zoologicae Botanicae Fennicae Vanamo 6:1-231.

Robertson, C. R., S. C. Zeug, and K. O. Winemiller. 2008. Associations between hydrological connectivity and resource partitioning among sympatric gar species (Lepisosteidae) in a Texas river and associated oxbows. Ecology of Freshwater Fish 17:119-129.

Ross, D. A., and R. K. Anderson. 1990. Habitat use, movements, and nesting of *Emydoidea blandingii* in central Wisconsin. Journal of Herpetology 24:6-12.

Rowe, J. W., and E. O. Moll. 1991. A radiotelemetric study of activity and movements of the Blanding's turtle (*Emydoidea blandingii*) in northeastern Illinois. Journal of Herpetology 25:178-185.

Schoener, T. W. 1974. Resource partitioning in ecological communities. Science 185:27-39.

Sebastiá, M-T. 2004. Role of topography and soils in grassland structuring at the landscape and community scale. Basic and Applied Ecology 5:331-346.

Sexton, O. J. 1995. Miscellaneous comments on the natural history of Blanding's turtle (*Emydoidea blandingii*). Transactions of the Missouri Academy of Science 29:1-13.

Souza, F. L., and A. S. Abe. 1998. Resource partitioning by the neotropical freshwater turtle, *Hydromedusa maximiliani*. Journal of Herpetology 32:106-112.

Swihart, R. K., J. J. Lusk, J. E. Duchamp, C. E. Rizkalla, and J. E. Moore. 2006. The roles of landscape context, niche breadth, and range boundaries in predicting species responses to habitat alteration. Diversity and Distributions 12:277-287.

Toft, C. A. 1985. Resource partitioning in amphibians and reptiles. Copeia 1985:1-21.

Tucker, J. K., N. I. Filoramo, and F. J. Janzen. 1999. Size-biased mortality due to predation in a nesting freshwater turtle, *Trachemys scripta*. American Midland Naturalist 141:198-203.

Vogt, R. C. 1981. Food partitioning in three sympatric species of map turtle, genus *Graptemys* (Testudinata, Emydidea). American Midland Naturalist 105:102-111.

Vogt, R. C., and S. G. Guzman. 1988. Food partitioning in a neotropical freshwater turtle community. Copeia 1988:37-47.

Williams, T. A., and J. L. Christiansen. 1981. The niches of two sympatric softshell turtles, *Trionyx muticus* and *Trionyx spiniferus*, in Iowa. Journal of Herpetology 15:303-308.

TABLES

Table 2.1 Proportions of available macro-habitat used by ten *C. guttata* (CLGU), 18 *E. blandingii* (EMBL), seven *C. serpentina* (CHSE), nine *S. odoratus* (STOD), and six *C. picta* (CHPI) radio-located at a preserve in Will County, Illinois during 2006.

Proportion Available		Proportion Used				
Macro-habitat		CLGU	EMBL	CHSE	STOD	CHPI
Mesic Prairie	0.11	0.06	0.01	0.00	0.00	0.00
Dry Prairie	0.25	0.01	0.01	0.00	0.00	0.00
Floodplain	0.20	0.00	0.09	0.10	0.00	0.00
River	0.16	0.00	0.21	0.15	0.12	0.07
Marsh	0.23	0.81	0.51	0.23	0.06	0.22
Sedge Meadow	0.04	0.12	0.06	0.03	0.00	0.00
Pond	0.02	0.00	0.10	0.50	0.82	0.70

Table 2.2 Macro-habitat niche overlap values for ten *C. guttata* (CLGU), 18 *E. blandingii* (EMBL), seven *C. serpentina* (CHSE), nine *S. odoratus* (STOD), and six *C. picta* (CHPI) radio-located at a preserve in Will County, Illinois during 2006. Measures of niche breadth for each species are underlined and appear on the diagonal.

Species	CLGU	EMBL	CHSE	STOD	CHPI
CLGU	0.34				
EMBL	59.7	0.56			
CHSE	25.5	59.5	0.52		
STOD	5.7	28.0	67.9	0.20	
CHPI	22.8	39.3	79.3	82.9	0.32

Table 2.3 The coefficients and loadings on principal component one (PC1) and two (PC2) retained for micro-habitat use variables collected for ten *C. guttata*, 18 *E. blandingii*, seven *C. serpentina*, nine *S. odoratus*, and six *C. picta* radio-located at a preserve in Will County, Illinois during 2006.

	Loadings		Coefficients	
Variable	PC1	PC2	PC1	PC2
% Water Surface Cover	-0.944	-0.083	-0.293	0.330
% Vegetation Surface Cover	0.933	0.127	-0.305	0.094
Vegetation Height (cm)	0.769	0.437	0.294	-0.053
Water Depth (cm)	-0.745	0.229	0.167	-0.734
% Understory Canopy Cover	0.619	0.571	0.110	0.388
% Overstory Canopy Cover	0.062	-0.831	0.184	0.246

FIGURES

Fig. 2.1 Mean wetland macro-habitat rankings derived using compositional analysis for ten *C. guttata* (CLGU), 18 *E. blandingii* (EMBL), seven *C. serpentina* (CHSE), nine *S. odoratus* (STOD), and six *C. picta* (CHPI) radio-located at a preserve in Will County, Illinois during 2006.

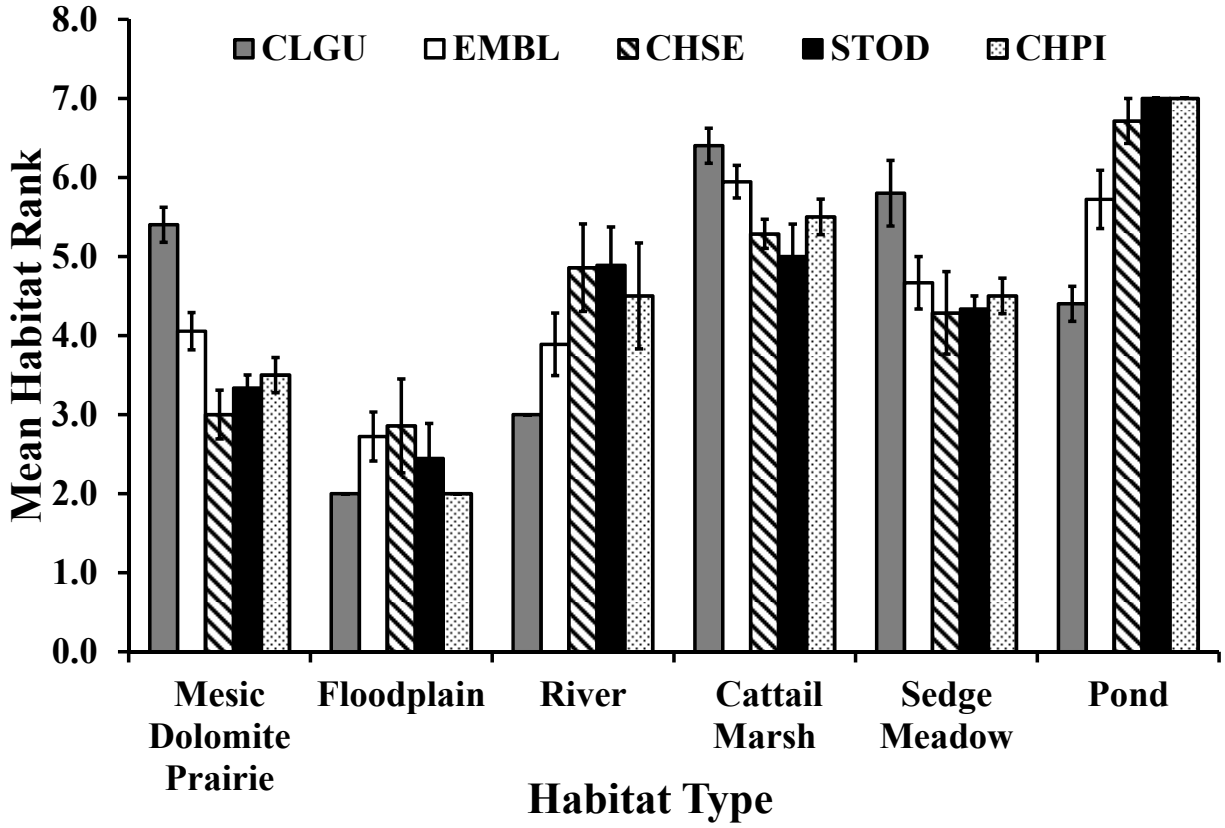


Fig. 2.2 Plot of mean pricipal component scores (PC1 vs PC2) calculated from micro-habitat variables collected at radio-locations for ten *C. guttata* (CLGU), 18 *E. blandingii* (EMBL), seven *C. serpentina* (CHSE), nine *S. odoratus* (STOD), and six *C. picta* (CHPI) radio-located at a preserve in Will County, Illinois during 2006. Polygons connect outermost points and illustrate relative micro-habitat niche breadth size and niche breadth overlap among species.

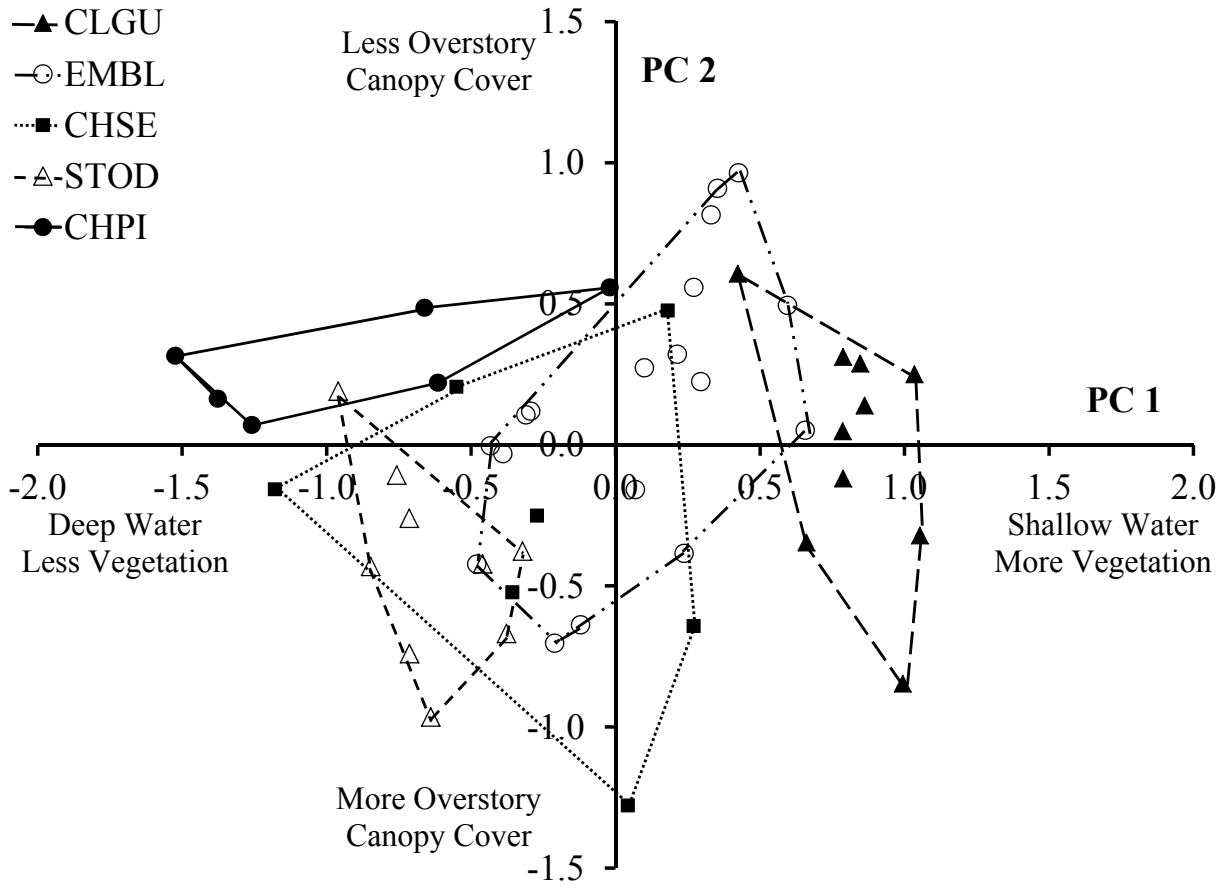


Fig. 2.3 Mean micro-habitat values and standard errors of A) proportion of water surface cover, B) proportion of vegetation surface cover, C) vegetation height, D) water depth, E) proportion of understory canopy cover, G) proportion of overstory canopy cover and F) proportion of locations having organic substrates for ten *C. guttata* (CLGU), 18 *E. blandingii* (EMBL), seven *C. serpentina* (CHSE), nine *S. odoratus* (STOD), and six *C. picta* (CHPI) radio-located at a preserve in Will County, Illinois during 2006.

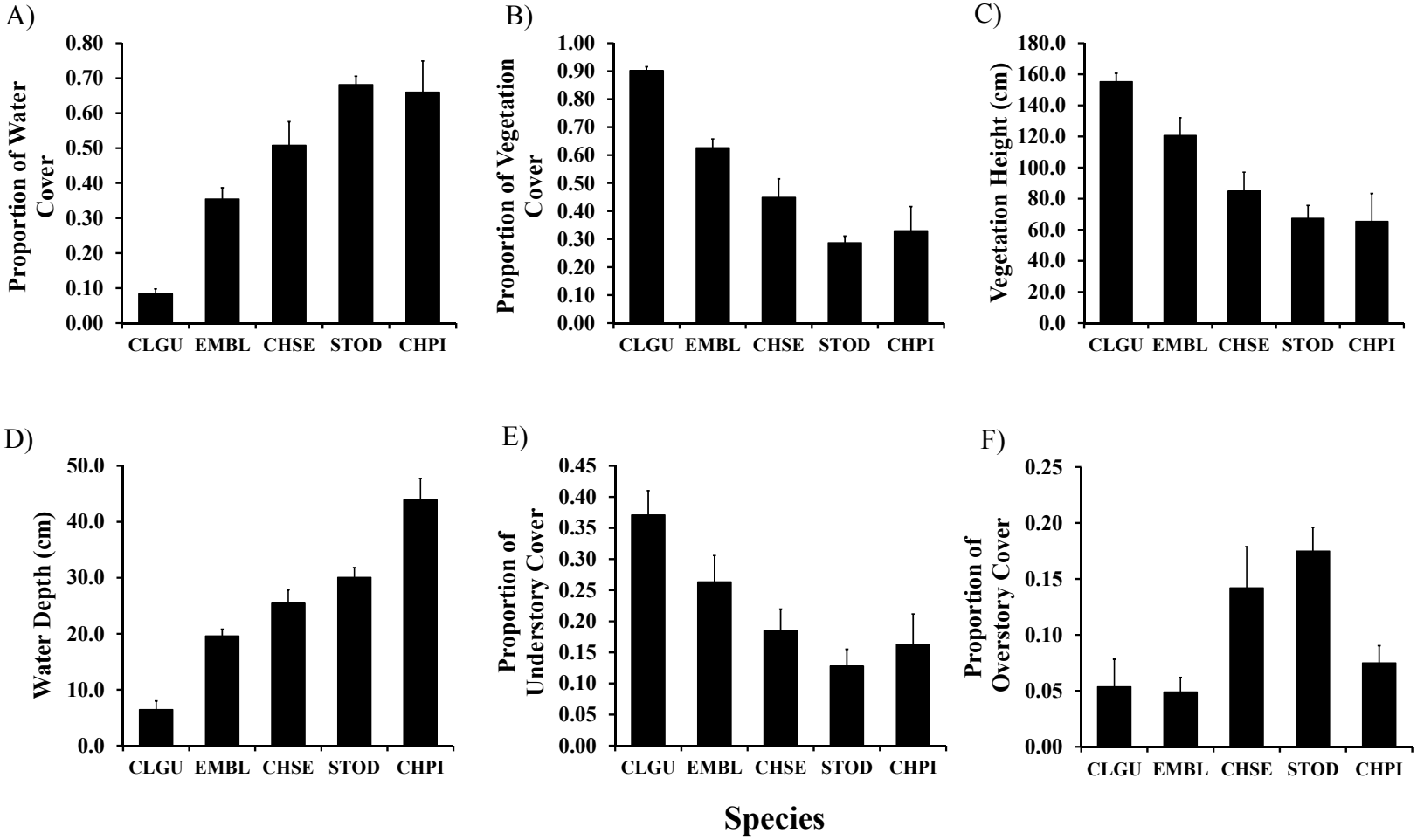


Fig. 2.3 (cont.)

F)

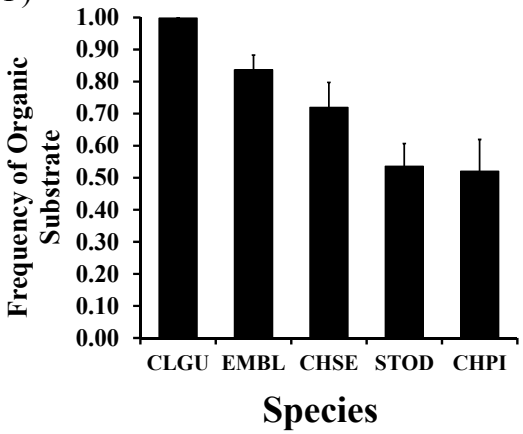
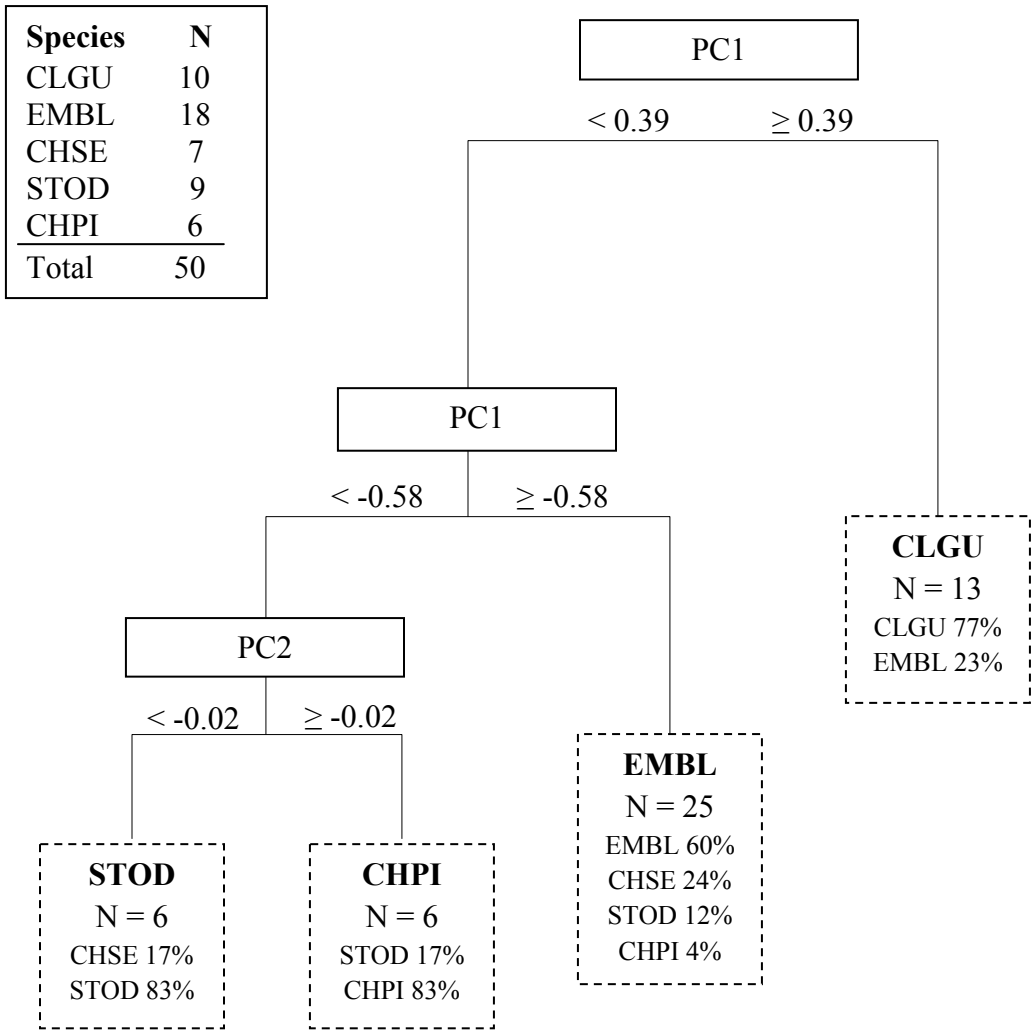

Frequency of Organic Substrate
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
CLGU
EMBL
CHSE
STOD
CHPI
Species

Fig. 2.4 Classification tree based on micro-habitat measures collected from radio locations for *C. guttata* (CLGU), *E. blandingii* (EMBL), *C. serpentina* (CHSE), *S. odoratus* (STOD), and *C. picta* (CHPI) radio-located at a preserve in Will County, Illinois during 2006. Increasing positive values for PC1 represent microhabitats with less water and more vegetation. Increasing positive values for PC2 represent microhabitats with less shoreline overstory canopy cover. The length of the vertical line below each split indicates variable importance in the separation. Sample size and species composition of resulting classification for each node is shown.



CHAPTER 3

COMPARISON OF POPULATION GENETIC STRUCTURE AMONG THREE SYMPATRIC FRESHWATER TURTLE SPECIES

INTRODUCTION

Anthropogenic landscape fragmentation results in small, isolated, remnant populations vulnerable to decreased levels of genetic diversity via genetic drift and reduced gene flow (Spradling *et al*. 2010, Reed *et al*. 2011). In many cases, this is compounded by increased levels of inbreeding. Loss of genetic diversity and inbreeding can lead to reduced fitness from the expression of deleterious genes and compromise survival, fertility, and general health (Westemeier *et al*. 1998) as well as impair the ability of populations to adapt to a changing environment (Willi *et al*. 2006).

Comparing genetic structure in sympatric species of similar taxa that vary in life history and ecological traits improves our understanding of how species respond to fragmentation (Steele *et al.* 2009, DiLeo *et al.* 2010, Goldberg and Waits 2010). Variation in species-specific traits such as dispersal ability, reproductive effort, and ecological specialization influences genetic processes among species. For example, three sympatric snake species that varied in body size and vagility exhibited marked differences in gene flow and genetic population structure in a subdivided island/mainland system (King and Lawson 2001). In turtles, lack of dispersal can result in the loss of gene flow between populations (Kou and Janzen 2004, Richtsmeier *et al*. 2008), and might ultimately lead to reduced genetic variation (Gray 1995, Parker and Whiteman 1993).

In this study, I examined genetic diversity and genetic divergence in three sympatric freshwater turtle species sampled from three fragmented and one intact site in Illinois. The

species represent two families; Emydidae [Blanding's turtle (*Emydoidea blandingii*), painted turtle (*Chrysemys picta*)] and Chelydridae [common snapping turtle (*Chelydra serpentina*)] and are of different conservation status (Ernst & Lovich 2009). These three species vary in a number of characteristics such as life history traits (Congdon *et al*. 1993, Congdon *et al*. 1994, Congdon *et al*. 2003, McGuire 2011, McGuire *et al.* 2011), vagility (Chapter One), and habitat use (Chapter Two), which can influence gene flow and loss of genetic diversity in a fragmented landscape. For example, compared to *C. picta* and *C. serpentina*, *E. blandingii* has lower reproductive output (clutch size, annual clutch frequency) as well as a longer generation time (Congdon *et al*. 1993, Congdon *et al*. 1994, Congdon *et al*. 2003, McGuire 2011, McGuire *et al.* 2011). In addition, *C. picta* and *C. serpentina* are widely distributed and abundant throughout much of the United States, whereas *E. blandingii* has a more restricted distribution and is considered rare throughout much of its range (Ernst & Lovich 2009).

I employed microsatellite DNA markers in three turtle species across four study sites to investigate the effects of fragmentation and species-specific differences in ecological/ life history traits on and genetic diversity and genetic divergence. I tested the following predictions: 1) All species will have decreased levels of genetic diversity in the fragmented sites compared to the intact site; 2) In the fragmented sites, *E. blandingii* will have lower levels of genetic diversity and higher levels of genetic divergence within and among species compared to the common species (*C. picta* and *C. serpentina*); 3) All species from the fragmented sites will show evidence of recent population bottlenecks; 4) Future levels of genetic diversity would be lower for *E. blandingii* than *C. picta* or *C. serpentina*. Predictions 2 and 4 stem from the lower reproductive output, longer generation time, and lower population size of *E. blandingii* (Ernst and Lovich, 2009). Finally, because females of many species of turtles are philopatric to nesting locations

(Congdon *et al*. 1983, Congdon *et al*. 1987, Valenzuela & Janzen 2001, Rowe *et al*. 2005), I predict lower levels of gene flow in females compared to males, for all species.

METHODS

Study sites

My study was conducted within the Lower Des Plaines River Valley (LDPRV) in northeastern Illinois. This area was once a prairie-dominated landscape (Bowles & McBride 2001) composed of semi-contiguous prairie-wetland matrices that allowed turtles to freely disperse along the river corridor without anthropogenic impediment. However, since the early 1800's there have been drastic environmental changes as a result of European settlement and associated anthropogenic alterations. Gradually, over the past 150 years, agriculture, shipping canals, railways, roadways, quarries, industrial parks, and towns have come to dominate the landscape. Remaining natural areas are effectively isolated from one another except for their connection along the narrow Des Plaines River riparian zone.

Turtles were sampled at four sites along the LDPRV; three small, isolated sites in Will County (Will 1-3); and one large, more intact site in Grundy County (Grundy; Fig. 3.1). The sites are located along a 40 km stretch of the Des Plaines River. Will 1 (95 ha) and Will 2 (188 ha) are separated by 1 km, and Will 2 and Will 3 (124 ha) by 6 km. The Grundy site (1247 ha) is the largest remnant prairie in Illinois, and is located near the confluence of the Des Plaines River and Kankakee rivers, approximately 34 km by river southwest of Will 3. The LDPRV sites are composed of a prairie-wetland matrix that is inhabited by a diverse turtle assemblage with the southernmost site (Grundy) providing habitat for large and presumably genetically diverse turtle populations (Banning *et al.* 2006, Dreslik *et al*. 2010, Dreslik *et al.* 2011).

DNA extraction

I collected tissue samples from adult *E. blandingii*, *C. picta*, and *C. serpentina,* captured during trapping and radio-telemetry surveys conducted from 2004 – 2009. Blood (0.1-0.3 cc) was collected from the sub-carapacial sinus (Fisher 2003) of live turtles using a 25 ½ gauge needle and 1 cc syringe. Tail clips and liver tissue were taken from dead turtles found on roads at the study sites. I preserved tissues in 95% ethanol or Queen's lysis buffer (Seutin *et al*. 1991) and stored samples at -80°C until DNA extraction. I extracted whole genomic DNA from tissue samples using the Qiagen DNeasy Blood & Tissue Kit (QIAGEN INC.) following the manufacturers protocol, with the exception that I digested tissue samples overnight in the proteinase K solution.

DNA amplification, linkage disequilibrium, and Hardy-Weinberg equilibrium

For *E. blandingii* and *C. picta*, I screened 21 microsatellite loci using primers developed for *E. blandingii* ([BTCA9; Libants *et al*. 2004] [Eb09, Eb17, Eb19; Osentoski *et al*. 2002]) and bog turtle (*Glyptemys muhlenbergii*; *Gmu*D21, *Gmu*D55, *Gmu*D70, *Gmu*D87, *Gmu*D90, *Gmu*D93, *Gmu*D121, *Gmu*B08, *Gmu*A18, *Gmu*A19, *Gmu*A32; King and Julian 2004). For *C. serpentina*, I screened nine microsatellite loci using primers developed for alligator snapping turtle (*Macrochelys temminckii*; *Mte*A105, *Mte*B103, *Mte*C1, *Mte*C112, *Mte*D2, *Mte*D9, *Mte*D106, *Mte*D109, *Mte*D111; Hackler *et al*. 2007). Based on the results of initial primer testing, I grouped favorable primers into multiplex panels (groups of fluorescent dye-labeled primers that successfully amplify target DNA regions under similar conditions using polymerase chain reaction [PCR)]). I determined that 15 primers amplified target DNA in *E. blandingii* and *C. picta* samples. I grouped those primers into four multiplex panels (Appendix H). Seven

primers amplified target DNA in *C. serpentina* samples and were grouped into two multiplex panels (Appendix H).

I conducted PCR for all panels in 10 µl volumes using 0.2-0.9 mM of each primer, 1X GoTaq Flexi buffer, 2.5-5.0 mM $MgCl_2$, 0.2 mM dNTP, 0.5-1.0 U of Flexi GoTaq DNA polymerase (Promega), and 1.0 µl template DNA. Multiplex reactions were carried out under the following conditions: initial denaturation at 95 ^oC for 3 min, followed by 15 cycles of 95 ^oC for 45 s, a panel-specific annealing temperature for 45 s, and a 72 ^oC elongation for 30 s, followed by an additional 25 cycles of 95 ^oC for 30 s, a panel-specific annealing temperature for 30 s, and a 72 ^oC elongation for 15 s, followed by a final extension at 72 ^oC for 20 min.

Fragment analysis of resulting PCR products was carried out on an automated Applied Biosystems (ABI) Prism 3730xl sequencer at the W. M. Keck Center at the University of Illinois, Champaign. An internal size standard (Liz 500) was run with each sample and I scored alleles using GENEMAPPER 4.1 software (ABI). Within each species, I identified possible null alleles, large allele dropout, and scoring errors due to stutter peaks using MICRO-CHECKER 2.2.3 (van Oosterhout *et al*. 2004). For each species at each study site I tested for linkage disequilibrium (Markov Chain parameters: 10000 dememorisation steps, 500 batches, 5000 iterations) between all pairs of loci and tested for departures from Hardy-Weinberg equilibrium (HWE) for each locus using exact tests in GENEPOP 4.0 (Rousset 2008). Sequential Bonferroni correction was used to control for multiple comparisons (Rice 1989).

Genetic diversity within species across sites

For each species and site, I estimated allele frequencies, observed heterozygosity (H_o), expected heterozygosity (H_e), and inbreeding coefficients (F_{IS}) using GENALEX 6.41 (Peakall &

Smouse 2006). In HP-RARE v. June-6-2006 (Kalinowski 2005) I calculated allelic richness (A_R) and private allelic richness (P_{AR}), measures of genetic diversity derived from rarefaction and corrected for variable sample sizes. I used a paired Wilcoxon rank sum test in SPSS 17.0 (SPSS Inc. Chicago, Illinois) to test for differences in the amount of genetic diversity (*i.e.* A_R, P_{AR}, H_o) in each species between the intact Grundy County and each of the fragmented Will County sites.

Genetic divergence within species

To assess genetic divergence among sites, I conducted pairwise F_{ST} analysis (999 permutations, interpolated missing data) and an analysis of molecular variance (AMOVA) in GENALEX. In addition, I used the Bayesian clustering method implemented in program STRUCTURE 2.3.3 (Pritchard *et al*. 2000) to further assess genetic structure among sampling locations. I tested two simulations, one without and one with prior sampling location information (LOCPRIOR) to assist clustering and assess levels of migration between sites (Pritchard *et al*. 2000). For remaining parameters, I selected the admixture ancestry model and the correlated allele frequency model parameter options for both simulations. Five replicate analyses were run for K values ranging from 1 to 4 (number of sampling locations) using a specified burn-in length of 500,000 iterations followed by 1,000,000 Markov Chain Monte Carlo (MCMC) replicates. I assumed no substructure in the intact Grundy County site. I determined the optimal number of clusters for each simulation by using the online software STRUCTURE HARVESTER 0.6.1 (Earl & vonHoldt 2011) to calculate ad hoc statistic 'ΔK' described by Evanno *et al*. (2005).

Genetic divergence among species

To compare genetic divergence among the three species, I averaged two standardized measures of genetic divergence G'_{ST} (Hedrick 2005, Ryman & Leimar 2009) and D_{est} (Jost 2008) for each species across sites. These measures allow for comparisons between species with different numbers of and variability among loci (Hedrick 2005, Jost 2008) and have been used in recent studies to compare divergence in sympatric species of salamanders (Steele *et al*. 2009) and bumble bees (Lozier *et al*. 2011). Both G'_{ST} and D_{est} were estimated with 95% confidence intervals (CIs) using 1000 bootstrap repetitions in the R package "DEMEtics" (Gerlach *et al*. 2010) implemented in R software 2.13.2. Significance was determined by the non-overlap of 95% CIs.

Sex-biased dispersal

Previous studies have documented nest-site fidelity of adult females in the turtle species used in this study (Congdon *et al*. 1983; Congdon *et al*. 1987; Valenzuela and Janzen 2001; Rowe *et al*. 2005). I assessed the presence of sex-biased gene flow among sites using the biased dispersal option in FSTAT V. 2.9.3.2 (Goudet 1995). I tested for differences in the mean assignment indices (*m*AIc), the variance in assignment indices (*v*AIc), F_{ST}, and F_{IS} between males and females (1000 permutations; Goudet 2002). To compare the potential impacts of fragmentation on gene flow patterns, I conducted tests for two scenarios; across all sites and across fragmented sites only. If males are dispersing more than females and sites consist of both resident and migrant males but mostly resident females, then males should have a negative *m*AIc whereas females should have a positive *m*AIc (Goudet *et al*. 2002). In addition, males should exhibit larger *v*AIc values than females and pairwise F_{ST} among sites should be greater for

females than males. Finally, measures of F_{IS} should be higher in males because sites should consist of both resident and migrant males, indicating a heterozygote deficiency (*i.e.* Wahlund effect; Goudet *et al*. 2002).

Bottlenecks

I examined sites for loss of genetic diversity using two different tests in the program BOTTLENECK 1.2.02 (Piry *et al*. 1999). For historically recent bottlenecks (0.2 - 4 N_e generations), I tested whether the observed heterozygosity was higher than expected under the assumption of mutation-drift equilibrium (Luikart & Cornuet 1998) using the two-phase mutation model (TPM) option. This model consists of a combination of single step and multiple step mutations, as recommended for microsatellite data (Di Rienzo *et al*. 1994, Piry *et al*. 1999) and the TPM mutation pattern has been observed in microsatellites documented in sea turtles (Hoekert *et al*. 2002). To test for historic population declines, I used the Wilcoxon sign test (Cornuet & Luikart 1996, Luikart & Cornuet 1998) to test for an excess of heterozygosity at each study site. The TPM model consisted of 95% single steps and 5% multiple steps with variance for mutation size set to 12 as recommended by Piry *et al*. (1999). Further, I tested for the effects of alterations in these parameters in the model by varying the frequency of single step (98%, 90%) and multiple step mutations (2%, 10%) in two additional scenarios (Rivalan *et al*. 2006). To test for more recent population declines (few dozen generations), I used a qualitative mode shift test (Luikart *et al.* 1998) to evaluate shifts in allele frequencies from loss of rare alleles. The input file for *C. picta* failed to run in program BOTTLENECK when the data set included the locus *Gmu*D70; thus this locus was excluded from Wilcoxon sign test and mode-shift test for this species.

I also assessed historic bottleneck effects using the M-ratio method of Garza & Williamson (2001). This method is used to detect bottlenecks by comparing the mean ratio of the number of alleles to the range in allele size under the TPM model and essentially measures the "gaps" between the largest and smallest allele, which would be larger in sites that had experienced genetic drift. Loss of alleles in a bottlenecked population would produce a smaller ratio compared to a population under mutation-drift equilibrium (Garza & Williamson 2001). I tested for significance in M values for each locus across each site by comparing estimated values of M to critical values of M (M_c) using the software programs M_P_VAL.EXE and CRITICAL_M.EXE (Garza & Williamson 2001). Both programs require three input parameters to estimate M values: percentage of single-step mutations (p_s), average size of non-stepwise mutations (Δ_g), and a population specific θ ($4N_e u$) where N_e is effective population size and u is the mutation rate. I used $p_s = 0.9$ and $\Delta_g = 3.5$ as suggested by Garza & Williamson (2001) but because pre-bottleneck population size was unknown, I tested θ for values ranging from 0.1 to 10 (*e.g.* Busch *et al.* 2007, Parga *et al*. 2012).

Future loss of genetic diversity

To predict and compare future loss of genetic variation among species from genetic drift, I used the program BOTTLESIM v.2.6 (Kuo & Janzen 2003) to simulate levels of allelic diversity and heterozygosity remaining over a 300-year period. This program includes a scenario for long-lived species with overlapping generations (*i.e.* turtles) and requires input of life history trait and demographic parameters such as longevity, age of maturity, mating system, population size, and sex ratios (Kuo & Janzen 2003, 2004). I conducted two simulations using current estimates of population size and sex ratios from mark-recapture data collected for *E. blandingii*, *C. picta*, and

C. serpentina at the Will 3 site (see Fig. 3.3, Banning *et al.* 2006). Demographic parameters remained constant for the 300-year duration. Estimates of longevity and ages of maturity for each species were obtained from estimates reported from long-term studies and datasets (Congdon *et al*. 1993, Congdon *et al.* 1994, Congdon *et al.* 2003, McGuire 2011). For the first simulation I selected the random mating system option, and for the second simulation I selected a skewed mating system option (*i.e*. one male sires all offspring each year) to model potential effects of demographic stochasticity.

RESULTS

Amplification success, linkage disequilibrium, and Hardy-Weinberg equilibrium

Emydoidea blandingii

I successfully genotyped 110 adult *E. blandingii* for 14 of the 15 microsatellite loci (Table 3.1). One individual was only genotyped for 12 loci but was included in analyses. One locus (*Gmu*D90) could not be confidently scored because of inconsistent amplification and was excluded from analyses. Presence of homozygous excess was detected at the Will 1 site for *Gmu*A18 and at Grundy site for *Gmu*D70. Nevertheless, the occurrence of null alleles at these loci is unlikely because tests of known mother-offspring genotype comparisons during parentage analyses failed to produce any genotype mismatches (*i.e*. indication of null alleles; see Chapter Five). Deviations from HWE were not detected after sequential Bonferroni correction (Table 3.2). Significant linkage disequilibrium ($P = 0.0004$; adjusted $\alpha = 0.0006$) was detected between *Gmu*D121 and *Gmu*D21 for the Grundy site after Bonferroni correction but these loci were retained for analyses because the significant relationship was restricted to one site.

Chrysemys picta

I successfully genotyped 331 adult *C. picta* for eight of the 15 microsatellite loci (Table 3.1). Eighteen individuals were genotyped for 6-7 loci and were included in analyses. One of the successful loci (Eb17) was fixed for the Grundy County site but polymorphic for the Will County sites. The seven remaining loci were excluded from analyses for various reasons: *Gmu*D90 and Eb19 could not be confidently scored because of inconsistent amplification, *Gmu*D121, *Gmu*D87, and *Gmu*A18 appeared to have null alleles (*i.e.,* many samples failed to amplify, homozygous excess), and Eb09 and BATC9 each only exhibited two alleles one repeat motif apart and could not be confidently scored because of stutter patterns. Deviations from HWE and significant linkage disequilibrium were not detected after sequential Bonferroni correction (Table 3.2).

Chelydra serpentina

I successfully genotyped 83 adult *C. serpentina* for six of the seven microsatellite loci (Table 3.1). One individual was only genotyped for two loci but was included in analyses. One of the six successful loci (*Mte*D2) was fixed for all study sites and was subsequently removed from further analyses. The seventh locus (*Mte*D106) could not be confidently scored and was also excluded from analyses. The Grundy site was fixed and the Will 1 site only had one heterozygote for the *Mte*C1 locus; however, because this locus exhibited low polymorphism, the lack of heterozygotes in the two sites was likely just an artifact of small sample size. Presence of homozygous excess was detected at the Will 1 site for *Mte*D9 but this also could be attributed to small sample size. All loci conformed to the assumptions of HWE (Table 3.2). Significant linkage disequilibrium ($P = 0.002$; adjusted $\alpha = 0.005$) was detected between *Mte*C1 and

*Mte*C112 for the Will 2 site after Bonferroni correction, but linkage comparisons across all sites were not significant.

Genetic diversity within species across sites

Emydoidea blandingii

For the 14 successful loci, I identified two to 13 alleles at each locus across all study sites (Table 3.2; Appendix I). Interestingly, one individual from Will 3 was genotyped for three alleles at three different loci (BATC9, *Gmu*D70, and *Gmu*D87) in each of two independent samples that were collected in different years. I included this individual in subsequent analyses, but for the triploid loci I only retained two of the three alleles that were most frequently observed in the Will 3 site. Allelic richness and private allele richness were estimated from 22 gene copies in each site to account for sample size variation. Mean number of observed alleles was greatest in the intact site (Grundy) but measures of allelic richness were similar between the Grundy and Will 1 sites (Table 3.2). Mean observed and expected heterozygosity were similar for all sites and mean inbreeding coefficients did not indicate a loss of genetic diversity (Table 3.2). Comparisons of genetic diversity (A_R, P_{AR}, H_o) did not differ between the intact Grundy County and the fragmented Will County sites (Wilcoxon tests; $P > 0.074$, adjusted $\alpha = 0.017$).

Chrysemys picta

For the eight successful loci, I identified two to 73 alleles at each locus across all study sites (Table 3.2; Appendix I). Allelic richness and private allele richness were estimated from 89 gene copies in each site to account for sample size variation. Mean allelic richness and total number of private alleles were greatest for the fragmented Will County sites (Table 3.2).

However, mean observed heterozygosity and mean expected heterozygosity were similar among sites (Table 3.2). Comparisons of genetic diversity (A_R, P_{AR}, H_o) did not differ between the intact Grundy County and the fragmented Will County sites (Wilcoxon tests; $P > 0.093$, adjusted $\alpha = 0.017$).

Chelydra serpentina

For the five successful loci, I identified two to 16 alleles at each locus across all study sites (Table 3.2; Appendix I). Allelic richness and private allele richness were estimated from 20 gene copies in each site to account for sample size variation. Mean allelic richness and total number of private alleles were greatest for the Will 3 and Grundy County sites (Table 3.2). Mean observed heterozygosity and mean expected heterozygosity varied slightly among sites and were highest for the Will 2 site (Table 3.2). Comparisons of genetic diversity (A_R, P_{AR}, H_o) did not differ between the intact Grundy County and the fragmented Will County sites (Wilcoxon tests; $P > 0.128$, adjusted $\alpha = 0.017$).

Genetic divergence within species

For *E. blandingii*, pairwise F_{ST} analysis detected significant divergence between the Grundy County and each of the Will County sites and between the Will 1 and Will 3 sites before and after sequential Bonferroni correction (Table 3.3). For *C. picta*, significant divergence was detected between Will 1 and Will 3 sites before but not after Bonferroni correction (Table 3.3). For *C. serpentina*, divergence was detected between the Will 1 and Will 2 and between the Will 2 and Will 3 sites before and after Bonferroni correction (Table 3.3). AMOVA indicated weak

but significant structure among sites for *E. blandingii* (F_{ST} = 0.020, P = 0.001), *C. picta* (F_{ST} = 0.002, P = 0.010), and *C. serpentina* (F_{ST} = 0.011, P = 0.010).

Both simulations (with and without prior location information) of the Bayesian clustering method indicated that there were three optimal clusters for *E. blandingii* and two optimal clusters for *C. picta* and *C. serpentina*. However, the program failed to consistently assign individuals to their respective sampling locations and assigned large proportions of individuals from one location to more than one cluster indicating a lack of strong genetic divergence among sites (Fig. 3.2A-C).

Genetic divergence among species

For divergence among species, mean values of D_{est} and G'_{ST} were low (< 0.04) and patterns of divergence were inconsistent between *C. picta* and *C. serpentina* (Table 3.4). For, D_{est}, *C. serpentina* was the least divergent among sites (CI included zero) but for G'_{ST}, *C. serpentina* was as highly divergent as *E. blandingii*. Further, significant differences in divergence (95 CIs did not overlap) were only detected in G'_{ST} comparisons; *E. blandingii* and *C. serpentina* were more divergent across sites than *C. picta*.

Sex-biased dispersal

Emydoidea blandingii exhibited subtle patterns of male-biased gene flow across all sites but these patterns were more pronounced across fragmented sites (Table 3.5). Only F_{IS} values across fragmented sites were significantly larger in males than females (Table 3.5). No significant differences in sex-biased dispersal were detected for *C. picta* or *C. serpentina*. In *C. picta*, subtle patterns of male-biased gene flow were evident for *m*AIc and *v*AIc values but not

F_{ST} (Table 3.5). Further, F_{IS} values were greater for female *C. picta* in both scenarios and little difference between values was observed between fragmented sites only and all sites. In *C. serpentina*, both scenarios showed subtle mixed patterns of sex-biased gene flow (Table 3.5). For males, only F_{IS} values indicated male-biased gene flow; whereas for females, *v*AIc and F_{ST} indicated female-biased gene flow. Further, *m*AIc values (*i.e.* positive and negative) switched between males and females in the comparison between fragmented sites only and all sites (Table 3.5).

Bottlenecks

No evidence of a past bottleneck (significant heterozygosity excess) was detected in any of the fragmented Will County sites or the intact Grundy County site for *E. blandingii* (P = 0.77-0.96), *C. picta* (P = 0.95-1.00), or *C. serpentina* (P = 0.44-0.97) regardless of TPM mutation parameters. All species also maintained a normal L-shaped distribution of allele frequencies across sites, indicating no substantial loss of rare alleles that would be expected in a bottlenecked population. The M-ratio tests also failed to show evidence of population declines ($M > M_c$) in all species across all sites.

Future loss of genetic diversity

In both simulations of future genetic drift based on current demographic parameters and allele frequencies, observed number of alleles decreased more quickly than observed heterozygosity over the 300 year period (Fig. 3.3). Overall, loss of genetic diversity was most pronounced in *E. blandingii* compared to the other two species. For the random mating simulation, 88%, 97%, and 99% of heterozygosity was retained and 72%, 95%, and 94% of

allelic diversity was retained for *E. blandingii*, *C. serpentina*, and *C. picta*, respectively after 300 years (Fig. 3.3). For the skewed mating simulation, resulting levels of genetic diversity were lower compared to those of the random mating system but patterns of loss between the two simulations varied among species. For example, patterns of genetic drift in *E. blandingii* were similar regardless of mating system but *C. serpentina* and *C. picta* lost more heterozygosity (3% and 4%) and substantially more allelic diversity (9% and 19%) in the skewed mating system compared to the random mating system.

DISCUSSION

Overall, within the Lower Des Plaines River Valley (LDPRV) I found little evidence that *E. blandingii*, *C. picta*, and *C. serpentina* in fragmented sites had less genetic variation when compared to those in an intact site. All species demonstrated moderate to high levels of genetic diversity. Further, I detected little genetic divergence among sites; however F_{ST} values among sites varied by species. Gene flow was male-biased in *E. blandingii* across the fragmented sites but differences in dispersal between males and females in *C. picta* and *C. serpentina* were not strong. I found no evidence of genetic population bottlenecks in any species but simulations of future genetic diversity suggest that *E. blandingii* is more vulnerable to loss of genetic diversity than *C. picta* or *C. serpentina*.

Levels of genetic diversity

Comparisons of within-species levels genetic diversity observed across the LDPRV sites were lower in *E. blandingii* when qualitatively compared to *C. picta* and *C. serpentina*. However, estimates for all species were moderate and comparable to levels reported in other

freshwater turtles (Kuo & Janzen 2004, Tessier *et al*. 2005, Pearse *et al*. 2006, Castellano *et al.* 2009, Escalona *et al.* 2009, Ye *et al.* 2009, Spradling *et al*. 2010, Molnár *et al*. 2011). In my study, inbreeding coefficients did not indicate inbreeding within species at any site. Estimates of observed heterozygosity in previous *E. blandingii* studies that sampled ≥ 10 individuals/site ranged from 0.71-0.80 in Illinois (Mockford *et al*. 2007, Klut 2011) and 0.61-0.64 in other Midwest populations (Mockford *et al*. 2007). Differences in levels of genetic diversity among species and studies can be attributed variability in locus polymorphism (Rubinsztein *et al*. 1995) as well as the number of loci used to estimate diversity parameters.

This is one of the first studies known to report population genetic structure and gene flow for *C. picta* and *C. serpentina*. Both of these species are common throughout their respective geographic distributions but have received less attention than species of conservation concern such as *E. blandingii*. With the exception of a DNA fingerprinting study that examined the genetic diversity of *C. picta* between small and large wetland sites (Parker & Whiteman 1993), previous genetic studies of *C. picta* and *C. serpentina* have focused on parentage analysis, genetic mating systems, and assessments of multiple paternity (Galbraith 1993, Pearse & Avise 2001, Pearse *et al*. 2001, 2002, McGuire 2011, McGuire *et al*. 2011) and taxonomic relationships (Phillips *et al*. 1996, Starkey *et al*. 2003).

Because turtle species examined in my study vary considerably in life history traits (Congdon *et al*. 1993, Congdon *et al*. 1994, Congdon *et al*. 2003, McGuire 2011, McGuire *et al.* 2011), spatial ecology (Chapter One), and habitat use (Chapter Two), I had expected to find differences in patterns of genetic diversity among species between the intact and fragmented populations. Specifically, I had predicted fragmented *E. blandingii* populations to have lost more genetic diversity and be more divergent between fragmented sites and the intact site than the two

common species, *C. picta* and *C. serpentina*. In a similar study that used DNA fingerprinting, Parker & Whiteman (1993) found that the rare spotted turtle (*Clemmys guttata*) exhibited greater differences in genetic diversity between small and large wetland complexes compared to the abundant *C. picta*. However, I failed to detect significant differences in genetic diversity for any of the three species between sites. Each of these species is capable of long-distance movements via the Des Plaines River (Chapter One); thus, vagility coupled with long generation times (Avise *et al.* 1992) and relatively recent fragmentation (Bennett *et al*. 2010) could account for the lag in detectable loss of genetic diversity in fragmented sites.

Measures of genetic divergence

I detected significant pairwise F_{ST} divergence in *E. blandingii* and *C. serpentina*. Although F_{ST} values were low, *E. blandingii* was divergent between the intact and each of fragmented sites as well as between two of the fragmented sites (Will 1 and Will 3). Conversely, *C. serpentina* was only divergent between Will 2 and Will 1, as well as Will 2 and Will 3. I suspect that the levels of divergence in *C. serpentina* are attributed to variation in sample size. Samples from female *C. serpentina* are lacking from the Will 1 and Will 3 sites compared to Will 2 and considering that female *C. serpentina* are known to be philopatric to nesting sites (Congdon *et al.* 1987), a male-biased sample pool could impact levels of divergence among sites.

In the direct comparisons among species, *E. blandingii* was the most divergent for both pairwise estimates (D_{est} and G'_{ST}). However, patterns of divergence were not consistent for *C. picta* and *C. serpentina*. Further, significant differences among species were only detected using the G'_{ST} estimates; *E. blandingii* and *C. serpentina* were more divergent than *C. picta*. The discrepancies between these two measures may be attributed to differences in the underlying

dependencies in heterozygosity and mutation rates (Hedrick 2005, Jost 2008, Ryman & Leimar 2009). Further, accuracy of G'_{ST} in measuring differentiation has been criticized (Jost 2008, Gerlach *et al*. 2010) and thus should be interpreted with caution. Variation in life history traits (*e.g.* longer generation time) could explain why *E. blandingii* is more divergent among sites compared to the other two species.

Sex-biased dispersal

Females of many species of turtles are philopatric to nesting locations, including *E. blandingii* (Congdon *et al*. 1983), *C. picta* (Valenzuela & Janzen 2001, Rowe *et al*. 2005), and *C. serpentina* (Congdon *et al*. 1987), whereas males are considered to be the dispersing sex (but see Sheridan *et al*. 2010). However, in this study sex biased gene flow was only evident for *E. blandingii* and was more apparent in fragmented sites alone than when including the intact Grundy County site. If the dispersing sex is more genetically similar across sites than the philopatric sex and contemporary fragmentation prevents successful dispersal among sites, then F_{IS} values should increase in the dispersing sex (*i.e*. males). Assemblages of *E. blandingii* found in the LDPRV fragmented sites are small and biased towards females (Banning 2006, Banning *et al*. 2006, Dreslik *et al*. 2011). Thus, fewer numbers of males across the fragmented sites could explain the stronger bias in levels of male F_{IS} compared to the scenario that included the intact site. Alternatively, stronger evidence for male-biased gene flow in the fragmented sites may be related to their closer proximity and potential for higher levels of historical gene flow than the more distant intact site. The lack of sex-biased gene flow in *C. picta* and *C. serpentina* could be caused by either a lack of male dispersers or a combination of male and female dispersers. For *C. picta*, high genetic diversity and no differentiation across sites suggest that gene flow was

historically high across sites and lends support to the latter dispersal explanation. Female natal philopatry as well as male and female dispersal has been reported in the diamondback terrapin (*Malaclemys terrapin*, Sheridan *et al*. 2010). For *C. serpentina*, because evidence for differentiation across sites is unclear, sex-biased gene flow may be present but undetected.

Bottlenecks

Although suitable turtle habitat has been lost and fragmented within the LDPRV, evidence of recent population declines was not evident for any species. Lack of genetic divergence and population bottlenecks, even in small isolated sites, are not uncommon in turtles (Parker & Whiteman 1993, Rubin *et al*. 2001a, Kuo & Janzen 2004, Mockford *et al.* 2007, Bennett *et al*. 2010, Spradling *et al.* 2010, Klut 2011) and have been attributed to a combination of long generation times, low metabolic and mutation rates (Avise *et al*. 1992), and relatively recent anthropogenic habitat fragmentation (Bennett *et al*. 2010). Both, spatial and temporal scale can affect power to detect patterns in landscape genetic studies and a lag time can exist between landscape change and a response in biological processes (Anderson *et al*. 2010). The turtle gene pools sampled in my study occur within a relatively localized scale; a 50 km stretch of the LDPRV. Historically, these groups were likely panmictic and movement and gene flow could occur throughout matrices of prairie and wetland habitats without anthropogenic impediment. Although contemporary movement among these remnant populations has been restricted to dispersal via the Des Plaines River and subtle differentiation is evident only in *E. blandingii* across sites, not enough time (*i.e.* generations) may have yet passed to detect the subsequent loss of genetic diversity and gene flow in *C. picta* and *C. serpentina*.

Future loss of genetic diversity

Simulations of future loss of genetic diversity demonstrated that differences in species-specific traits such as age of maturity, longevity, sex ratio, and abundance appear to affect the rates of genetic drift among *E. blandingii*, *C. picta*, and *C. serpentina* within the LDPRV. Loss of genetic diversity was substantially higher in *E. blandingii* than for *C. picta* or *C. serpentina*. This can be explained by the long time to maturity, greater longevity, and drastically smaller estimated population size in *E. blandingii* compared to *C. picta* and *C. serpentina*. Although *C. serpentina* appear to be more stable compared to *E. blandingii*, simulations of future genetic diversity suggest that *C. serpentina* is more vulnerable to genetic loss than *C. picta*. Its intermediate position of conservation concern is likely a result of the combination of demographic parameters and ecological specialization of *C. serpentina*. On one hand, this species is relatively abundant (Banning *et al*. 2006, Dreslik *et al*. 2011), capable of long-distance aquatic movements (Chapter One) that can potentially maintain gene flow among populations and is a habitat generalist that readily uses poorer quality habitats including the Des Plaines River (Chapter Two). However, *C. serpentina* also exhibits a longer time to sexual maturity and a longer life span than *C. picta* that is more similar to *E. blandingii* in these regards (Congdon *et al*. 1993, 1994, 2003). Alterations in the mating system settings (random vs. skewed) had the greatest impact on *C. serpentina* and *C. picta*. However, skewed mating extremes (*i.e.* only one male siring all offspring) do not reflect actual mating systems reported in populations of *C. serpentina* and *C. picta* (Pearse and Avise 2001, Pearse *et al.* 2002, McGuire 2011) and are unlikely for population with large numbers of individuals as estimated for the Will 3 site.

Conservation Implications

Loss of genetic diversity and divergence in fragmented sites compared to an intact site was not apparent within the LDPRV. However, lack of contemporary dispersal (Chapter One) and gene flow (Chapter Four) between sites is potentially masked by long-generation times and relatively recent landscape fragmentation. Long-term loss of genetic diversity is possible in all three turtle species but is particularly imminent in *E. blandingii* because of lower abundance and longer generation time of this species across sites compared to *C. picta* and *C. serpentina*. Because populations do not appear to be substantially different genetically, long-term management of LDPRV sites should try to maintain some level of gene flow and consider actions such as translocation of head-started hatchlings.

Literature Cited **(Formatted for the Journal of Molecular Ecology)**

Anderson, CD, Epperson BK, Fortin M-J E, Holderegger R, James PMA, Rosenberg MS, Scribner KT, Spear S (2010) Considering spatial and temporal scale in landscape-genetic studies of gene flow. Molecular Ecology **19**, 3565–3575.

Avise JC, Bowen BW, Lamb T, Meylan AB, Bermingham E (1992) Mitochondrial DNA evolution at a turtle's pace: evidence for low genetic variability and reduced microevolutionary rate in Testudines. Molecular Biological Evolution **9**, 457-473.

Banning WJ (2006) Ecology of the Blanding's Turtle (*Emydoidea blandingii*) at a Northeastern Illinois Wetland Community. Unpublished. Masters Thesis, University of Illinois Urbana Champaign, Illinois.

Banning WJ, Dreslik MJ, Phillips CA (2006) Continued study of the ecology of the freshwater turtle community at Lockport Prairie Nature Preserve: With special emphasis on the Blanding's turtle (*Emydoidea blandingii*). Illinois Natural History Survey, Center for Biodiversity, Technical Report 2006(4), 1–259pp.

Bennett AM, Keevil M, Litzgus JD (2010) Spatial ecology and population genetics of northern map turtles (*Graptemys geographica*) in fragmented and continuous habitats in Canada. Chelonian Conservation and Biology **9**, 185-195.

Bowles ML, McBride J (2001) Historical landscape vegetation pattern, composition, and structure of Will County, Illinois, as recorded by the U.S. Public Land Survey (1821-1838). http://www.greenmapping.org

Busch JD, Waser PM, DeWoody A (2007) Recent demographic bottlenecks are not accompanied by a genetic signature in banner-tailed kangaroo rats (*Dipodomys spectabilis*). *Molecular Ecology* **16**, 2450-2462.

Castellano CM, Behler JL, Amato G (2009) Genetic diversity and population genetic structure of the wood turtle (*Glyptemys insculpta*) at Delaware Water Gap National Recreation Area, USA. *Conservation Genetics* **10,** 1783-1788.

Congdon JD, Breitenbach GL, van Loben Sels RC, Tinkle DW (1987) Reproduction and nesting ecology of snapping turtles (*Chelydra serpentina*) in southeastern Michigan. Herpetologica **43**, 39-54.

Congdon JD, Dunham AE, van Loben Sels RC (1994) Demographics of common snapping turtles (*Chelydra serpentina*): Implications for conservation and management of long-lived organisms. American Zoologist **34**, 397-408.

Congdon JD, Nagle RD, Kinney OM, van Loben Sels RC, Quinter T, Tinkle DW (2003) Testing hypotheses of aging in long-lived painted turtles (*Chrysemys picta*). Experimental Gerontology **38**, 765-772.

Congdon JD, Tinkle DW, Breitenbach GL, van Loben Sels RC (1983) Nesting ecology and hatching success in the turtle *Emydoidea blandingii*. *Herpetologica* **39**, 417-429.

Congdon JD, van Loben Sels RC (1993) Relationships of reproductive traits and body size with attainment of sexual maturity and age in Blanding's turtles (*Emydoidea blandingii*). J. Evol. Biol. **6**, 547-557.

Cornuet JM, Luikart G (1996) Description and power analysis of two tests for detecting recent population bottlenecks from allele frequency data. *Genetics* **144**, 2001-2014.

DiLeo MF, Row JR, Lougheed SC (2010) Discordant patterns of population structure for two co-distributed snake species across a fragmented Ontario landscape. *Diversity and Distributions*, **16**, 571-581.

Di Rienzo A, Peterson AC, Garza JC, Valdes AM, Slatkin M, Freimer NB (1994) Mutational processes of simple-sequence repeat loci in human populations. *Proceedings of the National Academy of Sciences* **91**, 3166-3170.

Dreslik MJ, Banning WJ, Kirk D (2010) Population biology of the state endangered Blanding's turtle (*Emydoidea blandingii*) at Goose Lake Prairie State Natural Area. Illinois Natural History Survey, Technical Report 2010(11), 1-50pp.

Dreslik MJ, Banning WJ, Marioni NK, Phillips CA (2011) Monitoring of the Blanding's Turtle (*Emydoidea blandingii*) at the I-355 Des Plaines River Bridge Crossing: Final Report. Illinois Natural History Survey, Technical Report 2011(3), 1-237pp.

Earl DA, vonHoldt BM (2011) STRUCTURE HARVESTER: a website and program for visualizing STRUCTURE output and implementing the Evanno method. *Conservation Genetics Resources* DOI: 10.1007/s12686-011-9548-7.

Ernst CH, Lovich JE (2009) *Turtles of the United States and Canada*, 2nd edn. John Hopkins University Press, Baltimore.

Escalona T, Engstrom TN, Hernandez OE, Bock BC, Vogt RC, Valenzuela N (2009) Population genetics of the endangered South American freshwater turtle, *Podocnemis unifilis*, inferred from microsatellite DNA data. Conservation Genetics, **10**, 1683-1696.

Evanno G, Regnaut S, Goudet J (2005) Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. *Molecular Ecology* **14,** 2611-2620.

Fisher P (2003) Locating new venipuncture site in chelonians. *Exotic DVM Vet Magazine* **4**, 8.

Galbraith DA (1993) Multiple paternity and sperm storage in turtles. Herpetological Journal **3**, 117-123.

Garza JC, Williamson EG (2001) Detection of reduction in population size using data from microsatellite loci. *Molecular Ecology* **10,** 305-318.

Gerlach G, Jueterbock A, Kraemer P, Deppermann J, Harmand P (2010) Calculations of population differentiation based on G(ST) and D: forget G(ST) but not all statistics! *Molecular Ecology* **19**, 3845-3852.

Goldberg CS, Waits LP (2010) Comparative landscape genetics of two pond-breeding amphibian species in a highly modified agricultural landscape. *Molecular Ecology*, **19**, 3650-3663.

Goudet J (1995) FSTAT (version 1.2): A computer program to calculate F-statistics. Journal of *Heredity* **86**, 484-486.

Goudet J, Perrin N, Waser P (2002) Tests for sex-biased dispersal using bi-parentally inherited genetic markers. *Molecular Ecology* **11**, 1103-1114.

Gray EM (1995) DNA fingerprinting reveals a lack of genetic variation in northern populations of the western pond turtle (*Clemmys marmorata*). *Conservation Biology* **9**, 1244-1255.

Hackler JC, Van Den Bussche RA, Leslie Jr. DM (2007) Characterization of microsatellite DNA markers for the alligator snapping turtle, *Macrochelys temminckii*. *Molecular Ecology Notes* **7,** 474-476.

Hedrick PW (2005) A standardized genetic differentiation measure. *Evolution* **59**, 1633-1638.

Hoekert WE J, Neuféglise H, Schouten AD, Menken SBJ (2002) Multiple paternity and female-biased mutation at a microsatellite locus in olive ridley sea turtle (*Lepidochelys olivacea*). *Heredity* **89**, 107-113.

Jost L (2008) Gst and its relatives do not measure differentiation. *Molecular Ecology* **17**, 4015-4026.

Kalinowski ST (2005) HP-Rare: A computer program for performing rarefaction on measures of allelic diversity. *Molecular Ecology Notes* **5**,187-189.

King RB, Lawson R (2001) Patterns of population subdivision and gene flow in three sympatric natricine snakes. *Copeia* **2001**, 602-614.

King TL, Julian SE (2004) Conservation of microsatellite DNA flanking sequence across 13 Emydid genera assayed with novel bog turtle (*Glyptemys muhlenbergii*) loci. *Conservation Genetics* **5**, 719-725.

Klut, GM (2011) Genetic homogeneity among Blanding's turtle (*Emydoidea blandingii*) populations across the Chicago area. Western Illinois University Unpublished Masters Thesis.

Kuo C-H, Janzen FJ (2003) BOTTLESIM: a bottleneck simulation for long-lived species with overlapping generations. Molecular Ecology Notes **3**, 669-673.

Kuo C-H, Janzen FJ (2004) Genetic effects of a persistent bottleneck on a natural population of ornate box turtles (*Terrapene ornata*). *Conservation Genetics* **5**, 425-437.

Libants S, Kamarainen AM, Scribner KT, Congdon JD (2004) Isolation and cross-species amplification of seven microsatellite loci from *Emydoidea blandingii*. *Molecular Ecology Notes* **4,** 300-302.

Lozier JD, Strange JP, Stewart IJ, Cameron SA (2011) Patterns of range-wide genetic variation in six North American bumble bee (Apidae: *Bombus*) species. *Molecular Ecology* **20**, 4870-4888.

Luikart G, Allendorf FW, Cornuet J-M, Sherwin WB (1998) Distortion of allele frequency distributions provides a test for recent population bottlenecks. *Journal of Heredity* **89**, 238-247.

Luikart G, Cornuet J-M (1998) Empirical evaluation of a test for identifying recently bottlenecked population from allele frequency data. *Conservation Biology* **12**, 228-237.

McGuire JM (2011) Comparative analysis of factors influencing male reproductive success in sympatric freshwater turtles. Michigan State University, PhD Dissertation.

McGuire JM, Congdon JD, Scribner KT, Capps JD (2011) Variation in female reproductive quality and reproductive success of male Midland Painted Turtles (*Chrysemys picta marginata*). Canadian Journal of Zoology **89**, 1136-1145.

Mockford SW, Herman TB, Snyder M, Wright JM (2007) Conservation genetics of Blanding's turtle and its application in the identification of evolutionarily significant units. Conservation Genetics **8**, 209-219.

Molnár T, Lehoczky I, Molnár M, Benedek I, Magyary I, Jeney Z, Zsolnai A (2011) Genetic diversity of the European pond turtle (*Emys orbicularis*) in the south-west region of Hungary – first results. *Amphibia-Reptilia* **32**, 519-526.

Oliveira EJ, Pádua, J G, Zucchi MI, Vencovsky R, Vieira MLC (2006) Origin, evolution, and genome distribution of microsatellites. *Genetics and Molecular Biology* **29**, 294-307.

Osentoski MF, Mockford S, Wright JM, Synder M, Herman TB, Hughes CR (2002) Isolation and characterization of microsatellite loci from the Blanding's turtle, *Emydoidea blandingii*. *Molecular Ecology Notes* **2,** 147-149.

Parga JA, Sauther ML, Cuozzo FP, Jacky IAY, Lawler RR (2012) Evaluating ring-tailed lemurs (*Lemur catta*) from southwestern Madagascar for a genetic population bottleneck. *American Journal of Physical Anthropology* **147**, 21-29.

Parker PG, Whiteman HH (1993) Genetic diversity in fragmented populations of *Clemmys guttata* and *Chrysemys picta marginata* as shown by DNA fingerprinting. *Copeia* **1993**, 841-846.

Peakall R, Smouse PE (2006) GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. *Molecular Ecology Notes* **6**, 288-295.

Pearse DE, Arndt AD, Valenzuela N, Miller BA, Cantarelli V, Sites J (2006) Estimating population structure under nonequilibrium conditions in a conservation context: continent-wide population genetics of the giant Amazon river turtle, *Podocnemis expansa* (Chelonia; Podocnemididae). *Molecular Ecology* **15**, 985-1006.

Pearse DE, Avise JC (2001) Turtle mating systems: Behavior, sperm storage, and genetic paternity. *Journal of Heredity* **92**, 206-211.

Pearse DE, Janzen FJ, Avise JC (2001) Genetic markers substantiate long-term storage and utilization of sperm by female painted turtles. *Heredity* **86**, 378-384.

Pearse DE, Janzen FJ, Avise JC (2002) Multiple paternity, sperm storage, and reproductive success of female and male painted turtles (*Chrysemys picta*) in nature. *Behavioral Ecology and Sociobiology* **51**, 164-171.

Phillips CA, Dimmick WW, Carr JL (1996) Conservation genetics of the common snapping turtle (*Chelydra serpentina*). Conservation Biology **10**, 397-405.

Piry S, Luikart G, Cornuet JM (1999) BOTTLENECK: a computer program for detecting recent reductions in the effective population size using allele frequency data. Journal of Heredity **90**, 502-503.

Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using multilocus genotype data. *Genetics* **155**, 945-959.

Reed DH, Teoh V-H, Stratton GE, Hataway RA (2011) Levels of gene flow among populations of a wolf spider in a recently fragmented habitat: current versus historical rates. *Conservation Genetics*, **12**, 331-335.

Richtsmeier RJ, Bernstein NP, Demastes JW, Black RW (2008) Migration, gene flow, and genetic diversity within and among Iowa populations of ornate box turtles (*Terrepene ornata ornata*). *Chelonian Conservation Biology* **7**, 3-11.

Rivalan P, Dutton PH, Baudry E, Roden SE, Girondot M (2006) Demographic scenario inferred from genetic data in leatherback turtles nesting in French Guiana and Suriname. *Biological Conservation* **130**, 1-9.

Rice WR (1989) Analyzing tables of statistical tests. Evolution **43**, 223-225.

Rousset F (2008) GENEPOP'007: a complete re-implementation of the GENEPOP software for Windows and Linux. *Molecular Ecology Resources* **8,** 103-106.

Rowe JW, Coval KA, Dugan MR (2005) Nest placement, nest-site fidelity and nesting movements in midland painted turtles (*Chrysemys picta marginata*) on Beaver Island, Michigan. *American Midland Naturalist* **154**, 383-397.

Rubin CS, Warner RE, Bouzat JL, Paige KN (2001a) Population genetic structure of Blanding's turtles (*Emydoidea blandingii*) in an urban landscape. Biological Conservation **99**, 323-330.

Rubin CS, Warner RE, Ludwig DR (2001b) Habitat use and movements of radiotagged Blanding's turtles (*Emydoidea blandingii*) in a suburban landscape. *Chelonian Conservation Biology* **4**, 136–141.

Rubinsztein DC, Amos W, Leggo J, Goodburn S, Jain S, Li SH, Margolis RL, Ross CA, Fergusonsmith MA (1995) Microsatellite evolution – Evidence for directionality and variation in rate between species. *Nature Genetics* **10**, 337-343.

Ryman N, Leimar O (2009) G_{ST} is still a useful measure of genetic differentiation a comment on Jost's *D*. *Molecular Ecology* **18**, 2084-2087.

Selkoe, KA, Toonen RJ (2006) Microsatellites for ecologists: a practical guide to using and evaluating microsatellite markers. *Ecology Letters* **9**, 619-629.

Seutin G, White BN, Boag PT (1991) Preservation of avian blood and tissue samples for DNA analyses. *Canadian Journal of Zoology* **69**, 82-90.

Sheridan CM, Spotila JR, Bien WF, Avery HW (2010) Sex-biased dispersal and natal philopatry in the diamondback terrapin, *Malaclemys terrapin*. *Molecular Ecology* **19,** 5497-5510.

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**, 1667-1677.

Starkey DE, Shaffer HB, Burke RL, Forstner MRJ, Iverson JB, Janzen FJ, Rhodin AGJ, Ultsch GR (2003) Molecular systematics, phylogeography, and the effects of Pleistocene glaciation in the painted turtle (*Chrysemys picta*) complex. *Evolution* **57**, 119-128.

Steele CA, Baumsteiger J, Storfer A (2009) Influence of life-history variation on the genetic structure of two sympatric salamander taxa. *Molecular Ecology* **18**, 1629-1639.

Tessier N, Paquette SR, Rioux Lapointe F-J (2005) Conservation genetics of the wood turtle (Glyptemys insculpta) in Quebec, Canada. *Canadian Journal of Zoology* **83**, 765-772.

Valenzuela N, Janzen FJ (2001) Nest-site philopatry and the evolution of temperature-dependent sex determination. *Evolutionary Ecology and Research* **3**, 779-794.

van Oosterhout C, Hutchinson WF, Wills DPM, Shipley P (2004) MICRO-CHECKER: software for identifying and correcting genotyping errors in microsatellite data. *Molecular Ecology Notes* **4**, 535-538.

Westemeier RL, Brawn JD, Simpson SA, Esker TL, Jansen RW, Walk JW, Kershner EL, Bouzat JL, Paige KN (1998) Tracking the long-term decline and recovery of an isolated population. *Science* **282**, 1695-1698.

Willi Y, Buskirk JV, Hoffman AA (2006) Limits to the adaptive potential of small populations. *Annual Review of Ecology, Evolution, and Systematics* **37**, 433-458.

Williams BL, Brawn JD, Paige KN (2003) Landscape scale genetic effects of habitat fragmentation on a high gene flow species: *Speyeria idalia* (Nymphalidae) *Molecular Ecology*, **12**, 11-20.

Ye R, Zheng R, Wang L, Du W (2009) Polymorphic microsatellite loci in the Chinese pond turtle (*Chinemys reevesii*). *Conservation Genetics* **10**, 1045-1048.

TABLES

Table 3.1 Numbers of male (♂), female (♀), unknown (U), and total (T) adult individuals successfully amplified across selected microsatellite loci in *E. blandingii*, *C. picta*, and *C. serpentina* from three fragmented sites (Will 1-3) and one intact site (Grundy) within the Lower Des Plaines River Valley.

	E. blandingii			*C. picta*			*C. serpentina*			
Site	♂	♀	T	♂	♀	T	♂	♀	U	T
Will 1	8	14	22	68	38	106	15	5	1	21
Will 2	3	8	11	45	26	71	17	12	6	35
Will 3	10	20	30	57	53	110	12	5	0	17
Grundy	23	24	47	30	14	44	8	2	0	10
Total	44	66	110	200	131	331	52	24	7	83

Table 3.2 Mean estimates for number of alleles ($^{\#}A$), allelic richness (A_R), private allele richness (PA_R), observed heterozygosity (H_o), expected heterozygosity (H_e), inbreeding coefficients (F_{IS}), and probability of Hardy-Weinberg deviation (P_{HWE}) for *E. blandingii*, *C. picta*, and *C. serpentina* sampled from three fragmented (Will 1-3) and one intact site (Grundy) within the Lower Des Plaines River Valley. Data were derived from microsatellite analysis with numbers of loci analyzed in *E. blandingii* = 14, *C. picta* = 8, and *C. serpentina* = 5. Sample sizes for each species at each site are provided in Table 3.1.

Site	$^{\#}A$	A_R	PA_R	H_o	H_e	F_{IS}	P_{HWE}
E. blandingii							
Will 1	4.9	4.2	0.42	0.535	0.532	0.034	0.48
Will 2	4.1	4.1	0.38	0.552	0.535	-0.014	0.53
Will 3	4.9	4.0	0.17	0.552	0.537	-0.029	0.67
Grundy	5.6	4.3	0.43	0.506	0.522	0.001	0.56
C. picta							
Will 1	15.0	11.8	0.91	0.662	0.660	-0.011	0.66
Will 2	14.9	12.7	1.40	0.664	0.652	-0.014	0.65
Will 3	14.4	11.9	0.93	0.662	0.659	-0.020	0.57
Grundy	11.5	11.4	0.53	0.627	0.639	0.002	0.58
C. serpentina							
Will 1	6.2	5.1	0.05	0.543	0.579	0.024	0.46
Will 2	7.2	5.4	0.21	0.691	0.651	-0.058	0.65
Will 3	6.8	5.8	0.56	0.576	0.578	-0.006	0.84
Grundy	5.8	5.8	0.25	0.620	0.619	-0.003	0.39

Table 3.3 Pairwise estimates of F_{ST} (below diagonal) and *p*-values estimated from 999 permutations (above diagonal) for A) *E. blandingii*, B) *C. picta*, and C) *C. serpentina* among three fragmented (Will 1-3) and one intact site (Grundy) within the Lower Des Plaines River Valley. Significant F_{ST} values after sequential Bonferroni correction are denoted with an "*". Genetic data were derived from microsatellite DNA analysis with numbers of loci analyzed in *E. blandingii* = 14, *C. picta* = 8, and *C. serpentina* = 5. Sample sizes for each species at each site are shown in Table 3.1.

A) *E. blandingii*

	Will 1	Will 2	Will 3	Grundy
Will 1	----	0.072	0.003	0.002
Will 2	0.014	----	0.169	0.002
Will 3	0.023*	0.008	----	0.001
Grundy	0.018*	0.029*	0.026*	----

B) *C. picta*

	Will 1	Will 2	Will 3	Grundy
Will 1	----	0.155	0.011	0.134
Will 2	0.001	----	0.155	0.083
Will 3	0.003	0.001	----	0.081
Grundy	0.002	0.003	0.003	----

C) *C. serpentina*

	Will 1	Will 2	Will 3	Grundy
Will 1	----	0.010	0.475	0.408
Will 2	0.017*	----	0.001	0.421
Will 3	0.000	0.037*	----	0.167
Grundy	0.000	0.000	0.011	----

Table 3.4 Standardized estimates of D_{est} and G_{ST} (with 95% Confidence Intervals in parentheses) for *E. blandingii*, *C. picta*, and *C. serpentina* sampled from three fragmented (Will 1-3) and one intact site (Grundy) within the Lower Des Plaines River Valley. Genetic data were derived from microsatellite DNA analysis with numbers of loci analyzed in *E. blandingii* = 14, *C. picta* = 8, and *C. serpentina* = 5. Sample sizes for each species at each site are shown in Table 3.1.

Species	D_{est} (95% CIs)	G_{ST} (95% CIs)
E. blandingii	0.039 (0.018-0.063)	0.031 (0.020-0.042)
C. picta	0.017 (0.003-0.032)	0.008 (0.005-0.012)
C. serpentina	0.009 (-0.039-0.065)	0.031 (0.026-0.051)

Table 3.5 Tests for differences in mean assignment indices (*m*AIc), variance in assignment indices (*v*AIc), F_{ST}, and F_{IS} between male and female *E. blandingii*, *C. picta*, and *C. serpentina* from sites within the Lower Des Plaines River Valley. Parameters were estimated sites using the biased dispersal option in FSTAT V. 2.9.3.2 (Goudet 1995). Significance is indicated by an "*" and α = 0.05.

	*m*AIc			*v*AIc			F_{ST}			F_{IS}		
Sites	♂	♀	*P*	♂	♀	*P*	♂	♀	*P*	♂	♀	*P*
E. blandingii												
All Sites	-0.072	0.050	0.46	19.5	16.6	0.41	0.026	0.023	0.58	0.053	-0.006	0.08
Frag. Sites	-0.347	0.173	0.34	19.0	14.4	0.24	0.009	0.025	0.32	0.095	-0.045	**0.004***
C. picta												
All Sites	-0.200	0.303	0.07	9.7	8.6	0.19	0.001	0.005	0.11	-0.008	0.017	0.91
Frag. Sites	-0.150	0.215	0.14	9.9	9.0	0.27	0.001	0.002	0.36	-0.011	0.012	0.89
C. serpentina												
All Sites	0.012	-0.027	0.54	2.9	4.2	0.82	0.012	-0.022	0.96	0.024	0.005	0.57
Frag. Sites	-0.006	0.014	0.49	3.1	4.1	0.76	0.022	-0.014	0.97	0.016	-0.001	0.5

FIGURES

Fig. 3.1 Location of turtle sampling sites in northeastern Illinois, USA. Sites Will 1, Will 2, Will 3, and Grundy are indicated by red stars and are located from north to south, respectively, along the Des Plaines River.

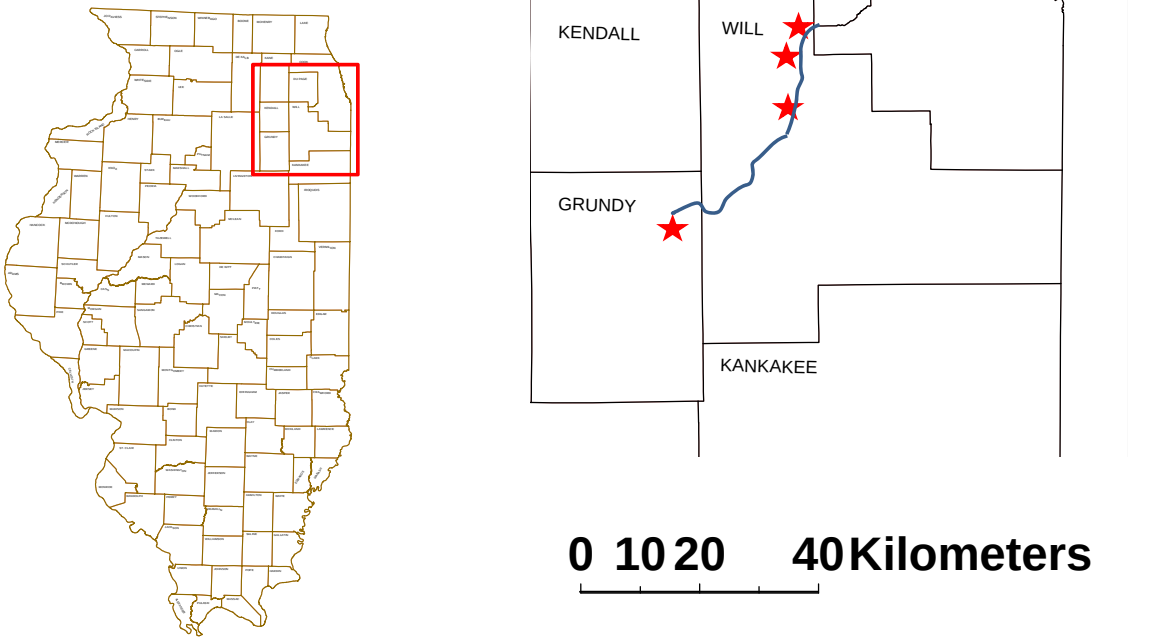
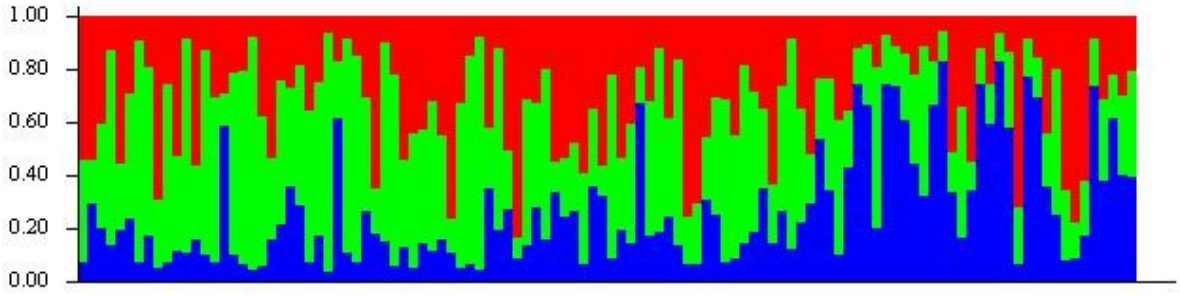
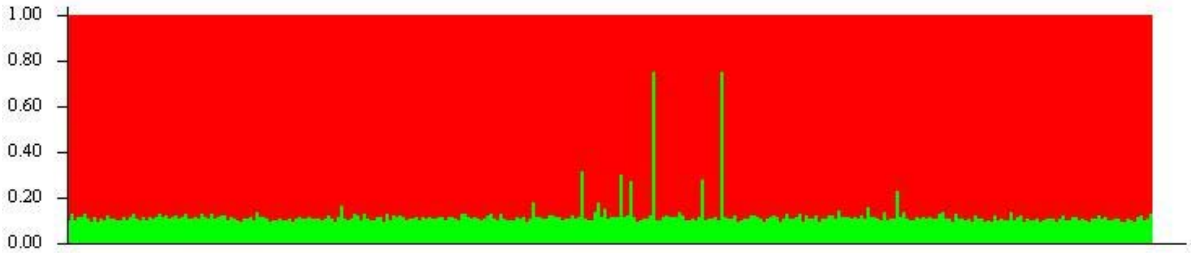


Fig. 3.2 Bayesian clustering results based on the LOCPRIOR option in STRUCTURE 2.3.3 (Pritchard *et al*. 2000) A) *E. blandingii* (3 clusters), B) *C. picta* (2 clusters), and C) *C. serpentina* (2 clusters) among three fragmented (Will 1-3) and one intact site (Grundy) within the Lower Des Plaines River Valley. DNA analysis with numbers of loci analyzed in *E. blandingii* = 14, *C. picta* = 8, and *C. serpentina* = 5. Sample sizes for each species at each site are shown in Table 3.1.

A)



B)



C)

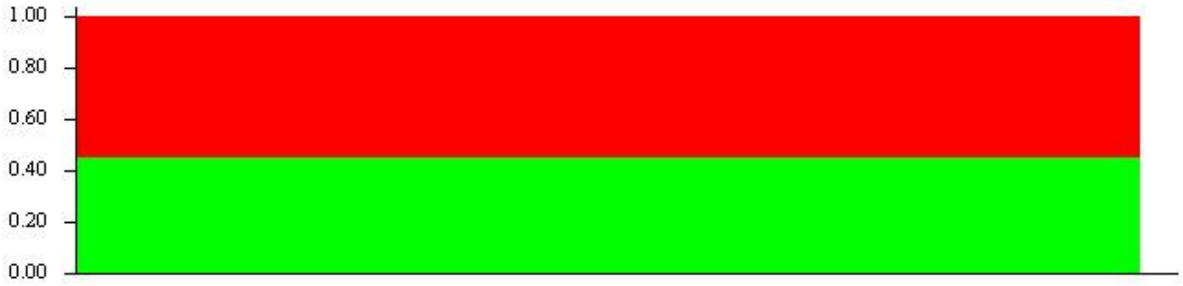
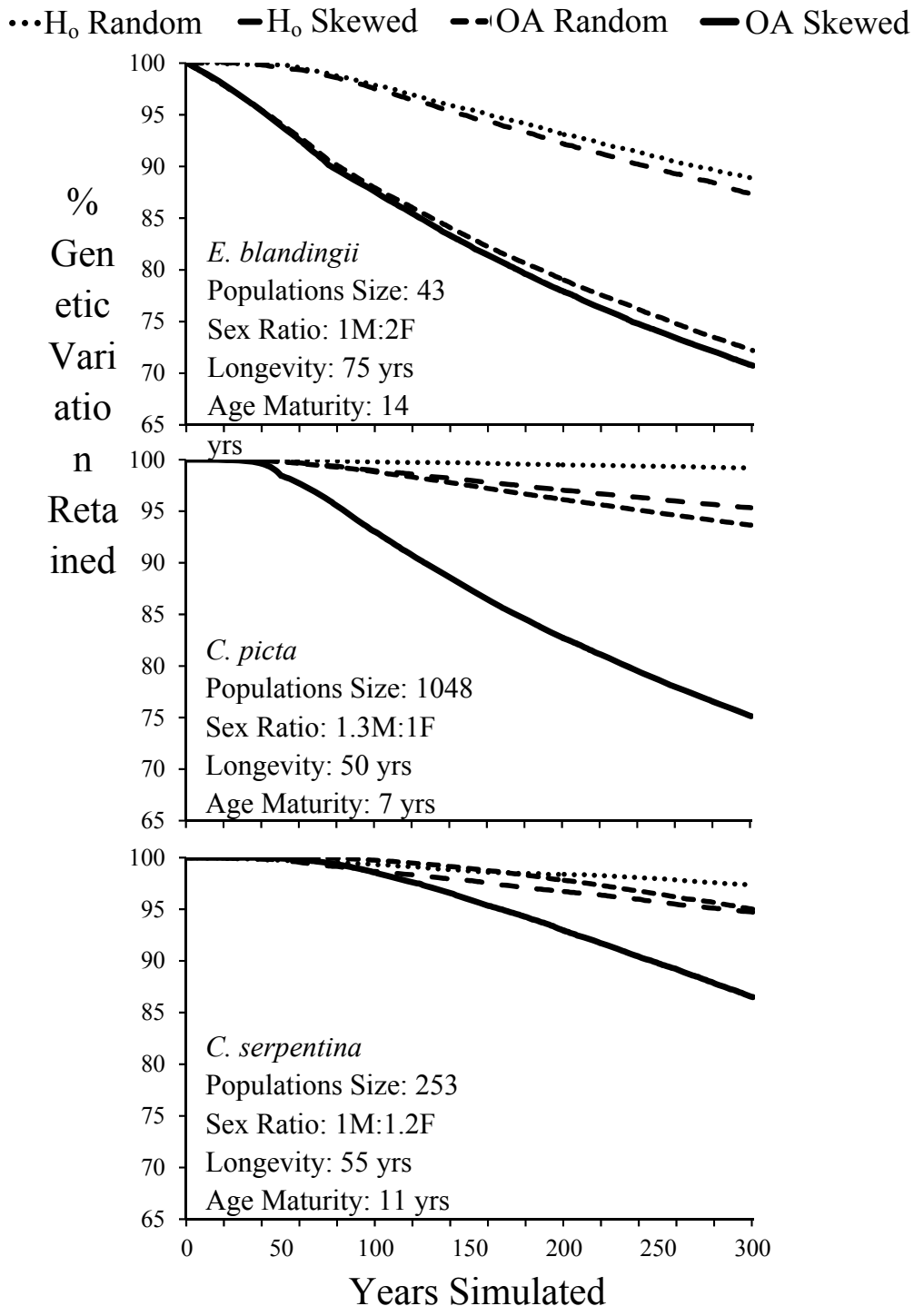


Fig. 3.3 Comparison of predicted genetic variation retained for observed # alleles (OA) and observed heterozygosity (H_o) over 300 years in populations of three turtle species from a preserve in Will County, Illinois. Simulations included the below demographic estimates and life history traits and were performed for random and skewed mating systems using the program BOTTLESIM v2.6 (Kuo and Janzen 2003).



CHAPTER 4

MATING SYSTEM AND REPRODUCTIVE SUCCESS IN A FRAGMENTED POPULATION OF BLANDING'S TURTLES (*EMYDOIDEA BLANDINGII*)

INTRODUCTION

Data on reproductive ecology are important for understanding population dynamics and demographics, and are an integral part of conservation planning. For example, the mating system of a species is an important life history component because the number of reproducing individuals directly influences effective population size N_e, genetic drift, and inbreeding (Caballero 1994) which have conservation implications for small fragmented populations (Willi et al. 2006, Allendorf and Luikart 2007, Mills 2007). In addition, fragmentation can alter distribution of mates (Lane et al. 2011) and elevate inbreeding risk (Andersen et al. 2004, Banks et al. 2005) by confounding dispersal patterns and disrupting gene flow among populations (Moore et al. 2008a). Remnant populations with limited dispersal may consist predominantly of related individuals and have lowered reproductive success because of inbreeding depression (Mills and Smouse 1994). In addition, because of Allee effects, small populations may simply lack sufficient numbers of individuals to ensure adequate encounter rates to facilitate mating (Tainaka and Itoh 1996, Stephens and Sunderland 1999, Dale 2001, Robertson and Butler 2009).

A mating system consists of number of mates, method of acquiring mates, pair bond characteristics, and manner of parental care (Emlen and Oring 1977). Compared to other taxa, non-avian reptiles have less complex mating systems because they typically lack pair bonds and parental care (Pearse and Avise 2001, Uller and Olsson 2008). However, widespread reproductive strategies among reptile taxa such as multiple paternity and sperm storage are not straightforward and lead to misinterpretations of mating system patterns (Uller and Olsson

2008). For example, single clutches sired by multiple males could stem from fertilization from stored and recently inseminated sperm (Pearse et al. 2001, 2002) and confound inferences of polyandry versus seasonal monogamy (Uller and Olsson 2008). Anecdotal observations of courtship and mating attempts are uncommon (Sexton 1959a) and do not necessarily equate to reproductive success (Fitzsimmons 1998). Further, mechanisms of cryptic female choice and sperm competition are not well documented (Galbraith 1993, Eberhard 1996, Uller and Olsson 2008, Olsson et al. 2010). Therefore, studies of mating systems are most informative when behavioral observations can be paired with parentage analysis in naturally occurring populations (Pearse et al. 2002, Moore et al. 2009, Uller and Olsson 2008).

In this study, I assessed the mating system and reproductive success of two adjacent populations of Blanding's turtle (*Emydoidea blandingii*) within a fragmented landscape by pairing field observations of mating behavior with genetic parentage analysis of offspring. *Emydoidea blandingii* is a species of conservation concern throughout its range largely because of habitat loss (Ernst and Lovich 2009). This species is capable of long overland movements (up to > 1 km) during nesting forays (Sexton 1995, Piepgras and Lang 2000, Joyal et al. 2001) and between wetlands (Piepgras and Lang 2000, Rowe and Moll 1991) but anthropogenic barriers such as roads prevent successful dispersal and gene flow in turtle species (Gibbs and Steen 2005). Recent studies of the mating system and parentage in *E. blandingii* have demonstrated multiple paternity (15-81%), repeat paternity (69%), and possible sperm storage (Refsnider 2009, McGuire 2011), but no study to date has compared behavioral observations of courtship to parentage or assessed the mating system of this species in fragmented landscapes.

My objectives were to determine 1) timing and frequency of mating attempts, 2) number of potential mates among individuals, 3) number of offspring and clutches sired by males across

four sequential breeding seasons, 4) determinants of male reproductive success, and 5) effects of male-female pair relatedness on reproductive success. Specifically, I predicted observations of mating attempts would correspond with DNA parentage analysis. Because larger males have larger home ranges (Chapter One), I expected that males with larger home range sizes should encounter more females and have more successful matings, which would lead to higher reproductive success. Body size has been shown to be a predictor of greater reproductive success in reptiles (Moore et al. 2009, Olsson et al. 2010, Tuberville et al. 2011), thus I also predicted that larger males could also sire more offspring because they would be more likely to defend females from other males and coerce females into successful matings. Because matings between related individuals (*i.e*. inbreeding) can reduce reproductive success, I expected related male-female pairs to have lower mating and hatching success than un-related pairs. I also expected low levels of gene flow because few individuals have been observed to move between sites (Chapter One).

METHODS

Reproductive ecology of Emydoidea blandingii

Emydoidea blandingii are long-lived (70+ years) with delayed sexual maturity at 14-20 years of age (Congdon et al. 1993). Females ovulate in May (Gibbons 1968) but the reproductive cycle is unknown in male *E. blandingii* (Ernst and Lovich 2009). Anecdotal accounts of courtship in natural populations of *E. blandingii* have been observed throughout the year (Carr 1952, Graham and Doyle 1979), and suggest that the timing of mating and fertilization may be decoupled (Devine 1984, Uller and Olsson 2008). Mature females produce one clutch per year but may not reproduce every year (Congdon et al. 1983, Congdon and van Loben Sels, 1993,

Banning 2007) and in Michigan, among-year clutch frequency and multiple paternity of clutches increases with female age (Congdon and van Loben Sels 1993, McGuire 2011). In Will County, Illinois, clutch size of *E. blandingii* may range from 8-19 eggs but average clutch size is 11-13 eggs (Banning 2007, Dreslik et al. 2011). Nesting occurs in evenings during late-May-early July with females being philopatric to nesting areas (Congdon et al. 1983, Banning 2007). Hatchlings emerge in August – October (Congdon et al. 1983, Anthonysamy et al. unpublished data).

Field methods

I radio-tracked adult *E. blandingii* 3-7 times per week during a radio-telemetry study conducted from 2006-2009 at two semi-connected preserves (Will 1 and Will 2) in Will County, Illinois. Radio-transmitters were removed from males in October 2009 but transmitters were left on females until June 2010 to collect an additional year of nesting data. Details on study sites and radio-telemetry methods are described in Chapter One. During radio-telemetry, I recorded all observations of mating attempts (mounting of females by males). Observations of mounting were considered to be only mating attempts as this behavior is part of a sequence of courtship that precedes copulation in *E. blandingii* but does not necessarily indicate that successful copulation occurred (Baker and Gillingham 1983). Repeated mating attempts between the same pairs were considered to be distinct events if they were separated by > 3 days (Rovero et al. 1999). I recorded temporal patterns of mating attempts, number of mating attempts, and number of potential mates observed for each turtle.

I determined whether females were gravid by palpating the inguinal pocket for presence of eggs during nesting season (late May–early July) and by radiography (Gibbons and Greene 1979). I obtained clutches during 2007-2010 by 1) radio-tracking females to nesting locations,

protecting nests with predator exclusion cages, and harvesting hatchlings from the cages; 2) radio-tracking females to nesting locations and collecting eggs from nest chambers; or 3) transporting gravid females to the Willowbrook Wildlife Center (Glen Ellyn, Illinois) to induce egg-laying with intramuscular injections of oxytocin (7.5 units/kg) or a combination of oxytocin (1.5 units/kg) and lutalyse (1.5 mg/kg). Clutches obtained from nest chambers were either placed in an incubator at a temperature of approximately 27-30 °C or were incubated at room temperature in plastic shoeboxes filled with moistened vermiculite. Clutches from induced females were placed in incubators with moistened vermiculite (constant temperature of 28 °C) at the Willowbrook Wildlife Center. Nests and incubated clutches were monitored periodically until hatchling emergence to determine hatching success and to collect tissue samples. I calculated hatching success as the proportion of live, non-deformed, and active hatchlings sampled from the total number of eggs collected for a clutch.

Lab methods

I collected blood (0.1-0.3 cc) from the sub-carapacial sinus (Fisher 2003) of adult turtles using a 25 ½ gauge needle and 1 cc syringe and collected 1-2 mm tail clips from hatchlings using sterilized cuticle scissors. I stored tissues in 95% ethanol or Queen's lysis buffer (Seutin et al. 1991) at -80°C until DNA extraction. I extracted whole genomic DNA from tissue samples using the QIAGEN DNeasy Blood & Tissue Kit (QIAGEN INC.) following the manufacturers protocol, with the exception that I digested tissue samples overnight in a proteinase K solution.

For each DNA sample, I amplified 14 microsatellite loci using primers developed for *E. blandingii* ([BTCA9; Libants et al. 2004] [Eb 09, Eb 17, Eb 19; Osentoski et al. 2002]) and bog turtle (*Glyptemys muhlenbergii*; *Gmu*D21, *Gmu*D55, *Gmu*D70, *Gmu*D87, *Gmu*D93, *Gmu*D121,

*Gmu*B08, *Gmu*A18, *Gmu*A19, *Gmu*A32; King and Julian 2004). Polymerase chain reaction (PCR) was carried out using the protocol described in Chapter Three. Fragment analysis of resulting PCR products was carried out on an automated Applied Biosystems (ABI) Prism 3730xl sequencer at the W. M. Keck Center at the University of Illinois, Champaign. An internal size standard was run with each sample (LIZ500). I scored alleles using GENEMAPPER 4.1 software (ABI) and identified possible null alleles, large allele dropout, and scoring errors due to stutter peaks using MICRO-CHECKER 2.2.3 (van Oosterhout et al. 2004).

Genetic analyses

Using only adult samples, I tested for linkage disequilibrium (Markov Chain parameters: 10000 dememorisation steps, 500 batches, 5000 iterations) between all pairs of loci and tested for departures from Hardy-Weinberg equilibrium for each locus using exact tests in GENEPOP 4.0 (Rousset 2008). I estimated allele frequencies, observed heterozygosity (H_o), and expected heterozygosity (H_e) using GENALEX 6.41 (Peakall and Smouse 2006).

Paternity analysis

To determine the number of offspring and clutches sired among males, I assigned paternity using GERUD 2.0 (Jones 2005) a software program that calculates exclusion probabilities for loci and reconstructs parental genotypes from arrays of full or half-sib progeny. Paternal genotypes were reconstructed based on genotypes of known mothers and their clutches and were then compared to genotypes of the 11 sampled candidate males in the population. I also used the results of the paternity analysis to determine if mating observations observed during radio-telemetry corresponded to sired offspring.

Determinants of male reproductive success

I examined the Pearson-product moment correlation coefficient (r) between male traits and reproductive success using the correlation (test.cor) function implemented in R software 2.13.2 (R Development Core Team 2011). Reproductive success was measured as total number of offspring sired over the course of the study. Male traits included body size (carapace length, CL), number of potential mates observed during radio-telemetry surveys, number of successful mates inferred from paternity analysis, and home range size (HR). For home range, I used 95% kernel density isopleth home range size that was estimated in Chapter One from all radio-locations collected for a respective male throughout its duration in the study. I also examined the correlation between CL vs. number of potential mates, CL vs. number of successful mates, HR vs. number of potential mates, and HR vs. number of successful mates. For all correlation analyses except number of successful mates vs. number of offspring, CL vs. number of successful mates, and CL vs. number of offspring I included only mature, radio-telemetered males that had sufficient locations to estimate multi-year home range size (N=7). One additional male with less than one year of location data was included in tests between number of successful mates vs. offspring, CL vs. number of successful mates, and CL vs. number of offspring.

Genetic compatibility and reproductive success

Genetic compatibility or effect of inbreeding avoidance on number of successful mates and clutch hatching success was assessed by estimating a relatedness coefficient (R) of male-female pairs in the program ML-RELATE (Kalinowski et al. 2006). Relatedness coefficients range from 0-1 with 0 indicating no relatedness and 1 indicating complete relatedness. I calculated a Pearson's product-moment correlation coefficient (r) between relatedness coefficients (R) and

successful pairings and hatching success. Because hatching success was low in 2007 and 2008, I tested the correlation between "R" and hatching success with and without the 2007 and 2008 data.

RESULTS

Reproductive and genetic data were collected from ten male and 19 female telemetry subjects (Table 4.1). Genetic data were also collected from three additional males and one female that were encountered during telemetry, but were not telemetry subjects. No other adult *E. blandingii* were encountered during 131,444 hours of trapping at the Will 1 site; thus, the numbers of males and females studied likely reflect a true female-biased sex ratio in the sites (Dreslik et al. 2011).

Timing and frequency of mating behavior

I recorded 39 distinct mating attempts between eight adult males and 15 adult females (Table 4.2). Mating attempts were observed throughout the active season except for June. Most attempts occurred during the spring and fall; however the greatest number of monthly observations was recorded in July (Fig.4.1). The total number of distinct mating attempts observed per male ranged from 0-10 and the total number of potential mates observed with a given male over the course the study ranged from 0-8 (Table 4.3). The total number of distinct mating attempts per female ranged from 0-5 and the total number of potential mates observed with a given female over the course the study ranged from 0-3. Two males (AXEL and RMEO) were never observed engaging in mating attempts (Table 4.3) and so were excluded from further analyses because although they exhibited secondary sexual characteristics, their size (plastron

lengths of 175 and 182 mm, respectively) suggests that they may not have been sexually mature (Ernst and Lovich 2009). In addition no clutches were obtained from two females (FRAN and CLET) because their transmitters failed early in the study and they were never recaptured. These females were also subsequently excluded from further analyses to reduce bias in comparisons between potential mating attempts and number of successful mates as inferred from paternity analyses.

Number of potential mates

Mean number of potential mates observed during radio-telemetry surveys varied among years and between telemetered males and females (Table 4.4A; Appendix J). Over four years of radio telemetry, males and females on average were observed with 3.8 and 1.5 potential mates, respectively. However, within-year estimates of potential mates were < 1 for two years in males and each of the four years in females (not all turtles were observed in mating attempts in each year). Average observed number of potential mates was lowest in 2006 (0.3) and highest in 2007 (1.3) but this variation likely reflects differences in the number of turtles radio-tracked during each year or differences in detection ability among field researchers between years. Nevertheless, males always averaged more potential mates than females (Table 4.4A). Four females were never observed engaging in mating behavior but each produced at least one clutch during the study. This demonstrates that we likely missed a number of mating observations during radio-telemetry surveys.

Clutch samples and hatching success

Most females (≥ 80%) produced a clutch in each nesting season in which they were monitored. However, some females had incomplete reproductive histories because I failed to locate six natural nests (four in 2007, two in 2008), transmitter failure before nesting season, or extremely short duration of telemetry. Two natural nests were completely depredated and one was partially depredated (clutch 27-08). One female (EDNA) monitored over four consecutive nesting seasons (2007-2010) never produced a clutch.

I collected 35 clutches (whole and partial) from 16 females for a total of 272 hatchlings with known mothers during 2007-2010 (Table 4.5). Number of hatchlings per clutch ranged from 1-18 hatchlings (mean = 8) and 28 clutches had at least three hatchlings; the minimum number necessary to detect more than two paternal alleles in a clutch (*i.e.* multiple paternity). I obtained hatchlings from one, two, and three clutches from five, seven, and four females, respectively, which allowed me to examine repeat paternity among years (see Parentage and Quantification of Mating Success section below).

Hatching success varied among years and among females but was lowest in 2007 and 2008 compared to 2009 and 2010 (Table 4.5) and is attributed to natural factors (*i.e.* flooding and ant infestation in 2007) and possibly to extended handling of clutches (transport of eggs to field station vs. immediate placement in incubator) and differences in incubation methods. Twenty-six clutches from naturally and artificially incubated nests contained 1-16 unviable eggs with no development, including four with a 100% failure rate (Table 4.5). Nine artificially incubated clutches produced 1-3 egg-bound or malformed/lethargic hatchlings. I assumed that malformed/lethargic individuals would not have emerged from the nest under natural

circumstances and did not consider them successful hatchlings when calculating hatching success.

Genetic analyses

All 33 adults and 272 hatchlings (alive and dead) were successfully genotyped across 14 microsatellite loci, but one non-telemetered female and one hatchling only yielded genotypes for 12 loci. For sampled adults, all loci conformed to the assumptions of Hardy-Weinberg equilibrium and no evidence of significant linkage disequilibrium was detected after Bonferroni correction (Table 4.6). Because the turtles at the Will 1 and Will 2 preserves were once part of a larger panmictic population and movement of individuals between sites has been documented (Chapter 1), and because pairwise F_{ST} comparisons between Will 1 and Will 2 showed no genetic differentiation (Chapter 3), I combined the two populations for subsequent analyses.

Male reproductive success

The program GERUD yielded either one (single paternity) or two (multiple paternity) possible sires for each clutch tested. Combined exclusion probabilities for the 14 loci with one parent known were > 0.99 (Table 4.6). Thus, paternity was easily established by comparing reconstructed paternal genotypes to the genotypes of the candidate male samples. Paternity was assigned to eight telemetered males and one un-sampled male (Table 4.5). The two telemetered males without any mating observations (AXEL and RMEO) failed to sire any offspring. The total number of offspring sired by each male was heavily skewed with one male siring 37% (N=102) of hatchlings (Fig. 4.2) and 36% of clutches (N=11; Tables 4.3 & 4.5; Fig. 4.3).

Quantification of mating success

Mean number of successful mating attempts varied among years and between telemetered males and females (Table 4.4B; Appendix J). Over four consecutive breeding seasons (2007-2010), males and females averaged 2.6 and 1.3 different mates, respectively. Six males (JAY, LIPA, EZRA, BIPA, VERN, and ZEB) sired offspring with 2-5 different females during the study. Six females (VLMA, MAUD, MRTH, HART, EZMR, and SMLY) sired offspring with two different males during the course of the study.

On 18 occasions, males attempted to mate with females with whom they were known to sire offspring at some point during the study. Of the 39 courtship observations documented during radio-telemetry, 22 observations could be compared to subsequent clutches acquired from females (Table 4.2). The remaining observations could not be used for comparisons because two females did not produce clutches during nesting seasons following observations that occurred in the preceding fall or spring and for 15 observations, mating success could not be determined because either nests could not be located, transmitter failure, or clutches had 100% hatch failure with no embryonic development. When considering the 23 clutches that were collected during the radio-telemetry project (clutches from 2007-2009 with at least one sampled hatchling) that could have been linked with behavioral data, nine out of the 22 observations (41%) corresponded with mating events that occurred during the fall or spring preceding the clutch (Tables 4.2 and 4.5). Conversely, there were 14 clutches with no apparent corresponding mating observation during the preceding fall or spring; however five of those clutches could potentially have been sired via stored sperm 1-2 years after the previous mating event but this is questionable because in most of those cases the females produced clutches sired by different males during that 1-2 year interim (Tables 4.2 and 4.5).

Determinants of male reproductive success

A significant positive correlation was observed for number of successful mates vs. number of offspring (r = 0.78, df = 6, $P = 0.022$) but no other male trait (CL, HR, number of potential mates) was related to number of offspring sired. No relationship between body size (CL) and number of potential or successful mates and no relationship between HR and number of potential or successful mates was detected.

Genetic compatibility and reproductive success

Relatedness coefficients (R) calculated for observed male-female pairs during radio-telemetry and male-female pairs that sired clutches ranged from 0-0.52 (Tables 4.2 and 4.5). At least 31% of observed pairings and 52% of clutches were produced from mated pairs with an $R > 0$. The correlation between relatedness and success of mating was negative but non-significant (r = -0.18, df = 39, $P = 0.272$). Further, I found no indication that relatedness affected hatching success with 2007 and 2008 clutches included (r = 0.09, df = 31, $P = 0.631$) or excluded (r = 0.17, df = 18, $P = 0.461$).

Detection of multiple paternity

Multiple paternity was detected in only three clutches (8%). Multiply sired clutches were produced by three different females (Table 4.5). At least three different paternal alleles were detected for the Eb09, BATC9, *Gmu*D70, *Gmu*A19, and *Gmu*B08 loci in clutch 40-09, BATC9, *Gmu*D70, and *Gmu*B08 in clutch 38-10, and *Gmu*D70 in clutch 26-08. One male (BIPA) contributed offspring in all three multiply sired clutches but sired a lower proportion of offspring in two of those clutches (Table 4.5). Paternity assignments for some males and multiple paternity

in some clutches could have gone undetected because I failed to locate six natural nests and four nests were completely unviable with no development and therefore no paternal DNA contribution.

Evidence of sperm storage

Across season sperm storage was confirmed in one clutch (11-08) that was sired by a male the nesting season (June 2008) following his death (August 2007). Circumstantial evidence suggests other possible instances of sperm storage. For example, female HART was observed in a mounted pair three times over a period of five days with male ZEB in September 2008 (Table 4.2); she had no clutch or other mating observations in 2009, but ZEB sired her entire clutch in 2010 (Table 4.5). Another male, BIPA, sired all of VLMA's offspring in 2009 and one offspring in VLMA's multiply sired clutch in 2010 suggesting that the one offspring in 2010 clutch was fertilized by stored sperm from the previous mating event. Further, repeat paternity between years was observed by three additional males (DRLD, EZRA, and JAY) and occurred in ten of 12 (83%) between-year, paired clutches. Only two females with singly sired paired clutches switched sires between years.

Levels of gene flow

Inter-population mating attempts were observed on three different occasions: one male (EZRA) from the Will 1 population was found mounting a female (LIMA) from the Will 2 population in 2008 and a Will 2 male (BIPA) was found mounting a Will 1 female (MAUD) in 2008 and 2009. However, one multiply sired clutch (26-08) was the only genetic evidence of male-mediated gene flow between populations.

DISCUSSION

In my study, behavioral observations were used to corroborate mating success and variation in reproductive success. This information provided insight into the social mating system as well as cryptic reproductive strategies such as mate choice and sperm storage. Using complementary methods of field observations of mating behavior with genetic parentage analysis of offspring, I was able to assess the mating system and reproductive success of *E. blandingii*. During four consecutive years of radio-telemetry monitoring, I observed male and female *E. blandingii* engaged in courtship behaviors with multiple individuals but parentage of clutches collected during 2007-2010 was strongly skewed towards one male and multiple paternity was rare. Male and females mated successfully with multiple individuals but successful matings did not always correspond with previously observed mating attempts. In males, number of mates was positively correlated with total number of offspring sired but I failed to detect inbreeding avoidance in observed mating pairs or a decrease in hatching success in related pairs. Previous chelonian mating system studies were important in documenting multiple paternity but were often limited to one breeding season without behavioral data and could only infer number of sires or assign paternity to candidate males (Valenzuela 2000, Ireland et al. 2003, Fantin et al. 2008, Refsnider 2009, Fantin et al. 2010). In such studies, it was not clear if multiply sired clutches were a result of polyandrous mating system or instead, a mix of a seasonally monogamous mating system with use of stored sperm from previous matings (Uller and Olsson 2008). More recent studies have examined parentage over multiple breeding seasons and have included field data to test hypotheses regarding sperm storage and multiple paternity (Pearse et al. 2001, 2002, Moore et al. 2009, Olsson et al. 2010, McGuire 2011, McGuire et al. 2011).

Timing and frequency of mating

Mating attempts in radio-telemetered *E. blandingii* were documented in every month except June (nesting season) and during the over-wintering period (mid-November to mid-March). These findings are similar to anecdotal observations in previous *E. blandingii* studies (Carr 1952, Graham and Doyle 1979). I observed most mating observations prior to overwintering in the fall and during post-emergence in the spring. Fall mating observations have been noted in Nova Scotia populations of *E. blandingii* (McNeil 2002) and could be attributed to aggregations of turtles at overwintering sites (Newton and Herman 2009). A high occurrence of mating has been documented in the spring for *E. blandingii* populations in Minnesota (Sajwaj and Lang 2000) and the Great Lakes Region (Harding 1997).

I recorded the highest number of mating observations in July; however seven of the ten July observations occurred in 2007. Most of the July 2007 courtship observations were clustered in the same wetland area and involved three and four different males and females, respectively. There was a white-tailed deer (*Odocoileus virginianus*) carcass in the marsh during that time that seemed to attract several turtles to this particular location, presumably to scavenge. The high density of turtles probably resulted in an increased encounter rate among individuals and the observed flurry of mating activity. It appears that mating attempts between individuals occur anytime there is an encounter and encounters are probably most frequent when turtles cluster or aggregate within the same areas such as those used for overwintering.

Number of potential mates

Because males and females were both observed with multiple partners during radio-telemetry surveys, the social mating system of *E. blandingii* in Will County, Illinois appears to

be promiscuous. Further, I observed male *E. blandingii* more frequently with multiple mates than females throughout the study. Similarly, Rovero et al. (1999) observed male European pond turtles (*Emys orbicularis*) to mount multiple females and females were mounted by multiple males. Kaufmann (1992) also reported that female wood turtles (*Glyptemys insculpta*) in central Pennsylvania mated with multiple males between nesting seasons. In my study, some courtship events were undetected. For example, there were 14 clutches sired by males with females for which no courtship pairing was observed in the field. Although much effort went into radio-tracking turtles multiple times a week, several mating events were likely undetected and observed courtship displays probably only represent a subset of total mating attempts in the population. Thus, number of courtship observations is likely to be underestimated and further supports a promiscuous mating system classification.

Male reproductive success

Males and females successfully mated with multiple individuals during the course of this study. McGuire (2011) and Refsnider (2009) also documented multiple mates for *E. blandingii* at the E. S. George Reserve in Michigan and a Minnesota population, respectively. In my study, although a total of nine males contributed offspring and two males sired offspring with at least five different females, parentage was strongly skewed towards one male that sired 37% of all offspring and 36% of all clutches. Disproportionate numbers of mates and skewed reproductive success among males have also been documented in other reptile populations (Roques et al. 2006, Moore et al. 2009). For example in a population of *E. orbicularis*, one male sired 57% of clutches (Roques et al. 2006). Although complete reproductive histories were missing for some turtles, it is still apparent that reproductive success was not equal among male *E. blandingii*.

Quantification of mating success

Conservatively, 41% of male mating attempts observed in the field resulted in sired offspring. This success rate is lower than that of 84% observed in a population of tuatara (*Sphenodon punctatus*), a seasonally monogamous reptile (Moore et al. 2009). In my study, over half of courtship observations in the field were not successful either because 1) females were not receptive and mounting behavior did not result in successful copulation, 2) post-copulation cryptic female mate-choice prevented successful fertilization, or 3) the prevalence of variation in sperm quality or sperm competition among males. In all observed courtship events, males displayed mounting behavior but copulation success was uncertain based on observations alone. In a group of wild-caught *E. blandingii* that were held in outdoor enclosures, only five copulations were observed out of more than 100 mating attempts (Baker and Gillingham 1983). Thus, low copulation frequency could explain why only a portion observed courtship events resulted in successful matings in my study.

Determinants of male reproductive success

Until recently, few reptile studies have evaluated the relationship between male traits and reproductive success (but see Kaufmann 1992, Pearse et al. 2002, Moore et al. 2009, Olsson et al. 2010, Tuberville et al. 2011). I predicted that males with larger home range sizes would encounter more females and subsequently have greater reproductive success. Only number of mates was positively correlated with number of offspring. There was no relationship between body size or home range size and reproductive success. Carapace length was also not a predictor of reproductive success in *C. picta* (Pearse et al. 2002) but body size was a predictor of reproductive success in *S. punctatus* (Moore et al. 2009), sand lizards (*Lacerta agilis*, Olsson et

al. 2010) and gopher tortoises (*Gopherus polyphemus*; Tuberville et al. 2011). Additionally, dominance in *G. insculpta*, as measured by observations of agonistic interactions during male-male encounters, was positively correlated to reproductive success (Kaufmann 1992, Galbraith and Kaufmann unpublished data). Amount of experience or age can also have an effect on reproductive success: older or more experienced individuals sire more offspring (Tuberville et al. 2011). Other than the two sub-adult males excluded from the study, I was unable to assess age of the remaining adult turtles because methods used to age young turtles such as annuli growth rings become indiscernible beyond sexual maturity (Sexton 1959b). Finally, small sample size may have obscured some relationships between male traits and reproductive success.

Genetic compatibility and reproductive success

Females may be reluctant to mate with particular males if they could detect a fitness disadvantage in the pairing, such as inbreeding (Amos et al. 2001, Stow and Sunnucks 2004, Miller et al. 2010). Levels of relatedness varied among male-female pairs but I found no indication that relatedness affected mating success or hatching success. Similar findings have been observed in the grand skink (*Oligosoma grande*), a promiscuous lizard from New Zealand (Berry 2006). Berry (2006) found that skinks mated with partners of varying relatedness but no effect of offspring survival was evident. However, inbreeding avoidance has been has been documented in fragmented populations of Cunningham's skink (*Egernia cunninghami*; Stow and Sunnucks 2004).

Detection of multiple paternity

Multiple paternity has been documented in many chelonian species (for recent reviews see, Uller and Olsson 2008, Refsnider 2009, Davy et al. 2011) and range from 4% (McTaggert 2000) to as high as 100% (Valenzuela 2000, Ireland et al. 2003, Fantin et al. 2008, Fantin et al. 2010). However, variation in sample sizes, proportions of clutches sampled, and number of loci used to infer paternity can make comparisons among studies difficult (Davy et al. 2011). In Will County, Illinois, I detected only 8% multiple paternity in 28 clutches; levels much lower than reported in previous studies of *E. blandingii*. Refsnider (2009) detected 56-81% multiple paternity in 16 clutches and McGuire (2011) detected on average 47% multiple paternity in 77 clutches. Discrepancies in levels of multiple paternity among populations have also been documented in studies of painted turtle (*Chrysemys picta*, 4-30%; McTaggert 2000, Pearse et al. 2001, 2002) and green sea turtle (*Chelonia mydas*, 9-61%; Fitzsimmons 1998, Lee and Hays 2004) that analyzed ≥ 18 clutches. Other freshwater chelonian studies with comparable sample sizes have also detected low estimates (~10%) of multiple paternity (Pearse et al. 2006, Roques et al. 2006). The low levels of multiple paternity detected in my study could be attributed to lower population density and a female biased sex ratio (Stephens and Sunderland 1999).

My estimate of multiple paternity is conservative because I was unable to locate some of the natural nests and some clutches were partially or completely depredated, thus some instances of multiple paternity may have been missed. Further, clutch size affects detection of multiple paternity (Kichler et al. 1999, Pearse et al. 2002, McGuire 2011) but I was able to detect multiple paternity in a clutch with as few as three hatchlings. Interestingly, one male (BIPA) contributed offspring to all three multiply sired clutches. Roques et al. (2006) also found that the same male contributed to both multiply sired clutches in their study of *E. orbicularis* and postulated that this

male may be of higher quality. Thus, BIPA may have higher sperm quality compared to other males, but little is known about sperm competition in turtles.

Hypotheses for the evolutionary advantages of multiple paternity include indirect female benefits such as increased genetic variation of offspring (Pearse et al. 2002, Pearse and Anderson 2009). However, Uller and Olsson (2008) argue that evidence for such benefits is lacking and that multiple paternity is more likely maintained by direct male fitness benefits from mating with multiple females, low female mating costs, and sperm competition. In his classic paper, Bateman (1948) noted that males are subject to stronger sexual selection and therefore should for strive for greater numbers of mates and exhibit more variable reproductive success than females. The results of my study are consistent with this pattern; number of mates and variation in reproductive success were higher among male than female *E. blandingii*. Though sample size precluded me from testing hatching success and genetic variation between single and multiply sired clutches, hatching success of both single and multiply sired clutches varied drastically (12-100%).

Evidence of sperm storage

Potential for sperm storage is high when females have multiple mates (Devine 1984). Discovery of oviductal sperm storage (Gist and Jones 1989, Gist and Congdon 1998) and the occurrence of offspring produced via stored sperm (Galbraith 1993, Pearse et al. 2001, 2002) have been documented in many chelonian species. I documented one confirmed instance of across-season sperm storage in *E. blandingii* when a male sired offspring the year after his death but also noted additional occurrences of potential sperm storage from repeat paternities and from comparisons of field observations with inferred parentage. Potentially, five clutches could have

resulted in fertilization using stored sperm 1-2 years after the observation. However, many of these females sired a clutch by another male during the interim, which raises questions about temporal viability in stored sperm and the effects of positional priority of sperm in the oviducts (see below).

Repeat paternities have been documented in multiple species including *C. picta* (Pearse et al. 2001, 2002, McGuire et al 2011), *E. orbicularis* (Roques et al. 2006), and *E. blandingii* (McGuire 2011). In species that produce multiple clutches within the same nesting season, repeat paternity is considered to be a result of sperm storage (Pearse et al. 2001, 2002, Roques et al. 2006, Sheridan 2010, McGuire et al. 2011) because of the low probability of a female remating with the same male during the interval between oviposition of and ovulation of successive clutches (Gist and Congdon 1998). Although stored sperm may also be used to fertilize clutches among years (Pearse et al. 2001, 2002, Sheridan 2010, McGuire et al. 2011), there is greater potential for remating to occur in the same pair of individuals between successive clutches for species that only lay one clutch per year. For example, *E. blandingii* often use the same core areas year after year (Congdon et al. 2011, Chapter One) and although turtles do not create pair bonds, turtles that tend to use the same core areas likely encounter the same mates over time. Thus repeated matings between some pairs of individuals are more likely than others. Intraspecific territoriality or mate guarding could also result in high variation in reproductive success and repeat matings (Emlen and Oring 1977). Some studies have documented intraspecific aggressive behaviors or dominance hierarchies in male freshwater turtles (Kaufman 1992, Rovero et al. 1999) but strong evidence for territoriality is lacking. I observed five instances of intrasexual mounting behavior between males during this study, involving five adult

males, one sub-adult male, and one juvenile male (unpublished data) but it is unclear whether these observations were dominance displays or misdirected mating attempts.

It is also not clear if the three multiply sired clutches in this study were fertilized by stored or recently inseminated sperm. The proportions of offspring sired by each male in the multiply sired clutches varied within each clutch. Proportions of offspring sired by males should depend on the contribution of sperm quantity or sperm quality of each male (Devine 1984). There is conflicting evidence regarding the relationship of fitness effects and the use of stored sperm. In *E. orbicularis*, use of stored sperm resulted in lowered hatching success and smaller hatchling size (Roques et al. 2006). Conversely, use of stored sperm had no effect on hatching success in *C. picta* (Pearse et al. 2002). In addition, the proportions of offspring sired by male *C. picta* in multiply sired clutches depended on mate order of the males: the last male to mate sired more offspring (Pearse et al. 2002). One instance of multiple paternity in my study supports this pattern of sperm storage; one male (BIPA) sired an entire female's clutch (38-09) in 2009 but only sired one of seven offspring in that female's clutch (38-10) the following year. The inference being that BIPA was the last mate in 2009, but may not have mated (sperm storage) or was other than last in 2010.

Conservation Implications

Because I was able to assign all offspring to eight sampled males and only one un-sampled male, and individuals had a tendency to be recaptured multiple times during the radio-telemetry project (Dreslik et al. 2011), I suspect that most individuals in our populations have been captured and that the number of adult samples is in accordance with actual population sizes for the preserves. Both locations consist of small remnant populations (~18 and ~ten adult

individuals for Will 1 and Will 2, respectively) with limited dispersal and gene flow occurring between them as evidenced by radio-telemetry surveys (Chapter One) and the parentage analysis conducted in this study. High variation in reproductive success and low levels of multiple paternity in the Will County populations compared to other *E. blandingii* populations (Refsnider 2009 and McGuire 2011) may be attributed to small population size, female biased sex ratios (Stephens and Sunderland 1999), and disruption of the mating system (Lane et al. 2011). Although males and females were observed with multiple partners, many of those mating attempts were unsuccessful. Whether this was caused by female-mate choice, sperm-competition, or lack of mate encounters (*i.e.* Allee effects) is not clear. It appears that mating success is related to number of mate encounters but identification of more refined determinants of male reproductive success will require additional research and long-term monitoring. This study examined reproductive success across four breeding seasons but this duration is still a short window of time considering the longevity (70+ years) and reproductive potential of *E. blandingii*.

Variation in reproductive success is thought to indirectly decrease effective population size N_e (Nunny 1993, Anthony and Blumstein 2000) and can result in loss of genetic diversity within just a few generations (Miller et al. 2009). Although I did not detect inbreeding avoidance or lowered reproductive success in related pairs, skewed reproductive success among so few individuals could have important genetic implications for the long-term persistence of remnant populations (Frankham 1996) as well as management efforts such as captive rearing (Moore et al. 2008b), reintroduction (Miller et al 2009), and translocation (Tuberville et al 2011). Further, turtles have life history traits such as delayed maturity and low juvenile survival that exacerbate declines and contribute to increased rates of genetic drift (Lee et al. 2011). Conservation plans

should seek to preserve or increase genetic variation for remnant turtle populations. Unfortunately, the most feasible way to achieve this goal at these sites is captive breeding or translocation of head-started individuals.

LITERATURE CITED

Allendorf, F.W., and G. Luikart. 2007. Conservation and the Genetics of Populations. Blackwell Publishing, Malden, Massachusetts.

Amos, W., J. Worthington Wilmer, K. Fullard, T.M. Burg, J.P. Croxall, D. Bloch, and T. Coulson. 2001. The influence of parental relatedness on reproductive success. Proceedings of the Royal Society of London B 268:2021-2027.

Andersen, L.W., K. Fog, and C. Damgaard. 2004. Habitat fragmentation causes bottlenecks and inbreeding in the European tree frog (*Hyla arborea*). Proceedings of the Royal Society of London, Series B, Biological Sciences 271:1293-1302.

Anthony, L.L. and D.T. Blumstein. 2000. Integrating behavior in wildlife conservation: the multiple ways that behavior can reduce N_e. Biological Conservation 95:303-315.

Baker R.F. and J.C. Gillingham. 1983. An analysis of courtship behavior in Blanding's turtle, *Emydoidea blandingii*. Herpetologica 39:166-173.

Banks, S.C., S.J. Ward, D.B. Lindenmayer, G.R. Finlayson, S.J. Lawson, and A.C. Taylor. 2005. The effects of habitat fragmentation on the social kin structure mating system of the agile antechinus, *Antechinus agilis*. Molecular Ecology 14:1789-1801.

Banning, W.J. 2007. Nesting ecology of the Blanding's turtle, *Emydoidea blandingii*, at the Lockport Prairie Nature Preserve, Will County, Illinois. INHS Technical Report 40:1-25.

Bateman, A.J. 1948. Intra-sexual selection in Drosophila. Heredity 2:349-368.

Berry, O.F. 2006. Inbreeding and promiscuity in the endangered grand skink. Conservation Genetics 7:427-437.

Caballero, A. 1994. Developments in the prediction of effective population size. Heredity 73:657-679.

Carr, A. 1952. Handbook of Turtles: The Turtles of the United States, Canada, and Baja California. Comstock Publishing Associates, Cornell University Press, Ithaca, New York, 542 pp.

Congdon, J.D., D.W. Tinkle, G.L. Breitenbach, and R.C. van Loben sels. 1983. Nesting ecology and hatching success in the turtle *Emydoidea blandingii*. Herpetologica 39:417-429.

Congdon, J.D., O.M. Kinney, and R.D. Nagle. 2011. Spatial Ecology and core-area protection of Blanding's turtle (*Emydoidea blandingii*). Canadian Journal of Zoology 89:1098-1106.

Congdon, J.D. and R.C. van Loben Sels. 1993. Relationships of reproductive traits and body size with attainment of sexual maturity and age in Blanding's turtles (*Emydoidea blandingii*). Journal of Evolutionary Biology 6:547-557.

Dale, S. 2001. Female-biased dispersal, low female recruitment, unpaired males, and the extinction of small and isolated bird populations. Oikos 91:344-356.

Davy, C.M., T. Edwards, A. Lathrop, M. Bratton, M. Hagan, B. Henen, K.A. Nagy, J. Stone, L.S. Hillard, R.W. Murphy. 2011. Polyandry and multiple paternities in the threatened Agassiz's desert tortoise, *Gopherus agassizii*. Conservation Genetics 12:1313-1322.

Devine, M.C. 1984. Potential for sperm competition in reptiles: behavioral and physiological consequences. In: Smith, R.L. (Ed.), Sperm Competition and the Evolution of Animal Mating Systems. Academic Press, London and New York, pp. 509-521.

Dreslik, M.J., W.J. Banning, N.K. Marioni, and C.A. Phillips. 2011. Monitoring of the Blanding's Turtle (*Emydoidea blandingii*) at the I-355 Des Plaines River Bridge Crossing: Final Report Illinois Natural History Survey Technical Report 2011(3):1-237pp.

Eberhard, W.G. 1996. Female Control: Sexual Selection by Cryptic Female Choice. Princeton University Press, Princeton, New Jersey, pp. 1-501.

Emlen, S.T. and L.W. Oring. 1977. Ecology, sexual selection, and the evolution of mating systems. Science 197:215-223.

Ernst, C.H. and J.E. Lovich. 2009. Turtles of the United States and Canada. 2nd edition. John Hopkins University Press, Baltimore. 827 pp.

Fantin, C., I.P. Farias, L.A.S. Monjeló, and T. Hrbek. 2010. Polyandry in the red-headed river turtle *Podocnemis erythrocepaphala* (Testudines, Podocnemididae) in the Brazilian Amazon. Genetics and Molecular Research 9:435-440.

Fantin, C., L.S. Viana, L.A.S. Monjeló, and I.P. Farias. 2008. Polyandry in *Podocnemis unifilis* (Pleurodira: Podocnemididae), the vulnerable yellow-spotted Amazon River turtle. Amphibia-Reptilia 29:479-486.

Fisher, P. 2003. Locating new venipuncture site in chelonians. Exotic DVM Vet Magazine 4:8.

Fitzsimmons, N.N. 1998. Single paternity of clutches and sperm storage in the promiscuous green turtle (*Chelonia mydas*). Molecular Ecology 7:575-584.

Frankham, R. 1996. Relationship of genetic variation to population size in wildlife. Conservation Biology 10:1500-1508.

Galbraith, D.A. 1993. Multiple paternity and sperm storage in turtles. Herpetological Journal 3:117-123.

Gibbons, J.W. 1968. Observations on the ecology and population dynamics of the Blanding's turtle, *Emydoidea blandingii*. Canadian Journal of Zoology 46:288-290.

Gibbons, J.W. and J.L. Greene. 1979. X-ray photography: a technique to determine reproductive patterns of freshwater turtles. Herpetologica 35:86-89.

Gibbs, J.P. and D.A. Steen. 2005. Trends in sex ratios of turtles in the United States: Implications of road mortality. Conservation Biology 19:552-556.

Gist, D.H. and J.D. Congdon. 1998. Oviductal sperm storage as a reproductive tactic of turtles. Journal of Experimental Zoology 282:526-534.

Gist, D.H. and J.M. Jones. 1989. Sperm storage within the oviduct of turtles. Journal of Morphology 199:379-384.

Graham, T.E. and T.S. Doyle. 1979. Dimorphism, courtship, eggs, and hatchlings of the Blanding's turtle, *Emydoidea blandingii*, (Reptilia, Testudines, Emydidae) in Massachusetts. Journal of Herpetology 13:125-127.

Harding, J.H. 1997. Amphibians and Reptiles of the Great Lakes Region. University of Michigan Press, pp. 378.

Ireland, J.S., A.C. Broderick, F. Glen, B.J. Godley, G.C. Hays, P.L.M. Lee, and D.O.F. Skibinski. 2003. Multiple paternity assessed using microsatellite markers, in green turtles *Chelonia mydas* (Linnaeus, 1758) of Ascension Island, South Atlantic. Journal of Experimental Marine Biology and Ecology. 291:149-160.

Jones, A.G. 2005. GERUD 2.0: a computer program for the reconstruction of parental genotypes from half-sib progeny arrays with known or unknown parents. Molecular Ecology Notes 5:708-711.

Joyal, L.A., M. McCollough, and M.L. Hunter, Jr. 2001. Landscape ecology approaches to wetland species conservation: a case study of two turtle species in southern Maine. Conservation Biology 15:1755–1762.

Kalinowski S.T, A.P. Wagner, and M.L. Taper. 2006. ML-Relate: a computer program for maximum likelihood estimation of relatedness and relationship. Molecular Ecology Notes 6:576-579.

Kaufmann, J.H. 1992. The social behavior of wood turtles, *Clemmys insculpta*, in central Pennsylvania. Herpetological Monographs 6:1-25.

Kichler, K., M.T. Holder, S.K. Davis, R. Márquez-M, and D.W. Owens. 1999. Detection of multiple paternity in Kemp's Ridley sea turtle with limited sampling. Molecular Ecology 8:819-830.

King, T.L. and S.E. Julian. 2004. Conservation of microsatellite DNA flanking sequence across 13 Emydid genera assayed with novel bog turtle (*Glyptemys muhlenbergii*) loci. Conservation Genetics 5:719-725.

Lane, J.E., M.N.K. Forrest, and C.K.R. Willis. 2011. Anthropogenic influences on natural animal mating systems. Animal Behaviour 81:909-917.

Lee, A.M., S. Engen, and B.-E. Saether. 2011. The influence of persistent individual differences and age at maturity on effective population size. Proceedings of the Royal Society of London, Series B, Biological Sciences 278:3303-3312.

Lee, P.L.M. and G.C. Hays. 2004. Polyandry in a marine turtle: females make the best of a bad job. Proceedings of the National Academy of Sciences 101:6530-6535.

Libants, S., A.M. Kamarainen, K.T. Scribner, and J.D. Congdon. 2004. Isolation and cross-species amplification of seven microsatellite loci from *Emydoidea blandingii*. Molecular Ecology Notes 4:300-302.

McGuire, J.M. 2011. Comparative analysis of factors influencing male reproductive success in sympatric freshwater turtles. Michigan State University, PhD Dissertation.

McGuire, J.M., J.D. Congdon, K.T. Scribner, and J.D. Capps. 2011. Variation in female reproductive quality and reproductive success of male Midland Painted Turtles (Chrysemys picta marginata). Canadian Journal of Zoology 89:1136-1145.

McNeil, J. 2002. Distribution, movements, morphology, and reproduction in a population of Blanding's turtles in an unprotected landscape in southwestern Nova Scotia. Acadia University, Wolfville, Nova Scotia, M.Sc. Thesis.

McTaggert, S.J. 2000. Good genes or sexy sons? Testing the benefits of female choice in the painted turtle, Chrysemys picta. University of Guelph, Ontario, M.S. Thesis.

Miller, K.A., N.J. Nelson, H.G. Smith, and J.A. Moore. 2009. How do reproductive skew and founder group size affect genetic diversity in reintroduced populations? Molecular Ecology 18: 3792-3802.

Miller, E.J., M.D.B. Eldridge, D.W. Cooper, and C.A. Herber. 2010. Dominance, body size and internal relatedness influence male reproductive success in eastern grey kangaroos (*Macropus giganteus*). Reproduction, Fertility and Development 22:539–549.

Mills, L.S. 2007. Predicting the dynamics of small and declining populations. In: Conservation of Wildlife Populations Demography, Genetics, and Management. Blackwell Publishing, Malden, Massachusetts, pp. 248-275.

Mills, S. and P.E. Smouse. 1994. Demographic consequences of inbreeding in remnant populations. American Naturalist 144:412-431.

Moore, J.A., C.H. Daugherty, S.S. Godfrey, and N.J. Nelson. 2009. Seasonal monogamy and multiple paternity in a wild population of a territorial reptile (tuatara). Biological Journal of the Linnean Society 98:161-170.

Moore, J.A., H.C. Miller, C.H. Daugherty, and N.J. Nelson. 2008a. Fine-scale genetic structure of a long-lived reptile reflects recent habitat modification. Molecular Ecology 17:4630-4641.

Moore, J.A., J.N. Nicola, S.N. Keall, and C.H. Daugherty. 2008b. Implications of social dominance and multiple paternity for the genetic diversity of a captive-bred reptile population (tuatara). Conservation Genetics 9:1243-1251.

Newton, E.J. and T.B. Herman. 2009. Habitat, movements, and behaviour of overwintering Blanding's turtles (*Emydoidea blandingii*) in Nova Scotia. Canadian Journal of Zoology 87:299-309.

Nunny, L. 1993. The influence of mating system and overlapping generations on effective population size. Evolution 47:1329-1341.

Olsson, M., E. Wapstra, T. Schwartz, T. Madsen, B. Ujvari, and T. Uller. 2010. In hot pursuit: Fluctuating mating system and sexual selection in sand lizards. Evolution 65:574-583.

Osentoski, M.F., S. Mockford, J.M. Wright, M. Synder, T.B. Herman, and C.R. Hughes. 2002. Isolation and characterization of microsatellite loci from the Blanding's turtle, *Emydoidea blandingii*. Molecular Ecology Notes 2:147-149.

Peakall, R., and P.E. Smouse. 2006. GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. Molecular Ecology Notes 6: 288-295.

Pearse, D.E. and E.C. Anderson. 2009. Multiple paternity increases effective population size. Molecular Ecology 18:3124-3127.

Pearse, D.E., F.J. Janzen, J.C. Avise. 2001. Genetic markers substantiate long-term storage and utilization of sperm by female painted turtles. Heredity 86:378-384.

Pearse, D.E., F.J. Janzen, J.C. Avise. 2002. Multiple paternity, sperm storage, and reproductive success of female and male painted turtles (*Chrysemys picta*) in nature. Behavioral Ecology and Sociobiology 51:164-171.

Pearse, D.E. and J.C. Avise. 2001. Turtle mating systems: Behavior, sperm storage, and genetic paternity. Journal of Heredity 92:206-211.

Pearse, D.E., R.B. Dastrup, O. Hernandez, and J.W. Sites Jr. 2006. Paternity in an Orinoco population of endangered Arrau river turtles, *Podocnemis expansa* (Pleurodira; Podocnemididae), from Venezuela. Chelonian Conservation and Biology 5:232-238.

Piepgras, S.A. and J.W. Lang. 2000. Spatial ecology of Blanding's turtle in central Minnesota. Chelonian Conservation and Biology 3:589-601.

Refsnider, J.M. 2009. High frequency of multiple paternity in Blanding's turtle (*Emys blandingii*). Journal of Herpetology 43:74-81.

Robertson, D.N. and M.J. Butler. 2009. Variable reproductive success in fragmented populations. Journal of Experimental Marine Biology and Ecology 377:84-92.

Roques, S., C. Díaz-Paniagua, A. Portheault, N. Pérez-Santigosa, and J. Hidalgo-Vila. 2006. Sperm storage and low incidence of multiple paternity in the European pond turtle, *Emys orbicularis*: a secure but costly strategy? Biological Conservation 129:236-243.

Rousset, F. 2008. GENEPOP'007: a complete re-implementation of the GENEPOP software for Windows and Linux. Molecular Ecology Resources 8:103-106.

Rovero, F., M. Lebboroni, and G. Chelazzi. 1999. Aggressive interactions and mating in wild populations of the European pond turtle *Emys orbicularis*. Journal of Herpetology 33:258-263.

Rowe, J.W. and E.O. Moll. 1991. A radiotelemetric study of activity and movements of the Blanding's turtle (*Emydoidea blandingii*) in northeastern Illinois. Journal of Herpetology 25:178-185.

Sajwaj, T.D. and J.W. Lang. 2000. Thermal ecology of Blanding's turtle in central Minnesota. Chelonian Conservation and Biology 3:626-636.

Seutin G., B.N. White, and P.T. Boag. 1991. Preservation of avian blood and tissue samples for DNA analyses. Canadian Journal of Zoology 69:82-90.

Sexton, O.J. 1959a. Spatial and temporal movements of a population of the painted turtle, *Chrysemys picta marginata* (Agassiz). Ecological Monographs 29:113-140.

Sexton, O.J. 1959b. A method of estimating the age of painted turtles for use in demographic studies. Ecology 40:716-718.

Sexton, O. J. 1995. Miscellaneous comments on the natural history of Blanding's turtle (*Emydoidea blandingii*). Transactions of the Missouri Academy of Science 29:1-13.

Sheridan, C.M. 2010. Mating system and dispersal patterns in the diamondback terrapin (*Malaclemys terrapin*). Drexel University, PhD Dissertation.

Stephens, P.A. and W.J. Sutherland. 1999. Consequences of the Allee effect for behaviour, ecology and conservation. Trends in Ecology and Evolution 14:401-405.

Stow, A.J. and P. Sunnucks. 2004. Inbreeding avoidance in Cunningham's skinks (*Egernia cunninghami*) in natural and fragmented habitat. Molecular Ecology 13:443-447.

Tainaka, K. and Y. Itoh. 1996. Glass effect in inbreeding-avoidance systems: Minimum viable population for outbreeders. Journal of the Physical Society of Japan 65:3379-3385.

Tuberville, T.D., T.M. Norton, B.J. Waffa, C. Hagan, and T.C. Glenn. 2011. Mating system in a gopher tortoise population established through multiple translocations: Apparent advantage of prior residence. Biological Conservation 144:175-183.

Uller T. and M. Olsson. 2008. Multiple paternity in reptiles: patterns and processes. Molecular Ecology 17:2566-2580.

Valenzuala, N. 2000. Multiple paternity in side-necked turtles *Podocnemis expansa*: evidence from microsatellite DNA data. Molecular Ecology 9:99-105.

van Oosterhout C., W.F. Hutchinson, D.P.M. Wills, P. Shipley. 2004. MICRO-CHECKER: software for identifying and correcting genotyping errors in microsatellite data. Molecular Ecology Notes 4:535-538.

Willi, Y., J. Van Buskirk, and A.A. Hoffman. 2006. Limits to the adaptive potential of small populations. Annual Review of Ecology, Evolution, and Systematics 37:433-458.

TABLES

Table 4.1 Turtle ID, site (Will 1 or Will 2), start of tracking duration, end of tracking duration, number of radio-locations (#Loc), carapace length in mm (CL) and 95% fixed kernel density isopleth in ha (95K) for 29 *E. blandingii* radio-tracked at two preserves in Will County, Illinois from 2006-2010.

ID	Site	Start	End	# Loc	CL	95K
Females						
EZMR	W1	28 MAY 2006	11 JUN 2008	277	195	9.5
PRMA	W1	14 JUN 2006	30 MAY 2010	475	200	18.4
JUDI	W1	23 JUN 2006	30 MAY 2010	435	212	22.8
FRAN	W1	15 JUL 2006	2 MAY 2007	113	199	10.4
BV	W1	2 JUL 2006	23 NOV 2009	463	200	20.7
CLET	W1	12 JUL 2006	8 AUG 2007	175	230	13.2
HART	W1	12 JUL 2006	27 MAY 2010	293	209	11.6
MRTH	W1	14 SEP 2006	30 MAY 2010	419	214	8.8
ETHL	W1	2 MAY 2007	23 MAY 2010	359	217	8.4
EDNA	W1	6 JUN 2007	7 JUN 2010	155	210	10.2
MILD	W1	18 JUN 2007	30 MAY 2010	293	194	13.1
CLRA	W1	14 NOV 2007	30 MAY 2010	234	211	16.2
MAUD	W1	16 MAY 2008	30 MAY 2010	219	208	9.3
LIMA	W2	6 MAY 2007	20 NOV 2009	375	195	12
BIMA	W2	11 MAY 2007	30 MAY 2010	362	205	11.9
VLMA	W2	23 APR 2008	30 MAY 2010	236	188	10.1
SMLY	W2	24 MAY 2008	15 APR 2010	208	201	20
NOEL	W2	17 NOV 2008	15 APR 2010	78	207	9.6
HOPE	W2	22 JUN 2009	30 MAY 2010	42	205	11.8
Males						
ZEB	W1	14 SEP 2006	19 OCT 2009	394	221	19.4
MNGO	W1	6 SEP 2006	15 OCT 2009	368	233	25.1
DRLD	W1	17 SEP 2006	13 OCT 2009	260	218	19.3
VERN	W1	29 MAR 2007	11 SEP 2007	104	226	12.6
JAY	W1	16 APR 2007	19 OCT 2009	302	234	23.7
EZRA	W1	29 JUL 2007	21 OCT 2009	276	221	19.1
RMEO	W1	26 AUG 2009	13 OCT 2009	10	184	.
AXEL	W2	7 MAY 2007	14 OCT 2009	266	185	8.7
BIPA	W2	23 JUL 2007	14 OCT 2009	309	230	15.6
LIPA	W2	3 AUG 2007	21 OCT 2009	287	196	14.6

Table 4.2 Mating attempts documented between 8 male and 15 female *E. blandingii* during radio-telemetry from 2006-2009 in Will County, Illinois. The relatedness coefficient (*R*) for each pair was calculated using ML-RELATE (Kalinowski et al. 2006). Mating attempts were considered successful if the observed pair parented a clutch during the nesting season following the observation. Mating success of observed pairs is denoted by a "?" when mating success could not be determined because nests could not be located, transmitters, or clutches had 100% hatch failure. Mating success is denoted by "N/A" when females did not produce a clutch during the nesting season following a documented mating attempt that occurred in the preceding fall or spring. The potential for sperm storage was noted for pairs that had no apparent mating success in the subsequent nesting season but that successfully produced clutches ≥ 1 year after the observation.

Observed Pair ♂	Observed Pair ♀	Month	Year	*R*	Mating Success	Potential Sperm Storage
BIPA	BIMA	JULY	2007	0.00	?	
BIPA	MAUD	MAY	2008	0.00	YES	
BIPA	MAUD	MAY	2009	0.00	?	
BIPA	VLMA	SEPT	2008	0.00	YES	
DRLD	JUDI	APRIL	2008	0.26	NO	
EZRA	LIMA	JULY	2008	0.00	?	
JAY	BV	OCT	2007	0.00	NO	
JAY	BV	APRIL	2009	0.00	NO	
JAY	CLET	JULY	2007	0.06	?	
JAY	CLET	AUG	2007	0.06	?	
JAY	EZMR	JULY	2007	0.00	NO	
JAY	FRAN	APRIL	2007	-----	?	
JAY	HART	MAY	2008	0.00	YES	
JAY	JUDI	SEPT	2008	0.00	YES	
JAY	MRTH	JULY	2007	0.16	NO	2 YRS
JAY	CLRA	NOV	2007	0.11	YES	.
LIPA	BIMA	OCT	2007	0.00	YES	
LIPA	BIMA	OCT	2008	0.00	?	
LIPA	LIMA	OCT	2007	0.13	YES	
LIPA	NOEL	NOV	2008	0.16	YES	
LIPA	VLMA	SEPT	2008	0.00	NO	2 YRS
LIPA	VLMA	OCT	2008	0.00	NO	2 YRS
LIPA	VLMA	APRIL	2009	0.00	NO	1 YR
MNGO	EDNA	SEPT	2008	0.00	N/A	
MNGO	ETHL	MAY	2007	0.00	?	2 YRS
MNGO	MAUD	APRIL	2009	0.00	?	
VERN	BV	JULY	2007	0.00	NO	
VERN	CLET	APRIL	2007	0.09	?	
VERN	EZMR	APRIL	2007	0.06	YES	
VERN	FRAN	MARCH	2007	-----	?	

Table 4.2 (Cont.)

Observed Pair ♂	♀	Month	Year	R	Mating Success	Potential Sperm Storage
VERN	FRAN	APRIL	2007	-----	?	
ZEB	BV	OCT	2007	0.38	NO	
ZEB	CLET	JULY	2007	0.00	?	
ZEB	CLET	JULY	2007	0.00	?	
ZEB	EZMR	SEPT	2006	0.00	NO	2 YRS
ZEB	HART	SEPT	2008	0.00	N/A	2 YRS
ZEB	JUDI	MAY	2009	0.00	NO	
ZEB	MRTH	JULY	2008	0.12	NO	
ZEB	BV	SEPT	2006	0.38	?	

Table 4.3 Number of potential mates and number of mating attempts observed during radio-telemetry surveys conducted from 2006-2009 as well as number of successful mates, clutches, and offspring inferred from parentage analysis from 2007-2010 for 19 female and 11 male *E. blandingii* from two forest preserves (Will 1 and Will 2) in Will County, Illinois. Females FRAN and CLET were radio-tracked for only a short duration and excluded from further analyses. Male UNKN was an un-sampled male detected during paternity analysis.

Name	Site	# Potential Mates	# Mating Attempts	# Successful Mates	# Clutches	# Offspring
Females						
EZMR	W1	3	3	2	2	14
MRTH	W1	2	2	2	3	30
ETHL	W1	1	1	1	1	18
EDNA	W1	1	1	0	0	0
PRMA	W1	0	0	1	3	26
MILD	W1	0	0	1	3	28
CLRA	W1	1	1	1	2	20
MAUD	W1	3	4	2	2	11
JUDI	W1	3	3	1	3	31
FRAN*	W1	2	3	0	0	0
BV	W1	3	5	1	2	9
CLET*	W1	3	5	0	0	0
HART	W1	2	2	2	2	18
BIMA	W2	2	3	1	1	4
LIMA	W2	2	2	1	2	20
VLMA	W2	2	4	2	2	15
SMLY	W2	0	0	2	1	10
NOEL	W2	1	1	1	1	9
HOPE	W2	0	0	1	1	9
Males						
MNGO	W1	3	3	1	1	18
DRLD	W1	1	1	1	2	9
VERN	W1	4	5	2	2	16
JAY	W1	8	10	5	8	102
EZRA	W1	1	1	2	3	37
RMEO	W1	0	0	0	0	0
ZEB	W1	6	8	2	1	21
AXEL	W2	0	0	0	0	0
BIPA	W2	3	4	3	3	14
LIPA	W2	4	7	5	4	46
UNKN*	W2	.	.	1	1	9

Table 4.4 Mean estimates of A) potential mating attempts and B) successful mating attempts for 19 female and ten male *E. blandingii* observed during radio-telemetry surveys conducted from 2006-2009 and inferred from parentage analysis of clutches obtained 2007-2010.

A)

Groups	2006	2007	2008	2009	All Years
Females	0.1	0.9	0.8	0.3	1.5
Males	0.7	2.0	1.7	0.7	3.8
Combined	0.3	1.3	1.0	0.4	2.2

B)

Groups	2007	2008	2009	2010	All Years
Females	0.8	0.9	0.9	1.0	1.3
Males	0.4	1.5	1.6	1.3	2.6
Combined	0.5	1.1	1.1	1.1	1.7

Table 4.5 Incubation method (natural vs. captive nest), year of oviposition, site (Will 1 vs. Will 2), known mother (♀), putative sire(s) (♂), number of eggs sampled (#Eggs), number of unviable eggs (#Unvbl.), number of dead/malformed hatchlings (#Dead), number of live hatchlings (#Live), total number of hatchlings sampled (N), relatedness coefficient (*R*) for male-female pairs, and hatching success for 35 clutches collected from 16 female *E. blandingii* in Will County, Illinois during 2007-2010. Clutches in bold indicate the sire was observed with the female during the spring or fall preceding the clutch. An "*" indicates that a clutch was multiply sired. A "+" indicates that a clutch was partially depredated before complete emergence. A "#" indicates that a clutch had 100% hatch failure and no sire could be determined.

Clutch	Incb.	Year	Site	♀	♂	#Eggs	#Unvbl.	#Dead	#Live	N	*R*	Hatch Success
01-07	Nat	2007	W1	EZMR	VERN	11	3	4	4	8	0.06	0.36
20-07#	Cap	2007	W2	LIMA	-----	16	16	0	0	0	-----	0
27-07#	Nat	2007	W2	BIMA	-----	14	14	0	0	0	-----	0
05-08	Cap	2008	W1	BV	DRLD	11	10	1	0	1	0.09	0
22-08	Cap	2008	W1	MILD	EZRA	15	0	2	13	16	0	0.87
26-08*	Cap	2008	W1	MAUD	BIPA/EZRA	18	15	1	2	3	0/0.01	0.11(0.11/0.0)
02-08	Cap	2008	W1	PRMA	JAY	14	12	0	2	2	0.52	0.14
03-08	Cap	2008	W1	JUDI	JAY	14	10	0	4	4	0	0.29
24-08	Cap	2008	W1	CLRA	JAY	14	7	3	4	7	0.11	0.29
11-08	Cap	2008	W1	MRTH	VERN	13	5	2	6	8	0.07	0.46
07-08	Cap	2008	W1	HART	JAY	15	12	1	2	3	0	0.13
01-08	Cap	2008	W1	EZMR	ZEB	11	5	3	3	6	0	0.27
16-08#	Cap	2008	W1	ETHL	-----	16	16	0	0	0	-----	0
20-08	Nat	2008	W2	BIMA	LIPA	11	9	0	4	4	0	0.36
27-08+	Nat	2008	W2	LIMA	LIPA	16	9	0	7	7	0	0.44
05-09	Cap	2009	W1	BV	DRLD	8	0	0	8	8	0.09	1
22-09	Cap	2009	W1	MILD	EZRA	11	9	2	0	2	0	0
26-09#	Cap	2009	W1	MAUD	-----	15	15	0	0	0	----	0
02-09	Cap	2009	W1	PRMA	JAY	14	1	0	13	13	0.52	0.93
03-09	Cap	2009	W1	JUDI	JAY	12	0	0	12	12	0	1
11-09	Cap	2009	W1	MRTH	JAY	11	4	0	7	7	0.07	0.64

Table 4.5 (Cont.)

Clutch	Incb.	Year	Site	♀	♂	#Eggs	#Unvbl.	#Dead	#Live	N	*R*	Hatch Success
24-09	Cap	2009	W1	CLRA	JAY	13	0	0	13	13	0.11	1
16-09	Cap	2009	W1	ETHL	MNGO	19	1	0	18	18	0	0.95
43-09	Cap	2009	W2	HOPE	UNKN	13	4	0	9	9	----	0.69
38-09	Nat	2009	W2	VLMA	BIPA	9	2	0	7	7	0	0.78
41-09	Nat	2009	W2	NOEL	LIPA	16	7	0	9	9	0.16	0.56
40-09*	Nat	2009	W2	SMLY	LIPA/BIPA	12	2	0	10	10	0/0.03	0.83(0.50/0.33)
22-10	Cap	2010	W1	MILD	EZRA	10	0	0	10	10	0	1
26-10	Cap	2010	W1	MAUD	EZRA	12	4	0	8	8	0.01	0.67
02-10	Cap	2010	W1	PRMA	JAY	11	0	2	9	11	0.52	0.82
03-10	Cap	2010	W1	JUDI	JAY	16	1	0	15	15	0	0.94
11-10	Cap	2010	W1	MRTH	JAY	15	0	0	15	15	0.07	1
07-10	Cap	2010	W1	HART	ZEB	15	0	0	15	15	0	1
27-10	Cap	2010	W2	LIMA	LIPA	13	0	2	11	13	0.13	0.85
38-10*	Cap	2010	W2	VLMA	LIPA/BIPA	8	0	0	8	8	0/0	1.00(0.88/0.13)

Table 4.6 Number of alleles, observed heterozygosity (H_o), expected heterozygosity (H_e), probability of violating Hardy-Weinberg equilibrium (*P*-HWE), and parentage exclusion probability for 14 loci amplified for 33 adult *E. blandingii* sampled from two preserves in Will County, Illinois. Significance level $\alpha = 0.004$ after Bonferroni correction.

Locus	**A**[#]	**H_o**	**H_e**	***P*-HWE**	**Exclusion Probability**
BATC9	12	0.818	0.837	0.17	0.68
Eb09	9	0.758	0.729	0.84	0.53
Eb17	6	0.727	0.675	0.35	0.42
Eb19	3	0.667	0.617	0.42	0.32
*Gmu*A18	2	0.212	0.351	0.03	0.15
*Gmu*A19	5	0.688	0.755	0.35	0.52
*Gmu*A32	2	0.182	0.165	1.00	0.08
*Gmu*B08	3	0.152	0.169	0.22	0.09
*Gmu*D121	6	0.455	0.592	0.02	0.38
*Gmu*D21	2	0.121	0.213	0.05	0.10
*Gmu*D55	5	0.727	0.670	0.47	0.43
*Gmu*D70	11	0.906	0.804	0.50	0.64
*Gmu*D87	8	0.667	0.618	0.76	0.35
*Gmu*D93	2	0.333	0.351	0.65	0.15

FIGURES

Fig. 4.1 Total number of unique mounting behavior (*i.e.* potential mating) observations of male-female pairs among eight male and 15 female *E. blandingii* during radio-telemetry surveys from 2006-2009 at two forest preserves in Will County, Illinois.

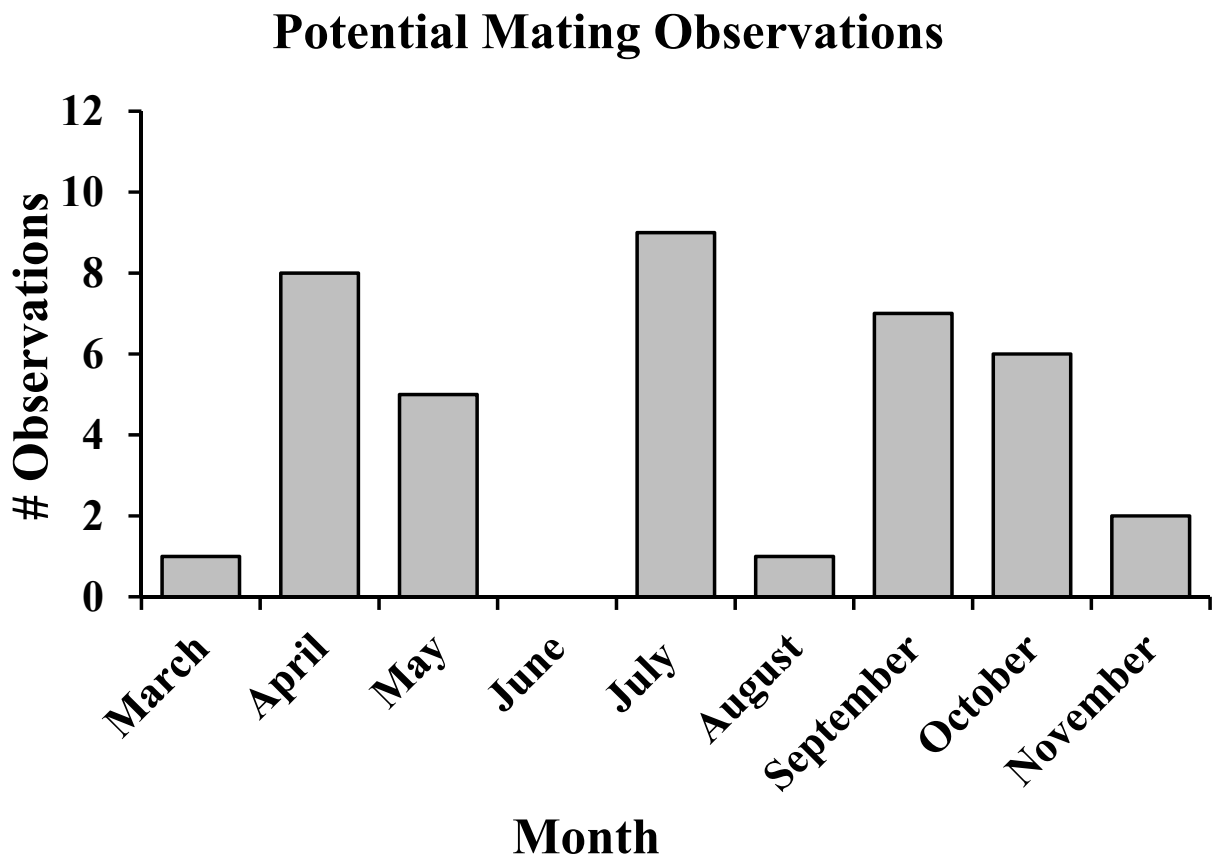


Fig. 4.2 Total number offspring sired by nine male *E. blandingii* from 2007-2010 at two forest preserves in Will County, Illinois.

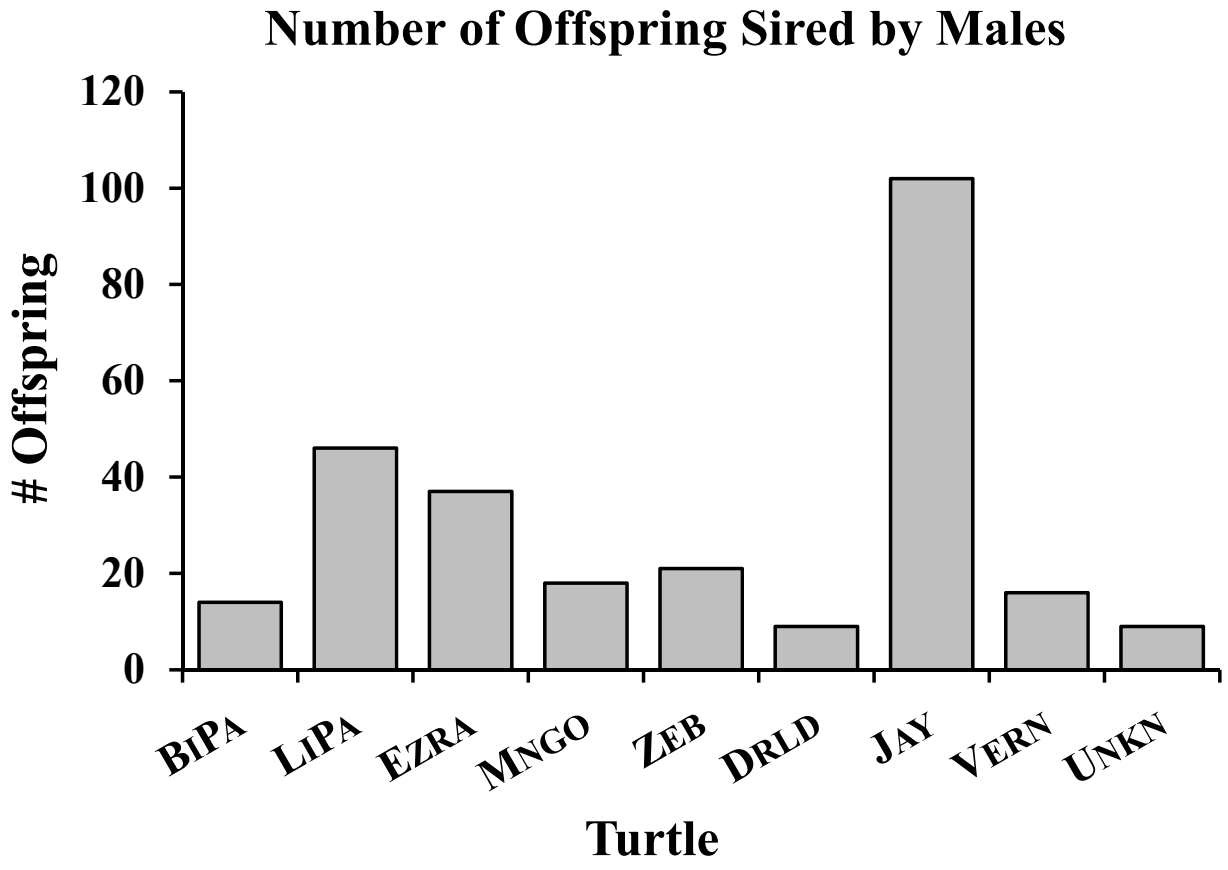
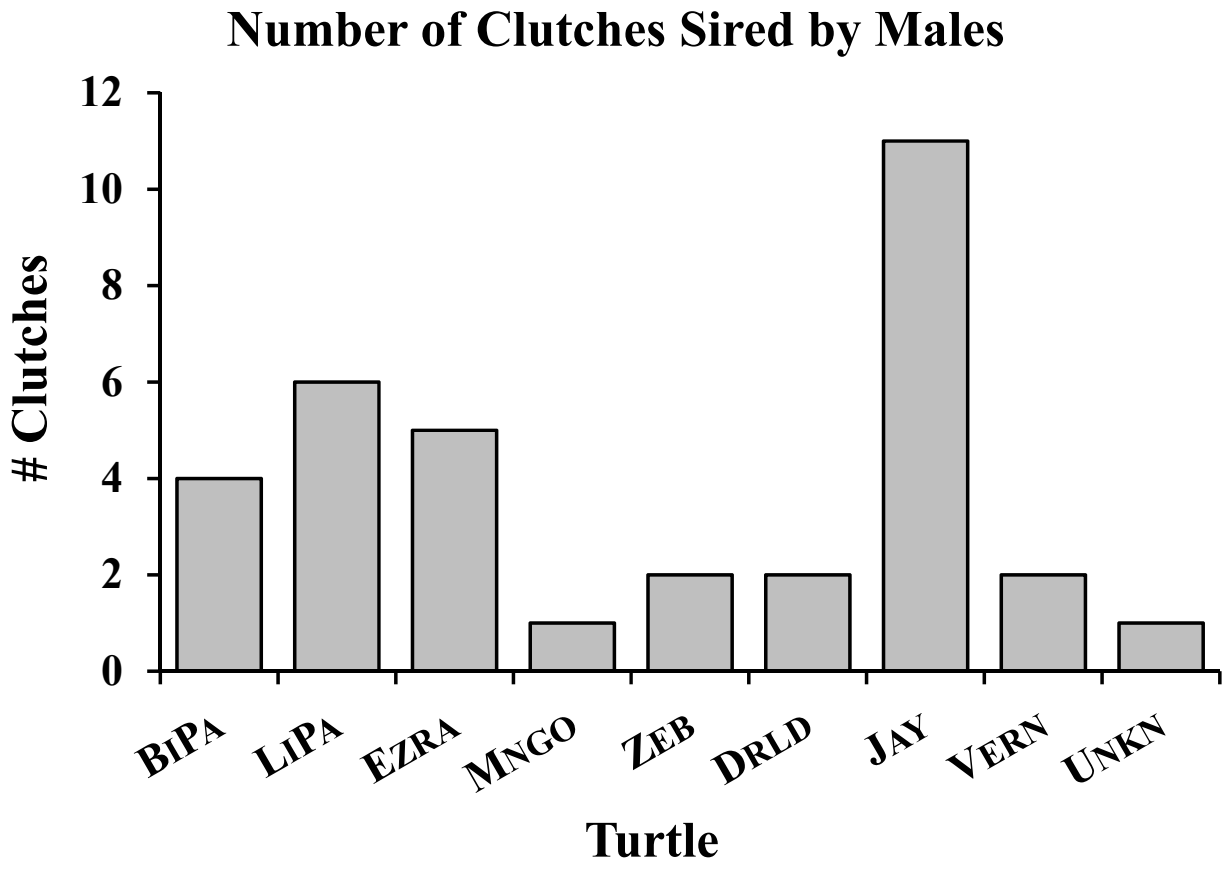


Fig. 4.3 Total number clutches sired by nine male *E. blandingii* from 2007-2010 at two forest preserves in Will County, Illinois.



CHAPTER 5

SUMMARY

Landscape alteration has been identified as the primary cause of species declines and loss of biodiversity worldwide (Ballie et al. 2004, Stuart et al. 2004, Thomas et al. 2004). The most serious impacts of landscape alteration are those attributed to habitat fragmentation such as habitat loss, decreased patch size, and isolation (Fahrig 2003, Ewers and Didham 2005). Habitat fragmentation can have serious implications for the population viability of long-lived organisms such as turtles (Gibbons et al. 2000, Mitchell and Klemens 2000, Beaudry et al. 2008) that have life history traits, such as delayed maturation, that tend to exacerbate declines (Congdon and van Loben Sels 1993, Congdon et al. 1993, 1994). In addition, variation in traits among turtle species such as dispersal ability, body size, abundance, and ecological specialization are proposed to influence response to fragmentation (Ewers and Didham 2005). Assessing such traits among species will aid in understanding species-specific sensitivity to landscape change and assist in conservation strategies for turtles.

The main goal of this study was to examine attributes of a turtle assemblage that could create variation in connectivity and long-term persistence among species within a fragmented landscape in northeastern Illinois. I studied five freshwater turtle species that occur in remnant preserves within Lower Des Plaines River Valley (LDPRV). These species vary in traits (e.g. longevity, rarity) that should affect how they are responding to recent (past 150 years) anthropogenic fragmentation. I used contemporary techniques such as radio-telemetry as well as biochemical tools such as nuclear markers to address the study's objectives. First, I analyzed movement among Blanding's turtle (*Emydoidea blandingii*) across three fragmented sites, spotted turtle (*Clemmys guttata*) across two fragmented sites, and eastern musk turtle

(*Sternotherus odoratus*), common snapping turtle (*Chelydra serpentina*), and painted turtle (*Chrysemys picta*) at one isolated site. I then examined habitat partitioning and measures of niche breadth among those five species at the isolated site. Next, I assessed the genetic diversity and gene flow among *E. blandingii*, *C. picta*, and *C. serpentina* among three fragmented and one intact site within the LDPRV. Finally, I examined the mating system and reproductive success of *E. blandingii* across two adjacent remnant sites.

Movement and home range estimates were larger for adult than juvenile *E. blandingii*. Of the five species, differences between males and females were evident only in *C. guttata*, with females having larger mean daily distances (MDD) and a greater number of core home range areas (#C) than males. Such differences have been attributed to nesting forays of gravid females in previous studies of *C. guttata* (Wilson 1994, Litzgus and Mousseau, 2004). In addition, significant differences in MDD, minimum convex polygon home range estimates (MCP), and home range length (HRL) were detected between sites in *E. blandingii* and *C. guttata*. Variation in amount, type, and distribution of wetland area across sites likely explains why individuals moved farther at one site versus another. I also detected differences in movement and home range among species at the Will 3 site. Adult *E. blandingii* and *C. picta* had larger home range estimates than *C. guttata*. In addition, all species moved greater daily distances (MDD) than *C. guttata*. Studies have shown that *E. blandingii* are capable of making long overland forays (> 1 km) between wetlands and to nesting sites (Ernst and Lovich, 2009, Chapter One), whereas the other species were more restricted to movements within wetlands. I observed three *E. blandingii* to move between sites (Will 1 and Will 2) during this study. Although, *E. blandingii* are considerably more vagile than the other species in this study*, S. odoratus*, *C. serpentina*, and *C. picta* were also capable of making long distance aquatic movements (≥ 1 km) via the Des Plaines

River. Conversely, *C. guttata* made the shortest movements and had the lowest home range estimates compared to all other species.

Patterns of macro- and micro-habitat use also varied among the five species. All species used multiple macro-habitat types but the rare turtle species, *E. blandingii* and *C. guttata*, most frequently used cattail marsh macro-habitats whereas the common species (*C. picta*, *C. serpentina*, and *S. odoratus*) most frequently used pond macro-habitats. In addition, use of mesic prairie, sedge meadow, river, and pond macro-habitats differed between *C. guttata* and common species while only use of pond macro-habitats differed between *E. blandingii* and two common species, *S. odoratus*, and *C. picta*. I found that species most strongly partitioned micro-habitat along an axis comprised of water depth, water and vegetative surface cover, vegetation height, and understory canopy cover. Proportion of organic substrates at radio-locations was also an important variable that differentiated habitat use among species in this study; use of organic substrates was highest among *C. guttata* and *E. blandingii*. In both levels of habitat analyses, *C. guttata* appeared to be the most restricted in use of habitat and appears to be a habitat specialist whereas *E. blandingii* and *C. serpentina* broadly and similarly used macro- and micro-habitats and maintained a relatively large measure of niche breadth suggesting that they are habitat generalists. My results suggest that *C. guttata* is most vulnerable to degradation of high quality interior shallow cattail marsh, sedge meadow, and mesic dolomite prairie from siltation caused by flooding of the Des Plaines River and that broad variation in water and vegetation micro-habitat characteristics is necessary to support a diverse freshwater turtle community.

All species (*E. blandingii*, *C. picta*, *C. serpentina*) demonstrated moderate to high levels of genetic diversity and no indication of inbreeding. In comparisons between the intact and fragmented LDPRV sites, none of the species demonstrated lower levels of genetic diversity in a

fragmented site. Standardized comparisons of genetic divergence among species showed that *E. blandingii* was more differentiated across sites than *C. picta* or *C. serpentina* and I only detected significant pairwise F_{ST} differentiation in *E. blandingii* and *C. serpentina*. Although F_{ST} values were low (0.018-0.029), *E. blandingii* were differentiated between the intact and each of fragmented sites as well as between two of the fragmented sites. Conversely, significant differentiation of *C. serpentina* between fragmented sites is likely a result of small sample sizes across sites. Gene flow was male-biased in *E. blandingii* across the fragmented sites but patterns of dispersal between males and females in *C. picta* and *C. serpentina* were not strong. I found no evidence of genetic population bottlenecks in any species but simulations of future genetic diversity suggest that *E. blandingii* is more vulnerable to loss of genetic diversity than *C. picta* or *C. serpentina*.

During four consecutive years of radio-telemetry monitoring, I observed promiscuous mating behavior in *E. blandingii* as both males and females engaged in mating attempts with multiple individuals. A total of nine males contributed offspring. Two males sired offspring with at least five different females but parentage was strongly skewed towards one male that sired 37% of all offspring and 36% of all clutches collected during 2007-2010. Male and females mated successfully with multiple individuals but successful matings did not always correspond with observed mating attempts; only 41% of male mating attempts observed in the field resulted in sired offspring. In males, number of mates was positively correlated with total number of offspring sired but I failed to detect a relationship between inbreeding avoidance in observed mating pairs or a decrease in hatching success and relatedness between male and female pairs.

Potential for sperm storage is high when females have multiple mates (Devine 1984) and sperm storage has been documented in freshwater turtle species (Galbraith 1993, Pearse and

Avise 2001, Pearse et al. 2001, 2002). Although I documented many repeat paternities in clutches among years, I only documented one confirmed instance of across season sperm storage in *E. blandingii* when a deceased male sired offspring the year after he died. I also detected only 8% multiple paternity in 28 clutches; levels much lower than reported in previous *E. blandingii* studies (Refsnider 2009, McGuire 2011). High variation in reproductive success and low levels of multiple paternity in the Will County populations compared to other *E. blandingii* populations (Refsnider 2009 and McGuire 2011) may be attributed to small population size, female biased sex ratios (Stephens and Sunderland 1999), and disruption of the mating system (Lane et al. 2011).

Conclusion

Characteristics examined in this study including vagility, niche breadth, genetic diversity, and reproductive success are all elements that contribute to the viability of species in altered landscapes (Ewers and Didham 2005). Each species in this study has its own unique combination of traits and requirements that should affect how it is responding to the recent anthropogenic habitat loss and fragmentation within the LDPRV. Variation in abundance (endangered vs. common) and life history traits such as generation time and reproductive frequency vary among these species and will affect population growth accordingly.

The response of state-listed species, *E. blandingii* and *C. guttata*, is of particular concern to wildlife management agencies in this region. For *E. blandingii*, the ability for long distance movements (Chapter One) and broad niche breadth, including the use of the Des Plaines River (Chapter Two), should increase connectivity in the fragmented landscape of the LDPRV. However, remnant sites have relatively few *E. blandingii* (Banning 2006, Banning et al. 2006,

Dreslik et al. 2011) and evidence for loss of genetic diversity and genetic drift (Chapter Three). Thus, successful dispersal among sites is probably limited at best. Reproductive success in this species was skewed but inbreeding avoidance and inbreeding effects were not apparent suggesting that loss of genetic diversity may not be an immediate threat in such a long-lived species. For *C. guttata*, restricted use of high quality marsh and sedge meadow habitats put it at greater risk of habitat degradation (e.g. siltation) but its smaller home range size and shorter movements compared to the other species may actually decrease its vulnerability to isolation than the other species. Genetic diversity and differentiation has yet to be assessed for this species.

The "common" species, *C. picta*, *C. serpentina*, and *S. odoratus*, appear to be capable of long distance movements via the Des Plaines River (Chapter One) and generally use habitats of less quality (Chapter Two) indicating that they are more resilient to habitat degradation and isolation. However, unlike *E. blandingii*, no marked individuals of these species have been recaptured at sites other than their site of original capture (Dreslik et al 2011). Although I found no evidence of loss of genetic diversity in *C. picta*, genetic patterns across sites were less clear for *C. serpentina* (Chapter Three). Additional sampling is needed to confirm subtle instances of divergence that I observed in *C. serpentina*.

LITERATURE CITED

Ballie, J.E.M., C. Hilton-Taylor, and S.N. Stuart. 2004. 2004 IUCN Red List of Threatened Species: A global species assessment. IUCN, Gland, Switzerland and Cambridge, UK. xxiv + 191 pp.

Banning W.J. .2006. Ecology of the Blanding's Turtle (*Emydoidea blandingii*) at a Northeastern Illinois Wetland Community. Unpublished. Masters Thesis, University of Illinois Urbana Champaign, Illinois.

Banning W.J., M.J. Dreslik, C.A. Phillips. 2006. Continued study of the ecology of the freshwater turtle community at Lockport Prairie Nature Preserve: With special emphasis on the Blanding's turtle (*Emydoidea blandingii*). Illinois Natural History Survey, Center for Biodiversity, Technical Report 2006(4):1–259pp.

Beaudry, F., P.G. deMaynadier, M.L. Hunter Jr. 2008. Identifying road mortality threat at multiple scales for semi-aquatic turtles. Biological Conservation 141:2550-2563.

Congdon, J.D., A.E. Dunham, and R.C. van Loben Sels. 1993. Delayed sexual maturity and demographics of Blanding's turtles (*Emydoidea blandingii*): Implications for conservation and management of long-lived organisms. Conservation Biology 7:826–833.

Congdon, J. D., A.E. Dunham, and R.C. van Loben Sels. 1994. Demographics of common snapping turtles (*Chelydra serpentina*): Implications for conservation and management of long-lived organisms. American Zoologist 34:397–408.

Congdon, J.D. and R.C. van Loben Sels. 1993. Relationships of reproductive traits and body size with the attainment of sexual maturity and age in Blanding's turtles (*Emydoidea blandingii*). Journal of Evolutionary Biology 6:547-557.

Devine, M.C. 1984. Potential for sperm competition in reptiles: behavioral and physiological consequences. In: Smith, R.L. (Ed.), Sperm Competition and the Evolution of Animal Mating Systems. Academic Press, London and New York, pp. 509-521.

Dreslik, M.J., W.J. Banning, N.K. Marioni, and C.A. Phillips. 2011. Monitoring of the Blanding's Turtle (*Emydoidea blandingii*) at the I-355 Des Plaines River Bridge Crossing: Final Report Illinois Natural History Survey Technical Report 2011(3):1-237pp.

Ernst, C.H. and J.E., Lovich. 2009. Turtles of the United States and Canada. 2nd edition. John Hopkins University Press, Baltimore.

Ewers, R.M. and R.K. Didham. 2006. Confounding factors in the detection of species responses to habitat fragmentation. Biological Review 81:117-142.

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

Galbraith, D.A. 1993. Multiple paternity and sperm storage in turtles. Herpetological Journal 3:117-123.

Gibbons, J.W., D.E. Scott, T.J. Ryan, K.A. Buhlmann, T.D. Tuberville, B.S. Metts, J.L. Green, T. Mills, Y. Leiden, S. Poppy, and C.T. Winne. 2000. The global decline of reptiles, déjà vu amphibians. BioScience 50:653-666.

Lane, J.E., M.N.K. Forrest, and C.K.R. Willis. 2011. Anthropogenic influences on natural animal mating systems. Animal Behavior 81:909-917.

Litzgus, J.D., and T.A. Mousseau. 2004. Home range and seasonal activity of southern spotted turtles (*Clemmys guttata*): Implications for management. Copeia 2004:804-817.

McGuire, J.M. 2011. Comparative analysis of factors influencing male reproductive success in sympatric freshwater turtles. Michigan State University, PhD Dissertation.

Mitchell, J.C. and M.W. Klemens. 2000. Primary and secondary effects of habitat alteration. In: Klemens, M.W. (Ed.), Turtle Conservation. Smithsonian Institution Press, Washington, pp. 5-32.

Pearse, D.E., F.J. Janzen, and J.C. Avise. 2001. Genetic markers substantiate long-term storage and utilization of sperm by female painted turtles. Heredity 86:378-384.

Pearse, D.E., F.J. Janzen, and J.C. Avise. 2002. Multiple paternity, sperm storage, and reproductive success of female and male painted turtles (*Chrysemys picta*) in nature. Behavioral Ecology and Sociobiology 51:164-171.

Pearse, D.E. and J.C. Avise. 2001. Turtle mating systems: Behavior, sperm storage, and genetic paternity. Journal of Heredity 92:206-211.

Refsnider, J.M. 2009. High frequency of multiple paternity in Blanding's turtle (*Emys blandingii*). Journal of Herpetology 43:74-81.

Stephens, P.A. and W.J. Sutherland. 1999. Consequences of the Allee effect for behaviour, ecology and conservation. Trends in Ecology and Evolution 14:401-405.

Stuart, S.N., J.S. Chanson, N.A. Cox, B.E. Young, A.S.L. Rodrigues, D.L. Fischman, and R.W. Waller. 2004. Status and trends of amphibian declines and extinctions worldwide. Science 306:1783-1786.

Thomas, J.A., M.G. Telfer, D.B. Roy, C.D. Preston, J.J.D. Greenwood, J. Asher, R. Fox, R.T. Clarke, and J.H. Lawton. 2004. Comparative losses of British butterflies, birds, and plants and the global extinction crisis. Science 303:1879-1881.

Wilson, T.P. 1994. Ecology of the spotted turtles, *Clemmys guttata*, at the western range limit. Masters Thesis, Eastern Illinois University, Charleston, Illinois. 97 pp.

APPENDIX A

SPATIAL METRICS FOR EMYDOIDEA BLANDINGII

Spatial metrics for 80 *E. blandingii* radio-tracked at Will County, Illinois from 2005-2010. Listed are: turtle identification number (#), site, sex, carapace length (CL), start of tracking duration, end of tracking duration, number of radio-locations (#Loc), minimum convex polygon (MCP), mean daily distance moved (MDD), 95% fixed kernel density isopleth (95K), 50% fixed kernel density isopleth (50K), number of 50% fixed kernel density isopleths (#C), and home range length (HRL).

#	Site	Sex	CL (mm)	Start	End	# Loc	MCP (ha)	MDD (m)	95K (ha)	50K (ha)	#C	HRL (m)
1	KPFP	F	195	28 May 2006	11 Jun 2008	277	13.5	30.8	9.5	1.4	1	721.8
2	KPFP	F	200	14 Jun 2006	30 May 2010	475	26.0	29.7	18.4	1.5	2	1108.8
3	KPFP	F	212	23 Jun 2006	30 May 2010	435	49.6	48.4	22.8	3.0	2	1535.2
4	KPFP	F	199	15 Jul 2006	2 May 2007	113	14.2	16.1	10.4	1.0	1	614.6
5	KPFP	F	200	2 Jul 2006	23 Nov 2009	463	29.7	29.3	20.7	1.1	1	1060.8
6	KPFP	F	230	12 Jul 2006	8 Aug 2007	175	30.2	49.9	13.2	1.3	1	1052.1
7	KPFP	F	209	12 Jul 2006	27 May 2010	293	43.2	31.9	11.6	1.1	1	1366.2
8	KPFP	F	177	7 Jul 2006	20 Jul 2006	10	.	.	.	.	.	.
9	KPFP	M	221	14 Sep 2006	19 Oct 2009	394	37.6	43.0	19.4	2.1	2	960.3
10	KPFP	M	233	6 Sep 2006	15 Oct 2009	368	94.2	79.4	25.1	1.7	2	2603.0
11	KPFP	F	214	14 Sep 2006	30 May 2010	419	23.6	31.0	8.8	1.3	1	873.1
12	KPFP	M	218	17 Sep 2006	13 Oct 2009	260	40.9	56.6	19.3	1.1	1	1127.8
13	KPFP	J	155	27 Oct 2006	30 May 2010	419	62.4	35.4	11.9	1.8	1	2066.0
14	KPFP	M	226	29 Mar 2007	11 Sep 2007	104	14.4	50.7	12.6	2.1	2	1043.9
15	KPFP	J	141	23 Apr 2007	15 May 2007	19	.	.	.	.	.	.
16	KPFP	F	217	2 May 2007	23 May 2010	359	20.9	39.3	8.4	1.1	1	1333.9
17	KPFP	M	234	16 Apr 2007	19 Oct 2009	302	73.4	71.9	23.7	1.0	1	2149.5
18	KPFP	F	210	6 Jun 2007	7 Jun 2010	155	34.2	59.0	10.2	1.0	1	1955.8
19	KPFP	J	156	25 May 2007	15 Oct 2009	334	13.1	37.3	6.2	1.3	1	1275.8
20	KPFP	J	128	7 Jul 2007	15 Oct 2009	328	7.1	27.9	4.1	1.1	1	741.9
21	KPFP	J	150	7 Jul 2007	15 Oct 2009	145	2.7	28.0	4.8	1.3	1	327.7
22	KPFP	F	194	18 Jun 2007	30 May 2010	293	33.2	41.1	13.1	1.3	1	1272.0
23	KPFP	M	221	29 Jul 2007	21 Oct 2009	276	109.3	94.4	19.1	2.3	1	4231.9
24	KPFP	F	211	14 Nov 2007	30 May 2010	234	21.5	38.2	16.2	1.1	1	995.7
25	KPFP	M	180	26 Apr 2008	21 Oct 2009	230	26.4	47.5	8.4	1.2	1	1210.4
26	KPFP	F	208	16 May 2008	30 May 2010	219	10.4	33.7	9.3	1.1	1	948.7
27	KPFP	F	195	23 Mar 2009	21 Jul 2009	60	8.4	44.7	13.6	2.4	3	1277.5
28	KPFP	F	181	10 Apr 2009	13 Oct 2009	80	24.9	43.9	18.6	2.4	2	1041.3
44	KPFP	J	106	5 Jul 2009	15 Oct 2009	27	.	.	.	.	.	.

#	Site	Sex	CL (mm)	Start	End	# Loc	MCP (ha)	MDD (m)	95K (ha)	50K (ha)	#C	HRL (m)
45	KPFP	M	184	26 Aug 2009	13 Oct 2009	10	.	.	.	.	.	.
46	KPFP	F	199	14 Sep 2009	14 Apr 2010	10	.	.	.	.	.	.
1	LPNP	F	195	21 Apr 2005	4 Jul 2007	269	52.9	27.5	9.1	1.0	1	1534.3
2	LPNP	M	211	16 May 2005	7 Nov 2006	200	26.9	11.0	7.5	1.0	1	797.8
3	LPNP	M	217	26 May 2005	1 Sep 2006	178	37.1	34.7	14.5	2.4	3	1208.0
4	LPNP	J	114	8 May 2005	6 Nov 2006	244	2.9	9.1	4.7	1.0	1	326.0
5	LPNP	F	206	11 May 2005	17 May 2007	282	43.9	24.1	25.6	3.8	3	1218.2
6	LPNP	F	192	11 May 2005	12 Jul 2006	92	14.7	50.4	13.9	1.1	1	1255.3
7	LPNP	F	198	17 May 2005	28 Jun 2007	291	45.7	41.5	22.2	1.9	2	1263.2
8	LPNP	F	174	15 May 2005	21 Jun 2007	251	35.0	18.0	8.1	1.1	1	803.9
9	LPNP	J	139	15 May 2005	28 Jul 2005	26	.	.	.	.		.
10	LPNP	F	131	18 May 2005	20 Jun 2005	13	.	.	.	.		.
11	LPNP	F	196	26 Jun 2005	28 Jun 2007	264	4.5	12.4	3.6	1.1	1	498.8
12	LPNP	J	100	27 May 2005	6 Nov 2006	132	1.2	13.8	3.2	1.0	1	228.7
13	LPNP	J	143	27 Jun 2005	6 Nov 2006	198	7.1	13.9	10.4	1.8	2	418.9
14	LPNP	J	127	7 Jun 2005	8 Nov 2006	215	7.1	13.6	7.6	1.0	1	794.9
15	LPNP	J	104	27 May 2005	22 Sep 2006	125	6.1	13.8	7.8	1.6	2	659.7
16	LPNP	F	200	6 Jun 2005	28 Jun 2007	293	17.7	22.2	10.8	2.3	2	895.0
17	LPNP	M	194	25 Jun 2005	26 Jun 2006	140	37.2	28.2	10.4	1.0	2	1234.6
18	LPNP	F	204	12 Jun 2005	28 Jun 2007	277	7.2	9.4	6.7	1.2	1	554.5
21	LPNP	F	203	23 Jun 2005	28 Jun 2007	107	28.5	12.1	7.8	1.0	1	1173.7
22	LPNP	F	178	25 Jun 2005	28 Jun 2007	137	39.2	48.5	22.8	2.0	3	1086.9
23	LPNP	J	131	22 Jun 2005	6 Nov 2006	242	5.4	11.4	5.9	1.1	1	427.9
24	LPNP	F	198	22 Jun 2005	14 Jul 2005	7	.	.	.	.		.
25	LPNP	F	216	20 Jun 2005	28 Jun 2007	288	12.7	26.6	13.2	2.4	3	761.9
26	LPNP	M	212	20 Jun 2005	6 Nov 2006	235	6.3	10.2	9.0	1.3	1	382.2
27	LPNP	M	187	22 Jun 2005	9 Aug 2005	25	.	.	.	.	.	.
35	LPNP	F	206	10 May 2006	9 Jun 2007	125	9.3	32.6	13.7	3.4	2	589.9
36	LPNP	F	210	1 Apr 2006	28 Jun 2007	165	36.2	73.7	23.7	2.5	2	1429.0
39	LPNP	J	119	23 Apr 2006	5 Oct 2006	115	8.7	24.1	9.9	1.1	1	1215.7
42	LPNP	M	233	1 May 2006	22 Mar 2007	85	9.3	37.6	9.6	1.2	2	583.8
46	LPNP	J	148	7 May 2006	8 Nov 2006	115	0.7	14.7	3.3	1.0	1	191.7
47	LPNP	J	153	6 May 2006	8 Nov 2006	112	29.7	32.4	4.7	1.0	1	1124.4
53	LPNP	J	114	21 May 2006	14 Nov 2006	107	1.4	8.4	4.7	1.2	1	297.9
63	LPNP	F	195	29 May 2006	1 Jul 2006	20	.	.	.	.		.
90	LPNP	F	215	11 Jul 2005	23 Jun 2006	106	0.8	4.4	4.2	1.3	1	191.1
7	RPNP	J	110	23 Apr 2007	6 Oct 2009	372	20.3	16.5	9.7	2.0	2	841.1
16	RPNP	J	145	2 May 2007	29 Sep 2008	97	15.9	37.7	15.4	2.4	1	753.8

#	Site	Sex	CL (mm)	Start	End	# Loc	MCP (ha)	MDD (m)	95K (ha)	50K (ha)	#C	HRL (m)
20	RPNP	F	195	6 May 2007	20 Nov 2009	375	30.1	42.6	12.0	1.6	1	901.8
26	RPNP	J	137	13 May 2007	24 Feb 2009	264	21.9	21.0	7.5	2.0	1	1254.4
27	RPNP	F	205	11 May 2007	30 May 2010	362	19.4	33.0	11.9	2.1	1	619.5
28	RPNP	M	185	7 May 2007	14 Oct 2009	266	53.5	37.1	8.7	1.2	1	1946.2
33	RPNP	M	230	23 Jul 2007	14 Oct 2009	309	151.9	60.5	15.6	1.1	1	2645.4
34	RPNP	M	196	3 Aug 2007	21 Oct 2009	287	21.9	52.4	14.6	1.6	1	941.3
38	RPNP	F	188	23 Apr 2008	30 May 2010	236	76.3	52.0	10.1	2.9	1	2733.9
40	RPNP	F	201	24 May 2008	15 Apr 2010	208	38.7	66.2	20.0	3.8	1	1591.9
41	RPNP	F	207	17 Nov 2008	15 Apr 2010	78	31.3	39.6	9.6	1.1	1	1345.1
42	RPNP	J	86	23 Apr 2008	14 Oct 2009	66	5.6	20.9	7.5	1.5	1	360.1
43	RPNP	F	205	22 Jun 2009	30 May 2010	42	7.7	20.3	11.8	2.9	1	435.2
44	RPNP	J	112	22 Jun 2009	13 Oct 2009	51	4.5	15.6	5.5	1.1	1	394.0
45	RPNP	F	210	17 Jul 2009	6 Aug 2009	8	.	.	.	.	.	.
Average						**197.4**	**27.5**	**33.8**	**11.8**	**1.6**	**1.4**	**1084.2**
S.E.						**14.1**	**3.2**	**2.3**	**0.7**	**0.1**	**0.1**	**82.4**

APPENDIX B

SPATIAL METRICS FOR CLEMMYS GUTTATA

Spatial metrics for 36 *C. guttata* radio-tracked at Will County, Illinois from 2005-2008. Listed are: turtle identification number (#), site, sex, carapace length (CL), start of tracking duration, end of tracking duration, number of radio-locations (#Loc), minimum convex polygon (MCP), mean daily distance moved (MDD), 95% fixed kernel density isopleth (95K), 50% fixed kernel density isopleth (50K), number of 50% fixed kernel density isopleths (#C), and home range length (HRL).

#	Site	Sex	CL (mm)	Start	End	# Loc	MCP (ha)	MDD (m)	95K (ha)	50K (ha)	#C	HRL (m)
19	LPNP	F	108	18 May 2005	14 Nov 2006	232	10.3	12.2	1.5	0.2	2	954.6
20	LPNP	M	137	17 May 2005	30 Oct 2005	99	5.4	6.7	0.9	0.1	1	469.8
34	LPNP	F	112	1 Jul 2005	14 Nov 2006	196	5.1	7.5	1.5	0.1	3	530.8
37	LPNP	F	107	6 Apr 2006	14 Nov 2006	96	0.3	8.2	0.7	0.2	2	85.6
38	LPNP	F	108	22 Apr 2006	16 May 2006	18	.	.	.	.	.	.
43	LPNP	M	102	7 May 2006	14 Nov 2006	84	1.7	3.3	0.9	0.2	1	340.2
44	LPNP	F	108	7 May 2006	6 Nov 2006	85	1.8	12.2	1.0	0.1	1	214.5
45	LPNP	M	113	9 May 2006	14 Nov 2006	82	1.4	9.4	1.0	0.1	1	161.3
48	LPNP	M	107	7 May 2006	31 Oct 2006	80	1.3	6.6	0.5	0.1	1	302.7
49	LPNP	F	103	15 May 2006	14 Nov 2006	81	1.3	5.5	0.9	0.1	2	218.1
50	LPNP	M	103	14 May 2006	14 Nov 2006	78	0.1	4.5	0.4	0.1	1	65.7
52	LPNP	M	102	21 May 2006	14 Nov 2006	73	0.4	4.4	0.8	0.1	1	136.3
96	LPNP	F	108	31 Jul 2006	5 Sep 2006	15	.	.	.	.	.	.
1	RPNP	F	98	2 Apr 2007	18 Jun 2008	194	0.9	15.3	1.2	0.1	2	143.8
2	RPNP	M	89	19 Mar 2007	12 Jun 2008	119	0.6	11.5	0.8	0.1	1	96.4
3	RPNP	M	103	16 Apr 2007	6 Jun 2008	185	9.1	15.8	1.1	0.2	2	734.5
4	RPNP	M	95	23 Apr 2007	13 May 2008	111	1.3	12.9	1.3	0.2	3	241.7
5	RPNP	F	86	23 Apr 2007	17 Jun 2007	39	0.6	6.5	0.6	0.1	1	204.8
6	RPNP	F	96	24 Apr 2007	14 Nov 2008	281	1.2	11.9	1.0	0.2	2	156.9
8	RPNP	M	101	19 Mar 2007	21 Oct 2008	158	0.9	12.4	1.2	0.4	1	127.3
9	RPNP	F	106	25 Apr 2007	12 Dec 2008	291	3.7	17.9	1.1	0.3	2	298.5
10	RPNP	F	100	17 Apr 2007	15 May 2008	146	1.3	16.2	1.7	0.3	3	263.9
11	RPNP	M	108	18 Mar 2007	4 Jun 2008	51	1.5	15.0	1.4	0.2	1	191.9
12	RPNP	F	104	23 Apr 2007	14 Apr 2008	149	2.7	18.1	2.1	0.2	2	301.7
13	RPNP	F	96	24 Apr 2007	1 May 2008	34	1.5	12.0	0.8	0.2	2	262.6
14	RPNP	M	89	1 May 2007	16 Oct 2008	51	4.2	14.4	2.2	0.3	4	416.4
15	RPNP	F	105	1 May 2007	14 Nov 2008	269	9.5	22.7	1.7	0.2	2	737.2
17	RPNP	M	100	30 Apr 2007	10 Oct 2008	253	1.2	22.5	1.2	0.3	1	198.0
18	RPNP	M	101	1 May 2007	30 Sep 2008	37	1.3	15.2	1.3	0.1	1	169.8

#	Site	Sex	CL (mm)	Start	End	# Loc	MCP (ha)	MDD (m)	95K (ha)	50K (ha)	#C	HRL (m)
19	RPNP	M	96	1 May 2007	21 Mar 2009	235	2.2	20.0	2.2	0.2	1	241.7
24	RPNP	F	105	17 Apr 2007	29 Jul 2008	181	3.7	28.4	1.9	0.3	2	350.5
29	RPNP	M	104	14 May 2007	20 Oct 2008	241	2.1	20.4	1.6	0.2	2	271.1
31	RPNP	F	95	16 May 2007	14 Nov 2008	256	1.1	14.6	1.1	0.3	1	157.3
35	RPNP	M	83	22 Aug 2007	13 Nov 2008	184	2.0	9.4	0.7	0.1	1	211.4
36	RPNP	M	96	21 Sep 2007	11 Sep 2008	134	3.4	14.5	1.8	0.1	2	333.8
37	RPNP	F	103	3 Oct 2007	8 Oct 2008	130	3.4	25.4	1.5	0.3	3	379.2
Average						**101.6**	**2.6**	**13.3**	**1.2**	**0.2**	**1.7**	**293.2**
S.E.						**12.8**	**0.4**	**1.1**	**0.1**	**0.0**	**0.1**	**33.7**

APPENDIX C

SPATIAL METRICS FOR STERNOTHERUS ODORATUS

Spatial metrics for 15 *S. odoratus* radio-tracked in Will County, Illinois from 2005-2006. Listed are: turtle identification number (#), site, sex, carapace length (CL), start of tracking duration, end of tracking duration, number of radio-locations (#Loc), minimum convex polygon (MCP), mean daily distance moved (MDD), 95% fixed kernel density isopleth (95K), 50% fixed kernel density isopleth (50K), number of 50% fixed kernel density isopleths (#C), and home range length (HRL).

#	Site	Sex	CL (mm)	Start	End	# Loc	MCP (ha)	MDD (m)	95K (ha)	50K (ha)	#C	HRL (m)
28	LPNP	M	93	21 Jun 2005	21 Jun 2005	1	.	.	.	.	.	.
29	LPNP	F	101	20 Jun 2005	10 Jul 2005	13	.	.	.	.	.	.
30	LPNP	M	97	21 Jun 2005	24 Aug 2005	22	58.2	93.7	7.0	0.7	1	1970.8
31	LPNP	M	102	21 Jun 2005	22 Sep 2005	61	1.1	16.5	4.6	1.5	2	205.7
32	LPNP	F	114	20 Jun 2005	22 Sep 2005	52	30.7	54.4	4.3	0.8	1	1628.2
33	LPNP	F	111	20 Jun 2005	6 Jul 2005	6	.	.	.	.	.	.
55	LPNP	M	122	26 May 2006	10 Aug 2006	53	1.5	26.1	2.6	0.8	1	290.4
58	LPNP	F	119	28 May 2006	25 Sep 2006	80	1.9	15.3	3.9	0.8	1	315.6
64	LPNP	F	109	29 May 2006	26 Sep 2006	74	9.5	33.4	11.2	1.7	2	701.3
65	LPNP	F	122	29 May 2006	26 Sep 2006	62	1.2	27.4	3.8	0.9	1	263.7
71	LPNP	M	107	31 May 2006	26 Sep 2006	59	3.0	26.1	3.0	0.8	1	317.5
72	LPNP	F	111	31 May 2006	25 Sep 2006	84	0.7	19.9	3.5	1.3	1	142.2
75	LPNP	F	109	2 Jun 2006	26 Sep 2006	62	5.0	29.8	5.0	0.8	1	487.9
88	LPNP	M	101	6 Jun 2006	16 Jul 2006	35	1.5	27.7	5.3	0.8	1	360.0
89	LPNP	M	105	6 Jun 2006	25 Sep 2006	64	4.0	27.8	7.2	0.9	2	367.7
Average						**54.9**	**9.9**	**33.2**	**5.1**	**1.0**	**1.3**	**587.6**
S.E.						**6.2**	**5.0**	**6.2**	**0.7**	**0.1**	**0.1**	**169.7**

APPENDIX D

SPATIAL METRICS FOR CHELYDRA SERPENTINA

Spatial metrics for 11 *C. serpentina* radio-tracked in Will County, Illinois in 2006. Listed are: turtle identification number (#), site, sex, carapace length (CL), start of tracking duration, end of tracking duration, number of radio-locations (#Loc), minimum convex polygon (MCP), mean daily distance moved (MDD), 95% fixed kernel density isopleth (95K), 50% fixed kernel density isopleth (50K), number of 50% fixed kernel density isopleths (#C) and home range length (HRL).

#	Site	Sex	CL (mm)	Start	End	# Loc	MCP (ha)	MDD (m)	95K (ha)	50K (ha)	#C	HRL (m)
54	LPNP	M	315	24 May 2006	15 Sep 2006	83	0.8	16.6	2.5	0.7	1	160.1
56	LPNP	F	234	26 May 2006	25 Sep 2006	72	8.9	38.5	3.6	0.4	1	541.6
57	LPNP	M	214	26 May 2006	2 Jun 2006	7	.	.	.	.	.	.
59	LPNP	M	271	29 May 2006	26 Sep 2006	75	3.7	15.8	1.4	0.4	1	467.9
60	LPNP	F	293	28 May 2006	26 Sep 2006	23	10.2	64.3	8.5	0.6	2	839.2
61	LPNP	M	238	28 May 2006	25 Sep 2006	75	4.1	37.2	2.3	0.4	1	419.1
62	LPNP	M	266	30 May 2006	26 Sep 2006	82	0.2	5.4	1.3	0.4	1	160.2
73	LPNP	F	252	1 Jun 2006	25 Sep 2006	80	2.0	15.6	3.2	0.4	1	221.6
74	LPNP	F	253	1 Jun 2006	19 Jun 2006	17	.	.	.	.	.	.
86	LPNP	F	233	28 May 2006	25 Sep 2006	65	11.4	50.6	6.9	0.7	1	985.5
87	LPNP	M	289	2 Jun 2006	6 Aug 2006	42	10.8	66.3	6.4	1.0	1	965.1
Average						**56.5**	**5.8**	**34.5**	**4.0**	**0.5**	**1.1**	**528.9**
S.E.						**8.7**	**1.5**	**7.5**	**0.9**	**0.1**	**0.1**	**110.4**

APPENDIX E

SPATIAL METRICS FOR CHRYSEMYS PICTA

Spatial metrics for nine *C. picta* radio-tracked in Will County, Illinois in 2006. Listed are: turtle identification number (#), site, sex, carapace length (CL), start of tracking duration, end of tracking duration, number of radio-locations (#Loc), minimum convex polygon (MCP), mean daily distance moved (MDD), 95% fixed kernel density isopleth (95K), 50% fixed kernel density isopleth (50K), number of 50% fixed kernel density isopleths (#C), and home range length (HRL).

#	Site	Sex	CL (mm)	Start	End	# Loc	MCP (ha)	MDD (m)	95K (ha)	50K (ha)	#C	HRL (m)
76	LPNP	F	165	1 Jun 2006	20 Jun 2006	19	.	.	.	.	.	.
77	LPNP	M	144	1 Jun 2006	26 Sep 2006	21	17.9	205.4	15.3	2.1	1	1716.6
78	LPNP	F	158	4 Jun 2006	25 Sep 2006	56	3.0	35.9	7.4	2.0	1	462.8
80	LPNP	F	139	5 Jun 2006	29 Jul 2006	37	0.7	20.9	5.1	1.8	1	224.9
81	LPNP	M	153	2 Jun 2006	18 Sep 2006	60	6.0	62.7	9.5	2.0	1	549.8
82	LPNP	M	145	2 Jun 2006	26 Sep 2006	58	2.7	27.6	11.0	3.6	1	224.5
83	LPNP	M	132	2 Jun 2006	25 Sep 2006	68	7.6	22.1	11.6	1.8	1	488.3
84	LPNP	M	131	2 Jun 2006	15 Sep 2006	59	3.4	36.2	8.0	1.9	1	337.1
85	LPNP	F	128	2 Jun 2006	28 Jul 2006	20	7.9	15.1	10.0	1.8	1	1599.6
Average						**44.2**	**6.1**	**53.2**	**9.8**	**2.1**	**1**	**700.4**
S.E.						**6.6**	**1.9**	**22.4**	**1.1**	**0.2**	**0**	**213.4**

APPENDIX F

SAMPLE SIZES FOR HABITAT PARTITIONING ANALYSES

Number of locations and sample sizes included in statistical analyses for five turtle species radio-located from May-September 2006 at a preserve in Will County, Illinois.

Species		Male	Female	Total
E. blandingii	# Locations	318	1041	1359
	(*N*)	(5)	(13)	(18)
C. guttata	# Locations	334	356	690
	(N)	(5)	(5)	(10)
C. picta	# Locations	189	62	251
	(N)	(4)	(2)	(6)
C. serpentina	# Locations	278	187	465
	(N)	(4)	(3)	(7)
S. odoratus	# Locations	162	294	456
	(N)	(4)	(5)	(9)

APPENDIX G

HABITAT PARTITIONING POST-HOC STATISTICAL RESULTS

P-values for MANOVA macro-habitat and ANOVA micro-habitat post-hoc tests between 18 *E. blandingii* (EMBL), 10 *C. guttata* (CLGU), six *C. picta* (CHPI), seven *C. serpentina* (CHSE), and nine *S. odoratus* (STOD) at a preserve in Will County, Illinois from May-September 2006. Variables are as follows: mesic prairie (MP), floodplain (FP), river (R), marsh (M), sedge meadow (SM), pond (P), principal component 1 (PC1), principal component 2 (PC2), and proportion of organic substrates (SUB). Significance levels were accepted at $\alpha = 0.05$.

		MANOVA Post-Hoc						ANOVA Post-Hoc		
Species 1	**Species 2**	**MP**	**FP**	**R**	**M**	**SM**	**PD**	**PC1**	**PC2**	**SUB**
EMBL	CLGU	0.06	1.00	1.00	0.50	0.18	0.12	0.00*	1.00	0.02*
EMBL	CHPI	0.81	1.00	0.63	0.99	0.00*	0.00*	1.00	0.00*	0.00*
EMBL	CHSE	0.77	0.81	0.08	1.00	1.00	0.01*	0.31	0.21	0.16
EMBL	STOD	0.69	1.00	0.06	0.75	0.54	0.00*	0.00*	0.03*	0.00*
CLGU	CHPI	0.01*	1.00	0.40	0.69	0.11	0.00*	0.00*	0.87	0.00*
CLGU	CHSE	0.01*	0.64	0.05*	0.87	0.12	0.00*	0.00*	0.81	0.00*
CLGU	STOD	0.00*	0.98	0.04*	0.06	0.01*	0.00*	0.00*	0.35	0.00*
CHPI	CHSE	1.00	0.92	1.00	1.00	1.00	1.00	0.03*	0.15	0.73
CHPI	STOD	1.00	1.00	1.00	0.98	1.00	1.00	0.83	0.03*	1.00
CHSE	STOD	1.00	1.00	1.00	0.84	1.00	1.00	0.36	1.00	0.68

APPENDIX H

MULTIPLEX PANELS

Multiplex panel (MP#), primer, fluorescent labeling dye, and annealing temperature (T_A) for PCR reaction conditions designed for amplification of *E. blandingii*, *C. picta*, and *C. serpentina.*

E. blandingii & *C. picta*

Panel	Locus	Dye	T_A	Panel	Locus	Dye	T_A
MP1	BATC9	6-FAM	58/48	MP2	*Gmu*B08	6-FAM	58
MP1	*Gmu*D70	VIC	58/48	MP2	*Gmu*D90	VIC	58
MP1	*Gmu*D121	NED	58/48	MP2	*Gmu*D55	NED	58
MP1	*Gmu*A19	PET	58/48	MP2	*Gmu*D21	PET	58
MP3	*Gmu*A32	6-FAM	57	MP5	Eb09	6-FAM	55
MP3	*Gmu*A18	VIC	57	MP5	Eb19	VIC	55
MP3	Eb17	NED	57	MP5	*Gmu*D93	NED	55
MP3	*Gmu*D87	PET	57				

C. serpentina

Panel	Locus	Dye	T_A	Panel	Locus	Dye	T_A
MP6	*Mte*C1	VIC	57	MP7	*Mte*B103	6-FAM	51
MP6	*Mte*C112	NED	57	MP7	*Mte*D106	VIC	51
MP6	*Mte*D111	PET	57	MP7	*Mte*D2	NED	51
				MP7	*Mte*D9	NED	51

APPENDIX I

GENETIC DIVERSITY INDICES

Standard genetic diversity indices for loci that successfully amplified in *E. blandingii*, *C. picta*, *C. serpentina* samples collected within the Lower Des Plaines River Valley. Listed are number of samples (N) genotyped, detected number of alleles ($^{\#}$A), size range of alleles in base pairs, number of private alleles (P_A), observed heterozygosity (H_o), expected heterozygosity (H_e), inbreeding coefficient (F_{IS}), and probability of rejecting Hardy-Weinberg equilibrium (P_{HWE}). Bonferroni adjusted α=0.004.

Locus	N	$^{\#}$A	Size	A_R	PA_R	H_o	H_e	F_{IS}	P_{HWE}
Will 1 (*E. blandingii*)									
Eb19	22	3	98-107	3.0	0.00	0.727	0.599	-0.214	0.323
Eb17	22	5	94-112	4.0	0.50	0.727	0.632	-0.150	0.225
Eb09	22	9	137-167	6.6	1.34	0.773	0.724	-0.067	0.962
BATC9	22	11	146-184	8.1	1.57	0.818	0.818	0.000	0.353
GmuD121	22	5	140-160	4.8	0.07	0.500	0.663	0.246	0.044
GmuB08	22	3	194-200	2.3	0.01	0.136	0.129	-0.056	1.000
GmuA32	22	2	139-145	1.8	0.00	0.091	0.087	-0.048	1.000
GmuA19	21	5	145-165	4.9	0.01	0.714	0.745	0.041	0.038
GmuA18	22	2	119-121	2.0	0.00	0.136	0.325	0.581	0.016
GmuD93	22	2	198-230	2.0	0.00	0.318	0.325	0.022	1.000
GmuD87	22	6	196-248	4.5	0.83	0.636	0.618	-0.030	0.880
GmuD70	21	10	225-265	8.5	1.58	1.000	0.821	-0.218	0.209
GmuD55	22	4	177-193	4.0	0.00	0.773	0.687	-0.125	0.584
GmuD21	22	2	153-157	2.0	0.00	0.136	0.268	0.490	0.058
Will 2 (*E. blandingii*)									
Eb19	11	3	98-107	3.0	0.00	0.727	0.579	-0.257	0.312
Eb17	11	4	94-109	4.0	0.01	0.727	0.640	-0.135	0.113
Eb09	11	8	129-163	8.0	1.31	0.818	0.769	-0.065	0.948
BATC9	11	7	146-182	7.0	0.51	0.636	0.727	0.125	0.260
GmuD121	11	5	140-156	5.0	0.01	0.636	0.632	-0.007	0.254
GmuB08	11	3	197-203	3.0	1.01	0.182	0.244	0.254	0.143
GmuA32	11	2	139-145	2.0	0.01	0.455	0.351	-0.294	1.000
GmuA19	11	4	145-155	4.0	0.08	0.727	0.698	-0.041	0.518
GmuA18	11	2	119-121	2.0	0.00	0.455	0.483	0.060	1.000
GmuD93	11	2	198-230	2.0	0.00	0.182	0.165	-0.100	1.000
GmuD87	11	5	196-252	5.0	1.26	0.818	0.657	-0.245	0.395
GmuD70	11	6	217-257	6.0	0.17	0.727	0.736	0.011	0.930
GmuD55	11	5	177-213	5.0	1.00	0.455	0.508	0.106	0.225
GmuD21	11	2	153-157	2.0	0.00	0.182	0.298	0.389	0.277

Locus	N	#A	Size	A_R	PA_R	H_o	H_e	F_{IS}	P_{HWE}
Will 3 (*E. blandingii*)									
Eb19	30	3	98-107	3.0	0.00	0.733	0.645	-0.137	0.867
Eb17	30	5	94-109	4.8	0.16	0.867	0.754	-0.150	0.728
Eb09	30	9	137-163	6.4	0.31	0.733	0.731	-0.004	0.489
BATC9	30	8	146-182	7.4	0.23	0.900	0.859	-0.047	0.791
GmuD121	30	5	144-160	4.4	0.02	0.567	0.597	0.051	0.809
GmuB08	30	3	194-200	2.7	0.29	0.267	0.313	0.147	0.258
GmuA32	30	2	139-145	2.0	0.00	0.233	0.206	-0.132	1.000
GmuA19	30	6	145-165	4.7	0.44	0.600	0.672	0.107	0.137
GmuA18	30	2	119-121	2.0	0.00	0.333	0.320	-0.042	1.000
GmuD93	30	2	198-230	2.0	0.00	0.367	0.375	0.022	1.000
GmuD87	30	7	196-268	4.8	0.55	0.700	0.637	-0.099	0.301
GmuD70	30	9	217-261	6.5	0.08	0.767	0.777	0.013	0.498
GmuD55	30	5	177-221	3.8	0.37	0.467	0.453	-0.031	0.538
GmuD21	30	2	153-157	1.9	0.00	0.200	0.180	-0.111	1.000
Grundy (*E. blandingii*)									
Eb19	47	3	98-107	2.5	0.00	0.490	0.510	0.040	0.900
Eb17	47	5	94-109	4.8	0.02	0.633	0.733	0.137	0.131
Eb09	47	10	129-163	6.0	0.17	0.551	0.644	0.144	0.122
BATC9	47	8	146-186	7.3	0.73	0.796	0.852	0.066	0.004
GmuD121	47	7	140-164	5.2	0.45	0.653	0.609	-0.073	0.465
GmuB08	47	3	194-200	2.3	0.01	0.265	0.235	-0.130	1.000
GmuA32	47	2	139-145	1.6	0.00	0.082	0.078	-0.043	1.000
GmuA19	47	8	145-169	5.9	1.44	0.714	0.766	0.068	0.520
GmuA18	47	3	119-123	2.2	0.22	0.265	0.262	-0.012	1.000
GmuD93	47	2	198-230	1.9	0.00	0.163	0.150	-0.089	1.000
GmuD87	47	7	196-240	5.4	1.70	0.714	0.732	0.024	0.160
GmuD70	47	13	217-269	9.3	0.90	0.776	0.875	0.114	0.022
GmuD55	47	5	177-217	4.0	0.40	0.653	0.550	-0.187	0.550
GmuD21	47	2	153-157	2.0	0.00	0.286	0.273	-0.046	1.000

Locus	N	#A	Size	A_R	PA_R	H_o	H_e	F_{IS}	P_{HWE}
Will 1 (*C. picta*)									
Eb17	93	2	82-88	2.0	0.00	0.065	0.062	-0.033	1.000
GmuB08	106	9	213-240	7.8	0.15	0.755	0.794	0.049	0.712
GmuA32	93	2	130-132	2.0	0.00	0.247	0.233	-0.063	1.000
GmuA19	106	13	126-160	11.0	0.84	0.783	0.812	0.036	0.175
GmuD93	106	17	132-228	13.9	1.42	0.840	0.824	-0.019	0.721
GmuD70	106	54	178-566	37.9	4.79	0.981	0.964	-0.018	0.486
GmuD55	106	11	165-209	9.1	0.11	0.774	0.753	-0.028	0.260
GmuD21	106	12	146-198	10.5	0.00	0.849	0.838	-0.013	0.901
Will 2 (*C. picta*)									
Eb17	71	2	82-88	1.9	0.00	0.042	0.041	-0.022	1.000
GmuB08	70	11	213-240	9.9	1.06	0.886	0.828	-0.070	0.872
GmuA32	71	2	130-132	2.0	0.00	0.183	0.189	0.031	0.562
GmuA19	71	11	126-160	10.0	0.00	0.887	0.812	-0.093	0.650
GmuD93	70	16	132-228	12.3	0.85	0.757	0.761	0.005	0.624
GmuD70	71	55	170-562	44.5	8.32	1.000	0.973	-0.028	0.961
GmuD55	70	10	165-217	9.6	0.98	0.757	0.780	0.029	0.446
GmuD21	71	12	146-198	11.2	0.00	0.803	0.830	0.033	0.055
Will 3 (*C. picta*)									
Eb17	110	2	82-88	2.0	0.00	0.152	0.140	-0.082	1.000
GmuB08	110	9	213-237	8.5	0.34	0.750	0.786	0.046	0.009
GmuA32	110	2	130-132	2.0	0.00	0.152	0.140	-0.082	1.000
GmuA19	110	13	126-160	11.8	1.32	0.866	0.848	-0.021	0.194
GmuD93	109	16	132-216	11.4	1.07	0.757	0.768	0.015	0.878
GmuD70	110	51	166-436	39.2	3.71	0.964	0.969	0.005	0.292
GmuD55	110	11	165-209	10.3	1.01	0.821	0.776	-0.058	0.626
GmuD21	110	11	146-194	10.2	0.00	0.830	0.843	0.016	0.583

Locus	N	#A	Size	A_R	PA_R	H_o	H_e	F_{IS}	P_{HWE}
Grundy (*C. picta*)									
Eb17	44	2	82-88	2.0	0.00	0.022	0.022	-0.011	.
GmuB08	44	8	213-237	8.0	0.01	0.667	0.755	0.117	0.247
GmuA32	44	2	130-132	2.0	0.00	0.222	0.198	-0.125	1.000
GmuA19	44	10	126-160	10.0	0.03	0.800	0.831	0.037	0.861
GmuD93	44	11	132-200	10.9	0.66	0.756	0.777	0.028	0.104
GmuD70	44	38	166-464	37.7	2.36	0.978	0.960	-0.018	0.576
GmuD55	44	9	165-205	9.0	1.07	0.800	0.745	-0.074	0.605
GmuD21	43	12	146-198	12.0	0.15	0.773	0.826	0.064	0.681
Will 1 (*C. serpentina*)									
MteB103	21	6	128-156	5.3	0.01	0.619	0.737	0.160	0.095
MteC1	21	2	140-144	1.5	0.18	0.048	0.046	-0.024	.
MteC112	21	5	342-454	4.1	0.01	0.524	0.434	-0.206	1.000
MteD9	21	7	238-270	6.4	0.00	0.619	0.813	0.238	0.118
MteD111	21	11	160-287	8.5	0.07	0.905	0.865	-0.046	0.621
Will 2 (*C. serpentina*)									
MteB103	35	6	128-156	5.8	0.08	0.886	0.809	-0.095	0.999
MteC1	35	2	140-144	1.6	0.02	0.086	0.082	-0.045	1.000
MteC112	35	6	342-454	5.0	0.20	0.743	0.720	-0.031	0.073
MteD9	35	9	238-278	6.3	0.29	0.829	0.793	-0.045	0.658
MteD111	35	13	160-287	8.5	0.46	0.914	0.852	-0.073	0.537
Will 3 (*C. serpentina*)									
MteB103	17	6	128-156	5.7	0.03	0.765	0.753	-0.016	0.873
MteC1	17	2	140-144	1.9	0.18	0.176	0.161	-0.097	1.000
MteC112	17	4	374-454	3.5	0.00	0.294	0.311	0.056	0.411
MteD9	17	7	242-270	6.2	0.59	0.706	0.760	0.071	0.953
MteD111	17	15	160-283	11.5	2.01	0.941	0.903	-0.042	0.953

Locus	N	#A	Size	A_R	PA_R	H_o	H_e	F_{IS}	P_{HWE}
Grundy (*C. serpentina*)									
MteB103	10	5	128-153	5.0	0.01	0.700	0.770	0.091	0.420
MteC1	10	1	140	1.0	0.00	0.000	0.000	.	.
MteC112	10	5	342-454	5.0	0.31	0.700	0.635	-0.102	0.137
MteD9	10	8	238-270	8.0	0.55	0.700	0.815	0.141	0.215
MteD111	10	10	160-287	10.0	0.38	1.000	0.875	-0.143	0.800

APPENDIX J

NUMBER OF POTENTIAL AND SUCCESSFUL MATES

Number of potential mates observed during radio-telemetry surveys conducted from 2006-2009 and number of successful mates inferred from paternity analysis from clutches sampled from 2007-2010 in 19 female and 10 male *E. blandingii* in two preserves in Will County, Illinois. A "." indicates that a turtle was not tracked during a time period or was excluded from analyses.

	# Potential Mates					# Successful Mates				
Turtle	2006	2007	2008	2009	Total	2007	2008	2009	2010	Total
FEMALES										
EZMR	1	2	0	.	3	1	1	.	.	2
MRTH	0	1	1	0	2	1	1	1	1	2
ETHL	.	1	0	0	1	1	1	1	1	1
EDNA	.	0	1	0	1	0	0	0	0	0
PRMA	0	0	0	0	0	1	1	1	1	1
MILD	.	0	0	0	0	.	1	1	1	1
CLRA	0	1	0	0	1	.	1	1	1	1
MAUD	.	.	1	2	3	.	1	1	2	2
JUDI	0	0	2	0	3	1	1	1	1	1
FRAN*	.	.	.	.	.	.	.	.	.	.
BV	0	3	0	1	3	0	1	1	.	1
CLET*	.	.	.	.	.	.	.	.	.	.
HART	0	0	2	0	2	.	1	0	1	2
BIMA	.	2	1	0	2	1	1	1	.	1
LIMA	.	1	1	0	2	1	1	1	1	1
VLMA	.	.	2	1	2	.	1	1	2	2
SMLY	.	.	0	0	0	.	1	2	.	2
NOEL	.	.	1	0	1	.	.	1	.	1
HOPE	.	.	.	0	0	.	.	1	0	1
MALES										
MNGO	0	1	1	1	3	0	0	1	0	1
DRLD	0	0	1	0	1	0	1	1	0	1
VERN	.	4	.	.	4	1	1	.	.	2
JAY	.	6	2	1	8	0	4	4	3	5
EZRA	.	0	1	0	1	0	2	1	2	2
RMEO	.	.	.	.	.	.	.	.	.	.
ZEB	2	2	2	1	6	1	1	0	1	2
AXEL	.	.	.	.	.	.	.	.	.	.
BIPA	.	1	2	1	3	0	1	2	1	3
LIPA	.	2	3	1	4	0	2	2	2	5