Herpetological Conservation and Biology 14(3):668–679.
Submitted: 15 November 2018; Accepted: 4 November 2019; Published: 16 December 2019.

A REGIONAL ANALYSIS OF *GLYPTEMYS INSCULPTA* (WOOD TURTLE) SURVIVAL IN THE UPPER MIDWEST OF THE USA

CARLY N. LAPIN[1,7], *JEFFREY W. TAMPLIN*[2], *MADALINE M. COCHRANE*[3,4], *JAMES E. WOODFORD*[1], *DONALD J. BROWN*[5,6], *AND RON A. MOEN*[3]

[1] *Wisconsin Department of Natural Resources, 107 Sutliff Avenue, Rhinelander, Wisconsin 54501, USA*
[2] *Department of Biology, University of Northern Iowa, 1227 West 27th Street, Cedar Falls, Iowa 50614, USA*
[3] *Natural Resources Research Institute, University of Minnesota-Duluth, 2013 Miller Trunk Highway, Duluth, Minnesota 55811, USA*
[4] *Present address: Division of Biological Sciences, University of Montana, 32 Campus Drive, Missoula, Montana, 59812, USA*
[5] *West Virginia University, School of Natural Resources, PO Box 6125, 322 Percival Hall, Morgantown, West Virginia 26506, USA*
[6] *U.S. Forest Service, Northern Research Station, Parsons, West Virginia 26287, USA*
[7] *Corresponding author, email: Carly.Lapin@Wisconsin.gov*

Abstract.—**The Wood Turtle (*Glyptemys insculpta*) is a species of conservation concern in the Upper Midwest of the USA. State agencies and partners in the region are working collaboratively to identify threats to *G. insculpta* populations and to implement effective management actions. One component of this conservation initiative is to improve our understanding of the impacts of different management strategies on long-term viability of populations. This requires estimates of population vital rates, which are currently lacking for most *G. insculpta* populations in the Upper Midwest and across the range of the species. In this study, we used individual-level monitoring data to estimate annual survival of adult *G. insculpta* in Iowa (two populations, four monitoring years, 52 individuals), Minnesota (one population, two monitoring years, 29 individuals), and Wisconsin (two populations, two monitoring years, 32 individuals). We estimated annual survival for each sex, population, and year using a known-fates analysis with a binomial model. Twenty-three (20%) of the monitored individuals died during the study. For 12 turtles for which we knew the cause, predation was responsible for most (n = 9; 75%) mortalities. Estimated annual survival of males and females ranged from 0.49–1.00 and 0.64–1.00, respectively, among populations and years. Estimated survival of all individuals was 0.86 in Iowa for 2012–2015, 0.89 in Minnesota for 2015–2016, and 0.87 in Wisconsin for 2014–2015. This study increases our understanding of adult *G. insculpta* survival rates and causes of mortality in the western Great Lakes portion of the range of the species and provides useful vital rate estimates for population viability analyses.**

Key Words.—adult; Iowa; Midwest; Minnesota; modeling; population; predation; Wisconsin

INTRODUCTION

The Wood Turtle (*Glyptemys insculpta*) is a medium-sized, semi-terrestrial freshwater turtle that ranges from northern Virginia to Nova Scotia in eastern North America, through the southern Canadian provinces of New Brunswick, Quebec, and Ontario, and into the western Great Lakes states of Michigan, Wisconsin, and eastern Minnesota; an isolated population occurs in northeastern Iowa, USA (Ernst and Lovich 2009; Spradling et al. 2010). *Glyptemys insculpta* occur in relatively clear, hard-bottomed (sand, gravel, or cobble substrates) rivers and streams with moderate to fast-flowing water adjacent to forested riparian areas and suitable nesting habitat (Vogt 1981; Harding 1997; Ernst and Lovich 2009; Kenneth Bowen and James Gillingham, unpubl. report). *Glyptemys insculpta* are terrestrial habitat generalists and often make use of forest edges or open canopy habitats during the warm months for foraging and thermoregulation (Compton et al. 2002; Dubois et al. 2009; Ernst and Lovich 2009).

Populations of *G. insculpta* in the Upper Midwest states of Iowa, Minnesota, and Wisconsin in the USA are the westernmost of the range of the species. In Iowa, *G. insculpta* occur only in the Iowa-Cedar River watershed (Christiansen and Bailey 1997; Spradling et al. 2010). In Minnesota, *G. insculpta* populations are discontinuous, with one population in the Lake Superior watershed in the northeastern region of the state and two other populations, likely isolated from the first, in the Mississippi River watershed to the south and east (Buech et al. 1997; Moriarty and Hall 2014). In Wisconsin, *G. insculpta* have been documented in the Lake Michigan, Lake Superior, and Mississippi River watersheds (Vogt

1981; Wisconsin Department of Natural Resources [WDNR] 2015a).

Glyptemys insculpta have undergone population declines across much of their geographic distribution (Burger and Garber 1995; Daigle and Jutras 2005; Willoughby et al. 2013; Cochrane et al. 2018). Currently, *G. insculpta* are considered Globally Endangered by the International Union for the Conservation of Nature (IUCN; van Dijk and Harding 2011). The species is state-listed as endangered in Iowa (Iowa Natural Resource Commission. 2009. Chapter 77: Endangered and Threatened Plant and Animal Species. Available from https://www.legis.iowa.gov/docs/ACO/chapter/571.77.pdf [Accessed 24 October 2018]), state-listed as threatened in both Minnesota and Wisconsin (Moriarty and Hall 2004; WDNR 2015b), and is currently under review for listing under the Endangered Species Act by the U.S. Fish and Wildlife Service (USFWS. 2015. Species profile for Wood Turtle [*Glyptemys insculpta*]. Available from https://ecos.fws.gov/ecp0/profile/speciesProfile?spcode=C06A [Accessed 24 October 2018]).

Across the distribution of the species, a variety of factors may be impacting *G. insculpta* population viability: habitat loss, degradation, and fragmentation (Garber and Burger 1995; Buech et al. 1997); reduced productivity due to heavy nest predation or nest flooding (Brooks et al. 1992; Daigle and Jutras 2005; Harding 2008; Spradling et al. 2010); increased juvenile and adult mortality from predators, vehicles, and agricultural equipment (Brooks et al. 1992; Saumure et al. 2007; Parren 2013); and collection of wild turtles for the commercial pet trade (Levell 2000). State agencies and partners in the Upper Midwest of the USA (i.e., Iowa, Michigan, Minnesota, and Wisconsin) are working to identify regional threats to *G. insculpta* populations.

Two regional initiatives, the foci of this study, are quantification of survival rates and identification of causes of mortality for adults. Similar to most turtle species, *G. insculpta* is a long-lived species with low fecundity and delayed reproductive maturity (Harding and Bloomer 1979), a life-history strategy that requires high juvenile and adult survival rates to maintain stable populations (Congdon et al. 1993, 1994). Adult survival estimates are currently lacking for *G. insculpta* populations in the Upper Midwest, with the exception of an increasing population in the Lower Peninsula of Michigan (Schneider et al. 2018). Thus, it is currently unknown if management actions focused on reducing adult mortality of *G. insculpta* are needed for these Upper Midwest populations. In addition, adult survival estimates are needed for a complementary regional research initiative and for creation of local and regional-scale population viability models (Pe'er et al. 2013).

The purposes of this study were to estimate annual adult survival for *G. insculpta* populations in Iowa, Minnesota, and Wisconsin, based on individual-level monitoring data, and to identify causes of adult mortality. We used radio-telemetry data collected between 2012 and 2016, with a total of 113 individuals tracked for one or more monitoring years. Results of this study will increase our understanding of adult *G. insculpta* survival rates and causes of mortality in the western Great Lakes portion of the range of the species and provide useful vital rate estimates for population viability analyses.

MATERIALS AND METHODS

Study sites.—The study sites in Iowa, USA, were located in two adjacent counties within the Iowa-Cedar River watershed: Black Hawk (hereafter population BH) and Butler (hereafter population BU; Fig. 1). Each study site encompassed approximately 3.5 km of linear stream distance based on individual relocation data. The total sizes of the BH and BU study sites were 299 ha and 434 ha, respectively, assuming 300 m surrounding streams represented potential habitat (Arvisais et al. 2002; Brown et al. 2016). The Iowa study sites contained a mixture of floodplain forest (BH = 193 ha [65% of the study site], BU = 253 ha [58%]), agricultural fields (BH = 26 ha [9%], BU = 71 ha [16%]), and open-canopy clearings containing various grasses and forbs (BH = 13 ha [4%], BU = 58 [13%]; Otten 2017). Both study sites contained a mixture of public (BH = 129 ha [43%]; BU = 238 ha [55%]) and private land. The BH population occurred within a landscape context more heavily influenced by housing development compared to the BU population. Total area of human development within the study sites was 28 ha (9%) in BH and 5 ha (1%) in BU (Otten 2017).

The Minnesota study site was in Lake and St. Louis counties along 28.0 km of river in the Lake Superior watershed (Fig. 1). The total size was 1,456 ha, assuming 300 m surrounding streams represented potential habitat. The specific location is withheld in compliance with the data practices law of Minnesota for species listed as endangered or threatened. The study site contained a mixture of wetland types (674 ha [46%]), upland forests (545 ha [37%]) dominated by evergreens (61%) and mesic forest types (24%), and scrub/shrub habitat types (147 ha [10%]). This study site was largely undeveloped (1,366 ha [94%]) and contained 922 ha (63%) public land (Homer et al. 2015).

Study sites in Wisconsin were located along stretches of two rivers in Oneida County (study site total length = 30.3 km; population ON) and stretches of two rivers in Washburn and Burnett counties (study site total length = 62.3 km; population WB; Fig. 1), all within the Mississippi River watershed. The total

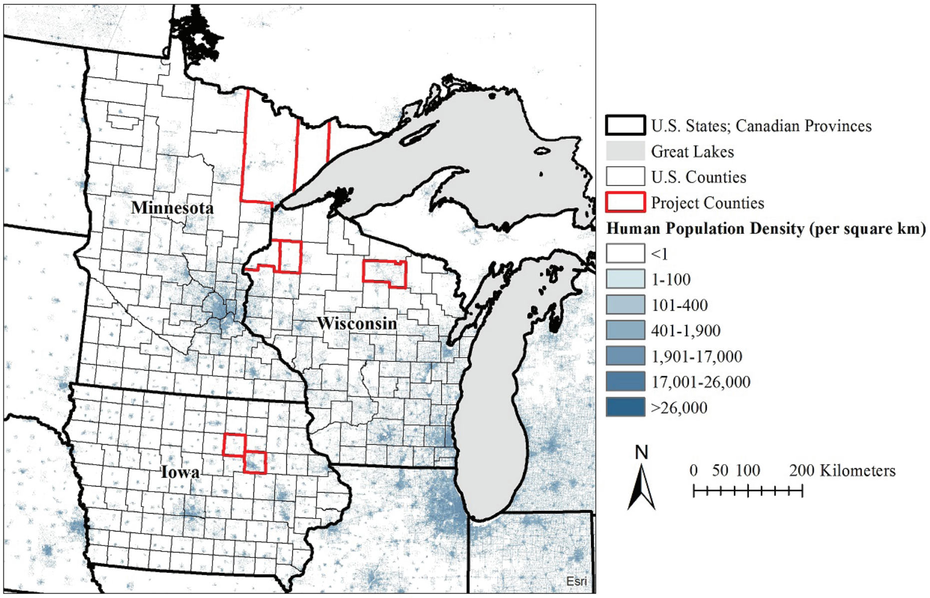

Figure 1. Counties where adult *Glyptemys insculpta* (Wood Turtle) were radio-tracked in Iowa (2012−2015), Minnesota (2015−2016), and Wisconsin (2014−2015), USA. (Esri World Population Density Estimate 2016. https://www.arcgis.com/home/item.html?id=0f83177f15d640ed911bdcf6614810a5).

size of the ON and WB study sites was 1,688 ha and 3,625 ha, respectively, assuming 300 m surrounding streams represented potential habitat. The study sites contained a mixture of coniferous and deciduous upland forests (ON = 1,010 ha [60%], WB = 2,724 ha [75%]), open and scrub/shrub wetlands (ON = 306 ha [18%], WB = 101 ha [3%]), and forested wetland (ON = 331 ha [20%], WB = 583 ha [16%]; WDNR. 2016. Wiscland 2.0. Available from https://dnr.wi.gov/maps/WISCLAND.html [Accessed 24 October 2018]). There was a limited amount of development in each study site (ON = 8 ha [<1%], WB = 62 ha [2%]; WDNR. 2016. *op. cit.*). Public lands comprised approximately 60% (1,012 ha) of study site ON, and 87% (3,141 ha) of study site WB. Study site ON had few roads, most of them local (primarily gravel), and one county highway that crossed one river. Study site WB had more local roads (primarily paved), one county highway that crossed each river, and one busy state highway that paralleled one of the rivers within 300 m for approximately 10.9 km.

Data collection.—We captured adult *G. insculpta* during population surveys conducted annually in April and May and also on opportunistic encounters. We attached radio transmitters to captured turtles (Iowa: Model R2220, 49 g, battery life 9.5 y, Advanced Telemetry Systems [ATS], Isanti, Minnesota, USA; Minnesota: Model R1680, 4 g, battery life 1 y, ATS; Wisconsin: Model A1-2F, 35 g, battery life 2 y, Holohil Systems Ltd., Carp, Ontario, Canada). We selected individuals for radio transmitters as they were encountered and so that the combined weight of the transmitter, antenna, and epoxy for *G. insculpta* typically totaled < 5% of the weight of each individual (maximum = 7% for some Iowa turtles). In Wisconsin, we selected more female *G. insculpta* for tracking to assist with locating nesting sites. We attached the transmitters to the right costal scutes of the carapace using epoxy PC-7 (Protective Coating Co., Allentown, Pennsylvania, USA). Upon capture, we held turtles for 24–48 h to allow the epoxy to cure and subsequently released at their capture site. In Iowa, Minnesota, and Wisconsin, we used a Model R410 telemetry receiver (ATS), Model R2000 telemetry receiver (ATS), and a Model R1000 telemetry receiver (Communication Specialists, Inc., Orange, California, USA), respectively. In all states we used a collapsible three-element Yagi antenna (Model 13860, ATS), and in Wisconsin we also used a flexible H type antenna (Model RA-23, Telonics, Mesa, Arizona, USA).

We radio-tracked 113 *G. insculpta* (40 males, 73 females) across multiple years in the three states. Radio-tracked individuals were added to the sample in a staggered entry fashion throughout the duration of the tracking effort in each state. In Iowa, we tracked 52 adult turtles (15 males and 14 females from population BH; nine males and 14 females from population BU) from 2012−2015. We relocated individuals once per week during winter brumation and two to three times per week during active periods. In Minnesota, we tracked 29 adults (10 males, 19 females) once a month from May to October 2015 and April to August 2016. In Wisconsin, we tracked 32 adults (four males, 10 females from population ON; two males, 16 females from

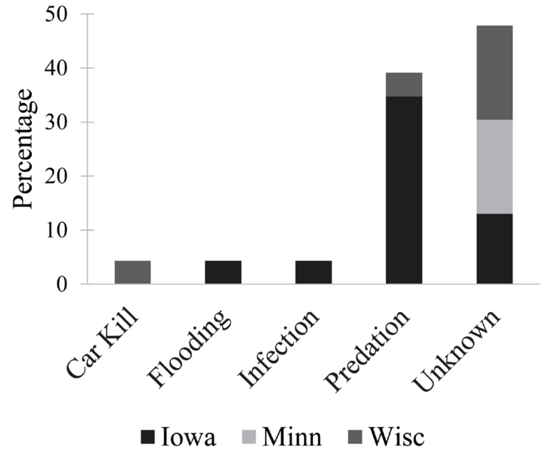

Figure 2. Causes of mortality for radio-tracked adult *Glyptemys insculpta* (Wood Turtle) in Iowa (2012−2015, n = 13), Minnesota (2015−2016, n = 4), and Wisconsin (2014−2015, n = 6), USA.

population WB) one or more times per week during the active season and one time per month during winter brumation from April 2014 to October 2015.

Throughout the course of the study, we documented *G. insculpta* mortality and cause when possible as they were observed. Individuals were labeled censored if we could not relocate them during the study due to radio failure or for an unknown reason and we subsequently removed them from the sample (White and Burnham 1999). We removed radio transmitters from all study animals in Minnesota and Wisconsin at the conclusion of the study (late summer 2016 and 2015, respectively).

Statistical analysis.—We estimated annual *G. insculpta* survival (*S*) using a known-fates model with the logit link function in Program MARK (White and Burnham 1999). This model uses binomial likelihoods to estimate survival probability when sampling probabilities are one because the status (fate) of each individual is known at each sampling occasion. For this analysis, we organized the radio telemetry data into monthly encounter histories. In Iowa, we calculated survival in each year for 2012–2015 and for the entire study period. We grouped Iowa data by sex only in 2012 and 2013 (we only tracked one population, BH, during these years) and by sex and population (n = 2) in 2014 and 2015. We grouped Minnesota data by sex and calculated survival in 2015 and 2016 and for the entire study period. We grouped Wisconsin data by sex and population (n = 2), and calculated survival in 2014 and 2015 and for the entire study period.

We report annual survival estimates for each sex, population, and year in each state, for all individuals within a year in each state, and across all study years for each state to maximize the information available for local and regional-scale population viability analyses; however, we also assessed the strength of evidence for differences in annual survival based on sex and population using a model selection approach. We tested for a sex effect in all years in the Iowa and Minnesota data, and we tested for a population effect in 2014 and 2015 in the Iowa and Wisconsin data. We did not test for a sex effect in the Wisconsin data due to small sample size for male *G. insculpta* (only four males were tracked in population ON and two in population WB). We identified the most parsimonious models using the Akaike Information Criterion corrected for small sample size (AIC_c; White and Burnham 1999; Burnham and Anderson 2002). Following Burnham et al. (2011), we calculated the difference between the model with the best (lowest) AIC_c and all other models in the subset (Δ_i) and considered all models with $\Delta_i < 7.0$ as having substantial support.

Results

Twenty-three (20%) of the monitored individuals died during the study (Table 1). Most mortalities (n = 20; 87%) occurred in May, June, and July (n = 4, 8, and 8, respectively). We could identify the cause of 52% (n = 12) of mortality events; predation accounted for 75% of these events (n = 9; Fig. 2). Each state and year of analysis had more than one model with fairly strong support based on Δ_i (i.e., $\Delta_i < 7.0$ of the top model; Table 2). Models with constant survival (null model) were supported in every test, and sex and population variables also received support for every model in which the predictors could be tested (sex effect was not tested in Wisconsin).

Iowa.—Of the 52 *G. insculpta* monitored, 25% died (n = 13; five males, six females from population BH; two males from population BU) and 10% were censored (n = 5; two males, one female from BH; one male, one female from BU). Mortalities occurred from March to October, with the highest rates occurring in May (n = 4) and June (n = 5). Causes of mortality included being buried in sediment during extreme flooding (n = 1), jaw dislocation and possible infection resulting from a predator attack (n = 1), predation (n = 8), and unknown (n = 3; Fig. 2). Two of the unknown mortalities were female *G. insculpta* from population BH found dead in September 2013. They had last been encountered in May 2013, after which severe flooding prohibited tracking until September. Mortalities due to predation were documented in March, May, June, July, September, and October. Maximum monthly survival estimates for all groups and years ranged from 0.95 ± 0.02 (standard deviation [SD]) in June to 1.00 ± 0.00 (Fig. 3). Estimated annual male survival ranged from 0.67 ± 0.16 to 0.89 ± 0.11. Estimated annual female

Table 1. Sample size (n), number of mortalities (m), and the number of *Glyptemys insculpta* (Wood Turtle) censored within years using radio telemetry in Iowa, Minnesota, and Wisconsin, USA, by year and population. We monitored 113 unique turtles for one or more years, for a total of 219 turtle-year combinations. The acronyms BU = Iowa Butler County population, BH = Iowa Black Hawk County population, ON = Wisconsin Oneida County population, and WB = Wisconsin Washburn and Burnett counties population. In 2013 in Iowa, turtles were not tracked due to severe flooding June to August.

				Male			Female			Total		
State	Population	Year	Months Tracked	n	m	c	n	m	c	n	m	c
Iowa	BH	2012	January to December	11		1	11	1		22	1	1
Iowa	BH	2013	January to May, September to December	9	1	1	11	3		20	4	1
Iowa	BH	2014	January to December	10	1		8	1	1	18	2	1
Iowa	BU	2014	January to December	8	1		11		1	19	1	1
Iowa	BH	2015	January to November	10	3		9	1		19	4	
Iowa	BU	2015	January to November	8	1	1	13			21	1	1
Minnesota		2015	June to September	9	2		17	1	3	26	3	3
Minnesota		2016	April to August	8		2	15	1	1	23	1	3
Wisconsin	ON	2014	May to October	4		2	8			12		2
Wisconsin	WB	2014	May to October	2			8	1		10	1	
Wisconsin	ON	2015	April to September	2	1		10	3		12	4	
Wisconsin	WB	2015	April to September	2			15	1		17	1	
Total				83	10	7	136	13	6	219	23	13

survival ranged from 0.64 ± 0.16 to 1.00 ± 0.00. The combined survival estimate for all groups and years was 0.86 ± 0.03 (Table 3).

Minnesota.—Of the 29 *G. insculpta* we monitored, 14% died (n = 4; two males, two females) and 21% were censored (n = 6; two males, four females). All documented mortalities occurred in the month of July. The causes of mortalities were unknown. All four mortalities were missing most of their internal organs and soft tissue when located. In addition, one female was decapitated, and we did not find any evidence of teeth or claw marks on any of the shells. Maximum monthly survival estimates for both sexes for the duration of monitoring ranged from 0.91 ± 0.04 (SD) in July to 1.00 ± 0.00 (Fig. 3). Estimated annual male survival was 0.74 ± 0.16 in 2015 and 1.00 ± 0.00 in 2016. Estimated annual female survival was 0.93 ± 0.06 in 2015 and 0.92 ± 0.08 in 2016. The combined survival estimate for all individuals in both years was 0.89 ± 0.05 (Table 3).

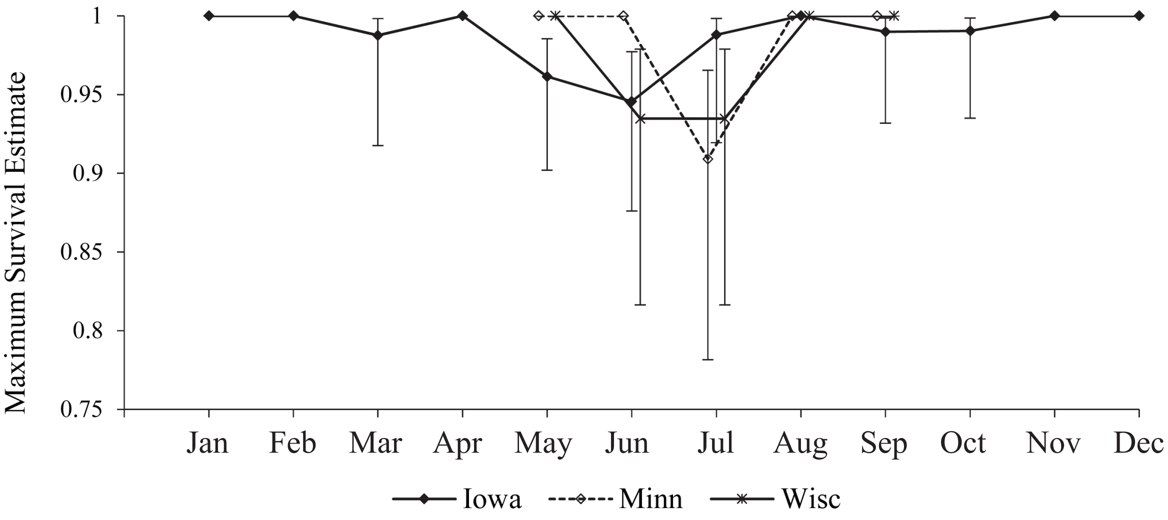

Figure 3. Monthly maximum survival estimates for radio-tracked adult *Glyptemys insculpta* (Wood Turtle) in Iowa (2012−2015), Minnesota (2015−2016), and Wisconsin (2014−2015), USA. Error bars are 95% confidence intervals.

Table 2. Models with some support ($\Delta_i < 7.0$) for predicting adult *Glyptemys insculpta* (Wood Turtle) survival by year in Iowa, Minnesota, and Wisconsin, USA. Variables are (.) = constant; (s) = sex; (p) = population; (t) = time (month). Notation follows Burnham and Anderson (2002): AIC_c = Akaike Information Criterion corrected for small sample size; Δ_i = difference between current model AIC*c* and lowest AIC*c*; w_i = Akaike weight; *K* = number of parameters.

State	Year	Model	AIC_c	Δ_i	w_i	*K*
Iowa	2012	S(.)	14.60	0.00	0.56	1
		S(s)	15.12	0.51	0.77	2
	2013	S(.)	38.97	0.00	0.66	1
		S(s)	40.32	1.35	0.34	2
	2014	S(.)	36.10	0.00	0.50	1
		S(s)	37.69	1.60	0.22	2
		S(p)	37.99	1.90	0.19	2
		S(s+p)	39.66	3.57	0.08	3
		S(s*p)	40.17	4.07	0.06	4
	2015	S(s)	54.08	0.00	0.20	2
		S(s+p)	54.18	0.10	0.19	3
		S(p)	54.72	0.64	0.15	2
		S(.)	55.20	1.12	0.12	1
		S(s*p)	55.50	1.42	0.10	4
		S(s+p+t)	55.94	1.86	0.08	13
		S(s+t)	56.19	2.11	0.07	12
		S(p+t)	56.63	2.55	0.06	12
		S(t)	57.26	3.18	0.04	11
Minnesota	2015	S(t)	26.83	0.00	0.37	4
		S(s+t)	27.34	0.51	0.29	5
		S(.)	28.15	1.31	0.19	1
		S(s)	28.57	1.74	0.15	2
	2016	S(.)	12.97	0.00	0.65	1
		S(s)	14.25	1.28	0.33	2
		S(t)	18.58	5.61	0.04	5
Wisconsin	2014	S(.)	13.55	0.00	0.54	1
		S(p)	13.91	0.36	0.46	2
	2015	S(p+t)	43.22	0.00	0.43	7
		S(p)	44.04	0.82	0.28	2
		S(t)	45.14	1.92	0.16	6
		S(.)	45.67	2.45	0.13	1

Wisconsin.—Of the 32 *G. insculpta* we monitored, 19% died (n = 6; one male, three females from population ON; two females from population WB) and 6% were censored (n = 2, both males from population ON). All of the documented mortalities occurred during the months of June and July (n = 3 in each month). One mortality was the result of a vehicle collision, one was determined by necropsy to be from predation, and four were the result of unknown causes (Fig. 2). Maximum monthly survival estimates for all groups for the duration of monitoring ranged from 0.93 ± 0.04 (SD) in June and July to 1.00 ± 0.00 (Fig. 3). Estimated annual male survival ranged from 0.49 ± 0.35 to 1.00 ± 0.00. Estimated annual female survival ranged from 0.68 ± 0.15 to 1.00 ± 0.00. The combined survival estimate for all individuals in both years was 0.87 ± 0.05 (Table 3).

DISCUSSION

Our results indicated average adult annual survival for our *G. insculpta* populations from the Upper Midwest during the study period was < 0.9 (Table 3), similar to *G. insculpta* adult survival estimates reported from a population in an agricultural-forested landscape in Québec (i.e., 0.90 and 0.87 in 1998 and 1999, respectively; Saumure et al. 2007). The Québec population was believed to be declining due to unsustainable adult mortality rates resulting from agricultural practices and was expected to be extirpated without intervention (Daigle and Jutras 2005; Saumure et al. 2007). For our Upper Midwest populations, additional knowledge of population-specific recruitment and juvenile survival rates is required to determine if these survival rates are high enough for long-term population persistence (Skalski et al. 2005). Average annual adult survival rates of > 0.95 may be required for long-term population stability; a *G. insculpta* population simulation model indicated that an adult survival rate of 0.96 resulted in a stable population, whereas the population declined when adult survival was reduced to about 0.94 (Compton 1999). An empirical study in Michigan conducted over an 18-y study period estimated an annual adult survival rate of 0.970 ± 0.016 (SD), which was associated with a positive population growth rate (Schneider et al. 2018).

The life-history traits of *G. insculpta* and many other chelonians are such that populations are likely unable to recover from sustained high levels of adult mortality (Brooks et al. 1991; Congdon et al. 1993). Freshwater turtle populations are susceptible to even low rates of adult mortality, which can cause rapid population declines and even extirpation (Brooks et al. 1992; Heppell 1998). Congdon et al. (1994) showed that an increase in annual adult *Chelydra serpentina* mortality of 10% from baseline rates could halve the number of adults in a population in fewer than 20 y without density-dependent compensation. In a modeled population of 100 adult *G. insculpta*, Compton (1999) projected that for a population in New England, removal of three breeding adults per year would lead to extirpation in 50 y. Additional monitoring data from our Iowa and Minnesota study populations supports the high adult mortality rates inferred from the telemetry

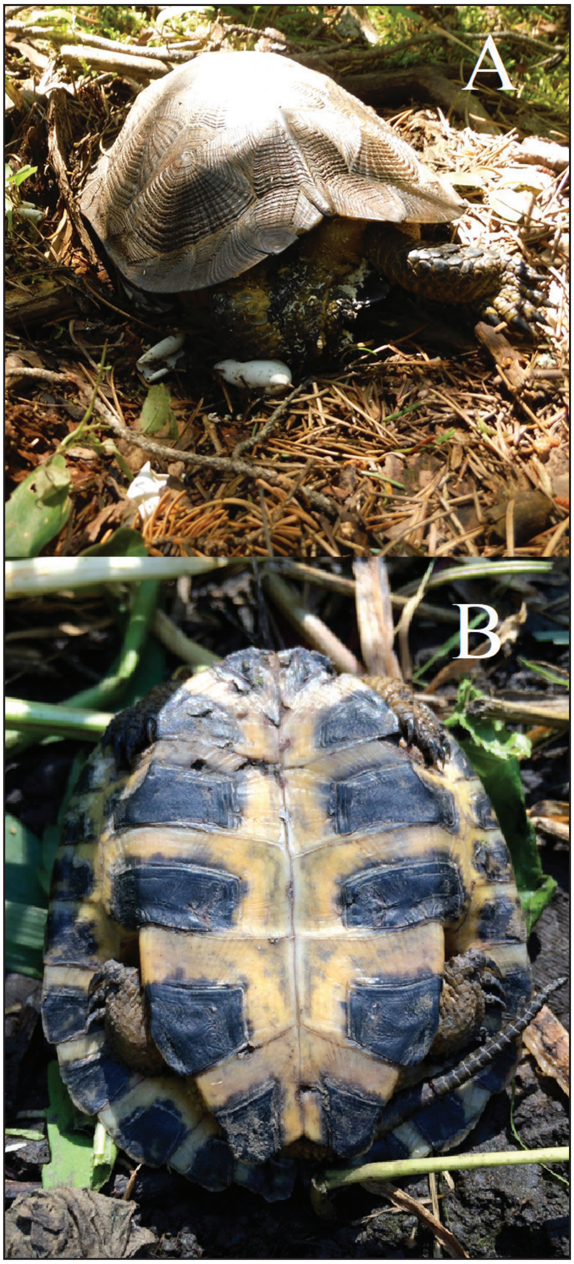

Figure 4. Successful and attempted predation of *Glyptemys insculpta* (Wood Turtle) by mesopredators in the Upper Midwest, USA. (A) Recently decapitated female *G. insculpta* found at a known nesting site surrounded by predated eggs in Minnesota in June 2016. (B) Juvenile *G. insculpta* in Iowa that survived a suspected predation attempt by *Mustela* sp. in May 2016. (A photographed by Madaline Cochrane and B photographed by Jeffrey Tamplin).

data analyses. For the Iowa populations, 36 of 141 *G. insculpta* marked between 2003–2018 have died. Seven mortalities occurred from 2003–2012 and 29 mortalities occurred from 2013–2018, including 18 of 45 marked turtles in the suburban BH population. For the Minnesota population, we encountered 50 dead *G. insculpta* from 2016–2017, including 13 individuals in 2017 that were known to be alive in 2016 (Cochrane et al. 2018).

Predation.—Many of the mortalities (39%) of adult *G. insculpta* wearing radio transmitters documented in this study were the result of predation. All of them occurred during the active period of March to October, and many during the nesting period of May to July, indicating that, at least in the Upper Midwest, *G. insculpta* appear to be most vulnerable to predation when they are using terrestrial environments. In most cases (eight of nine), these animals had been located within the previous 2−10 d and exhibited no signs of abnormal behavior or illness prior to mortality. We did not directly observe any predation events, but we believe most, if not all, predatory attacks were caused by mesopredators based on track presence, bite marks, types of soft tissue damage, and the species assemblage present at our study sites (Cochrane et al. 2018; Carly Lapin, pers. obs.; Jeff Tamplin, pers. obs.). In Iowa, turtles that were predated included carcasses found with chewed radio antennae, scratches and gnaw marks evident on the transmitter or on the shell, and/or extensive soft-tissue damage, including decapitation (Fig. 4A). In Wisconsin and Minnesota, we suspect the deaths were the result of predation due to the timing of mortality and the lack of evidence of any other cause (e.g., road mortality, disease). In August 2015, we collected oral swab and blood samples from seven turtles (two males, five females) from population ON for disease testing at the Wildlife Epidemeology Lab of the University of Illinois (Urbana, Illinois, USA) for ranavirus and herpesvirus, and all results were negative.

Raccoons (*Procyon lotor*) are known predators of *G. insculpta* across the species range and are suspected to have caused population declines in Michigan (Harding and Bloomer 1979; Farrell and Graham 1991; Ernst et al. 1994; Wusterbarth 2000; MacGregor and Elderkin 2003). *Procyon lotor* populations have increased range-wide in association with increased agriculture, development, human activity, and reductions in apex predator populations (Riley et al. 1998; Odell and Knight 2001; Kuehl and Clark 2002; MacGregor and Elderkin 2003). Based on track abundance and proximity, *P. lotor* was suspected to be responsible for most predation events in Iowa, which is perhaps not surprising given the dominant surrounding land use for these populations (i.e., agriculture and development). In contrast, camera trapping in 2015 and 2016 at *G. insulpta* nesting sites in Minnesota showed that American Badgers (*Taxidea taxus*; 56% of captures) were a far more prevalent mesopredator than *P. lotor* (13% of captures; Cochrane et al. 2017). The primary predators of adult *G. insculpta* in the primarily forested region of northern Minnesota and Wisconsin remain unknown, however.

Table 3. Annual and cumulative survival for radio-tracked adult *Glyptemys insculpta* (Wood Turtle) in Iowa, Minnesota, and Wisconsin, USA. The abbreviation S = survival estimate, and acronyms are BH = Iowa Black Hawk County population, BU = Iowa Butler County population, ON = Wisconsin Oneida County population, and WB = Wisconsin Washburn and Burnett counties population.

						95% CI	
State	Year	Group	n	*S*	SE	Lower	Upper
Iowa	2012	Male, BH	11	0.88	0.11	0.47	0.98
		Female, BH	11	1.00	0.00	1.00	1.00
		Combined	22	0.94	0.05	0.69	0.99
Iowa	2013	Male, BH	9	0.84	0.15	0.38	0.98
		Female, BH	11	0.64	0.16	0.31	0.88
		Combined	20	0.72	0.12	0.46	0.89
Iowa	2014	Male, BH	10	0.89	0.11	0.50	0.98
		Female, BH	8	0.86	0.13	0.44	0.98
		Male, BU	8	0.80	0.18	0.31	0.97
		Female, BU	11	1.00	0.00	1.00	1.00
		Combined	37	0.89	0.06	0.72	0.97
Iowa	2015	Male, BH	10	0.67	0.16	0.34	0.89
		Female, BH	9	0.88	0.11	0.49	0.98
		Male, BU	8	0.86	0.13	0.43	0.98
		Female, BU	13	1.00	0.00	1.00	1.00
		Combined	40	0.86	0.06	0.71	0.94
Iowa	2012−2015	Combined	52	0.86	0.03	0.78	0.92
Minnesota	2015	Male	9	0.74	0.16	0.36	0.93
		Female	17	0.93	0.06	0.65	0.99
		Combined	26	0.87	0.07	0.66	0.96
Minnesota	2016	Male	8	1.00	0.00	1.00	1.00
		Female	15	0.92	0.08	0.59	0.99
		Combined	23	0.94	0.05	0.69	0.99
Minnesota	2015−2016	Combined	29	0.89	0.05	0.74	0.96
Wisconsin	2014	Male, ON	4	1.00	0.00	1.00	1.00
		Female, ON	8	1.00	0.00	1.00	1.00
		Male, WB	2	1.00	0.00	1.00	1.00
		Female, WB	8	0.86	0.13	0.42	0.98
		Combined	22	0.95	0.05	0.72	0.99
Wisconsin	2015	Male, ON	2	0.49	0.35	0.06	0.94
		Female, ON	10	0.68	0.15	0.35	0.89
		Male, WB	2	1.00	0.00	1.00	1.00
		Female, WB	15	0.93	0.07	0.62	0.99
		Combined	29	0.63	0.15	0.33	0.85
Wisconsin	2014−2015	Combined	32	0.87	0.05	0.74	0.94

In addition to *P. lotor*, one (perhaps two) kill(s) in Iowa circumstantially appeared to be by River Otters (*Lontra canadensis*), where we found two *G. insculpta* at the same time and place in the water one week after observed mating. Mink (*Mustela vison*) tracks were also abundant at the Iowa sites, and one juvenile *G. insculpta* survived what appeared to be a *M. vison* (or other mustelid) attack at the BU site in May 2016 (Fig. 4B). In addition to mortalities, we observed evidence of several predator attacks that resulted in nonlethal limb amputation or large areas of shell damage in all three states.

Flooding.—As has been documented in other areas of the range of this species (Jones and Sievert 2009), flooding played a role in *G. insculpta* mortality in Iowa. A severe flooding event in May 2013 in Iowa resulted in the direct mortality of one female *G. insculpta* from population BH and may have directly or indirectly contributed to the mortality of two other females. Outside of the study period, another adult female in the BU population was directly killed by flooding in October 2005 (Jeff Tamplin, pers. obs.); this turtle was swept several km downstream by flash flooding and subsequently found dead under a newly formed sandbar. Despite only a few adult turtle deaths directly attributed to flooding, flooding is a significant factor in nest destruction and greatly limits recruitment, particularly in the Iowa populations (Spradling et al. 2010).

Vehicle mortality.—Road mortality is a well-documented, localized threat to *G. insculpta* and other turtle populations in North America (Brooks et al. 1992; Burger and Garber 1995; Gibbs and Shriver 2002; MacGregor and Elderkin 2003). Road mortalities were rare among tracked individuals in our study areas. During the course of this study, we only documented one (4% of total) radio-tracked *G. insculpta* road mortality, a female in population WB in Wisconsin that was killed in June 2014 when struck on a bridge during the nesting season. We discovered at least five *G. insculpta* not wearing radio transmitters during the study period that were road mortalities (two in Minnesota and three in Wisconsin); however, all were associated with nesting season movements (Cochrane et al. 2017; Carly Lapin, pers. obs.). Although direct mortality from vehicles was not observed in Iowa during the study period, one female at BU was evidently struck by farm equipment. We recovered the radio transmitter of this turtle in an agricultural field, dislodged and damaged by a farm implement. We searched the area thoroughly but we never located the turtle or carcass. In all states, we commonly observed female *G. insculpta* using gravel roads and road shoulders for nesting, and several road mortalities have been reported for *G. insculpta* at or near the BU site in the past decade, including one gravid female in 2019 (Jeff Tamplin, pers. obs.). Management to reduce road mortality (e.g., road barriers, Dodd et al. 2004) could be an effective strategy to reduce threats to *G. insculpta* in locations where it occurs.

Study implications.—The low estimated annual survival rates for all of our focal *G. insculpta* populations is a cause for concern, and regional efforts to conduct population viability analyses and establish long-term monitoring are warranted (Brown et al. 2017; Kenneth Bowen and James Gillingham, unpubl. report). Long-term monitoring would contribute to our knowledge of survival over time and help us to understand whether the potentially lower-than-sustainable survival probabilities calculated here are truly a cause for concern (Gibbons et al. 2000). In addition, continued documentation of the causes and timing of adult *G. insculpta* mortality would help to establish effective conservation actions to maximize survival.

Acknowledgments.—Glyptemys insculpta research in Iowa was funded by the Iowa Department of Natural Resources (Permit No. SC-648) through a Competitive State Wildlife Grant (No. F14AP00013) contracted to the University of Northern Iowa (UNI; Jeff Tamplin, Principle Investigator). We thank Samuel W. Berg, Jeremy P. George, Joshua G. Otten, and Jessica J. Williams (M.S. students at the University of Northern Iowa) for assistance with radio telemetry and field work and the Department of Biology and the College of Humanities, Arts, and Sciences of the University of Northern Iowa for funding.

Glyptemys insculpta research in Minnesota was funded by the Minnesota Department of Natural Resources through a Competitive State Wildlife Grant (No. F14AP00028), with additional financial support provided to Madaline Cochrane through a summer fellowship of the University of Minnesota Integrated Biosciences Graduate Program. Donald Brown was supported during manuscript preparation by the McIntire Stennis project WVA00122 of the National Institute of Food and Agriculture of the U.S. Department of Agriculture, and the West Virginia Agricultural and Forestry Experiment Station. The Institutional Animal Care and Use Committee of the University of Minnesota (Protocol No. 1504-32514A) approved sampling and handling methods, and the Minnesota Department of Natural Resources permitted this research. We thank Katelin Goebel, Kelcy Huston, Cord Reno, and Ashlee Ricci for assistance with radio telemetry and field work.

Glyptemys insculpta research in Wisconsin was funded by the Wisconsin Department of Natural Resources through a Competitive State Wildlife Grant (No. F14AP00041), with additional financial support provided by the Natural Resources Foundation of Wisconsin. The Animal Care and Use Committee of the Wisconsin Department of Natural Resources (No. 14_Lapin_01) approved sampling and handling methods. We thank Andrew Badje, Tiffany A. Bougie, Joel Flory, Laura Jaskiewicz, Kathy Kafura, Matt Schumaker, and Erik Wild for assistance with radio telemetry and field work.

LITERATURE CITED

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

Brooks, R.J., G.P. Brown, and D.A. Galbraith. 1991. Effects of a sudden increase in natural mortality of adults on a population of the Common Snapping Turtle (*Chelydra serpentina*). Canadian Journal of Zoology 69:1314–1320.

Brooks, R.J., C.M. Shilton, G.P. Brown, and N.W.S. Quinn. 1992. Body size, age distribution, and reproduction in a northern population of Wood Turtles (*Clemmys insculpta*). Canadian Journal of Zoology 70:462–469.

Brown, D.J., M.D. Nelson, D.J. Rugg, R.R. Buech, and D.M. Donner. 2016. Spatial and temporal habitat-use patterns of Wood Turtles at the western edge of their distribution. Journal of Herpetology 50:347–356.

Brown, D.J., M.M. Cochrane, and R.A. Moen. 2017. Survey and analysis design for Wood Turtle population modeling. Journal of Wildlife Management 81:868–877.

Buech, R.R., L.G. Hanson, and M.D. Nelson. 1997. Identification of Wood Turtle nesting areas for protection and management. Pp. 383–391 *In* Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles - an International Conference. Van Abbema, J. (Ed.). New York Turtle and Tortoise Society, New York, New York, USA.

Burger, J., and S.D. Garber 1995. Risk assessment, life history strategies, and turtles: could declines be prevented or predicted? Journal of Toxicology and Environmental Health 46:483–500.

Burnham, K.P., and D.R. Anderson. 2002. Model Selection and Multi-model Inference: A Practical Information-theoretic Approach. 2nd Edition. Springer-Verlag, New York, New York, USA.

Burnham, K.P., D.R. Anderson, and K.P. Huyvaert. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behavioral Ecology and Sociobiology 65:23–35.

Christiansen, J.L., and R.M. Bailey. 1997. The lizards and turtles of Iowa. Iowa Department of Natural Resources, Nongame Technical Series No. 3, Des Moines, Iowa, USA. 20 p.

Cochrane, M.M., D.J. Brown, and R.A. Moen. 2017. Wood Turtle nest monitoring and mortality surveys. NRRI/TR-2017-06 Release 1.0, Natural Resource Research Institute, Duluth, Minnesota, USA. 40 p.

Cochrane, M.M., D.J. Brown, M.D. Nelson, R.R. Buech, M. Schrage, D. Ryan, and R.A. Moen. 2018. Status of a *Glyptemys insculpta* (Wood Turtle) population in northeastern Minnesota. Herpetological Conservation and Biology 13:273–282.

Compton, B.W. 1999. Ecology and conservation of the Wood Turtle (*Clemmys insculpta*) in Maine. M.Sc. Thesis, University of Maine, Orono, Maine, USA. 91 p.

Compton, B.W., J.M. Rhymer, and M. McCollough. 2002. Habitat selection by Wood Turtles (*Clemmys insculpta*): an application of paired logistic regression. Ecology 83:833–843.

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 serptentina*): implications for conservation and management of long-lived organisms. American Zoologist 34:397–408.

Daigle, C., and J. Jutras. 2005. Quantitative evidence of decline in a southern Québec Wood Turtle (*Glyptemys insculpta*) population. Journal of Herpetology 39:130–132.

Dodd, C.K., Jr., W.J. Barichivich, and L.L. Smith. 2004. Effectiveness of a barrier wall and culverts in reducing wildlife mortality on a heavily traveled highway in Florida. Biological Conservation 118:619–631.

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

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

Ernst, C.H., J.E. Lovich, and R.W. Barbour. 1994. Turtles of the United States and Canada. Smithsonian Institution Press, Washington, D.C., USA.

Farrell, R.F., and T.E. Graham. 1991. Ecological notes on the turtle *Clemmys insculpta* in northwestern New Jersey. Journal of Herpetology 25:1–9.

Garber, S.D., and J. Burger. 1995. A 20-yr study documenting the relationship between turtle decline and human recreation. Ecological Applications 5:1151–1162.

Gibbons, J.W., D.E. Scott, T.J. Ryan, K.A. Buhlmann, T.D. Tuberville, B.S. Metts, J.L. Greene, T. Mills, Y. Leiden, S. Poppy, et al. 2000. The global decline of reptiles, déjá vu amphibians. BioScience 50:653–666.

Gibbs, J.P., and W.G. Shriver. 2002. Estimating the effects of road mortality on turtle populations. Conservation Biology 16:1647–1652.

Harding, J.H. 1997. Amphibians and Reptiles of the

Great Lakes Region. University of Michigan Press, Ann Arbor, Michigan, USA.

Harding, J.H. 2008. Wood Turtles, humans, and raccoons: burning the candle at both ends. World Chelonian Trust Newsletter 3:1−4.

Harding, J.H., and T.J. Bloomer. 1979. The Wood Turtle, *Clemmys insculpta*... a natural history. Bulletin of the New York Herpetological Society 15:9−26.

Heppell, S.S. 1998. Application of life-history theory and population model analysis to turtle conservation. Copeia 1998:367−375.

Homer, C., J. Dewitz, L. Yang, S. Jin, P. Danileson, G. Xian, J. Coulston, N. Herold, J. Wickham, and K. Megown. 2015. Completion of the 2011 National Land Cover Database for the Conterminous United States - Representing a Decade of Land Cover Change Information. Photogrammetric Engineering and Remote Sensing 81:346−354.

Jones, M.T., and P.R. Sievert. 2009. Effects of stochastic flood disturbance on adult Wood Turtles, *Glyptemys insculpta*, in Massachusetts. Canadian Field-Naturalist 123:343−322.

Kuehl, A.K., and W.R. Clark. 2002. Predator activity related to landscape features in northern Iowa. Journal of Wildlife Management 66:1224−1234.

Levell, J.P. 2000. Commercial exploitation of Blanding's Turtle, *Emydoidea blandingii*, and the Wood Turtle, *Clemmys insculpta*, for the live animal trade. Chelonian Conservation and Biology 3:665−674.

MacGregor, M.K., and M.F. Elderkin. 2003. Protecting and conserving Wood Turtles: a stewardship plan for Nova Scotia. Biodiversity Program, Wildlife Division, Nova Scotia Department of Natural Resources, Kentville, Nova Scotia, Canada. 23 p.

Moriarty, J.J., and C.D. Hall. 2014. Amphibians and Reptiles in Minnesota. University of Minnesota Press, Minneapolis, Minnesota, USA.

Odell, E.A., and R.L. Knight. 2001. Songbird and medium-sized mammal communities associated with exurban development in Pitkin County, Colorado. Conservation Biology 15:1143−1150.

Otten, J.G. 2017. Factors influencing Wood Turtle (*Glyptemys insculpta*) home range size in Iowa: a comparison between suburban and rural populations. M.Sc. Thesis, University of Northern Iowa, Cedar Falls, Iowa, USA. 162 p.

Parren, S.G. 2013. A twenty-five year study of the Wood Turtle (*Glyptemys insculpta*) in Vermont: movements, behavior, injuries, and death. Herpetological Conservation and Biology 8:176−190.

Pe'er, G., Y.G. Matsinos, K. Johst, K.W. Franz, C. Turlure, V. Radchuk, A.H. Malinowska, J.M.R. Curtis, I. Naujokaitis-Lewis, B.A. Wintle, et al. 2013. A protocol for better design, application, and communication of population viability analyses. Conservation Biology 27:644−656.

Riley, S.P.D., J. Hadidian, and D.A. Manski. 1998. Population density, survival, and rabies in Raccoons in an urban national park. Canadian Journal of Zoology 76:1153−1164.

Saumure, R.A., T.B. Herman, and R.D. Titman. 2007. Effects of haying and agricultural practices on a declining species: the North American Wood Turtle, *Glyptemys insculpta*. Biological Conservation 135:581−591.

Schneider, A.C., T.W. Arnold, P.W. Huber, and T.L. Lewis. 2018. An 18-year mark-recapture study of Wood Turtles (*Glyptemys insculpta*) in Michigan. Journal of Herpetology 52:193−200.

Skalski, J.R., K.E. Ryding, and J.J. Millspaugh. 2005. Wildlife Demography: Analysis of Sex, Age, and Count Data. Academic Press, San Diego, California, USA.

Spradling, T.A., J.W. Tamplin, S.S. Dow, and K.J. Meyer. 2010. Conservation genetics of a peripherally isolated population of the Wood Turtle (*Glyptemys insculpta*) in Iowa. Conservation Genetics 11:1667−1677.

van Dijk, P.P., and J. Harding. 2011. *Glyptemys insculpta* [errata version published in 2016]. The International Union for the Conservation of Nature Red List of Threatened Species 2011. www.IUCN.org.

Vogt, R.C. 1981. Natural History of Amphibians and Reptiles in Wisconsin. Milwaukee Public Museum Press, Milwaukee, Wisconsin, USA.

White, G.C., and K.P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46(supplement):S120−139.

Willoughby, J.R., M. Sundaram, T.L. Lewis, and B.J. Swanson. 2013. Population decline in a long-lived species: the Wood Turtle in Michigan. Herpetologica 69:186−198.

Wisconsin Department of Natural Resources [WDNR]. 2015a. Wisconsin Wood Turtle Species Guidance. PUB-ER-684, Bureau of Natural Heritage Conservation, Wisconsin Department of Natural Resources, Madison, Wisconsin, USA. 10 p.

Wisconsin Department of Natural Resources [WDNR]. 2015b. Wisconsin Endangered and Threatened Species Laws & List. PUB-ER_001 2004 REV June 2015, Bureau of Natural Heritage Conservation, Wisconsin Department of Natural Resources, Madison, Wisconsin, USA. 5 p.

Wusterbarth, T.L. 2000. Nest predation and effects of human recreation on the Wood Turtle (*Clemmys insculpta*) of a western Michigan river. M.Sc. Thesis, Central Michigan University, Mt. Pleasant, Michigan, USA. 44 p.

Carly N. Lapin is a Regional Ecologist for the Bureau of Natural Heritage Conservation, Wisconsin Department of Natural Resources, based in Rhinelander, Wisconsin, USA, where she manages a number of State Natural Areas and assists with rare species conservation. She received her B.A. in Conservation Biology from the University of Wisconsin - Madison, USA, in 2005 and a M.Sc. degree from the University of Minnesota, Duluth, USA, in 2010. (Photographed by Tiffany Bougie).

Jeffrey W. Tamplin is a Professor of Biology at the University of Northern Iowa. Cedar Falls, USA, who has been studying Wood Turtle ecology in Iowa since 2003. Jeff earned a B.A. in Biology in 1986 from Augustana College, Rock Island, Illinois, USA, and earned his M.Sc. (1988) and Ph.D. (1999) in Zoology from Louisiana State University, Baton Rouge, USA. At the University of Northern Iowa, Jeff teaches courses in Introductory Biology, Ecology and Evolution, Field Herpetology, and Vertebrate Zoology. (Photographed by Emily Reisberg).

Madaline M. Cochrane is currently working on her doctorate at the University of Montana, Missoula, USA, where she studies Appalachian stream salamander population and spatial ecology. She completed her M.Sc. at the University of Minnesota, Duluth, USA, in 2017. She received her B.A. in Biology and Environmental Studies from Macalester College, St. Paul, Minnesota, USA. (Photographed by Kelcy Huston).

James E. Woodford is the Field Operations Section Chief within the Bureau of Natural Heritage Conservation, Wisconsin Department of Natural Resources, based in Rhinelander, Wisconsin, USA. He has a B.Sc. degree in Wildlife Management from the University of Wisconsin-Stevens Point, USA, and a M.Sc. degree in Wildlife Ecology from the University of Wisconsin-Madison, USA. (Photographed by Michele Woodford).

Donald J. Brown is a Research Assistant Professor in a joint position with West Virginia University, Morgantown, USA, and the U.S. Forest Service, Northern Research Station, Parsons, West Virginia, USA. He received his B.Sc. in Fisheries & Wildlife from the University of Minnesota-Twin Cities, St. Paul, USA, and his M.Sc. and Ph.D. from Texas State University, San Marcos, USA, in Wildlife Ecology and Aquatic Resources, respectively. Donald's lab conducts research that contributes to conservation of wildlife populations and communities under changing environmental and management conditions, with a focus on amphibian and reptile species of concern. (Photographed by Andrew Badje).

Ron A. Moen is an Associate Professor in the Department of Biology and a Senior Research Associate with the Natural Resources Research Institute at the University of Minnesota Duluth, USA. He received his B.Sc. in Ecology from Cornell University, Ithaca, New York, USA, and his M.Sc. and Ph.D. from the University of Minnesota, St. Paul, USA, in Wildlife Conservation. Ron's lab generally conducts research on habitat use and population dynamics of mammals, with occasional work on other taxonomic groups. (Photographed by Brett Groehler).