

Variation and repeatability of home range in a forest-dwelling terrestrial turtle: implications for prescribed fire in forest management

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Keywords

behavior; controlled burn; disturbance; Eastern Box Turtle; Longleaf Pine; site fidelity; spatial ecology; *Terrapene carolina*.

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Abstract

Animal movements and use of space are in part determined by interactions between individual attributes such as sex and body size and extrinsic environmental factors such as the seasonal availability, quality and spatial configuration of resource patches in the landscape. Fire is a common and widespread disturbance process that has the potential to affect animal movements through modifications to the environment. Using radiotelemetry, we examined the contribution of these factors to variation in movements and home range over a 5-year period in a forest-dwelling terrestrial turtle, *Terrapene carolina*, at fire-maintained and unburned habitats in the southeastern United States. Female turtles had annual home-range sizes twice as large as males and moved longer distances per day during the nesting season (June and July), but males exhibited greater spatial fidelity from year to year. Turtles at the unburned site had home-range sizes twice as large as those at the fire-maintained site, and home-range size also decreased with increasing frequency and extent of fire, but this latter effect was strongest in females. Home-range behavior was highly repeatable within individuals of both sexes over time. This is the first evidence that fire influences the spatial ecology and movements of turtles, most likely through fire's impact on the spatial configuration, availability and quality of critical resources. That individuals behaved consistently through time, but differently from one another according to both intrinsic individual attributes and extrinsic environmental factors provides strong evidence of consistent inter- and intra-population variation in space use and movement behaviors in *T. carolina*. Such intra-specific behavioral variation suggests applying caution when extrapolating results to other sites across the geographic range of a species for use in conservation and management.

Introduction

Information on animal movements and use of space is essential for understanding their ecology, life history, population dynamics and conservation because such behaviors in part determine fitness costs and benefits (Swingland & Greenwood, 1983). Individuals typically position themselves spatially and temporally relative to critical resources, with the seasonal availability, quality, spatial configuration and heterogeneity of resource patches shaping movements and space use (Haskell, Ritchie & Olf, 2002; Roe, Kingsbury & Herbert, 2004; Börger *et al.*, 2006; Roe & Georges, 2008; Saïd *et al.*, 2009). Movements and space use can also be influenced by intrinsic individual attributes such as body size (Blouin-Demers, Bjorgan & Weatherhead, 2007; Hyslop *et al.*, 2014), sex (Relyea, Lawrence & Demarais, 2000; Carfagno & Weatherhead, 2008), reproductive status (Tufto, Anderson & Linnell, 1996; Marshall, Manning & Kingsbury, 2006) and temperament (Ward-Fear *et al.*, 2018). Studying the additive and interactive effects

of both intrinsic and extrinsic environmental factors can yield insight into the proximal mechanisms shaping intra-specific variation in movement and space use, both between populations and among individuals within a population.

A common and useful measure of an individual's use of space is the home range, defined as the area traversed during behaviors required for survival and reproduction over a defined time period (Burt, 1943; Börger *et al.*, 2006). Movements within the home range may include routine behaviors such as resource acquisition (i.e. food and water), social interactions and reproduction (i.e. mate searching and nest site selection) and refuge from predators or environmental extremes (i.e. overwintering and estivation). However, the needs of individuals and locations of suitable habitat patches in the landscape can change on a predictable basis according to seasonal variation or episodic unpredictable disturbance events (Wingfield, 2005), requiring individuals to alter movement and space use behaviors (Duda, Krzysik & Freilich, 1999; Saïd & Servanty, 2005; Roe & Georges, 2008). Thus, the consistency of

behavior and stability of home-range size and geographic location may vary among individuals depending on environmental context. It is especially important to examine behavioral responses of long-lived animals to dynamic environments over sufficiently long time periods that encompass both seasonal and stochastic environmental disturbance events that contribute to population regulation in the short term, and evolutionary responses in the long term (Clutton-Brock & Sheldon, 2010).

Fire is a natural and widespread disturbance process in ecosystems worldwide (Keeley & Rundel, 2005; Pausas & Keeley, 2009), with prescribed fire being increasingly used by natural resource practitioners for diverse management goals including wildfire hazard reduction, invasive species control and for grazing, silviculture, game management and biodiversity conservation (Haines, Busby & Cleaves, 2001; Pastro, Dickman & Letnic, 2011). One such pyrogenic system is the Longleaf Pine (*Pinus palustris*) savanna of the southeastern United States, which historically burned as low- to moderate-intensity surface fires at a frequencies of 1–6 years (Frost, 1998; Van Lear *et al.*, 2005). Fire alters understory vegetation and structure in ways that could temporarily affect forest microenvironments and distribution of critical resources on broader spatial scales (Williamson & Black, 1981; York, 1999; Iverson & Hutchinson, 2002; Greenberg & Waldrop, 2008; Hossack *et al.*, 2009; Mitchell *et al.*, 2009). Fire thus has the potential to also affect animal movements and space use behavior, either directly through movements to escape approaching fire fronts, or indirectly in response to changes in habitat quality after fire (Russell, Van Lear & Guynn, 1999).

The Eastern Box Turtle, *Terrapene carolina*, is a long-lived species that inhabits terrestrial forests over a broad geographic range in eastern North America (Dodd, 2001; Keister & Willey, 2015). Several studies have examined *T. carolina* responses to prescribed fire, with turtles suffering high mortality, injury and reduced body condition in fire-managed forests (Platt, Liu & Borg, 2010; Howey & Roosenburg, 2013; Roe, Wild & Chavez, 2019), but to our knowledge, none have examined movement and home-range behaviors in fire-disturbed environments in *Terrapene*. Of the few studies examining turtle behavioral responses to fire, none have found significant changes to home ranges or movement patterns associated with fire disturbance (Yager *et al.*, 2007; Lovich *et al.*, 2011; Sanz-Aguilar *et al.*, 2011). However, as most *Terrapene* are nominally terrestrial turtles with limited mobility owing to slow walking speeds (Zani & Kram, 2008), we expect *T. carolina* to be particularly vulnerable to fire disturbance and to modify movements and space use in fire-managed forests. Here, we compare movements and space use in two *T. carolina* populations at sites that differ in their historic and current use of fire, and examine numerous potential sources of individual variation including sex, body size, season and spatial and temporal heterogeneity of fire. We predict individuals will constrain movements and home ranges within fire refuge habitat patches in or near aquatic resources and mesic forest types, and maintain higher fidelity to these areas over time. As *T. carolina* is a species of conservation concern that is in decline in many parts of range (Keister & Willey, 2015), such information is needed to assess whether and how *T. carolina*

responds to management practices involving fire and apply this knowledge to inform conservation and management strategies.

Materials and methods

Study sites

The study was conducted at two North Carolina State Parks, including Weymouth Woods Sandhills Nature Preserve (hereafter Weymouth Woods) and the Lumber River State Park (hereafter Lumber River). Weymouth Woods is *c.* 200-ha site in the Sandhills Level IV Ecoregion (Griffith, Omernik & Comstock, 2002), and is comprised of a forest mosaic of mixed pine and hardwood forests (Fig. 1), including Longleaf Pine and Loblolly Pine (*Pinus taeda*), along with several species of hardwood such as oak (*Quercus* spp.), hickory (*Carya* spp.), Red Maple (*Acer rubrum*), Sweetgum (*Liquidambar styraciflua*), American Holly (*Ilex opacum*), Sassafras (*Sassafras albidum*) and Tuliptree (*Liriodendron tulipifera*). The majority of the site is xeric uplands with a small stream network and associated bottomlands (Fig. 1). Prescribed fire has been used regularly in forest management since 1974, with 76% of the area being managed using low-intensity controlled burns ranging in size from 0.9 to 23.9 ha (5.2 ± 3.2 ha; mean \pm sd), with a historic mean burn frequency of every 5.9 years (range: 1.5–17 years) from 2000 to 2016 (Weymouth Woods Sandhills Nature Preserve, unpubl. data).

The Lumber River site is *c.* 225-ha reserve in the Atlantic Southern Loamy Plains and Southeastern Floodplains and Low Terraces Level IV Ecoregions (Griffith *et al.*, 2002). The habitat of Lumber River includes extensive riverine bottomland swamp forests with Bald Cypress (*Taxodium distichum*), tupelo (*Nyssa* spp.), Tuliptree, Sweetgum, Red Maple and Atlantic White Cedar (*Chamaecyparis thyoides*) along with upland mixed pine and hardwood forests comprised of Loblolly and Longleaf Pine, oaks and hickory (Fig. 1). A prescribed burn program was initiated in March 2017, but prior to this and for the duration of this study, fire had not been used in management since designation as a state park in 2001 (Lumber River State Park, unpubl. data).

Field data collection

To capture variation resulting from environmental heterogeneity, we captured individuals from a variety of forest types spread out across each site, including from burn units and areas where fire has been historically excluded at the fire-maintained site (Weymouth Woods). We equipped turtles with radiotransmitters (RI-2B, 10–15 g; Holohil Systems Ltd., Carp, ON, Canada) using 5-min epoxy gel (Devcon, Solon, OH, USA). From April 2012 to March 2017, we tracked 57 turtles (14 males and 14 females from Weymouth Woods, 15 males and 14 females from Lumber River) for periods of 12–60 months. Upon initial capture, we measured midline carapace length (CL) to the nearest 0.1 mm using Vernier calipers and mass to the nearest gram using a spring scale. We determined sex by observing several sexually dimorphic features, with males typically having a concave posterior plastron,

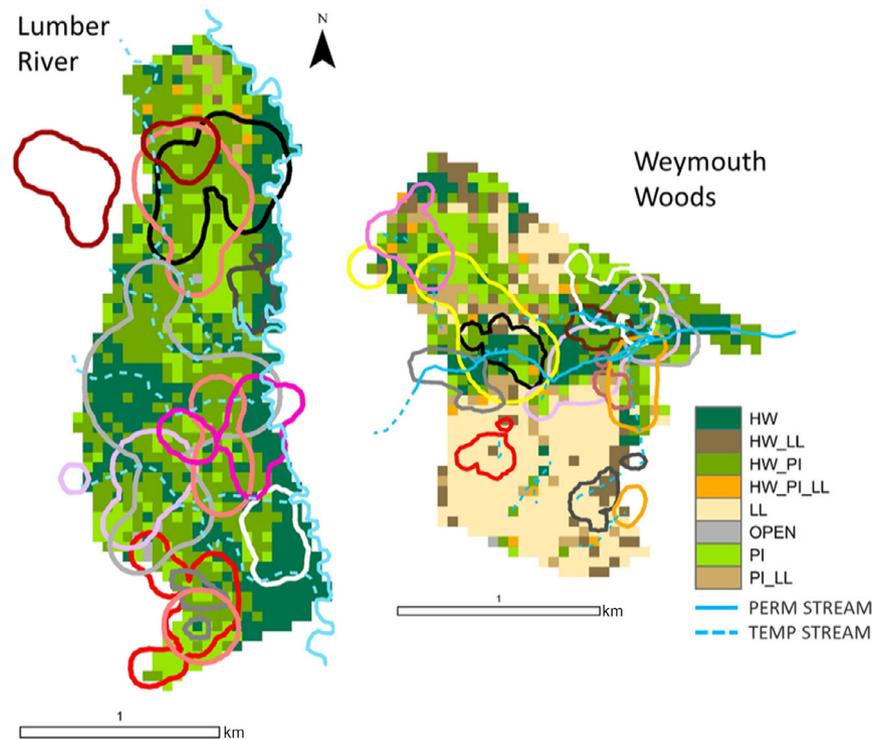


Figure 1 Maps of habitats and 95% kernel density home ranges for *Terrapene carolina* from unburned Coastal Plain (Lumber River) and fire-maintained Sandhills (Weymouth Woods) sites in North Carolina, USA. We only show a single year of data from a subset of individuals (12 per site) for simplicity. Forest habitat abbreviations are hardwood (HW), Longleaf Pine (LL) and non-Longleaf Pine (PI). See Roe *et al.* (2019) for description and mapping of habitat types.

stouter and longer curved claws on hind feet, a red iris and thicker and longer tails compared to females (Palmer & Braswell, 1995).

We located telemetered turtles using a receiver (R-1000; Communication Specialists, Orange, CA, USA) and Yagi antenna at a frequency of once per week during the active season (May–September), every two weeks during brumation ingress (October–November) and egress (March–April) and once per month for the remainder of the brumation period (December–February). Turtles at each site were divided into local spatial clusters and each cluster was radiotracked on a rotating order each visit, with the majority of observations occurring between 09:00 and 12:00 h (71.9% and 75.2% of observations at Lumber River and Weymouth Woods, respectively). At each location, we determined the coordinate position using a hand-held GPS (≤ 7 m accuracy) and plotted locations on maps using ArcMap 10.2.2.

Space use and movement variable estimation

We calculated several movement and space use variables for each turtle. Given the debate over whether minimum convex polygon (MCP) or kernel density techniques are more appropriate (Row & Blouin-Demers, 2006; Laver & Kelly, 2008;

Nilsen, Pedersen & Linnell, 2008), we used both methods to estimate annual home-range size. Using all active season locations and one overwintering location per year, we calculated 100% MCPs, and for kernel density, we used the fixed kernel method and the likelihood cross-validation (CVh) smoothing parameter with 50 m cell size output raster to estimate the size of area within the 95% isopleths. We chose the CVh smoothing parameter because this method is recommended for small sample sizes (< 50 , Horne & Garton, 2006). For individuals tracked over multiple years, we quantified home-range overlap (i.e. geographic fidelity) using the following equation:

$$\text{home range overlap} = \frac{\text{area overlap } ij(\text{ha})}{\text{area year } i(\text{ha}) + \text{area year } j(\text{ha}) - \text{area overlap } ij(\text{ha})}$$

where years i and j are sequential years, and area overlap was calculated using the Intersect function in ArcMap 10.2.2 (Refsnider, Strickland & Janzen, 2012). Lastly, we measured movement rates as straight-line distances between sequential locations divided by the number of days elapsed between observations. We used Geospatial Modeling Environment (Beyer, 2012) and (R Core Team, 2017) as extensions of ArcMap 10.2.2 to estimate movement distances and home-range sizes.

Statistical analyses

We performed statistical analyses with SPSS v. 25.0 (SPSS Inc., Chicago, IL, USA). Where appropriate, we examined assumptions of homogeneity of variances and normality and made appropriate transformations when data failed to meet assumptions. We accepted statistical significance at $\alpha \leq 0.05$ unless otherwise noted. Values are reported as mean \pm 1 se unless otherwise stated.

For individuals tracked over multiple years, repeatability of home-range size was assessed using a Spearman's rank-order correlation test, running one overall analysis combining sites and sexes. For turtles tracked more than 2 years, we randomly selected only 2 years for inclusion in repeatability analyses.

We examined variation in home range using linear mixed models, with \log_{10} -transformed home-range size and arcsine-transformed spatial overlap as the dependent variables, site, sex, year and interactions as the independent variables, \log_{10} -transformed CL as a covariate and individual as a repeated variable. In the above analyses, we ran separate models for MCP and 95% kernel density estimates. We used linear mixed models to examine variation in movement rates with \log_{10} -transformed movement rate (m day^{-1}) as the dependent variable, site, sex, month and interactions as the independent variables, \log_{10} -transformed CL as a covariate and individual as a repeated variable. We only examined months that coincide with the active season (April–October) in movement analyses.

At the fire-maintained site (Weymouth Woods), we used linear mixed models to assess how intrinsic attributes of the individual (sex and size) and spatial and temporal heterogeneity of fire influenced home-range size and home-range overlap. We used \log_{10} -transformed home-range size and arcsine-transformed spatial overlap as dependent variables, sex, year and sex \times year as independent variables, individual as a repeated variable and \log_{10} -transformed fire risk index as the fire heterogeneity covariate. The fire risk index was calculated using the following equation:

$$\text{fire risk index} = \frac{\text{locations in fire units}(n)}{\text{total locations}(n)} \times \text{fire frequency}$$

where fire frequency is the mean number of times the units that the turtle visited was burned during the study period (Roe *et al.*, 2019). We ran separate models for MCP and 95% kernel density estimates. We also used linear mixed models to examine how fire heterogeneity influenced \log_{10} -transformed movement rates (dependent variable), with sex and month (April–October) as independent variables, individual as a repeated variable and \log_{10} -transformed fire risk index as the fire heterogeneity covariate.

Results

Body size

Male turtles from Weymouth Woods had mean (\pm sd) initial CL of 130.5 ± 7.5 mm (range: 121.3–149.6 mm) and Weymouth Woods females had initial CL of 126.7 ± 9.7 mm

(range: 109.3–137.7 mm). Male turtles from Lumber River had initial CL of 138.9 ± 10.4 mm (range: 124.1–151.7 mm) and Lumber River females had initial CL of 132.7 ± 7.9 mm (range: 126.1–149.1 mm). Transmitter weight ranged from 2.4% to 4.5% of turtle initial body mass.

Home range

We obtained 27.5 ± 5.4 (mean \pm sd) and 26.0 ± 2.0 locations per year for female and male turtles, respectively, at Weymouth Woods, and 25.9 ± 3.2 and 24.5 ± 4.8 locations per year for female and male turtles, respectively, at Lumber River. For the 35 individuals tracked over multiple years, home-range size was repeatable, with an individual's home-range size in 1 year being a strong predictor of its home-range size in subsequent years, accounting for 64.5–76.5% of variation (95% kernel density: $r_s = 0.645$, $P < 0.001$; MCP: $r_s = 0.765$, $P < 0.001$; Fig. 2). Home-range size varied by sex for both 95% kernel density and MCP estimators, with females using areas twice as large as males at both study sites (Tables 1 and 2, Fig. 1). Home-range size also varied by site for the 95% kernel density method, but not for the MCP method (Tables 1 and 2). Turtles at the Lumber River had home-range sizes approximately twice as large as those at Weymouth Woods, and this difference was consistent for both sexes (Tables 1 and 2, Fig. 1). There was no annual variability in home-range size for individuals tracked for multiple years, and body size did not influence home-range size (Table 2).

Individuals exhibited strong fidelity to particular areas from year to year, with home-range spatial overlap varying by sex, but not site, year, body size or any interactions among variables (Tables 1 and 3). Spatial overlap of home ranges in consecutive years was *c.* 10% greater for males than females, but

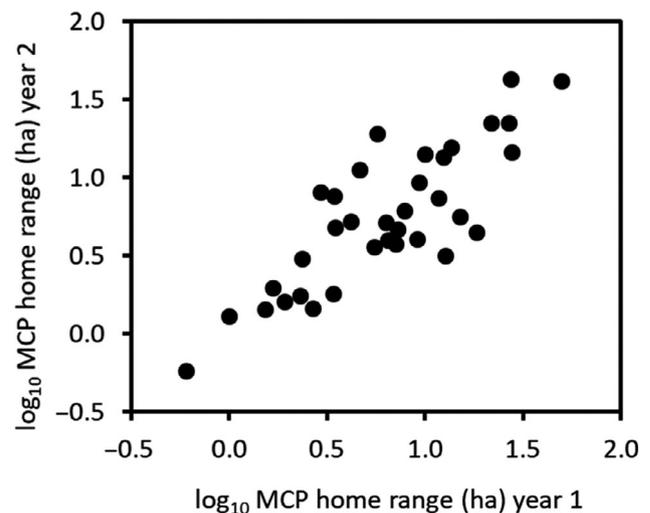


Figure 2 Repeatability of home-range size (minimum convex polygon) for individual *Terrapene carolina* radiotracked for multiple years from two sites in North Carolina, USA. For individuals tracked more than 2 years, only 2 years were randomly chosen for inclusion in repeatability analyses.

this difference was only significant for the 95% kernel density method (Tables 1 and 3).

Individuals at the fire-maintained site (Weymouth Woods) were found within 4.1 ± 0.4 (range: 1–8) fire management units which were burned between zero and three times during the study, spending $30.7 \pm 5.9\%$ (range: 0–100%) of their time in fire management units. The fire risk index was a predictor of

individual home-range size, but this relationship depended upon sex for both the MCP (sex: $F_{1,10.618} = 23.498$, $P = 0.001$, year: $F_{4,5.773} = 0.615$, $P = 0.668$, sex \times year: $F_{4,5.773} = 0.546$, $P = 0.710$, fire risk index: $F_{1,47.788} = 8.208$, $P = 0.006$, sex \times fire risk index: $F_{1,47.788} = 9.000$, $P = 0.004$) and 95% kernel density methods (sex: $F_{1,10.592} = 26.514$, $P < 0.001$, year: $F_{4,6.018} = 0.620$, $P = 0.665$, sex \times year: $F_{4,6.081} = 0.662$,

Table 1 Home-range variables for male and female *Terrapene carolina* from a fire-maintained Sandhills population (Weymouth Woods) compared to an unburned Coastal Plain site (Lumber River)

Site	Sex	MCP (ha)		95% kernel density (ha)		MCP overlap (%)		95% kernel density overlap (%)	
		Mean (SE) ^a	Range ^b	Mean (SE) ^a	Range ^b	Mean (SE) ^a	Range ^b	Mean (SE) ^a	Range ^b
Lumber River	F	17.3 (4.2)	2.6–113.1	32.8 (8.3)	4.7–211.7	36.8 (3.5)	10.5–48.2	37.5 (3.3)	8.2–58.2
	M	9.1 (2.9)	0.6–42.9	17.2 (5.0)	1.5–74.4	44.2 (3.1)	23.4–72.2	49.2 (3.9)	26.3–76.7
Weymouth Woods	F	9.5 (1.4)	1.4–35.6	18.4 (3.1)	2.8–67.5	37.0 (4.0)	7.2–69.8	38.5 (3.4)	10.6–65.0
	M	4.7 (0.8)	1.0–31.9	9.9 (1.8)	2.3–60.4	48.8 (4.1)	0.0–76.2	49.2 (4.4)	8.6–72.0

MCP, minimum convex polygon.

^aWe calculated a mean value for individuals radiotracked for multiple years, which we then used to calculate the overall population mean.

^bRanges are minimum and maximum annual values before individual means were calculated for individuals radiotracked for multiple years.

Table 2 Results for linear mixed effects models examining sources of variation in home-range size in *Terrapene carolina* from two sites in North Carolina, USA

Source	95% kernel density				Minimum convex polygon			
	Num d.f.	Den d.f.	<i>F</i>	<i>P</i>	Num d.f.	Den d.f.	<i>F</i>	<i>P</i>
Site	1	14.541	4.623	0.049	1	12.857	3.712	0.076
Sex	1	12.987	19.063	0.001	1	11.486	19.414	0.001
Year	4	9.820	2.719	0.092	4	9.771	2.024	0.168
Site \times sex	1	60.853	0.012	0.912	1	65.218	0.000	0.989
Site \times year	4	9.704	0.300	0.871	4	9.703	0.232	0.914
Sex \times year	4	9.775	0.455	0.767	4	9.744	0.463	0.762
Site \times sex \times year	3	30.931	0.225	0.879	3	30.490	0.305	0.822
\log_{10} carapace length	1	107.060	1.569	0.213	1	107.061	2.027	0.157

One study site (Weymouth Woods) was in a fire-maintained Longleaf Pine sandhills ecosystem, whereas the other (Lumber River) was in an unburned mixed pine and hardwood coastal plain forest. Home-range estimates were derived using both the 95% kernel density and minimum convex polygon methods.

Table 3 Results for linear mixed effects models examining sources of variation in the degree of home-range spatial overlap in 35 *Terrapene carolina* radiotracked for 2–5 years from two sites in North Carolina, USA

Source	95% kernel density				Minimum convex polygon			
	Num d.f.	Den d.f.	<i>F</i>	<i>P</i>	Num d.f.	Den d.f.	<i>F</i>	<i>P</i>
Site	1	13.100	0.891	0.362	1	7.787	1.992	0.197
Sex	1	8.605	10.832	0.010	1	6.812	3.424	0.108
Year	3	8.612	1.562	0.268	3	7.815	1.803	0.226
Site \times sex	1	10.434	0.171	0.687	1	48.086	0.865	0.357
Site \times year	3	8.411	1.190	0.371	3	7.751	1.070	0.416
Sex \times year	3	8.355	1.475	0.290	3	7.793	1.552	0.277
Site \times sex \times year	3	8.345	0.767	0.543	2	39.987	0.040	0.961
\log_{10} carapace length	1	56.691	2.269	0.137	1	52.402	1.045	0.311

One study site (Weymouth Woods) was in a fire-maintained Longleaf Pine sandhills ecosystem, whereas the other (Lumber River) was in an unburned mixed pine and hardwood coastal plain forest. Home-range estimates were derived using both the 95% kernel density and minimum convex polygon methods.

$P = 0.641$, fire risk index: $F_{1,48.207} = 16.595$, $P < 0.001$, sex \times fire risk index: $F_{1,48.207} = 14.334$, $P < 0.001$; Fig. 3). Female home-range size decreased with increasing fire extent and frequency (MCP: $t = -3.000$, d.f. = 47.788, $P = 0.004$; 95% kernel density: $t = -3.786$, d.f. = 48.207, $P < 0.001$), but male home-range size did not vary with according to the fire risk index (Fig. 3). Home-range spatial overlap varied by sex, but not the fire risk index for either the MCP (sex: $F_{1,15.534} = 5.270$, $P = 0.036$, year: $F_{3,6.807} = 2.845$, $P = 0.117$, fire risk index: $F_{1,30.235} = 0.100$, $P = 0.753$, sex \times fire risk index: $F_{1,30.069} = 0.188$, $P = 0.668$) or 95% kernel density estimates (sex: $F_{1,12.492} = 6.697$, $P = 0.023$, year: $F_{3,7.637} = 3.003$, $P = 0.098$, fire risk index: $F_{1,29.263} = 0.891$, $P = 0.353$, sex \times fire risk index: $F_{1,28.621} = 0.000$, $P = 0.991$).

Movements

Movement rates differed between months and were dependent on body size, sex and the sex \times month interaction, but did not vary by site or any other examined interactions (sex: $F_{1,329.141} = 8.435$, $P = 0.004$; site: $F_{1,332.674} = 3.327$, $P = 0.069$; month: $F_{6,84.623} = 18.715$, $P < 0.001$; \log_{10} CL: $F_{1,333.093} = 12.477$, $P < 0.001$; sex \times site: $F_{1,323.577} = 0.811$, $P = 0.368$; site \times time: $F_{6,84.623} = 1.138$, $P = 0.347$; sex \times time: $F_{6,84.623} = 3.733$, $P = 0.002$; site \times sex \times month: $F_{6,84.623} = 0.539$, $P = 0.777$). Movement rates for both sexes increased from spring to summer, peaked in July, then decreased from late summer through fall (Fig. 4). Females moved at greater rates (20.7–24.0 m day⁻¹) than males (10.8–14.0 m day⁻¹) in June and July (Fig. 4), and larger turtles moved at greater rates than smaller turtles ($t = 3.532$, d.f. = 333.093, $P < 0.001$). Movement rates at the fire-maintained site did not vary according to the fire risk index for either sex (fire

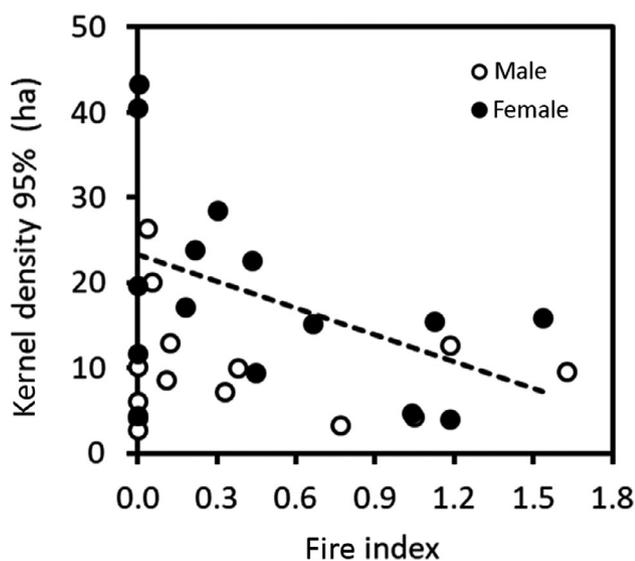


Figure 3 Relationship between *Terrapene carolina* home-range size (95% kernel density) and the frequency and extent of prescribed fire (fire index) at a fire-maintained site (Weymouth Woods) in the Sandhills of North Carolina, USA.

risk index: $F_{1,166.264} = 1.242$, $P = 0.267$, sex \times fire risk index: $F_{1,166.264} = 2.843$, $P = 0.094$).

Discussion

Our large sample size of turtles radiotracked for a 5-year period at two sites that differ in natural environmental conditions and land management practices allowed us to examine how numerous proximal intrinsic and extrinsic environmental factors influence movement and space use in a long-lived terrestrial vertebrate. The most important findings relevant to behavioral ecology and forest management practices were that (1) nearby populations of the same species demonstrated considerable variation in home-range size in response to differences in local environmental conditions; (2) home-range size depended on spatial and temporal heterogeneity of prescribed fire management; (3) intrinsic factors such as sex and body size influenced movements and space use, sometimes interacting with extrinsic factors such as fire and season; and (4) home-range size and spatial location in the landscape were consistent over time within individuals. These results, together with those of other studies (Rittenhouse *et al.*, 2008; Roe, Wild & Lunn, 2018; Roe *et al.*, 2019), demonstrate a variety of behavioral responses both within and among populations of *T. carolina* that allow this wide-ranging species to adjust to diverse local environmental conditions.

Behavioral responses to environmental heterogeneity can take the form of both between- and within-individual variation, and partitioning such variation between these categories and in relation to intrinsic and extrinsic covariates is a central goal of behavioral ecology (Sih *et al.*, 2012; Dingemanse & Dochtermann, 2013; Ward-Fear *et al.*, 2018). We found three lines of evidence supporting a high degree of within-individual repeatability of home-range behavior in *T. carolina*. First, annual home-range size did not differ over time within individuals through 5 years of study, and this trend was consistent for both sexes in two distinct populations and environmental contexts. Second, geographic fidelity of home ranges was high,

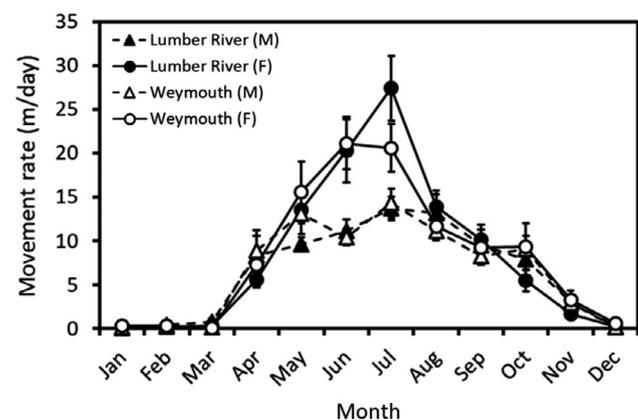


Figure 4 Monthly mean (\pm SE) movement rates for *Terrapene carolina* from unburned Coastal Plain (Lumber River) and fire-maintained Sandhills (Weymouth Woods) sites in North Carolina, USA.

with individual home ranges overlapping 37–49% of the previous year's home-range area the next year. Third, an individual's home-range size in 1 year was a strong predictor of its home-range size in subsequent years. The repeatability of home-range behavior in *T. carolina* compliments other studies demonstrating a high degree of behavioral consistency within *Terrapene*, including home-range overlap similar to turtles in our study (36–42%, Refsnider *et al.*, 2012), repeatability of spring emergence timing (DeGregorio *et al.*, 2017), overwintering site selection (Refsnider *et al.*, 2012), temperament (Kashon & Carlson, 2017) and habitat selection (Rittenhouse *et al.*, 2008). Our estimates of repeatability of home-range size (0.65–0.77) are considerably higher than a wide range of behaviors in numerous taxa (0.37, Bell, Hankison & Laskowski, 2009), and contribute to a growing understanding of behavioral consistency in turtles (Janzen & Morjan, 2001; Spencer & Thompson, 2003; Kamel & Mrosovsky, 2004, 2005; Carter *et al.*, 2016). Behavioral repeatability is often interpreted as indirect evidence for heritable behavioral genetic variation (Boake, 1989), which would make such traits subject to selection and evolution in response to environmental changes. However, establishing links between behavioral repeatability and genetic variation in the field is logistically difficult in organisms with long generation times such as turtles, and plasticity in response to early environmental cues can also result in behavioral consistency (Wiens, 1970; Davis & Stamps, 2004; Stamps & Swaisgood, 2007). Regardless of the proximal causes and eventual consequences of behavioral consistency, the ability to measure such variation and account for it in comparisons among individuals increases power in analysis of how differences in intrinsic attributes of the individual and extrinsic environmental heterogeneity influence behavior.

Numerous intrinsic factors such as sex, life-cycle stages and body size influence the movements and space use of terrestrial and semi-aquatic turtles (Litzgus & Mousseau, 2004; Iglay, Bowman & Nazdrowicz, 2007; Walston *et al.*, 2015; Slavenko *et al.*, 2016; Sullivan *et al.*, 2016; Castellón, Rothermel & Bauder, 2018). In our study, larger turtles moved at greater rates than smaller individuals, but body size did not influence any measure of space use over the size range examined. Sex was a more consistent predictor of movements and space use, with females traversing home ranges twice as large as males, moving at greater rates than males seasonally, and exhibiting lower home-range geographic fidelity than males. When such consistent variation is observed, it suggests differences in sexual reproductive strategies are in part responsible. In turtles, the 'reproductive strategies hypothesis' predicts males should traverse longer distances at times of peak mating activity to increase encounters with females, and females should increase movements during peak nesting activity in search of ovoposition sites (Morreale, Gibbons & Congdon, 1984). Mating behavior and male-male aggressive encounters occur at our sites throughout the entire active season (April–October), with highest incidences during May, July, August and September (unpubl. data). While male movements are generally greatest during this period, they never exceed movement rates for females, ruling out mate searching by males as a cause for the observed sex-specific differences. Alternatively, if suitable nest

environments are not available in the same areas where foraging, overwintering and other important activities occur, female turtles must travel potentially long distances to and from ovoposition sites. As *T. carolina* is a forest-dwelling species and exhibits strong selection of hardwood forest habitats (Dodd, 2001; Greenspan, Condon & Smith, 2015; Keister & Willey, 2015; Roe *et al.*, 2018) that typically remain cooler than more open habitats (Parlin *et al.*, 2017; Roe, Wild & Hall, 2017), females often seasonally migrate to open habitats and ecotones for nesting (Filtz & Mullin, 2006). In our study, most females made annual round-trip movements of several hundred meters (maximum 4.6 km) during the nesting season (June and July) to open successional habitats and forest edges. The greater movement rates of females during these months suggests searching for nesting habitat as a likely cause of the observed seasonality in sex-specific movements. Such nesting migrations would also increase home-range size, and if females do not exhibit fidelity to particular nest sites, spatial overlap of an individual's annual home ranges may be smaller for females. While it has not been documented in *Terrapene*, a return to the same general nest site is common in turtles (Congdon *et al.*, 1983; Valenzuela & Janzen, 2001; Freedberg *et al.*, 2005). Nest-site philopatry need not be a return to specific geographic nesting locations, but rather a consistent selection of microenvironmental cues (Janzen & Morjan, 2001; Kamel & Mrosovsky, 2004). Turtles can select new nest locations when environmental changes affect the quality of previously used nesting environments or availability of new areas (Kolbe & Janzen, 2002; Najbar & Szuskiewicz, 2007; Beaudry, deMaynadier & Hunter, 2010). We observed occasional shifts in summer migrations of several hundred meters from formerly open habitats that had become shaded through succession to recent forest openings following forestry practices such as timber harvest and controlled burns. It should be noted that we rarely observed nesting activity directly, and acknowledge that female summer migrations may also be to locate temporarily available food resources (e.g. berries), for thermoregulation, or other purposes. Additionally, our observation method and regime underestimates home-range size and especially daily movement rates by interpreting linear rather than sinuous tracks, and missing small-scale movements within a core activity area (Claussen, Finkler & Smith, 1997; Christensen & Chow-Fraser, 2014).

Our observations of sex-specific movement are in contrast to other studies of *T. carolina*, where males typically move at greater or similar rates to females (Penick *et al.*, 2002; Iglay *et al.*, 2007; Currylow, MacGowan & Williams, 2012). Likewise, this is the first statistically supported evidence of home-range size variation between sexes in any single published study of *T. carolina* (Dodd, 2001; Keister & Willey, 2015), but a recent range-wide meta-analysis identified females as having home-range sizes 27% larger than males (Habeck *et al.*, 2019). While the direction of the sex-specific differences in our study are in agreement with Habeck *et al.* (2019), females traversed home ranges nearly 100% larger than males. The unique sex-specific patterns observed in our study suggest that perhaps site- or region-specific factors such as climate, the spatial configuration and quality of resources, or other local

environmental variables may interact with reproductive strategies to influence behavior in *T. carolina*.

An important extrinsic environmental factor that influences behavioral variation in turtles is the frequency, type and magnitude of disturbances (Duda *et al.*, 1999; Roe & Georges, 2008; Rees, Roe & Georges, 2009; Anthonysamy, Dreslik & Phillips, 2013), including in *T. carolina* (Dodd, Ozgul & Oli, 2006; Iglay *et al.*, 2007; Currylow *et al.*, 2012). Prescribed fire is one such disturbance that could affect habitat quality by altering microclimates and distribution of critical structural components (York, 1999; Iverson & Hutchinson, 2002; Greenberg & Waldrop, 2008; Hossack *et al.*, 2009). Such disturbances, along with the risk of injury or death from fire (Platt *et al.*, 2010; Howey & Roosenburg, 2013; Roe *et al.*, 2019) would likely have a strong influence on the behavior of *T. carolina* and other forest-dwelling terrestrial turtles. We found two lines of evidence that fire influenced space use in *T. carolina*. First, home ranges were approximately twice as large at the unburned site (Lumber River) compared to the fire-maintained site (Weymouth Woods). However, our inter-population comparison (on its own) should be viewed with caution given we only studied two sites that differ in several factors other than fire regime, including topography, soils, hydrology and forest plant communities, each potentially influencing *T. carolina* home-range size and other behaviors. More convincing evidence of the influence of fire on *T. carolina* behavior was that individuals occupying parts of the fire-maintained site that were burned more frequently and extensively had smaller home ranges. We propose two potential mechanisms that could explain such variation. First, individuals in the most fire-prone areas may limit home ranges to small patches of fire refugia, including mesic hardwood forests, bottomlands and streams, all of which are habitat components limited in availability and strongly selected by *T. carolina* at the fire-maintained site (Roe *et al.*, 2018). Individuals that stray too far from these fire refuges suffer higher mortality from fire (Roe *et al.*, 2019). Alternatively (or in addition), fire disturbance increases ground temperature by opening the understory and increasing solar radiation (Roe *et al.*, 2017) and may thus increase the availability of favorable nearby thermal opportunities for nesting (Filtz & Mullin, 2006), an explanation supported by the observation that female home ranges were influenced more strongly by fire heterogeneity. Indeed, other species of turtles nest in recently burned areas, sometimes with benefits to nest success depending on fire frequency and return interval (Reid, Thiel & Peery, 2015; Dziadzio *et al.*, 2016). Changes in movements and home range in response to fire have been observed in more mobile mammals (Herzog *et al.*, 2014; Berry *et al.*, 2017), but this is the first documentation of home-range variation in response to fire disturbance in turtles (Yager *et al.*, 2007; Lovich *et al.*, 2011; Sanz-Aguilar *et al.*, 2011).

That individuals behaved consistently through time but differently from one another according to both intrinsic individual attributes (sex) and extrinsic environmental factors (site, season and fire) provides strong evidence of repeatable inter- and intra-population variation in space use and movement behaviors in *T. carolina*. Such intra-specific behavioral variation

suggests applying caution when extrapolating results from particular locations to other sites across the geographic range of a species for use in conservation and management. To be most effective, land management practitioners require information that allows prediction of biotic responses to controlled disturbances such as prescribed burning in forest ecosystems. Our study of *T. carolina* in fire-maintained Longleaf Pine forests identified a reduction in home range size associated with the most frequently and extensively burned areas, most likely through fire's impact on the spatial configuration and quality of critical resources, though the effects of fire appear to be sex-specific and proximal mechanisms for this response are not yet clear. Despite the fire-related impacts to space use, annual home-range size for most turtles was large enough to span multiple small burn management units, allowing individuals opportunities to move among a mosaic of habitats with different fire-return intervals to access resources, overwintering locations and fire shelter sites. We suggest small-scale management units with alternating burn cycles would be most compatible with *T. carolina* space use requirements, a recommendation that has been proposed for other species of turtles (Dziadzio *et al.*, 2016). Due to their low energy expenditures, *T. carolina* may be uniquely suited to survive periods of resource scarcity without depleting energy reserves (Penick *et al.*, 2002), making it possible to remain in small habitat patches when required and await the return of favorable conditions. However, the overall quality of fire-maintained areas for *T. carolina* may be reduced relative to unburned habitats owing to higher mortality rates (Roe *et al.*, 2019). We caution that these findings not be extrapolated too broadly to other systems, as turtle responses to fire may vary among species (Esque *et al.*, 2003; Yager *et al.*, 2007; Ashton, Engelhardt & Branciforte, 2008; Lovich *et al.*, 2011; Sanz-Aguilar *et al.*, 2011; Pawelek & Kimball, 2014) and depend on habitat type, fire regime and other aspects of the local environment within species (Platt *et al.*, 2010; Howey & Roosenburg, 2013). However, behavioral flexibility in *T. carolina* may allow for some capacity to respond to disturbance events (Dodd & Dreslik, 2008; Currylow *et al.*, 2012; Dodd, Hyslop & Oli, 2012), and assuming critical resources remain available in nearby habitats and mortality is minimal, long-lived turtles may be resilient to some forms of small-scale natural and anthropogenic forest disturbances. We also stress the importance of animal behavior studies that test hypotheses about ecological processes responsible for shaping and maintaining variability in space use and movements within and among populations.

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