Novel habitat use supports population maintenance in a reconfigured landscape

C. J. O'Bryan,[1],† J. A. Homyack,[2] R. F. Baldwin,[1] Y. Kanno,[1] and A.-L. Harrison[3,4]

[1]Department of Forestry and Environmental Conservation, Clemson University,
132 Lehotsky Hall, Clemson, South Carolina 29634 USA
[2]Weyerhaeuser Company, 1785 Weyerhaeuser Road, Vanceboro, North Carolina 28586 USA
[3]Institute for Parks, Clemson University, 263 Lehotsky Hall, Clemson, South Carolina 29634 USA

Abstract.   Given the limited scope of unaltered, protected areas in most regions, understanding the contributions to imperiled species conservation by landscapes in which habitat elements have been reconfigured is critical. Commercial forestry has been a driver of altered structure and composition of forests and of distribution and character of aquatic systems. In eastern North America, extensive historical wetland drainage reconfigured hydrologic environments from low-gradient wet flats and isolated wetlands to connected networks of linear ditches. Landscapes where both uplands and aquatic environments differ from historic conditions may affect most ecological aspects of semi-aquatic species, including reptiles. Our objective was to determine if habitat selection and use decisions by spotted turtles (*Clemmys guttata*), a rare semi-aquatic species, supported population maintenance in a reconfigured forest landscape in eastern North Carolina, USA. We captured 280 individuals and radiomarked 31 adults to examine habitat selection at multiple spatial scales with paired logistic regression, movements and home ranges with location data and utilization distributions (UDs), survival with a known-fate model, and abundance with N-mixture modeling. Across local and landscape scales, turtles selected features associated with ditches despite abundant, more natural aquatic depressions across the study area. Habitat metrics describing understory closure and substrate characteristics were important at local scales, and closed canopy forest and habitat heterogeneity was positively associated with activity areas at landscape-scale spatial grains. Both movements and home ranges were centered on ditches, and turtles exploited ditches to access mates, nest sites, or uplands for estivation. In this highly reconfigured landscape, this species appeared to have sufficient behavioral plasticity to acquire key resources contributing to high survival and an abundant population. Isolation from road traffic and collection, both which negatively affect turtles elsewhere, was facilitated by limited public access. Our results suggest that conservation and management of rare species should not rely solely on habitat information gained from studies in more pristine areas because such results may not demonstrate the range in variation in behavior that might allow persistence in novel environments, absent key threats.

Key words: behavioral plasticity; *Clemmys guttata*; ditch; habitat selection; intensive forestry; plantation; reconfigured landscape; spatial ecology; spotted turtle.

[4] Present address: Migratory Bird Center, Smithsonian Conservation Biology Institute, National Zoological Park, MRC 5503, Washington, District of Columbia 20013, USA
† **E-mail:** obryancj@gmail.com

INTRODUCTION

Reconfigured landscapes where one or more primary habitat elements are anthropogenically modified can negatively affect populations by reducing required resources, introducing competitors or subsidized predators (Didham et al. 2007), increasing salient threats (Chevin et al. 2010) or creating ecological traps (Schlaepfer et al. 2002). However, some species have plastic responses in behavior that allow maintenance of populations in novel environments (Rosenstock et al. 1999, Schlaepfer et al. 2002, Gross et al. 2010, Graves 2014) through spatial use of optimal habitats (Garshelis 2000). Given that protected natural areas, a primary management tool for maintaining biodiversity and imperiled species, only comprise approximately 15% of the terrestrial surface globally (Deguignet et al. 2014), they will only conserve a subset of species (Noss et al. 2012). Consequently, understanding population responses to unprotected, anthropogenically modified landscapes is critical, yet is often undervalued in conservation frameworks (Chapin et al. 1998).

Throughout many portions of North America, commercial forestry has produced modified landscapes on an expansive scale with altered structure, age class distribution, and species composition. For example, from 1952 to 2012, planted pine forest increased from 0.7 to nearly 19 million ha (19% of forestland) in the Southeastern United States (Fox et al. 2007, U.S. Department of Agriculture 2015). Much of this region, particularly the Atlantic Coastal Plain, once had expansive freshwater wetlands that were extensively drained by the 1980s via networks of ditches to support agriculture, forestry, and peat mining (Richardson 1983, Cashin et al. 1992). Thus, the current low-relief landscape of the Atlantic Coastal Plain has been reconfigured with vegetation structure and composition and hydrological regimes of these anthropogenically modified landscapes differing greatly from natural systems (Fox et al. 2007, Jones et al. 2010). These reconfigurations can be expected to positively, negatively, or neutrally influence retention of native species, but species dependent on the terrestrial-aquatic interface may be particularly susceptible to these landscape-level changes (Bormann and Likens 1979, Urban 2004).

Quantifying the population level consequences of individual habitat selection and use decisions is critical for conservation of imperiled organisms. Globally, many turtle species are at-risk or declining from a myriad of factors including habitat modification, collection for pet trade, and vehicle mortality (Gibbons et al. 2000, Steen et al. 2006), and a dearth of information regarding rare turtles may be hindering conservation actions (Lovich and Ennen 2013). Semi-aquatic turtles require aquatic habitat types to meet life history needs, but also make upland movements for nesting and thermoregulation. Therefore, landscapes with ongoing alteration of both terrestrial and aquatic habitats may affect most aspects of semi-aquatic turtle ecology.

Our objective was to determine if habitat selection and use decisions of spotted turtles (*Clemmys guttata*), a rare semi-aquatic species, supported population maintenance in an anthropogenically modified landscape with remnants of more natural habitat types. To do so, we examined four pieces of evidence: habitat selection and use; movement patterns and home range characteristics; adult survival; and population abundance. We predicted that turtles would select local and landscape features associated with ditches and that extensive movements and home ranges would be centered on ditches, which would provide suitable habitat and protection from key threats. As a result, we predicted survival and abundance would be comparable to estimates from landscapes dominated by more natural habitat types.

METHODS

Study area

We conducted this study on timberlands owned and managed by Weyerhaeuser Company in the Atlantic Coastal Plain of North Carolina, United States. Due to the threat from illegal collection of our study species, we do not provide a more specific location. Our study landscape was a large (>24 100 ha), forested matrix dominated (86%) by loblolly pine (*Pinus taeda*) plantations with smaller components of hardwood buffers around streams and wetlands, ecological set-asides, natural pine stands, and unimproved forest roads. The regional setting was a mixture of agriculture, rural housing,

and managed forests. Silvicultural treatments used in plantations during a rotation included mechanical site preparation (shearing with a tractor implemented with a V-shaped blade and bedding), planting of seedlings at about 1100/ha, intermediate fertilizations and herbicide applications, commercial thinning to ≈220 trees/ha, and a final clear-cut harvest 27–30 yrs after planting.

Pine stands were intersected by a network of inner-stand ditches draining into roadside ditches that were constructed from the early 1900s through the 1970s (Homyack et al. 2014). Ditch networks improve operability for forest management activities and increase pine survival by reducing surface waters (DeBell et al. 1982). The study area contained ≈735 km of roadside ditches parallel to unimproved forest roads and ≈1305 km of smaller ditches in forest stands. At about a 25-yr interval and prior to final harvest of adjacent plantations, ditches were returned to their original configuration and dredged with an excavator that scours the bottom and deposits spoils along the perimeter. Vegetation succession occurs quickly within and adjacent to ditches, and eventually provides low shade and vertical structure, creating a spatially and temporally dynamic matrix of ditches across the landscape (Homyack et al. 2014). During our study, roadside shoulders were occasionally mowed, but many ditches received no disturbance. Roadside ditches were typically 1.8–5.5 m wide and within-stand ditches were <1.5 m wide. Ditch water depth ranged approximately from 0.1 to 1.5 m. In addition to ditches, small ephemeral depressions that are managed with the surrounding plantation are abundant on the study area and provide more natural aquatic habitat features for semi-aquatic organisms (Leonard et al. 2012).

Study organism

Spotted turtles occur across portions of the eastern and midwestern United States and Canada (Ernst and Lovich 2009) and are of conservation concern in many jurisdictions. They are considered globally endangered, federally endangered in Canada, and were petitioned to be listed under the US Endangered Species Act (van Dijk 2013). Spotted turtles use shallow wetland habitats including ephemeral pools, bogs, marshes, and small woodland streams

(Joyal et al. 2001, Litzgus and Mousseau 2004a). Due to low fecundity, low egg survival, and delayed sexual maturity, persistence of spotted turtles is most sensitive to adult survival, particularly of females (Steen et al. 2006, Enneson and Litzgus 2008, O'Bryan 2014). Loss and degradation of wetlands, collection for the pet trade, and vehicle-related mortality contribute to population declines (Ernst and Lovich 2009).

Capture and radiotelemetry

We captured 280 turtles January 2012–April 2013 in ditches, ephemeral wetlands, and on forest roads using visual encounter surveys (VES), hoop traps (Memphis Net & Twine, Memphis, Tennessee, USA), or opportunistically (O'Bryan 2014). We uniquely marked captured turtles by notching the carapace and plastron using a modification of Cagle's (1950) method and recorded locations of captures and recaptures with high-accuracy GPS (Trimble Navigation Ltd., Sunnyvale, California, USA; error < 5 m). We measured plastron length (mm) with a straight-line ruler and mass (g) with a spring scale (Pesola, Baar, Switzerland). We sexed turtles by minimum size at sexual maturity and morphological characteristics (Ernst and Lovich 2009).

We selected apparently healthy adult turtles for radiotelemetry that were large enough to receive transmitters <8% of body mass and to achieve an even sex ratio. We attached Holohil RI-2B very high frequency (VHF) transmitters (Holohil Systems Ltd., Carp, Ontario, Canada) to the anterior carapace of 16 adult males and 15 adult females with high-strength, fast-curing epoxy (ITW Devcon, Danvers, Massachusetts, USA). We located turtles using an R-1000 VHF receiver (Communication Specialists, Inc., Orange, California, USA) handheld unit with a "rubber ducky" (RA-23K VHF) antenna (Telonics, Inc., Mesa, Arizona, USA). Between January 2012 and June 2013, we located radiotagged turtles ≈1–2 times per week with ≥48 h between locations to balance fine-scale movement and minimize serial autocorrelation (Compton et al. 2002). We located turtles between 0600 and 2000 h (>90% of locations between 0800 and 1700 h). When possible, we recorded GPS coordinates at the visual location of the animal. When animals could not be visually located (18% of locations), we used

local triangulation to estimate the location. We handled, marked, and released turtles within an hour of initial capture, and removed transmitters at the end of the study.

Habitat measurements

Previous studies demonstrate that turtles select habitat structure based on micro and macro conditions operating at different spatial scales (Compton et al. 2002, Spencer and Thompson 2003). We quantified vegetation structure and abiotic metrics immediately after we located radiomarked turtles at a 1 m^2 circular plot centered on each location of radiomarked turtles representing used habitat and at two, paired 1 m^2 plots at 2 and 20 m along a random azimuth representing available habitat. At each plot, we visually estimated percent cover on the ground or aquatic substrate of deciduous leaves, pine needles, grasses/sedges, moss, bare soil, open water, coarse woody debris (CWD, ≥10 cm diameter), sticks/branches (<10 cm diameter), woody shrubs, and herbaceous vegetation with a modified version of Daubenmire's (1959) cover classes (1 = 0%, 2 = 1–5%, 3 = 6–25%, 4 = 26–50%, 5 = 51–75%, 6 = >75%). At plot centers, we measured substrate temperature (soil or water; °C), air temperature (°C), and relative humidity (%) with a soil thermometer or thermo-psychrometer (Optimum Energy Products Ltd., Alberta, Canada), and understory openness from the turtle's perspective at ground-level using a spherical convex densiometer. We estimated surrounding basal area with a 10-BAF cruising prism. We qualitatively described animal locations (e.g., road, upland, wetland, or ditch) and measured distance (m) from the nearest visible CWD and standing water. All handling and marking of spotted turtles was approved under a Clemson University Institutional Animal Care and Use Committee Protocol (number 2011-024) and a North Carolina Wildlife Resources Commission Wildlife Collection License (number 13-SC00579).

Local-level habitat selection

We investigated habitat selection of radiomarked individuals at two local scales with case–control, paired logistic regression (North and Reynolds 1996, Keating and Cherry 2004). We developed an a priori set of models and evaluated the relative strength of each in an information theoretic framework (Burnham and Anderson 2002). To reduce redundancy, we ran a Spearman's non-parametric rank-correlation coefficient matrix on our 40 habitat variables across all location plots. We removed inter-correlated ($r \geq 0.4$) variables and metrics with limited measurements (Williams et al. 2002). Resulting covariates were standardized with a mean of zero and a standard deviation of one. We constructed eight a priori candidate models (Appendix A) including combinations of 10 habitat variables that described hypothesized biological relationships with spotted turtles (Appendix B) based on previously selected habitats by spotted turtles (Ernst 1976, Litzgus and Brooks 1998, Milam and Melvin 2001). We assessed model goodness-of-fit using a global Chi-square test to examine whether the global model differs from the null model ($\beta = 0$) (Allison 1999).

We ran paired logistic regressions for each turtle with ≥30 locations and paired random plots ($n = 27$ individuals) separately at the 2 and 20 m scale. Conducting analyses separately by individuals allowed turtles to be the experimental unit, avoided sample size bias from variable numbers of locations/animal, and permitted us to make inferences of the larger population (Garshelis 2000, Millspaugh and Marzluff 2001). We used small-sample Akaike's Information Criterion (AIC$_c$) to evaluate a priori models for parsimony and fit (Akaike 1974). As AIC values are conditional on the data, they cannot be compared across individuals (Burnham and Anderson 2002).

Thus, to make inferences of the study population, we examined the relative strength of models across individuals by scale (i.e., 2 or 20 m) with cumulative ranks and with summed model weights (w_i). First, we adapted the cumulative ranks approach from the low point scoring system commonly used in sports for comparing individual results across multiple races to identify a "winner" for a series (International Sailing Federation 2012). For each turtle, we ranked models from 1 to 8 based on ΔAIC$_c$ values where "1" was the top-ranked model (i.e., ΔAIC$_c$ = 0) and "8" had the greatest ΔAIC$_c$ value. Next, we summed

model ranks across turtles to produce a cumulative rank for the model set at each scale. The most supported model across individuals had the lowest cumulative rank. Secondly, because the mathematical relationships within the cumulative rank approach are ordinal, we also summed associated model weights and across all turtles as another approach. Together, we examined the weight of evidence from the cumulative rank and summed model weights to summarize model selection results across individuals.

Landscape-level habitat selection

To assess selection of landscape features by radiomarked spotted turtles, we compared individual turtle activity areas with random areas. We defined activity areas for each turtle as those areas encompassing the 10% UD density isopleth of the T-LoCoh (see Utilization distributions), which contained intensively used areas by each turtle (Getz et al. 2007). We excluded two turtles without sufficient locations to construct a 10% isopleth. We identified centroids for each activity area polygon, and generated an equal number of random points that were constrained to aquatic habitat types (i.e., ditch network and ephemeral wetlands) in the outermost boundaries of all animal locations. Ephemeral wetlands were delineated in a prior study that used a LiDAR-derived, local-relief model to predict depressions on our study area (Leonard et al. 2012). We separated random points from each other by at least 600 m. To ensure independence of activity areas, we estimated the mean of environmental variables for three turtles that had multiple activity areas (Compton et al. 2002). We constructed buffers around activity area centroids and random points with four radial distances: 30, 60, 175, and 300 m (Bodie 2001). We chose 30 m because it represented mean daily distance moved by radiomarked turtles, 175 m because it represented mean weekly distance moved, and 300 m as a recommended terrestrial buffer for reptiles (Semlitsch and Bodie 2003). We included 60 m post hoc to examine sensitivity between 30 and 175 m.

At each scale, we compared landscape features, including % of the buffer in forest stand age classes with specific thinning regimes as a proxy for canopy openness and understory structure (young and open: 0–5 yrs old; closed canopy: 5–10 yrs old, prethinned only; old-thinned: 12+ yrs old with commercial thinning), total length (m) of ditches (sum of within-stand and roadside), and distance to nearest wetland originating from Leonard et al. (2012). We validated stand conditions and ditch presence by visual confirmation and using 2012 National Agricultural Imagery Program orthoimagery. We used stepwise, backward-elimination logistic regression to produce candidate models for habitat selection across activity areas for 29 turtles. Since stepwise model selection can produce a false reliance on a single best model (Whittingham et al. 2006), we included all competing models with $\Delta AIC_c \leq 2.0$ and used a weighted-model averaging technique for like variables (Burnham and Anderson 2002), which consolidates coefficients for top models using their weights and beta values. We conducted these analyses using JMP® v.10.0.0. (SAS Institute Inc., Cary, North Carolina, USA).

Seasonal movements

We estimated seasonal movements for each radiotagged turtle (n = 26) using distance between successive locations (Nieuwolt and Dec 1996), to provide understanding whether linear features facilitated movements and access to potential mates. We calculated mean daily distance moved by summing Euclidean movements during a season and dividing by the number of days in that season. We defined seasons based on spotted turtle activity; prenesting season occurred between emergence from hibernation and first detection of a gravid female (determined by palpation, Beaudry et al. 2010), nesting season occurred between detection of first gravid female and last known oviposition (determined by repeated palpation and monitoring of nesting activity), and postnesting season occurred between the last day of oviposition and last day of hibernation. We used a two-way analysis of variance (ANOVA) to examine differences in mean daily distance moved with sex and seasons as factors. Prior to analyses, we examined normality of data using a Shapiro–Wilk test and homogeneity of variances using a Bartlett's test. If necessary, data were transformed. For a significant ANOVA, we used Tukey's honestly

significant difference (HSD) multiple comparison of means test to examine differences among seasons. We calculated distance between turtle locations using the adehabitatLT package in Program R v.3.0.2 (Calenge 2006) and the ANOVA and HSD tests using Program R with alpha of 0.05.

Utilization distributions

We used a time-local convex hull approach (T-LoCoH) to estimate home ranges as UDs. T-LoCoH is a non-parametric UD estimator that incorporates time in estimation (Getz and Wilmers 2004, Getz et al. 2007) and is appropriate for animal movements centered on linear features (Lyons et al. 2013). A scaling factor based upon animal velocity is used to separate points (in the calculation of nearest neighbors) that may be close in space but far away in time. We used the fixed-k scaling method for identifying nearest neighboring points because it best represented space use of turtles by contouring home ranges to the linear movements we observed. Relocation time series were standardized to one location per week for all turtles. When multiple locations in a week were collected, we used the first location. We used the T-LoCoH package for R statistical software v.3.0.2 (Lyons et al. 2013) for all home range calculations. We used density isopleths to define individual turtle activity and core areas (see Landscape-level habitat selection).

Annual survival

We estimated adult monthly survival for radiomarked animals using known-fate models in Program MARK and extrapolated to annual estimates (White and Burnham 1999). We evaluated relative influence of sex (s), time (t) and a combination of factors compared to null models with four candidate models: (1) constant survival with no sex effect ($S(.)$), (2) time-dependent survival ($S(t)$), (3) constant survival with a sex effect ($S(.)(s)$), and (4) time-dependent survival with a sex effect ($S(t)(s)$). We evaluated the strength of evidence for models using AIC_c. We averaged real survival estimates across all supported models ($\Delta AIC_c \leq 2.00$), relying on weighted-average parameter estimates with unconditional standard errors (Burnham and Anderson 2002).

Abundance estimation

We estimated turtle abundance using an N-mixture modeling approach with spatially and temporally replicated count data (Royle 2004). From January 2012 to July 2013, we conducted VES across 15 ditch sites, ranging from 100 to 599 m (mean = 341 m) in length to locate adult turtles. Ditches used for VES ranged from 3 to 17 yrs since disturbance from dredging and were adjacent to plantations 1–33 yrs old (Homyack et al. 2014). When possible, turtles were captured by hand or with a dip net. For analysis, we chose a month in each year with the highest number of revisit samples; 16 d in February 2012 and 13 d in April 2013. We assumed that population dynamics were independent among sites because the mean distance between sites was 1300 m (minimum = 875 m) and our telemetry data suggested that movement of turtles between sites was unlikely. We further assumed that movement of turtles in and out of ditches was random because the sampled ditches were representative of surrounding ditches. Typical of N-mixture models, we assumed that the observed count data, $Y_{i,j}$ at site i and day j, were derived from mean abundance of turtles per 1000 m (λ) and detection probability of turtles (p). To account for variability in ditch lengths, we modeled true but imperfectly observed ditch-level abundance as: $N_i \sim$ Poisson ($\lambda \times$ [length i/1000]), where N_i indicates turtle abundance at ditch i. We further modeled observed data ($y_{i,j}$) as a realization of a binomial process such that: $Y_{i,j} \sim$ Binomial (N_i, p).

We analyzed N-mixture models with a Bayesian approach using Markov chain Monte Carlo (MCMC) methods in Program JAGS (Plummer 2003) called from Program R v.3.0.2 (R Development Core Team, 2014) with the "rjags" package (Plummer 2011). Uninformative priors were used for ditch-level abundance (λ) and detection probability (p). Posterior distributions of model parameters were estimated by taking every fifth sample from 5000 iterations of three chains after discarding 5000 burn-in iterations. We visually evaluated model convergence by examining plots of the MCMC chains for good mixture, as well as with the R-hat statistic. Models are considered to have converged when this value is <1.1 for all parameters (Gelman 2003) and R-hat
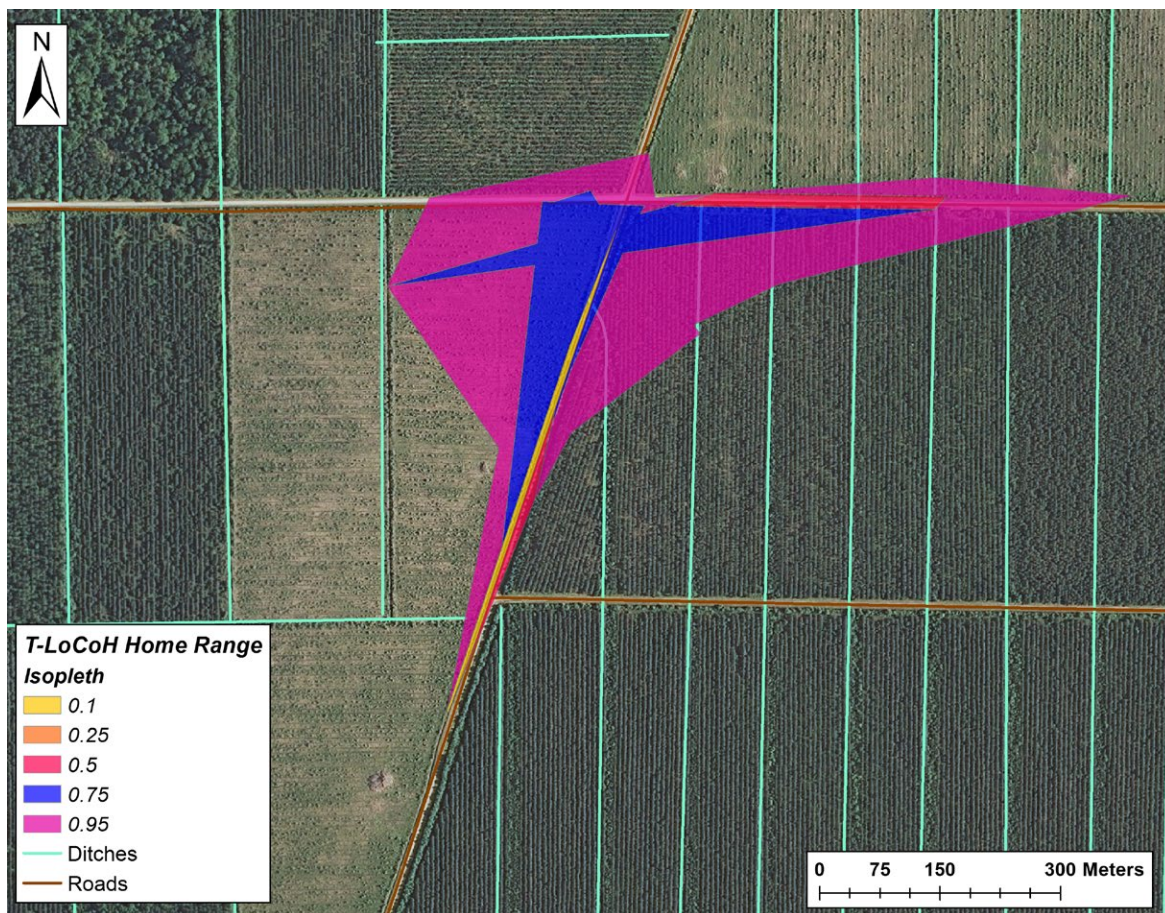
Fig. 1. Time local hull (T-LoCoH) home range for a male spotted turtle (*Clemmys guttata*) in a reconfigured landscape with managed pine forest uplands and a connected network of ditches in forest stands along both sides of roads in eastern North Carolina, USA, 2012–2013.

values were <1.05 for all estimated parameters in our models.

RESULTS

We captured and marked 280 unique spotted turtles and had 139 recaptures of 87 turtles, excluding radiomarked individuals. Most turtles were adults (92.4%, n = 268). Males (n = 174) were twice as common as females (n = 82), and juveniles (n = 12) and adults of unknown sex (n = 12) were least detected. We captured 73% of spotted turtles during the prenesting season, 21% during the nesting season, and 6% during the postnesting season. February (21%) and March (25%) accounted for most captures.

Most turtles (56%) were 81–90 mm in plastron length (O'Bryan 2014).

Local-level habitat selection

We estimated habitat metrics for 31 individual turtles at 2256 used and paired random plots at the 2 and 20 m scale. Nearly, 85% of used locations were in the ditch system, with the remaining in aquatic depressions (8.7%), uplands (6.6%), or crossing roads (0.2%) (Fig. 1). We analyzed habitat selection for turtles with ≥30 paired used and random plots and removed plots with missing habitat metrics, resulting in 1969 points for the 2 m scale and 1974 locations at the 20 m scale analyses for 27 turtles. We visually confirmed

Table 1. Comprehensive paired logistic regression models ($n = 8$) of habitat selection at the 2 m scale by spotted turtles in an anthropogenically altered landscape of Coastal North Carolina, USA 2012–2013, supported by Corrected Akaike's Information Criterion (AIC$_c$; $n = 27$).

Model Name	k	Sum Cumulative rank	Sum w_i (%)
Aquatic form protective cover	4	70	8.29 (30.7)
Soil foraging conditions	3	72	7.00 (25.9)
Woody debris foraging conditions	3	91	3.50 (13.0)
Deciduous leaf foraging conditions	3	96	2.43 (0.090)

Notes: Models were ranked by level of AIC$_c$ support and summed across individuals (maximum cumulative rank is 216, lower values have highest support). AIC weights (w_i) were summed across individuals (maximum weight is 27) and converted to percentages to account for total model weight. See Appendix C for models that received considerably less support (>10 consecutive ranks from previous model).

Table 2. Paired logistic regression model that best explains habitat selection at the 2 and 20 m scale across all spotted turtles ($n = 27$) in an anthropogenically altered landscape in eastern North Carolina, USA, 2012–2013.

Variable	Coefficient (median)	Odds ratio (median)	Odds ratio (interquartile range)
2 m scale			
Understory openness	−0.617	0.54	(0.320, 0.692)
Water cover	1.97	7.148	(5.39, 10.0)
Deciduous leaf cover	−0.383	0.682	(0.553, 0.863)
Pine needle cover	0.112	1.118	(0.780, 1.62)
20 m scale			
Substrate temp	0.226	0.877	(0.572, 1.83)
Water cover	3.12	22.659	(9.33, 37.6)
Deciduous leaf	0.213	1.127	(0.640, 2.23)

radiomarked turtles for >91% of locations and used 17 habitat variables for habitat selection analyses.

At the 2 m scale, the cumulative rank and sum of weights approaches selected the same top-ranked models for describing habitat selection of turtles. The model describing aquatic form protective cover received the most support (mean ΔAIC$_c$ = 0) for 23 of 27 turtles (total cumulative rank of 70, 30.7% of total model weight) (Table 1). The model describing soil cover foraging/thermoregulatory conditions was the second-highest ranked model for 20 of 27 turtles (total cumulative rank of 72, 25.9% of total model weight) (Table 1). Maximum likelihood coefficients describing aquatic form protective cover indicated that at the 2 m scale, turtles selected for increased canopy, water cover, and deciduous leaf cover, and less pine needle cover. The median odds ratios (Table 2) suggested that water was the most important descriptor of selection, with the likelihood of selection increasing >600% with every 1 SD increase in water cover. Furthermore, for every 1 SD increase in understory openness, there was 46% decrease in likelihood of selection, for every 1 SD increase in percent deciduous leaf cover there was a 32% decrease in likelihood of selection, and for every 1 SD increase in percent pine needle cover there was a 12% increase in likelihood of selection. For the next supported model (mean ΔAIC$_c$ = 0.5) with a total cumulative rank of 72% and 25.9% of total model weight, maximum likelihood coefficients indicated turtles selected for habitats with increased water cover, decreased substrate temperature, and increased percent soil cover. Like the first model, the median odds ratios suggested that water was the most important indicator of selection. However, with every 1 SD decrease in substrate temperature there was a 55% increase in likelihood of selection, and for every 1 SD

Table 3. Comprehensive paired logistic regression models ($n = 8$) of habitat selection at the 20 m scale by spotted turtles in an anthropogenically altered landscape of Coastal North Carolina, USA 2012–2013, supported by AIC_c ($n = 27$).

Model Name	k	Sum Cumulative rank	Sum w_i (%)
Deciduous leaf foraging conditions	3	74	5.63 (20.9)
Aquatic form protective cover	4	79	7.73 (28.6)
Pine needle foraging conditions	3	84	3.82 (14.1)
Woody debris foraging conditions	3	94	3.86 (14.3)
Soil foraging conditions	3	101	3.58 (13.3)

Notes: Models were ranked by level of AIC_c support and summed across individuals (maximum cumulative rank is 216, lower values have highest support). AIC weights (w_i) were summed across individuals (maximum weight is 27) and converted to percentages to account for total model weight. See Appendix D for models that received considerably less support (>10 consecutive ranks from previous model).

increase in percent soil cover there was a 75% increase in likelihood of selection. After the first top selected models, there was a break in the ranks by nearly 20 AIC_c units.

At the 20 m scale, the same models were supported as the 2 m scale, but the model describing deciduous leaf foraging/thermoregulatory conditions had the greatest total cumulative rank (74) and second-highest (20.8%) amount of total model weight across turtles (Table 3). The model describing aquatic form protective cover was the second-highest ranked model for 25 of 27 turtles (total cumulative rank of 72) and received the greatest (28.6%) summed model weight (Table 3). Maximum likelihood coefficients indicated turtles selected for habitats with increased water cover, increased deciduous leaves, and warmer substrate temperatures. The median odds ratios (Table 2) suggested that water was the best predictor of selection. For every 1 SD increase in substrate temperature (°C, either water or soil), there was a 12% increase in the likelihood of selection, and for every 1 SD increase in percent deciduous leaf cover there was a 13% increase in the likelihood of selection.

Landscape-level habitat selection

At the landscape scale, 19% of the activity areas (10% UD isopleths) overlapped with adjacent activity areas of other turtles. All individual turtle core activity areas (50% UD isopleths) were intersected by a ditch. For logistic regression describing placement of activity areas on the landscape, all parameters became uninformative (confidence intervals encompassed zero at each scale of analysis) after model averaging. Consequently, we considered parameters prior to model averaging for all scales except at 300 m, as the analysis did not converge at that scale. Ditch length had a positive effect on habitat selection at 30 m and 60 m scales, indicating that an increase in ditch length results in higher likelihood of activity area selection. Further, proximity to wetlands was positively associated with activity areas at the 60 m scale, but not at other scales. At the 175 m scale, an increase in young stands with closed canopies and old-thinned stands resulted in increased likelihood of activity area selection.

Movements

We quantified movements of 26 individual spotted turtles across all seasons and 2 yrs (1972 total locations, 9–106 locations/turtle). Mean daily distances moved were normally distributed for males ($W = 0.956$, $P = 0.127$), but not females ($W = 0.939$, $P = 0.035$), resulting in a square root transformation. Variances were homogenous between sexes ($k^2 = 0.399$, df = 1, $P = 0.528$). Mean distance moved was 173.4 m (±13.6 SE) between relocations. Mean daily distance moved was 29.7 m (±2.98 SE) for all turtles and differed among seasons ($F_{2,75} = 11.58$, $P < 0.001$) with the postnesting distance (26.4 m, ±3.91 SE) less than either prenesting (39.1 m, ±4.42 SE) or nesting season (43.4 m, ±4.05 SE) distances ($P < 0.001$). Mean daily distance moved also differed by sex ($F_{1,76} = 7.29$, $P = 0.009$), but there was not a

significant interaction between sex and season ($F_{2,72}$ = 2.90, P = 0.062). Mean daily distance was greater for males (32.62 m, ±3.43 SE) than females (26.91 m, ±4.74 SE).

Utilization distributions

We estimated UDs for spotted turtles with >40 locations (n = 28) and assessed differences between years for the 27 turtles tracked in both 2012 and 2013. The 95% UD isopleth represented the home range, eliminating the influence of extreme outliers. Across 2012 and 2013 the mean home range was 12.6 ha (±2.54 SE) across all seasons. Seasonal home ranges averaged 8.67 ha (±2.16 SE) during prenesting, 8.96 ha (±3.34 SE) during nesting, and 7.72 ha (±1.49 SE) during postnesting. There was a significant difference in home range size between years (Wilcoxon signed rank: z = 286, P = 0.019), with 2012 home ranges of 10.2 ha (±2.22 SE) and 2013 home ranges of 5.85 ha (±1.04 SE). Home range size did not differ among seasons ($F_{2,47}$ = 0.30, P = 0.750) or sex ($F_{1,48}$ = 2.12, P = 0.150), and there was not a season × sex interaction ($F_{2,44}$ = 0.77, P = 0.470).

Adult survival

We used radiotelemetry data on 31 adult turtles (16 males and 15 females) for known-fate survival estimation across 19 months (January 2012–July 2013). The candidate model with constant survival and a sex effect ($S(.)(s)$) received substantial support (ΔAIC_c = 0.00, w_i = 0.58) along with constant survival and no sex effect ($S(.)$) (ΔAIC_c = 0.67, w_i = 0.42). Other models were not well-supported (ΔAIC_c > 29, w_i = 0). Based on model-averaged estimates from supported models, monthly survival was slightly higher for females (0.998 ± 0.003) than males (0.993 ± 0.005), with annual survival extrapolated to 0.978 for females and 0.921 for males. We encountered two dead spotted turtles, both of which had been radio-tagged. Both mortalities were male and appeared to be from predation.

Abundance

Mean adult abundance per km of roadside ditch (λ) was estimated to be 2.1 turtles (95% credible intervals (CI): 0.7–5.1 turtles) in February 2012, and 1.6 turtles (95% CI: 0.6–3.2) in April 2013. Detection probability of turtles was 0.31 (95% CI: 0.10–0.51) in February 2012 and 0.50 (95% CI: 0.26–0.71) in April 2013.

DISCUSSION

Despite a novel configuration of terrestrial and aquatic landscape elements, we provide multiple lines of evidence to suggest turtles made behaviorally plastic habitat selection and use decisions that resulted in population maintenance. Both terrestrial and aquatic habitat types available to semi-aquatic wildlife in our study landscape have had extensive past and ongoing anthropogenic alteration, including modifying the spatial configuration of aquatic features from shallow wetlands and meandering streams, to a linear ditch network. Our results agree with our predictions that the ditch network, rather than more natural ephemeral habitat types, was the center of activity for movements and selection of the spotted turtles we marked. Although spotted turtles have been well-studied in wetland-dominated ecosystems with little habitat alteration, populations in reconfigured landscapes have not been studied extensively (but see Yagi and Litzgus 2012).

Multiscale habitat selection

Spotted turtles selected ditches across multiple spatial grains despite available and abundant ephemeral depressions and other more natural aquatic habitat types, suggesting their ability to exploit novel habitats may have been under-appreciated. Similarly, spotted turtles in a partially drained peat mine in Ontario extensively used drainage ditches, but opportunistically moved to flooded uplands when available (Yagi and Litzgus 2012). However, we note that our radiomarked turtles were initially captured in roadside ditches, and snapping turtles (*Chelydra serpentina*) can exhibit individual specialization on habitat types (Paterson et al. 2012) so that other spotted turtles in our study area could have focused on non-ditch habitat types. Given heterogeneity in habitat structure, spotted turtles typically use slow-moving permanent or ephemeral aquatic sites (Seburn 2003, Yagi and Litzgus 2012), but move upland for nesting, estivation, or when traversing to another aquatic feature (Beaudry et al. 2008).

For local-scale habitat selection, we determined that spotted turtles selected ditch habitats conducive for thermoregulation and feeding associations at both 2 and 20 m scales. We did observe turtles leaving ditches to use flooded plantations and natural depressions after heavy rain events. However, nearly 85% of turtle locations were in ditches despite the occurrence of >4600 depressions and other wetland features in the study area (Leonard et al. 2012). In addition, spotted turtles selected for a closed understory and thicker pine needle cover at the 2 m scale and for warmer substrate temperatures and deciduous leaf cover within and around the ditch system at the 20 m scale, which may indicate that they selected ditches based on thermal quality or shelter from predators (Yagi and Litzgus 2013). Spotted turtles, like other ectotherms, often create forms for protection from predators or thermoregulatory opportunities (Litzgus and Brooks 1998). We observed 19% of turtle locations under substrate and documented turtles estivating under a deep layer of leaves and needles in pine plantations. Occasionally, our presence may have caused turtles to seek protective cover, but turtles typically were located before they fled. Both observed behaviors further indicate that landscape reconfiguration did not prevent turtles from meeting life history requirements. Our two approaches to evaluating individual-based habitat models produced remarkably similar model selection results. We suggest either the cumulative ranks or summed model weights are suitable for evaluating information theoretic models across independent data sets, such as third-ordered habitat selection by radiomarked individuals (Johnson 1980).

Understanding fine-scale habitat selection in the context of local and landscape conditions is integral to informing conservation plans for imperiled species. Our multiscale results suggest that maintaining canopy closure near and around the ditch system comprised of both deciduous and pine trees may benefit semi-aquatic turtles. Ditches occurred in all activity areas at the landscape level, indicating their significance to spotted turtles at multiple spatial scales. Moreover, turtles focused activity areas closer to isolated wetlands at 60 m, corroborating the importance of a diverse suite of aquatic habitat types in forests for herpetofauna (Gibbs 1993, Werner

et al. 2007, Yagi and Litzgus 2012). Radiomarked turtles exhibited behavioral plasticity and exploited shallow aquatic environments with frequent movements upland to flooded plantations following heavy rains. For terrestrial habitats at a landscape scale, spotted turtles selected for habitat heterogeneity including both young, closed canopy and more mature thinned forest at the 175 m scale. This selection of heterogeneous landscape structure could indicate that turtles avoided stands with little overhead cover (e.g., recent clearcuts), but open habitats are important nesting areas (Beaudry et al. 2010, Rasmussen and Litzgus 2010). Active management of pine plantations contributes to the spatio-temporal mixture of stand ages and structural conditions that was selected for at a large spatial scale on this reconfigured landscape (Miller et al. 2009).

Spatial ecology

Reconfigured aquatic habitat types were used frequently by both sexes, particularly for mate searching by males during the prenesting period and for connectivity among landscape features (Litzgus and Mousseau 2004b). Both sexes accessed uplands by moving through the ditch network, which may have reduced overland movements, a primary source of mortality for turtles (Gibbs and Shriver 2002). Population persistence of aquatic and semi-aquatic herpetofauna is influenced by spatial configuration of wetlands (Joyal et al. 2001, Attum et al. 2008), so that the extensive ditch network likely facilitated connectivity among habitats and individuals. Despite significant annual variation in home range size, UDs of radiomarked turtles were centered on the ditch network in both years. This result provides additional confirmation that spotted turtles effectively exploited these spatially and hydrologically altered features to meet life history requirements.

Population ecology

Based on our abundance estimates and length of the ditch network, it appears that a robust population of spotted turtles occurred in this reconfigured landscape. In fact, we captured the largest number of spotted turtles in published literature (O'Bryan 2014). We captured twice as many males as females, but we suggest the longer distances moved and larger home

ranges by males likely resulted in higher detection rates and possibly lower survival. Adult turtles in our study population had high annual survival unrelated to sex or time, and female annual survival (0.978) was approximately 6% greater than males (0.921). These survival estimates are comparable to spotted turtles in a relatively unaltered area of southern Ontario (female = 0.965, males = 0.942) and greater than the estimated minimum value needed to support population growth for females (Litzgus 2006, Enneson and Litzgus 2008).

The high estimated annual survival of spotted turtles provides evidence that this population acquired key resources with little mortality on an extensively reconfigured landscape. Elsewhere, mortality from vehicles and removal for the pet trade are dominant threats that have lasting negative effects on populations (Gibbons et al. 2000, Beaudry et al. 2008, Enneson and Litzgus 2008). Female turtles are particularly vulnerable when making overland nesting movements, which can account for a large proportion of terrestrial activity (Steen et al. 2006, Beaudry et al. 2010). Here, turtles exploited the extensive ditch network to migrate to potential nesting areas and most (80%) of our observed nesting females oviposited directly on ditch banks (O'Bryan 2014). Our study area had extensive unimproved forest roads, but they received little traffic, and were gated and closed to the public. Across 2 yrs of traveling thousands of kilometers, we never observed a road-related mortality in this population. Thus, the reconfigured aquatic environment in conjunction with restricted public and vehicle access may have reduced exposure of females and hatchlings to mortality from terrestrial predators, vehicles, or collection. Dredging of ditches occurs approximately every 25 yrs and could cause mortality of spotted turtles. However, this activity occurs on a very small proportion of available ditches in any year, we did not observe mortality associated with ditch maintenance, and turtles likely can move away from equipment during the active season.

We allow the possibility that this population is a biological legacy that will decline due to a delayed response to habitat alteration and use of sub-optimal habitat (i.e., extinction debt; Kuussaari et al. 2009). Our captures were skewed toward older individuals; however, juvenile turtles may use different habitat types than adults (Cagle 1950) and are notoriously difficult to find in the field (Litzgus and Mousseau 2004a). Thus, the weight of evidence suggests that this rare turtle exhibited behavioral plasticity and opportunistically used ditch networks, suggesting that they can be locally abundant and more resilient to some forms of habitat alteration than typically recognized. Research focusing on population age structure, reproductive success, and habitat selection and survival of juvenile turtles in both reconfigured and unmanaged landscapes will enhance understanding of long-term population trends in this system.

CONCLUSIONS

Given that global rates of habitat conversion lag behind establishment of new protected areas, reconfigured landscapes are crucial resources for some at-risk species (Brockerhoff et al. 2008). However, populations may be extirpated following habitat modification if they are sensitive to removal of a key resource, enhancement of a critical threat, or are unable to make adaptive decisions (Schlaepfer et al. 2002, Chevin et al. 2010). Our research illustrates how managed forests, while subject to repeated disturbances from harvesting, silvicultural activities and hydrological alteration, may support some species sensitive to land use conversion into non-forest, road mortality, and unregulated collection (Gibbons et al. 2000). We suggest that future research of rare species on reconfigured landscapes consider behavioral plasticity as a potential response to habitat alteration and incorporate metrics of spatial and behavioral ecology as well as population responses into study designs. By doing so, ecologists may avoid using limited resources where species have adapted to novel environments and are maintaining populations.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1228/supinfo