



Research Article

Ecology of Neonate Eastern Box Turtles With Prescribed Fire Implications

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ABSTRACT Little is known about the movements and behavior of neonate eastern box turtles (*Terrapene carolina carolina*). We investigated spatial ecology of neonate eastern box turtles at 4 upland openings in the Manistee National Forest, Michigan, USA, 2012–2016. We protected nests and used radio-telemetry to document dispersal from nests, land cover types used for overwintering, and residency time of neonates in natal openings. We used binomial logistic regression to model probabilities of overwintering in natal openings versus adjacent forest and edge. We protected 64 nests, radio-fitted 64 neonates over 4 cohort years, tracked 46 neonates from nest emergence to their overwintering sites, and tracked 28 neonates for portions of their second activity season. Dispersal (straight-line distance from nest to overwintering site) was limited in the first activity season ($n = 46$ neonates, $\bar{x} = 19.9 \pm 2.4$ m [SE], range = 1.9–83.2 m) and 24 overwintered in natal openings, 4 overwintered in the forest edge, and 18 overwintered in forest. Our best logistic model included the predictor variables distance from nest to nearest forest edge and day of nest emergence. Probability of overwintering within a natal opening was greater for neonates from nests located farther from the forest edge and for neonates emerging from nests later in the year. By 1 June of their second activity season, all tracked turtles were still present in, or within 50 m, of their natal opening, but all neonates had dispersed into surrounding forest or wetlands by 1 July. Managers should be aware that neonates reside in or very near their natal openings for several months after nest emergence. When burning or otherwise intensively managing open canopy box turtle nesting areas, relaxing the interval (yr) between treatments and excluding forest edge and adjacent forest should allow neonates time to disperse, decreasing risk of mortality. © 2018 The Wildlife Society.

KEY WORDS barrens, dispersal, dry sand prairie, Manistee National Forest, neonate, prescribed fire, *Terrapene carolina carolina*, upland openings.

The magnitude of anthropogenic factors imperiling North American turtles and tortoises is daunting (Gibbons et al. 2000). Even in relatively large natural areas where anthropogenic population stressors may be less acute, many disturbance regimes (i.e., fire) that historically provided landscape mosaics of open canopy nesting habitat no longer exist. Thus, promoting long-term viability of many terrestrial chelonian populations, including the eastern box turtle (*Terrapene carolina carolina*), often requires vegetation management. Eastern box turtle and other chelonian populations respond slowly (decades) to positive changes

in habitat quality (i.e., “the ability of the environment to provide conditions appropriate for individual and population persistence;” Hall et al. 1997:178) yet may decline quickly if subjected to increases in mortality rates (Congdon et al. 1993, Heppell 1998, Dodd 2001, Dodd et al. 2016). Conservation strategies for eastern box turtle populations require a delicate balance between maintaining and restoring nesting habitat and avoiding undesirable levels of mortality during vegetation management activities (Gibson 2009, Cross 2016). Avoiding mortality during vegetation management is more difficult when aspects of a species’ life history are not well documented, and although adult eastern box turtles have been well-studied (Stickel 1950, Dodd 2001), less is known about pre-reproductive age classes.

Gravid eastern box turtles (i.e., box turtles) travel to upland open canopy sites to deposit eggs but return to forested areas

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shortly after nesting (Stickel 1950, Madden 1975, Dodd 2001, Wilson and Ernst 2005, Willey and Sievert 2012). Although box turtles are often associated with fire-adapted natural communities (Cohen 2000, Kost 2004) and open areas because of seasonal ecotonal and nesting habitat preferences (Fredericksen 2014), they do not appear to possess behavioral or physiological traits allowing them to consistently escape or withstand flames (Gibson 2009, Howey and Roosenburg 2013, Cross 2016, Greenberg et al. 2018). In southern Michigan (Gibson 2009) and Ohio, USA (Cross 2016), 10.7% and 27.2%, respectively, of radio-fitted adult box turtles present within burn units died as a result of injuries sustained in low-intensity prescribed fire. Dodd et al. (2016) modeled Florida box turtle (*Terrapene carolina bauri*) population responses to losses of individuals and concluded that repeated losses, even at low rates, greatly increased probabilities of local population extinctions. Although survival rates of neonates present during prescribed burns have not been evaluated in field studies, given they are slower and smaller than adults, it is reasonable to assume fire-related mortality occurs (Gibson 2009, Epperson and Heise 2003, Perry and McDaniel 2015, Cross 2016).

Neonates emerging from nests in relatively open canopy, xeric, fire-adapted systems would be expected to leave their natal areas eventually given adults seek out humid microclimates (Rossell et al. 2006, Fredericksen 2014) and inhabit mesic forested or lowland sites for much of the year (Dodd 2001). Despite advances in radio-telemetry products and concern regarding viability of box turtle populations (Williams and Parker 1987, Dodd 2001), few investigators have reported on the behavior of this age class. In New York, USA, Madden (1975) radio-fitted and monitored 2 neonates from fall nest emergence to overwintering (17–20 days) and reported 1 individual overwintering in the open canopy field where it hatched and the other overwintered in adjacent forest. Burke and Capitano (2011), also in New York, monitored 4 neonates from nest emergence to overwintering and reported approximately 10 m as the maximum distance dispersed from the nest. Because box turtles often nest in areas managed with fire, and dispersal from nests may be delayed because of onset of winter, additional information is needed to address current knowledge gaps and management implications regarding prescribed burning and neonates.

We conducted a multi-year observational field study on spatial ecology of neonate eastern box turtles at 4 open canopy nesting areas and adjacent forest in the Manistee National Forest, Michigan. Our objectives were to document nest emergence and dispersal from nests, land cover types used for overwintering, and residency time of neonates in natal openings. Our goal was to identify mitigation measures to reduce potential direct effects on neonates when prescribed fire and other management activities are implemented in box turtle nesting areas.

STUDY AREA

Our study sites were 4 upland openings and surrounding forest within a 3-km² area of the Manistee National Forest, Northwestern Lower Peninsula, Michigan. We omit specific

localities to deter potential poachers. Elevations ranged from 180 m to 220 m and topography was flat to gently rolling. The climate was temperate continental (Belda et al. 2014). Temperatures (mean monthly high temperatures and mean monthly low temperatures, respectively) in July were 26.7°C to 14.9°C, 14.9°C to 5.2°C in October, -1.0°C to -7.6°C in January, and 5.8°C to -3.9°C in March. A mosaic of fire-dependent barrens and dry sand prairie communities were historically present within a forest matrix, but they succeeded to forest because of fire suppression or were converted into red pine (*Pinus resinosa*) plantations in the last century (Kost et al. 2007, Albert et al. 2008).

The 3-km² study area was primarily forested and upland openings represented <4% of land cover (U.S. Department of Agriculture [USDA] Forest Service, unpublished data). The term opening is a broad classification used by the Huron-Manistee National Forests for non-forested sites although shrubs and trees were commonly present at low densities within sites classified as openings. Openings were periodically managed under individual prescriptions to provide habitat for wildlife species associated with openings and promote biodiversity in the Manistee National Forest (USDA Forest Service 2006). The 4 focal openings varied in size, basal area, canopy cover of trees within the openings, and disturbance history. Ecotones along opening boundaries were relatively hard edged and generally transitioned within a few meters from relatively open canopy settings to forest. Detailed descriptions and vegetation sampling data are reported in Laarman (2017). The largest opening (Savanna, 5.6 ha) had relatively flat topography and displayed the greatest structural complexity with the largest mean basal area of trees (5.9 m²/ha ± 0.7 [SE]) and largest mean overstory canopy cover (24.9 ± 4.6%). Turtle Bowl was a 1.9-ha oval-shaped geologic frost pocket with bowl-shaped topography, mean basal area of 1.8 ± 0.6 m²/ha, and mean overstory canopy cover of 8.3 ± 2.9%. Both Savanna and Turtle Bowl had been periodically managed with low-intensity prescribed burning, most recently in 2010. Gravel Pit was a 0.7-ha oval-shaped opening with bowl-shaped topography, with mean basal area of 1.5 ± 0.4 m²/ha and mean overstory canopy cover of 8.1 ± 2.8%. Gravel Pit was perpetually disturbed by illegal off-road vehicle use during the study period, which increased the prevalence of cobble and exposed mineral soil. This disturbance likely influenced nest-site selection by attracting gravid females to areas of exposed soil at Gravel Pit (Hughes and Brooks 2006, Altobelli 2017). East West was a 0.9-ha linear-shaped opening with a south-facing approximately 60% to 80% slope running its entire length. Mean basal area was 3.1 ± 0.7 m²/ha and mean overstory canopy cover was 20.8 ± 4.4%. Overstory trees present in the openings included oaks (*Quercus* spp.), jack pine (*Pinus banksiana*), red pine, and white pine (*Pinus strobus*). Understory vegetation in Savanna, Turtle Bowl, and East West was dominated by graminoids typical of dry sand prairie (Kost 2004) and oak-pine barrens communities (Cohen 2000). Understory vegetation in Gravel Pit was dominated by non-native invasive species including spotted knapweed (*Centaurea maculosa*), Saint

John's wort (*Hypericum perforatum*), and mullein (*Verbascum thapsus*). In all 4 openings, woody species comprised <12.0% and forbs comprised <5.0% of ground cover.

The forest surrounding openings was dry-mesic northern forest (Kost et al. 2007) and was similar across the study area with respect to overstory canopy cover and ground cover. Mean basal areas in forests surrounding each opening were $25.7 \pm 1.5 \text{ m}^2/\text{ha}$ at Savanna, $26.8 \pm 1.7 \text{ m}^2/\text{ha}$ at Turtle Bowl, $30.0 \pm 1.7 \text{ m}^2/\text{ha}$ at Gravel Pit, and $24.5 \pm 1.9 \text{ m}^2/\text{ha}$ at East West. Mean overstory canopy cover was $83.8 \pm 1.5\%$ at Savanna, $77.7 \pm 1.5\%$ at Turtle Bowl, $89.9 \pm 1.2\%$ at Gravel Pit, and $80.0 \pm 2.8\%$ at East West. At each site, the forest overstory was primarily comprised of oak, jack pine, and white pine although a red pine plantation bordered the west side of Savanna. The forest mid-story and shrub layers were generally sparse but contained primarily oak species, jack pine, white pine, or cherry (*Prunus* spp.). The herbaceous layer within the forest contained primarily Pennsylvania sedge (*Carex pensylvanica*), a mosaic of lowbush blueberry (*Vaccinium angustifolium*), and bracken fern (*Pteridium aquilinum*). A river floodplain with diverse land cover types including emergent vegetation, wet meadow, scrub-shrub, and lowland conifer was present within 1 km of all openings and was immediately adjacent to the Gravel Pit opening. Fauna at the study sites included 8 amphibian species, 16 reptile species, 42 mammal species, and 90 bird species (U.S. Department of Agriculture [USDA] Forest Service, unpublished data) although cryptic species and seasonal migrants were likely under-represented in these data.

METHODS

Nest Protection and Radio-Tracking

We annually surveyed upland openings from 2012 to 2016 during late morning or midday from 25 May to 25 June to locate gravid adult female box turtles. Following capture, we affixed 15-g very high frequency (VHF) radio-transmitters to each female's carapace (Model RI-2D Holohil Systems, Ontario, Canada or Model 1555 Advanced Telemetry Systems, Isanti, MN, USA). We returned to openings between 1900–2100 hours to monitor radio-fitted turtles for nesting activity and conducted surveys to locate additional nesting turtles. After females laid and covered their eggs, we protected each nest with a 61.0-cm \times 61.0-cm \times 30.5-cm wooden framed mesh predator enclosure. We recorded nest locations with a Trimble[®] Geo 7 \times global positioning system (GPS) unit. We monitored nest enclosures every 24 to 72 hours from 1 August to 5 November for emerging neonates and placed a handful of moist sphagnum moss or leaf litter in the corner of each enclosure to provide refugia. Neonates from the same clutch did not always emerge on the same day; thus, multiple dates could be used when calculating nest emergence statistics. When multiple neonates emerged from the same nest on the same day, we considered this a single emergence event in subsequent analysis.

After neonates emerged, we soaked them in a shallow dish of distilled water for approximately 5 minutes to minimize

stress and remove any debris accumulated during nest emergence. Following soaking, we dried each neonate and collected morphometric information including body mass (g). We used quick setting 2-part epoxy to attach series R1605 radio-transmitters (Advanced Telemetry Systems) to the carapace. Radio-transmitters were customized to the lowest possible pulse rates during production and signal range was approximately 50 m. We released neonates at their nest site outside the nest enclosures immediately after transmitter attachment with exception of a few individuals that emerged in evening without adequate time for processing and release before nightfall. We kept these individuals in their nest enclosures overnight and released them the following morning.

We released each radio-fitted neonate at a random outside corner of its nest enclosure. Following release at nests, we tracked neonates 1 to 3 times per week. During telemetry observations, we recorded land cover type (i.e., opening, forest, wetland) and marked each location with small drab colored flags labeled with the neonate identification number and observation date. Flagging allowed us to determine whether the neonate was in the same location it had been in during the previous observation. We recorded GPS coordinates of each neonate flagged location. We monitored neonates until we lost radio-contact, they were depredated, or they began overwintering (i.e., overwintering ingress). We defined the period from nest emergence to overwintering ingress as the first activity season. After overwintering ingress, we placed the same enclosures used to protect nests around overwintering neonates. After snow melted in spring and daily maximum temperatures exceeded 10°C, we monitored enclosures every 24 to 72 hours for evidence of overwintering egress. When neonates emerged, we noted depth (mm) of the overwintering refugia, removed the enclosure, collected morphometric data as above, affixed new transmitters, and released neonates at their overwintering sites. We defined the period after spring overwintering egress as the second activity season. We tracked neonates on a weekly basis until we lost contact or mortality occurred.

Transmitters plus epoxy were <8.0% total body mass (Beaupre et al. 2004). All handling techniques were approved by the Michigan Department of Natural Resources (Scientific Collectors Permits) and the Institutional Animal Care and Use Committee at Grand Valley State University (protocol 13-03A).

Analysis

We delineated boundaries of each opening by walking the perimeter and recording GPS coordinates. We buffered each opening boundary by 2.5 m and considered this edge. We chose a 2.5-m buffer because this metric captured the transition zone between relatively closed canopy forest and the relatively open canopy structure of each opening. For each opening, we calculated the distance from each box turtle nest to nearest forest edge using a geographic information system (ArcGIS 10, Environmental Systems Research Institute, Redlands, CA, USA). We also calculated distance to nearest forest edge from all 1-m² raster cells within the

polygon opening boundary and used these distances to calculate mean distance to nearest forest edge within each opening as a whole (Benson 2013). We then divided distance to nearest forest edge for each nest by mean distance to forest edge within that opening and compared these ratios to a mean of 1 using 1-sample *t*-tests (Conner and Plowman 2001).

Prior to using nest emergence dates for statistical applications, we converted calendar dates of nest emergence to ordinal day of year values, with year omitted (e.g., 1 Sep 2014 = 244). Because nest emergence occurred in summer and fall (see Results) and we omitted year, these data were not circular and we calculated descriptive statistics for nest emergence dates during our study period. We hereafter refer to nest emergence dates as day of nest emergence when used as a variable in analyses. For ease of interpretation, we converted day of nest emergence values back to calendar dates (with yr omitted) when reporting results in the text and tables. For each neonate, we also calculated in a geographic information system the straight-line distance between sequential telemetry locations, direction moved between sequential telemetry locations (i.e., azimuths, 0–359°), straight-line distance from nest to overwintering site, maximum straight-line distance from nest during the first activity season, and maximum straight-line distance from nest in the second activity season. We pooled movement rates (m/day) of all neonates and reported descriptive statistics regarding movement rates by season. We used Spearman rank correlations to test associations between distance from nest to overwintering site and 3 variables: day of nest emergence, body mass at nest emergence, and distance from nest to nearest forest edge.

We pooled first activity season movements of neonates belonging to the same clutch and tested for non-random mean directionality of movements away from the nest site using Rayleigh's tests (Zar 1984). We also tested for non-random mean directionality of all movements (i.e., pooled first and second activity season movements) for each individual neonate using Rayleigh's tests. Rayleigh's tests do not take length of movements into account and after reviewing movement patterns, we censored fine-scale movements ≤ 2 m before conducting Rayleigh's tests because we attributed them to thermoregulatory behavior, not dispersal. We applied Rayleigh's test to a clutch or individual neonate if we observed ≥ 6 movements meeting our criteria.

We used binomial logistic regression to model potential relationships between the type of land cover used by neonates for overwintering and 3 predictor variables. The binary response variable was overwintering land cover type (i.e., natal openings vs. surrounding forest and edge) used by each neonate. Explanatory variables included distance (m) from nest to nearest forest edge, day of nest emergence, and body mass (g) of neonates at nest emergence. We constructed 7 candidate models using all possible combinations of variables. Prior to model construction, we tested explanatory variables for correlations using Spearman rank correlations and considered variables correlated if $P \leq 0.05$. For all candidate models, we calculated Akaike's Information

Criterion for small sample sizes (AIC_c), and associated metrics: difference in AIC_c (ΔAIC_c) and AIC_c weight (w_i ; Akaike 1973, Burnham and Anderson 2002). We considered models equally supported if their AIC_c differed by < 2 . After selecting the most parsimonious model(s) based on ΔAIC_c , we converted the β coefficients (β) to odds ratios (OR) and their 95% confidence intervals (CI) and generated predicted probabilities of neonates overwintering in natal openings by holding predictor variables constant for a range of values that we considered biologically relevant based on our observations of nest locations and nest emergence.

Prior to parametric tests, we evaluated assumptions of normality and homogeneity of variances using Shapiro-Wilk and Bartlett's tests. Because of increased probability of type II errors associated with very small sample sizes, and the biological relevance potentially associated with directionality of lengthy dispersal movements, we set α at 0.10 for Rayleigh's tests (Toft and Shea 1983). For all other hypothesis tests, $\alpha = 0.05$. We used the statistical software program R version 2.15.1 (www.r-project.org, accessed Sep 2012) for analyses. We reported descriptive statistics as means \pm standard errors (SE).

RESULTS

Nests and First Activity Season

During the 5 years of nesting surveys (2012–2016), we documented 64 nests from 29 May to 21 June. Nest locations were farthest from forest edge at Savanna (Fig. 1). Nests were significantly closer to forest edge when compared to mean distances to forest edge within the overall opening at Turtle Bowl ($t = -9.04$, $P < 0.001$) and Gravel Pit ($t = -2.18$, $P = 0.049$) but not at Savanna ($t = 0.57$, $P = 0.578$) or East West ($t = -0.26$, $P = 0.795$).

Neonates emerged from nests between 16 August to 25 October, 2012–2016, and mean day of emergence was 18 September ± 2.5 days ($n = 31$ nests, $n = 42$ nest emergence events, all sites, 2012–2016). We radio-fitted 64 neonates from 20 clutches, during 2012 to 2015 (Table 1). We determined fates (i.e., mortality or survived to overwintering ingress) for 59 of 64 neonates (92.3%) during the first activity season.

During telemetry observations, neonates were commonly hidden in forms (Stickel 1950) within duff or leaf litter, root systems of graminoids and forbs, or next to coarse woody debris. The cumulative movement trajectories for individual neonates were relatively linear and neonates did not return to former activity areas after movements > 2 m (Fig. 2). Of the 24 neonates that moved to the forest edge before overwintering, only 2 returned to openings on subsequent telemetry observations. Sample size limitations (movements per neonate) prohibited testing directionality of movements for individual neonates in the first activity season, but we did detect non-random directionality (Rayleigh's Z , $P \leq 0.1$) in pooled within-clutch movements for 8 of 10 clutches although results should be interpreted with caution because of small sample sizes (movements/clutch). Directional means of movements for these 8 clutches were oriented toward

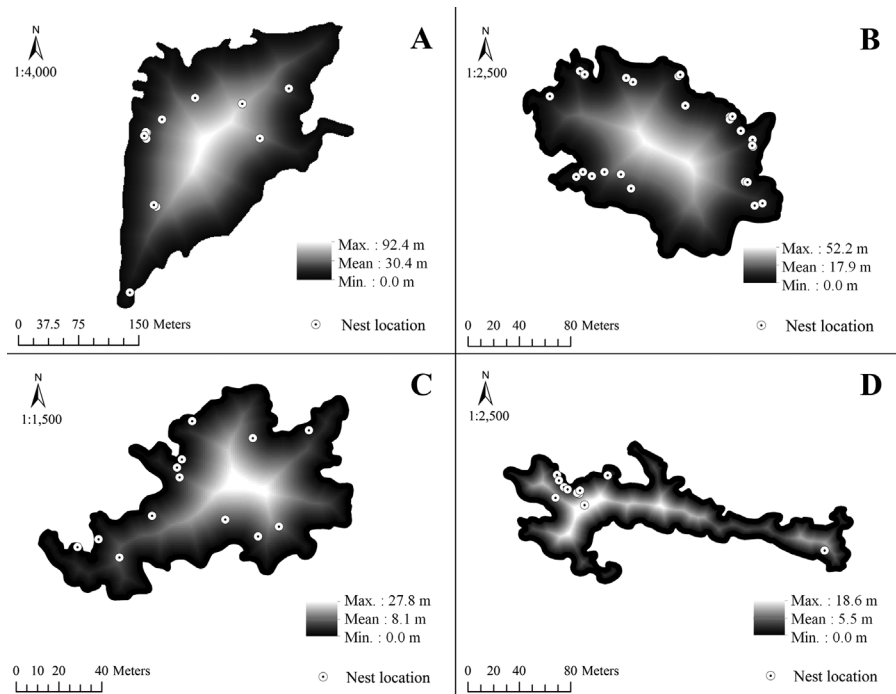


Figure 1. Spatial distribution of eastern box turtle nests ($n = 64$ nests) relative to forest edge at Savanna opening (A), Turtle Bowl opening (B), Gravel Pit opening (C), and East West opening (D), Manistee National Forest, Michigan, USA, 2012–2016. Grey-scale color ramps indicate maximum, minimum, and mean distances (m) of raster cell centroids (1-m^2 resolution) within each opening relative to the nearest forest edge (Benson 2013).

forest edges rather than interior portions of the openings (Fig. 2).

We tracked 46 radio-fitted neonates from nest emergence to overwintering ingress (Table 1). Movement rates (m/day)

were higher in August and September than in October and November (Fig. 3). No neonate dispersed >50 m beyond the boundary of its natal opening before overwintering (Fig. 2). Straight-line distances (m) from nests to overwintering sites

Table 1. Dispersal distance and land cover types used for overwintering (OW) of radio-fitted neonate eastern box turtles ($n = 64$) monitored during their first activity season at 4 forest openings in the Manistee National Forest, Michigan, USA, 2012–2015. Dispersal distance is the straight-line distance (m) from nest to overwintering site.

Opening	Yr	Clutches	Radio-fitted neonates	Survived to OW	Dispersal distance (m)				OW in opening	OW in edge	OW in forest
					\bar{x}	SE	Min.	Max.			
Turtle Bowl	2012	2	2	1	44.2						1
	2013	4	20	15	25.6	2.8	8.0	45.2	4	3	8
	2014	2	11	10	11.0	2.0	1.9	20.4	8		2
	2015	2	4	3	14.9	0.4	14.4	15.8		1	2
	Total or \bar{x}	10	37	29	20.1	2.2	1.9	45.2	12	4	13
Savanna	2012	1	1	1	28.4				1		
	2013	2	6	3	29.8	26.7	2.9	83.2	2		1
	2015	2	5	4	5.9	1.1	2.7	7.8	4		
	Total or \bar{x}	5	12	8	27.8	9.8	2.7	83.2	7		1
East West	2013	1	1	0							
	2014	1	7	6	28.1	6.1	17.3	49.2	2		4
	2015	2	4	2	3.3	0.4	2.9	3.6	2	0	
	Total or \bar{x}	4	12	8	21.9	6.1	2.9	49.2	4	0	4
Gravel Pit	2015	1	3	1	16.8				1		
All sites	2012	3	3	2	36.3	11.2	28.4	44.2	1		1
	2013	7	27	18	26.3	4.4	2.9	83.2	6	3	9
	2014	3	18	16	17.4	3.3	1.9	49.2	10		6
	2015	7	16	10	9.2	1.8	2.7	16.8	7	1	2
	Total or \bar{x}	20	64	46	19.9	2.4	1.9	83.2	24 (52.2%)	4 (8.7%)	18 (39.1%)

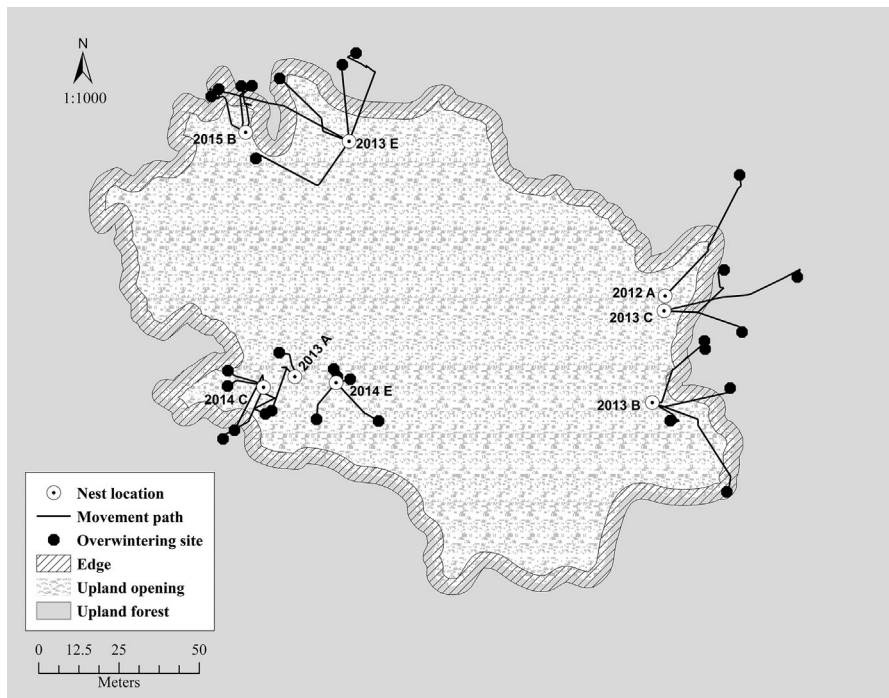


Figure 2. Movements and overwintering sites of 29 radio-fitted neonate eastern box turtles monitored from nest emergence to overwintering at the 1.9-ha Turtle Bowl opening, Manistee National Forest, Michigan, USA, 2012–2015. Nest emergence occurred between 16 August to 25 October and neonates began overwintering from the first week in October to the first week in November. Labels next to nest locations indicate the year and clutch identification. Because of scale of map, many fine-scale movements are obscured.

($n = 46$ neonates, $\bar{x} = 19.9 \pm 2.4$, range = 1.9–83.2) were close to maximum observed distances (m) from nests ($n = 46$ neonates, $\bar{x} = 20.6 \pm 2.4$, range = 1.9–83.2) and overwintering sites were equivalent to the maximum observed distance from nests for 29 (63.0%) neonates. Distance from nest to overwintering site was negatively correlated ($r_s = -0.668$, $P < 0.001$) with day of nest emergence. Distance (m) from nest to overwintering site was not correlated with distance (m) from nest to nearest forest edge ($r_s = -0.206$, $P = 0.169$) or with body mass (g) at nest emergence ($r_s = -0.182$, $P = 0.224$).

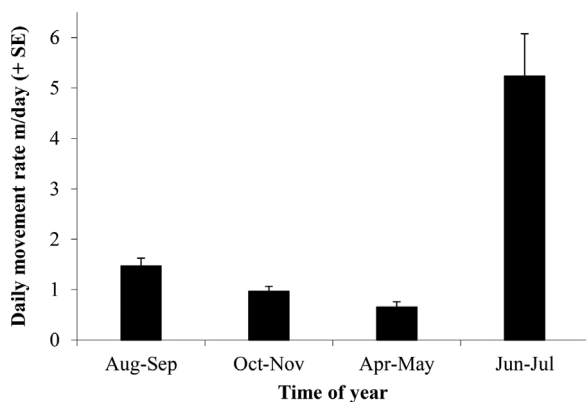


Figure 3. Mean movement rates (+SE) of 64 radio-fitted neonate eastern box turtles monitored up to 333 days after nest emergence ($n = 642$ telemetry locations) by time of year in the Manistee National Forest, Michigan, USA, 2012–2016.

Overwintering

Of the 46 neonates tracked successfully, 24 overwintered in natal openings, 4 overwintered in the forest edge, and 18 overwintered in forest (Table 1). Explanatory variables (distance from nest to nearest forest edge, day of nest emergence, and body mass of neonates at nest emergence) were not correlated (range of $r_s = -0.019$ to 0.238, $P \geq 0.112$), and thus we did not eliminate any variables prior to model construction. Based on ΔAIC_c , we selected distance from nest to nearest forest edge ($\beta = 0.094 \pm 0.039$ [SE], OR = 1.099, CI = 1.026–1.209) + day of nest emergence ($\beta = 0.098 \pm 0.043$ [SE], OR = 1.028, CI = 1.028–1.226) as the best model from the set of candidate models (Table 2). We considered this model to be supported because it had the greatest difference between residual deviance and deviance of the intercept-only model and the ratio of deviance to degrees of freedom (i.e., estimated dispersion) was closest to 1 (Table 2). Although the model distance from nest to nearest forest edge + day of nest emergence + mass had a ΔAIC_c value close to the 2 equivalence criterion (2.392), we considered distance from nest to nearest forest edge + day of nest emergence a more parsimonious model because it contained fewer predictive variables.

Using the best model, we generated a matrix of predicted probabilities of overwintering in natal openings using distance from nest to nearest forest edge values ranging from 1 to 110 m and day of nest emergence values ranging from 15 August to 30 October (Table 3). When we held day of nest emergence constant at 18 September (i.e., mean nest emergence day for all nests monitored from 2012 to 2016),

Table 2. Binomial logistic regression models and model selection criteria used to examine potential associations between 3 predictor variables and land cover types used for overwintering (natal opening vs. adjacent forest and edge) for 46 radio-fitted neonate eastern box turtles that survived from nest emergence to overwintering in the Manistee National Forest, Michigan, USA, 2012–2015. We calculated Akaike’s Information Criterion for small sample sizes (AIC_c), difference in AIC_c (ΔAIC_c), and AIC_c weight (w_i). Variables included distance (m) from nest to nearest forest edge (nestedge), ordinal day of nest emergence (emgdate), and body mass (g) of neonate turtles at nest emergence (mass).

Candidate models	Deviance _{df}	AIC_c	ΔAIC_c	w_i
Nestedge + emgdate	46.626 ₄₃	53.197	0.000	0.694
Nestedge + emgdate + mass	46.614 ₄₂	55.589	2.392	0.209
Emgdate	54.582 ₄₄	58.860	5.663	0.040
Nestedge	55.216 ₄₄	59.494	6.297	0.033
Emgdate + mass	54.307 ₄₃	60.878	7.681	0.014
Nestedge + mass	55.082 ₄₃	61.653	8.456	0.010
Mass	63.677 ₄₄	67.677	14.480	0.000
Intercept only (null) model	63.683 ₄₅			

the predicted probabilities of overwintering in natal openings increased when distance from nest to nearest forest edge increased (Table 3). Similarly, when the value of distance from nests to nearest forest edge was held constant, the probability of overwintering in natal openings increased with day of nest emergence (Table 3). When distances from nest to nearest forest edge exceeded 70 m, predicted probability of overwintering in natal openings approached 1 regardless of the day of nest emergence. When day of nest emergence was 15 October or later, predicted probabilities of overwintering in openings approached 1 for all nests >5 m from the forest edge (Table 3).

Neonates ($n = 46$) constructed overwintering burrows in duff or mineral soil or created shallow circular depressions in mineral soil or duff. Mean vertical depth of overwintering refugia into mineral soil was 29.9 mm \pm 2.9 (range = 0.0–101.8). The majority of neonates ($n = 39$) burrowed into

mineral soil at approximately 30° to 50° angles relative to the surface, but 7 neonates created shallow (<17 mm) circular depressions in mineral soil but their carapace was covered only in duff and leaf litter.

Second Activity Season

We re-fitted all neonates that survived the overwintering period ($n = 28$ total, $n = 2$ in 2013, $n = 18$ in 2014, and $n = 8$ in 2016) with radio-transmitters and monitored them weekly. Most neonates ($n = 27$, 96.4%) emerged from overwintering refugia ($n = 14$ in openings, $n = 10$ in forest, $n = 4$ in edge) between 19 April and 10 May and 1 emerged on 24 May. Through April and May, of the 14 neonates that previously overwintered in openings, 7 remained in openings, 2 moved to forest edge, 1 dispersed into forest, and we lost contact with 4 while they were in openings. Of the 14 neonates that previously overwintered in forest or forest edge, 13 remained in forest or edge, and 1 returned briefly to its natal opening in late-May. Regardless of the land cover types used and year, no neonate had dispersed >50 m beyond the boundary of its natal opening by the end of May.

We monitored 24 neonates for portions of June, July, and August and we opportunistically radio-fitted 1 natural recruit from a previously undetected nest on 11 June 2014 at Turtle Bowl. Of the 7 neonates that occupied natal openings in April and May, 5 were lost and 2 dispersed into forest in June. The natural recruit also dispersed into forest in June. Of the 20 neonates that used forest for portions of June, July, and August, none returned to openings although 1 neonate returned briefly to edge at Turtle Bowl (Fig. 4). We observed no use of openings in July or August (Fig. 4), although sample size during this period had diminished to 6 individuals. We eventually lost contact with the last neonate after 17 August (333 days after nest emergence).

Mean movement rate in April and May was <1 m/day, slightly lower than the first activity season (Fig. 3). Mean

Table 3. Predicted probabilities of neonate eastern box turtles overwintering within their natal openings for a range of nest emergence days and distances from nests to nearest forest edge, Manistee National Forest, Michigan, USA. Prior to using nest emergence dates for statistical applications, we converted the calendar dates of nest emergence to ordinal day of year values, with year omitted (e.g., 1 Sep 2014 = 244). For ease of interpretation, we converted ordinal day of year values back to calendar dates (with yr omitted) when reporting results. Nest emergence ($n = 31$ nests, $n = 42$ nest emergence events) ranged from 16 August to 25 October, 2012 to 2016. Mean day of nest emergence over the 5 field seasons was 18 September \pm 2.5 days (SE). We derived each prediction probability from a binomial logistic regression model with 3 parameters including an intercept, distance from nest to nearest forest edge (m), and day of nest emergence.

Distance from nest to forest edge (m)	Day of nest emergence					
	15 Aug	1 Sep	18 Sep	1 Oct	15 Oct	30 Oct
1	0.009	0.050	0.220	0.504	0.803	0.947
5	0.014	0.071	0.291	0.598	0.856	0.963
10	0.022	0.109	0.397	0.704	0.904	0.978
15	0.035	0.164	0.514	0.792	0.938	0.985
20	0.055	0.239	0.629	0.859	0.960	0.991
25	0.086	0.335	0.731	0.907	0.975	0.994
30	0.131	0.448	0.814	0.940	0.984	0.996
35	0.195	0.565	0.875	0.962	0.990	0.998
40	0.279	0.676	0.918	0.975	0.993	0.999
50	0.500	0.843	0.967	0.990	0.997	
60	0.720	0.932	0.988	0.996	0.999	
70	0.868	0.972	0.995	0.998	0.999	
80	0.944	0.989	0.998	0.999		
90	0.978	0.996	0.999			
100	0.991	0.999				
110	0.999					

movement rate in June and July increased >6 times (Fig. 3). We documented extensive movements away from openings in June and July for 8 neonates that dispersed >100 m away from their nest and overwintering sites before we lost contact (Table 4, Fig. 4). We detected non-random directionality (Rayleigh's Z , $P \leq 0.1$) of pooled first and second activity season movements for 11 of 17 neonates (Table 4) although results should be interpreted with caution because of small sample sizes (movements/turtle). Movement paths of second-year neonates can best be described as a wheel spoke pattern. Natal openings formed the wheel hub and dispersal trajectories of individual neonates formed the spokes into adjacent forest or wetland (Fig. 4).

DISCUSSION

We found that movement of neonatal box turtles was limited during their first activity season. Our observations were similar to anecdotal accounts from New York (Madden 1975, Burke and Capitano 2011). We also found movement increased by July of the second activity season, but we were unable to monitor neonates further as we lost contact with

most individuals during this period without determining their fates. We experienced instances of early transmitter failure during the second activity season, but we also suspect some disappearances resulted from predation and extensive neonate movements outside the tracking area.

Distances moved from nests to overwintering sites were close to the maximum distances moved from nests, indicating distance from nest to first overwintering site was a reasonable proxy for maximum dispersal distance in the first activity season. In northern portions of the species' range, thermal constraints limit movement and activity in the short period between nest emergence and first overwintering. Dispersal distance was associated with day of nest emergence but not distance from nest to nearest forest edge or to body mass. In addition to date of nest emergence, nest-site selection by gravid females greatly influenced which land cover types were available to neonates for overwintering. Although we collected evidence suggesting neonates dispersed toward the forest edge, some neonates successfully overwintered within openings. Neonates emerging from nests located away from forest edges may simply not have time (i.e., locomotive

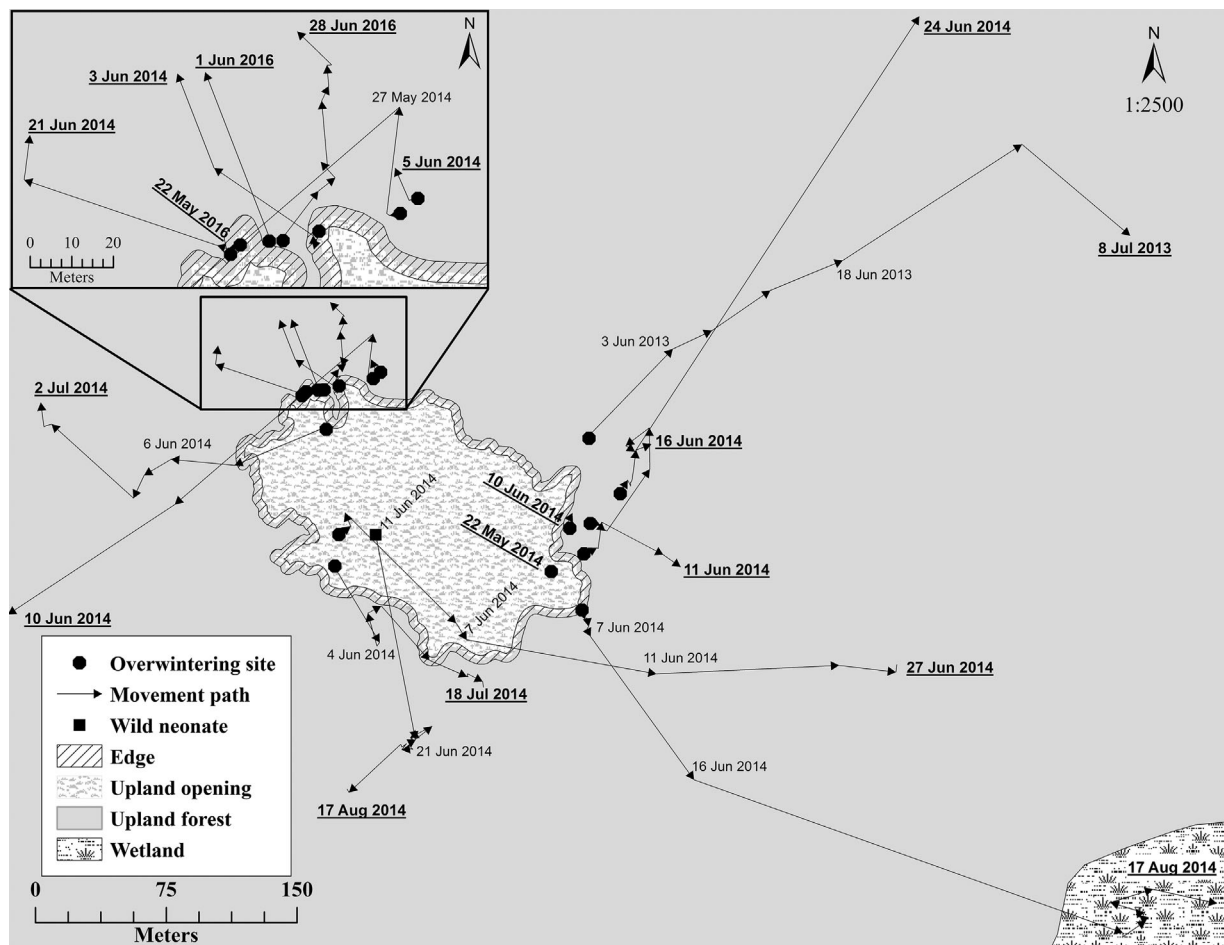


Figure 4. Movements of 17 radio-fitted neonate eastern box turtles (age 7–11 months) monitored weekly after emerging from overwintering sites in spring at the 1.9-ha Turtle Bowl opening, Manistee National Forest, Michigan, USA, 2013, 2014, and 2016. Neonates hatched from nests within the opening during the previous year and dispersed to their respective overwintering locations. We lost contact (i.e., mortality or disappearance) with all 17 radio-fitted neonates after 17 August. Underlined dates at the end of movement paths indicate the last observation before loss of contact. Wild neonate refers to a neonate we encountered and opportunistically radio-fitted on 11 June 2014 from a previously undetected nest.

Table 4. Results of Rayleigh's tests of mean directionality of movements for 17 radio-fitted neonate eastern box turtles monitored at 2 openings in the Manistee National Forest, Michigan, USA, 2012–2016. We included only movements ≥ 2 m in this analysis. We report directional means only for individual neonates with significant non-random ($\alpha = 0.10$) directionality of movements. TB = Turtle Bowl opening. SAV = Savanna opening.

Neonate identification	Site	Nest emergence	Last contact	Dispersal ^a (m)	<i>n</i> ^b	Z	P	Directional mean
2012A1	TB	26 Aug 2012	7 Jul 2013	367.3	10	7.16	<0.001	49.7°
2013A2	TB	9 Sep 2013	27 Jun 2014	322.1	11	1.57	0.212	
2013A4	TB	16 Sep 2013	18 Jul 2013	111.8	11	1.99	0.136	
2013B1	TB	18 Sep 2013	11 Jun 2014	79.8	7	3.50	0.024	77.3°
2013B3	TB	18 Sep 2013	17 Aug 2014	397.7	19	2.75	0.062	151.1°
2013B4	TB	18 Sep 2013	10 Jun 2014	33.0	7	1.68	0.190	
2013C4	TB	15 Sep 2013	24 Jun 2014	355.2	11	2.52	0.078	86.2°
2013C5	TB	18 Sep 2013	16 Jun 2014	70.8	11	2.40	0.089	57.0°
2013E1	TB	14 Sep 2013	2 Jul 2014	193.1	10	3.72	0.020	255.6°
2013E3	TB	14 Sep 2013	21 Jun 2014	100.7	8	4.04	0.012	287.2°
2013E4	TB	14 Sep 2013	3 Jun 2014	80.1	7	3.38	0.028	317.4°
2013E5	TB	15 Sep 2013	5 Jun 2014	35.0	7	2.89	0.049	324.2°
2015B2	TB	19 Sep 2015	28 Jun 2016	65.0	10	10.14	<0.001	6.9°
2015B4	TB	19 Sep 2015	22 May 2016	17.2	6	1.51	0.229	
2012B1	SAV	26 Aug 2012	27 May 2013	56.7	6	3.95	0.012	316.8°
2013F2	SAV	19 Sep 2013	4 Jul 2014	352.5	12	0.19	0.832	
2015L2	SAV	18 Sep 2015	28 Jun 2016	27.3	8	0.80	0.463	

^a Straight-line distance (m) from nest to location of last contact.

^b Number of movements ≥ 2 m.

limitations and thermal constraints to movement) to reach forest edges before onset of winter. Madden (1975) also observed variation in overwintering land cover use; 1 radio-fitted neonate overwintered within its natal field and 1 overwintered in adjacent forest. Thermal constraints in the first activity season probably also limit or exclude feeding opportunities; thus, efficient conservation of yolk-sac energy reserves is probably of greater consequence than dispersal during the first activity season (Congdon 1989, Nagle et al. 2003, Costanzo et al. 2004, Willette et al. 2005).

Movement rates in early spring of the second activity season (<1 m/day) were similar to values reported in Forsythe et al. (2004) who monitored 3 radio-fitted neonates from 30 March to 27 April in central Illinois, USA and reported the mean cumulative distance moved was 21.94 m. Madden (1975) maintained contact with 1 individual for 3 activity seasons after nest emergence and never observed the juvenile moving >100 m from the nest. Our observations of extensive movements in June and July were different. Neonates we monitored exhibited linear dispersal trajectories and did not return to former activity areas, whereas adults usually maintain fidelity to a home range and revisit certain areas consistently (Stickel 1950, 1989; Cross 2016). The openings, forest, and wetlands in our study area were within areas used by radio-fitted adult box turtles (Laarman 2017) and we do not attribute the extensive neonate movements to a lack of available habitat or unsuitable vegetation types (Krausman and Morrison 2016). Increased dispersal distance during the second activity season has been reported for other terrestrial chelonians (Epperson and Heise 2003, Pike 2006).

Nesting sites used by gravid females in our study area were located within graminoid-dominated forest openings with very low forb densities. Increased temperatures and low relative humidity common during summer probably renders

these openings less hospitable for neonates than does surrounding forest and wetland (Rossell et al. 2006, Fredericksen 2014). Nests were not clustered near the forest edge at Savanna, the largest and most structurally complex opening. The same structural characteristics (i.e., tree and shrub density, % leaf litter, herbaceous vegetation) potentially causing females to nest farther from forest edge may provide cover and thermoregulatory options for neonates, which could explain, in addition to distance from nests to forest edge, why 7 of 8 neonates overwintered in Savanna opening. In large openings, neonates may occupy their natal openings for longer periods than we observed. Furthermore, the forests surrounding openings in our study area contained abundant canopy gaps for basking and thermoregulation. In openings surrounded by closed canopy forest types, neonates may occupy or associate with forest-opening edges for longer periods of time than we observed in this investigation.

Because neonates remain in or near natal openings for months after hatching, this age class is vulnerable to mortality during implementation of management activities often used to promote disturbance-dependent natural communities. Prescribed burns and other common management activities (e.g., mechanical treatments, mowing, herbicides) conducted in spring or fall that encompass a nesting opening and adjacent forest (≤ 50 m from opening) have the potential to directly affect 100% of the cohort produced at the site from the prior nesting season. Rates of nest depredation or failure are often high, and neonate mortality is also affected by depredation and weather (Madden 1975, Congdon et al. 1983, Belzer et al. 2002, Willey and Sievert 2012, Altobelli 2017). In certain years, especially in small openings, very few, if any, neonates may be present at a given site. Thus, mortality of individual neonates during management activities conducted at appropriate

intervals may be compensatory or even be offset if nest survival rates increase because the management action improves habitat quality or increases availability of nesting habitat (Reid et al. 2016).

In scenarios where fire or other management-induced mortality is additive, intensively managed sites could function as reproductive sinks if they become increasingly attractive to gravid females but little or no recruitment occurs. Clearly, short-term perturbations affecting neonate survival rates during stand-level management would not affect long-term population growth rates in the same fashion as landscape-scale failures to maintain and restore open canopy nesting areas. In general, the more complicated and restrictive species-specific mitigation measures are, the more expensive, difficult, or unlikely project implementation becomes. No action could cause adverse indirect effects to localized populations if existing nesting areas are encroached by woody shrubs and trees and ultimately become unsuitable for nesting. However, neonates that survive the egg-stage bottleneck are important for recruitment (Congdon et al. 1993). Recognizing the appropriate level of risk to individual neonates during project implementation is an issue of scale and requires the proper context. The issue of fire and box turtle population response is likely complex, and cannot be adequately addressed without field studies of mortality rates during vegetation management activities and long-term monitoring of population response to habitat manipulations.

MANAGEMENT IMPLICATIONS

If managers are concerned with mortality risks to box turtles associated with management activities, we recommend avoiding implementation during the nesting season (Jun in our study area). The optimum seasonal window for management of open canopy nesting areas is the period after nesting and before nest emergence (1 Jul through 15 Aug at our study area) because neonates and adults are least likely to occupy openings during this period. We recommend not including the forest edge in treatment units or limiting edge treatments to hand-cutting of trees and shrubs. During the optimal seasonal window, mowing or mechanical treatments may be more feasible than prescribed fire because they can be planned in advance and implemented relatively independently of fuel conditions and weather. Mechanical treatments conducted during the overwintering period, when the ground is frozen or snow is present, may reduce risk of direct effects although neonates overwintering in shallow refugia may still be vulnerable to compaction. When the goal is to restore or maintain fire-dependent or early successional plant communities and the primary tool is prescribed burning, we expect the seasonal window optimal for box turtles may often prove incompatible with fuel conditions, desired vegetation response, or seasonal restrictions in place to protect other species of conservation priority. In such cases, we suggest increasing the time (yr) between burns to allow neonate cohorts to disperse between treatments, and excluding the forest edge and adjacent forest from the burn unit whenever possible. In larger openings, we also recommend splitting the opening into multiple units and burning units on a rotation to reduce

potential for site-wide direct impacts. If the recommendations above are not feasible, we recommend developing an inventory of known nesting areas, and managing sites on a rotation that allows productive sites to function as reserve areas during years when other sites are being intensively managed.

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