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Responses of a forest-dwelling terrestrial turtle, *Terrapene Carolina*, to prescribed fire in a Longleaf Pine ecosystem

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Abstract

Prescribed fire is commonly used as a tool to meet a range of forest management goals. Owing to their limited movement abilities, terrestrial turtles are likely to be at high risk of injury and mortality, and to experience other fitness consequences with population-level implications from fire. Using radiotelemetry, we studied the responses of Eastern Box Turtles, *Terrapene carolina carolina*, to prescribed fire management in a sandhills Longleaf Pine forest system over a five-year period and compared our results to a nearby population in an unburned coastal plain location. Individual variation in turtle survival was strongly dependent on how frequently and extensively the areas were burned, with annual survival rates of 94.5% in unburned areas decreasing to 45.9 % in the most extensively burned areas. Turtles at the fire-maintained sandhills site had annual survival rates 4.9 % less than at the unburned coastal plain site, and females had annual survival rates 6.8 % less than males. Survival varied seasonally, with greatest mortality rates in winter and spring, especially among females. Growth rates and body condition did not differ between sites, nor did they vary according to fire extent and frequency at the fire-maintained site. Although mortality was greater and spatially variable at the fire-maintained site, annual survival rates across the site (86 – 90 % for females and males, respectively) were comparable to other stable populations of *T. carolina*. The lesser than expected mortality rate at the fire-maintained site was likely the result of turtles' strong selection of mesic hardwood forests near bottomlands and streams – habitats that may serve as refugia from fire. In areas where *T. carolina* conservation is a priority, land managers should integrate maintenance of fire refuge habitats into burn planning to minimize unintended negative impacts to this imperiled species.

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Keywords

controlled burn; disturbance; Eastern Box Turtle; forest management; growth; mortality; survivorship

1. Introduction

Intentionally setting fire for management purposes, or prescribed fire, has become a common method used by natural resource practitioners to reduce wildfire hazards, control invasive pests, maintain habitat condition, and for grazing, silviculture, game management, and biodiversity conservation goals (Haines et al. 2001, Pastro et al. 2011). One such fire-dependent system is the Longleaf Pine (*Pinus palustris*) savanna of the southeastern Coastal Plain and Sandhills ecoregions of the United States, which historically burned at a frequency of 1 – 3 and 4 – 6 years, respectively, from natural wildfires (Frost 1998). The Longleaf Pine ecosystem is imperiled due in part to overharvest, land clearing, fire suppression and other mismanagement, resulting in a 97% decline from its historic extent (Noss 1989, Frost 1993). Prescribed fire is an essential tool used increasingly to restore this and other pyrogenic systems on public and private lands (Van Lear et al. 2005).

The Longleaf Pine ecosystem includes many plants and animals that are uniquely adapted to periodic fire disturbance (Means 2006), including some that are rare and at risk of extinction (Van Lear et al. 2005). Terrestrial reptiles may be particularly sensitive to aspects of fire regime, such as fire exclusion and alteration to seasonality, frequency, extent, and intensity of fires. For instance, the open understory maintained by frequent surface fires can increase light penetration and temperature, offering opportunities for ectothermic vertebrates to maintain optimal body temperature (Greenburg and Waldrop 2008, Roe et al. 2017, Wild and Gienger 2018). Fire can also promote vegetative regrowth and foraging opportunities for herbivores (MacDonald and Mushinsky 1988) and increase foraging success of insectivorous reptiles (Griffiths and Christian 1996). In such cases, some species respond positively to fire (Brisson et al. 2003, Steen et al. 2013, Fouts et al. 2017) and may even be considered specialists of fire-maintained habitats (Driscoll and Henderson 2007). Alternatively, other species may respond negatively to the altered microclimate conditions, changes to vegetative structure and distribution of resources, and increased risks of mortality and injury (Mushinsky 1992, Webb and Shine 2008, Lyet et al. 2009). Fire will thus not impact all species and populations equally, with responses varying according to the fire's characteristics as well as species-specific behaviors, environmental tolerances, and other aspects of biology that evolved under particular fire regimes (Pausas and Parr 2018).

Terrestrial turtles provide a unique opportunity to examine ectothermic vertebrate responses to fire. As with most fauna, turtle responses to fire vary among species, with some capable of coping and even thriving with such disturbance (Ashton et al. 2008, Powelek and Kimbal 2014), and others experiencing high mortality, injury, and other deleterious effects (Esque et al. 2003, Sanz-Aguilar et al. 2010, Platt et al. 2010, Howey and Roosenberg 2013). However, turtle populations are particularly vulnerable to additional sources of mortality owing to their life history of slow growth, delayed maturity, and high natural mortality in the egg and

juvenile life stages (Congdon et al. 1993). Additionally, compared to more mobile terrestrial vertebrates, we expect turtles to be limited in their ability to escape approaching fire fronts owing to slow walking speeds (Zani and Kram 2008). They may also be less capable of dispersing to distant unburned areas outside of their often small home ranges (Slavenco et al. 2016). Given such constraints, terrestrial turtles are likely to be at high risk of injury and mortality from direct exposure to fire, as well as from indirect effects on the environment following fire.

The Eastern Box Turtle (*Terrapene carolina*) is a nominally terrestrial turtle found in temperate forests and early successional mosaics throughout the eastern United States (Dodd 2001, Keister and Willey 2015), including Longleaf Pine forests of the southeast region (Greenspan et al. 2015). However, relatively little is known of their ecology in fire-prone systems of any kind (but see Platt et al. 2010, Howey and Roosenburg 2013, Roe et al. 2017), with only limited information on survivorship, growth rates, body condition, and other vital rates with population-level consequences. Such information is needed to assess whether and how *T. carolina* responds to management practices involving fire. Here, we compare vital rates in two *T. carolina carolina* populations in protected reserves that differ in their historic and current use of fire. We also examine individual variation in responses to spatial and temporal heterogeneity of fire at the fire-maintained site. *Terrapene carolina* is a species of conservation concern that is in decline in many parts of its broad geographic range (Keister and Willey 2015), and it may serve valuable functional roles in areas where it is still common (Liu et al., 2004; Dodd 2006; Jones et al. 2007; Lovich et al. 2018). It is thus important to understand responses of *T. carolina* to fire and other forest management practices and apply this knowledge to inform conservation and management strategies.

2. Materials and Methods

2.1. Study sites

The study was conducted at two North Carolina State Parks. One site was Weymouth Woods Sandhills Nature Preserve (hereafter Weymouth Woods), an approximately 200-ha park in the sandhills ecoregion of south-central North Carolina. The habitat is a mosaic of mixed pine and hardwood forests, consisting of 35% Longleaf Pine, 19% mixed Longleaf and Loblolly Pine, 15% hardwood, and 31% pine and hardwood mixtures (J. Roe, unpubl. data). The majority (92%) of the site is xeric uplands, with a small stream network and associated bottomlands (8%, (J. Roe, unpubl. data). The elevation ranges from 102 – 154 m. Prescribed fire has been used in forest management since 1974, with 76% of the area managed using low-intensity, small-scale controlled burns (Fig. 1).

Weymouth Woods is divided into 29 burn units ranging in size from 0.9 – 23.9 ha (Fig. 2). From 2000 – 2017, approximately 22% of the area under fire management was burned each year, with an historic mean burn frequency of 5 – 6 years for each unit. Fires occurred between January and September (Weymouth Woods Sandhills Nature Preserve, unpubl. data).

The other site, 24 km south, was the Lumber River State Park at Chalk Banks (hereafter Lumber River), an approximately 225-ha reserve in the Coastal Plain ecoregion adjacent to

the Lumber River. The habitat of Lumber River includes bottomland forest (35%) adjacent to the river and several small tributaries and swamps, along with upland forests (65%, J. Roe, unpubl. data). Forest types include hardwood (33%), mixed Longleaf and Loblolly Pines (21%), hardwood and pine mixtures (45%), and open habitats (1%, J. Roe, unpubl. data). The elevation ranges from 65 – 70 m. 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. Further descriptions of each study site can be found in (Roe et al. 2017).

2.2. Field data collection

To capture variation resulting from environmental heterogeneity in habitats, we intentionally captured individuals spread out from 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 radio-transmitters (RI-2B, 10 – 15 g, Holohil Systems Ltd., Carp, ON, Canada) using 5 minute epoxy gel (Devcon, Solon, OH). From April 2012 – March 2017, we tracked 65 individual turtles (18 males and 18 females from Weymouth Woods, 15 males and 14 females from Lumber River) for periods of 1 – 60 months. Transmitter weight did not exceed 4.5% of turtle body mass in any case.

We located telemetered turtles using a receiver (R-1000, Communication Specialists, Orange, CA) and Yagi antenna. We located individuals at least once per week during the active season (May – September), every two weeks around the times of winter ingress (October – November) and spring egress (March – April), and once per month for the remainder of the overwintering period (December – February). At each location, we determined the coordinate position using GPS (7 m accuracy) and plotted turtle locations on maps using ArcMap 10.1. We also assessed whether the turtle was alive or dead at each encounter. If a turtle was confirmed dead after an extended period where it could not be visually observed, we presumed it had been dead since the last confirmed visual observation or movement. For dead turtles, we noted confirmed or likely causes of mortality based upon evidence at the scene and condition of the individual preceding death. Detached transmitters, including those with extensive damage, were not considered evidence of mortality unless the turtle body was also recovered. We periodically captured each individual and measured CL to the nearest 0.1 mm using vernier calipers and mass to the nearest gram using a Pesola spring scale. We captured and measured turtles in the fall (prior to winter ingress) and spring (soon after winter egress). Transmitters were replaced in the field as needed.

2.3. Data analysis

We performed statistical analyses with SPSS 23.0 and the program MARK 8.2 (White and Burnham 1999). Where appropriate, we examined assumptions of homogeneity of variances and normality; when data failed to meet assumptions, they were transformed to approximate normal distributions and equal variances. Statistical significance was accepted at the α 0.05.

2.3.1. Survival—Maximum likelihood survival probabilities were estimated and compared using known fate models in the program MARK. Akaike Information Criterion

corrected for small sample sizes (AICc) was used to rank candidate models; if models had AICc values of < 2.0, they were considered as having some support. Time intervals were set as quarterly (Winter: Jan – Mar, Spring: Apr – Jun, Summer: July – Sep, Fall: Oct – Dec). Our first approach was to explore how survival varied among individuals at each site, depending on both intrinsic (sex, body size) and extrinsic (season) environmental variables relevant to both sites. We started with fully-saturated models where survival probability depended on season, sex, season × sex, and initial body size (CL) as a covariate. Next, using only the variables identified as important in the site-specific models, we examined models where survival probability was also dependent on site and interactions among relevant variables. Finally, at Weymouth Woods, we tested an additional model including a covariate reflecting the extent to which each turtle used fire-managed areas and the frequency of fires in such areas. A 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 the fire frequency is the mean number of times the units that the turtle visited was burned during the study period.

2.3.2. Growth and body condition—We calculated growth rates by dividing change in CL between initial and final captures by the total number of days elapsed, only including days within the approximately six-month active season each year (15 Apr – 15 Oct; 184 days). Growth rates (mm/yr) were then calculated by dividing the number of total days elapsed by 184. We then examined variation in growth rates using analysis of covariance (ANCOVA), with site, sex, and site × sex interaction as the independent variables, CL growth rate as the dependent variable, and initial log₁₀-transformed CL as the covariate.

Body condition indices (BCI) were compared between sites and sexes using the method described by Beaupre and Douglas (2009). BCI was estimated as the deviation (i.e., residuals) in observed mass from that predicted by the regression relationship between body mass and CL of all turtles, using mean mass and CL values for each individual over the study period. Both body mass and CL were log₁₀-transformed prior to analysis. We first examined whether BCI varied seasonally using repeated measures analysis of variance (ANOVA), with spring and fall BCI residuals as the within-subject factors, and site and sex and interacting variables. We then used ANOVA to test for overall BCI differences (spring and fall combined) between sex, site, and sex × site interactions. Lastly, we assessed whether growth rates and BCI were dependent on fire risk index for individuals at Weymouth Woods using linear regressions.

3. Results

3.1. Turtle body sizes

Male turtles from Weymouth Woods had mean (± standard deviation) initial carapace length (CL) of 131.7 ± 7.9 mm (range: 121.3 – 149.6 mm) and mass of 401 ± 66 g (range: 305 – 575 g), while Weymouth Woods females had initial CL of 128.4 ± 9.4 mm (range: 109.3 – 140.0 mm) and mass of 435 ± 86 g (range: 260 – 615 g). Male turtles from Lumber River

had initial CL of 138.7 ± 10.0 mm (range: 124.1 – 151.7 mm) and mass of 435 ± 78 g (range: 330 – 577 g), while Lumber River females has initial CL of 131.6 ± 7.8 mm (range: 122.1 – 149.1 mm) and mass of 462 ± 64 g (range: 385 – 615 g).

3.2. Survival

Thirteen telemetered turtles died over the five-year period, including nine from Weymouth Woods (3 males, 6 females) and four from Lumber River (1 male, 3 females). Sources of mortality at Weymouth Woods included direct burning from fire ($n = 2$), vehicle collision ($n = 1$), and disease ($n = 4$), with the cause of death unknown for the remaining individuals ($n = 2$). At Lumber River, sources of mortality included disease ($n = 1$), probable depredation ($n = 1$), and unknown causes ($n = 2$). Diseased individuals exhibited combinations of symptoms including swelling of the eyes, aural abscesses, discharge from the eyes, nose, or mouth, labored breathing, and lethargy. For the depredated individual, we observed extensive and fresh injuries to the body and teeth marks on the shell and transmitter, likely from a mammal predator.

Models for the Lumber River population indicated that season and sex were the primary factors influencing survival probability (season: $AICc = 0.00$, Weight = 0.26; sex: $AICc = 1.47$, Weight = 0.12). Models for Weymouth Woods identified sex as the only factor influencing survival probability (sex: $AICc = 0.17$, Weight = 0.23). Models without initial body size (CL) as a covariate received more support (mean difference of 7%) than models with the same main factors that included the CL covariate in all cases. Body size was thus not included in further models of survival probability.

In the analysis including individuals from both sites, survival models with sex, season, sex $\times$ season, and site all received some support, as did the model with constant survival ($AICc < 1.27$ in all cases, Table 1). The model with sex-specific variation in survival (holding all other variables constant) suggested that males have 6.8% greater survival than females over the seasonal time intervals. However, differences between sexes were also dependent on season, with male survival greater than females in winter and spring, but equivalent to females in summer and fall (Fig. 3). The model including only survival variation between sites indicates that turtles in the Lumber River population have 4.9% greater survival than Weymouth Woods over the seasonal time intervals. Model-averaged estimates for extrapolated annual survival probabilities for all site and sex group combinations ranged from 0.858 – 0.913 (Table 2).

At the fire-maintained site (Weymouth Woods), the most supported model was for survival probability varying according to the fire risk index as an individual covariate, holding all other variables constant (Table 3). Models including the fire risk index received more support than all other models with the same main factors of sex, season, and sex $\times$ season interaction (Table 3). Holding all other variables constant, survival probability decreased with increasing fire risk index (Fig. 4), with seasonal survival probability ranging from 0.986 (0.945 annual survival) for the lowest fire index to 0.823 (0.459 annual survival) for the greatest fire index.

3.3. Growth and body condition

Growth rates ranged from -2.0 to 5.6 mm/year, but did not differ between sexes, sites, or body sizes over the size range of our sample (site: $F_{1,43} = 0.51$, $p = 0.480$; sex: $F_{1,43} = 0.35$, $p = 0.556$; site $\times$ sex: $F_{1,43} = 0.76$, $p = 0.390$; CL: $F_{1,43} = 2.42$, $p = 0.127$; Fig. 5). One individual from Weymouth Woods was excluded from growth analysis owing to a shell injury that precluded consistent and accurate carapace measurements.

Body mass could be predicted by CL according to the equation: $\log_{10} \text{ mass} = 1.6788 \times \log_{10} \text{ CL} - 0.9229$ ($F_{1,63} = 73.37$, $p < 0.001$, $r^2 = 0.54$; Fig. 6). Body condition did not differ between spring and fall seasons for any site and sex group combination (season: $F_{1,49} = 2.44$, $p = 0.125$; season $\times$ site: $F_{1,49} = 1.91$, $p = 0.173$; season $\times$ sex: $F_{1,49} = 0.01$, $p = 0.935$; season $\times$ site $\times$ sex: $F_{1,49} = 0.116$, $p = 0.735$). Overall BCI was greater for females than males, but did not differ between sites (sex: $F_{1,61} = 47.02$, $p < 0.001$; site: $F_{1,61} = 0.01$, $p = 0.913$; sex $\times$ site $F_{1,61} = 0.34$, $p = 0.564$; Fig. 6). At the fire-maintained site (Weymouth Woods), neither growth rate nor BCI were dependent on the fire risk index (growth rate: $p = 0.244$, $r^2 = 0.05$; BCI: $p = 0.379$, $r^2 = 0.02$).

4. Discussion

Fire is an essential tool that can assist natural resource practitioners in meeting diverse management goals. Along with its utility, however, fire can expose non-target species to unintended negative consequences. *Terrapene carolina* is a terrestrial, forest-dwelling turtle that is vulnerable to the impacts of fire, including mortality or injury from burns (Babbitt and Babbitt 1951, Ernst et al. 1995, Platt et al. 2010, Howey and Roosenburg 2013). However, previous studies of *T. carolina* responses to fire are limited in number and unrepresentative of the variety of environments where they are found throughout their extensive range. Our study is the first to assess *T. carolina* responses to fire in the sandhills Longleaf Pine ecosystem, and together with Roe et al. (2017), it is also the most rigorous study of *T. carolina* behavior and vital rates in any natural fire-maintained system. The most important findings relevant to turtle interactions with fire were that 1) survivorship varied according to interactions among several intrinsic and extrinsic environmental variables, including sex, season, and fire, 2) survivorship varied spatially according to heterogeneity in the extent and frequency of fire, 3) overall population mortality rates from fire appeared to be low at our site, and 4) other important vital rates such as growth and body condition were unaffected by fire. These findings provide useful information that can help land managers project risks and responses of *T. carolina* and other terrestrial turtles to forest management practices, and to inform modifications to burn plans that minimize conflict with other management goals if necessary.

Our study design involved two complimentary approaches, including comparison of populations at fire-maintained and nearby unburned sites, coupled with a detailed examination of individual variation to fire spatial and temporal heterogeneity at a single site. Inter-population comparisons are informative in that estimated values for vital rates at the fire-maintained site can be generally interpreted against a benchmark where fire is not used in management, and the close proximity of sites coupled with their simultaneity of study using identical methods makes these comparisons more robust. However, such comparisons

are limited in samples size and complicated by differences in the underlying environments between sites in addition to the use of prescribed fire. In our case, the fire-maintained site (Weymouth Woods) occurs in the sandhills ecoregion with extensive xeric uplands and Longleaf Pine forests, whereas the unburned site (Lumber River) is in the Atlantic coastal plain ecoregion with extensive bottomlands and predominantly mixed hardwood and pine forests. On the other hand, a detailed examination of variation in individual responses at the fire-maintained site allowed us to isolate how one environmental factor (prescribed fire) affects vital rates over smaller spatial scales, although comparisons to other populations or species are more difficult to interpret and inferences are more limited.

Compared to other studies of turtle responses to fire, estimates of annual survival from the fire-maintained site (86 – 90 % for females and males, respectively) are high, with only 4.9 % greater annual mortality compared to the unburned site. In contrast, Hermann's Tortoise (*Testudo hermani*) populations had annual survival as low as 63 % in response to controlled burns, corresponding to an approximately 37 % increase in mortality, although the effect of fire varied considerably depending on life stage, season, and habitat (Hailey 2000). Likewise, Spur-thighed Tortoises (*Testudo graeca*) experienced additional mortality from wild fire between 12 – 100 % depending on life stage, with the greatest rates in juveniles (Sanz-Aguilar et al. 2010). We are aware of only one other published account of *T. carolina* mortality rates from fire, where Platt et al. (2010) estimated between 10 – 22 % of the population was killed by prescribed fires. In the study by Platt et al. (2010), mortality rates were determined by visual surveys of turtle carcasses in recently burned areas, and the numbers of dead individuals were compared to population abundance and density estimates. As the authors point out, such an approach is prone to inaccuracy if population estimates are imprecise, and it does not account for injured animals that may have dispersed from the search area before death. Our approach of following a large number of individuals via radio-telemetry allowed for a more detailed examination of animal fates that can be extrapolated to more accurate population mortality rates, assuming the sample is a representative subset of the site's adult population. Moreover, our estimates not only include mortality from direct interactions with fire ($n = 2$ in our study), but also indirect or delayed responses resulting from injury, the stress and dangers of forced displacement from typical activity areas, or as individuals contend with changes to the structure and microclimate of environments that could impact habitat quality. For instance, fire temporarily reduces or removes understory vegetation, leaf litter, and other surface debris (Iverson and Hutchinson 2002, Greenberg and Waldrop 2008, Hossack et al. 2009), all of which serve as important microsites for *T. carolina* (Rossell et al. 2006, Roe et al. 2017) and other terrestrial turtles (Lagarde et al. 2012, Attum et al. 2013). Fire may also affect the availability of preferred food items for *T. carolina* such as mushrooms, litter and soil invertebrates, and fruits (Dodd 2001). Even when accounting for delayed and indirect effects, our estimates of annual mortality are still well below those reported in other studies of turtle-fire interactions.

Interpreting survivorship and other measures characteristic of the typical individual in a population can be informative, but it is also useful to examine sources of individual variation within the population. In doing so, we identified considerable heterogeneity in survivorship according to the spatial extent and frequency of fire (i.e., fire risk index). As expected, turtles using areas with more extensive and frequent fires experienced greater mortality.

Individuals in the most fire-prone areas experienced up to 48.6 % extra annual mortality, a value more consistent with other studies of turtle-fire interactions (Hailey 2000, Platt et al. 2010, Sanz-Aguilar 2010). Areas of the site with the greatest mortality, injury, and numbers of turtle-fire interactions were in the predominantly xeric upland Longleaf Pine forests that have been prioritized (both recently and historically) for prescribed fire management (Fig. 2). The mortality risks associated with use of the fire-prone Longleaf Pine uplands is consistent with the general avoidance behavior of this habitat type in *T. carolina* (Greenspan et al. 2014, J. Roe unpubl. data), suggesting that fire disturbance may factor into habitat selection decisions.

Even though fire was an important factor in survival, other sources of mortality contributed to significant variation in survival probability, including demographics and season. Sex was the largest contributor to individual variation in survival probability, with females experiencing nearly 7 % greater mortality than males. Such differences may in part stem from the costs of reproduction. For instance, female turtles are often at greater risk of road mortality during nesting migrations that may require long-distance travel outside of typical activity centers, though asymmetry in risk between sexes is more apparent for aquatic than terrestrial turtles (Gibbs and Steen 2005, Steen et al. 2006). Consistent with this explanation, the only road mortality we observed was for a female moving to a nest site. Another proximate cause of mortality was disease, with all mortality in females and most occurring on a seasonal basis, peaking during winter and soon after spring emergence. Symptoms were consistent with an upper respiratory tract disease-like syndrome caused by mycoplasma, ranavirus, or herpesvirus infections (De Voe et al. 2004, Feldman et al. 2006), all of which have been detected in *T. carolina*; however, we did not confirm pathogen identification by laboratory assays. Disease epidemics have become more common in wild and captive *T. carolina* populations (Johnson et al. 2008, Allender et al. 2011), but details of disease epidemiology, including differences in susceptibility between sexes, remain largely unknown. The stresses of overwintering and spring emergence periods may compromise the ability of turtles to combat infection, including their ability to behaviorally thermoregulate (do Amaral et al. 2002). Nevertheless, our survival estimates for males and females in both populations were within the range reported for *T. carolina* elsewhere (Currylow et al. 2011, Keister and Willey 2015), but to our knowledge, this is the first statistically-supported documentation of either seasonal or sex-specific variation in survival in *T. c. carolina*. Our large sample sizes followed over an extended period, along with the known-fates approach to modelling survival probability using data from radio-telemetry, allowed us to generate among the most accurate and reliable estimates of *T. carolina* survivorship of any study to date with which to uniquely examine such variation.

Despite the considerable variation in survival, we identified only minimal variation in growth and body condition among groups. That females had greater body condition indices (BCI) than males is likely due in part to some females being gravid, but the lack of seasonal variation in BCI raises some doubt about this explanation. Some BCI variation could also be the result of sexually dimorphic shell morphology (Budischak et al. 2006). If such differences are an artefact of morphology, we caution against examining variation in BCI without first accounting for sex-specific variation. The observation that growth rates and body condition were similar between fire-maintained and unburned sites (for both sexes),

together with the independence of these measures relative to the fire risk index, suggests that fire had little measurable influence on long-term energy and water relations for surviving turtles. This finding is in contrast to Howey and Roosenburg (2013), who found that *T. carolina* in recently burned areas were in poorer condition (i.e., lesser body mass for equivalent carapace length) than in nearby unburned areas. Howey and Roosenburg (2013) hypothesized that the warmer temperatures, increased solar radiation, and frequent injuries to the epidermal scutes (20% of captured individuals) in the burned areas may have contributed to increased rates of evaporative water loss. In contrast, only one of the 36 telemetered turtles (2.8%) experienced and survived similar burn injuries in our study. It is noteworthy that the only turtle that survived burn injuries retreated to a mesic bottomland adjacent to a permanent stream where we found it frequently soaking in shallow water. However, its transmitter became detached two months later as more epidermal scutes were lost and we were thus unable to confirm whether it ultimately survived these injuries. In other studies of turtle responses to fire, Desert Tortoises (*Gopherus agassizii*) were also able to maintain body condition and reproductive output in the years following fire (Lovich et al. 2011), and *T. graeca* fecundity did not differ between burned and unburned areas (Sanz-Aguilar et al. 2010). We caution that we did not measure all aspects of resource investment, as reptiles allocate assimilated energy to the competing compartments of maintenance, growth, reproduction, and storage (Congdon et al. 1982). While our estimates of growth are robust, our BCI is only an indirect measure of energy storage that is also sensitive to variation in body water. We did not measure maintenance metabolic costs or reproductive output at either site, both of which are important metrics for understanding how surviving individuals respond to fire and other disturbances (Dodd and Dreslik 2008, Gienger and Urdiales 2017).

We were not involved in the planning or implementation of the burn management plan, nor did we give fire managers any specific information on the location of telemetered turtles prior to or during burns. Instead, our goals were to objectively assess how turtles responded to ongoing fire practices to inform managers of the effects to non-target biota. We determined that fire is just one of many challenges with which *T. carolina* must contend in any given environment, and researchers that assess survivorship or other vital rates must examine cumulative effects when attempting to project population-level implications and inform management strategies. Population models for turtles indicate a high-sensitivity to even slight increases in chronic adult mortality (Heppel 1998), with as little as 2 – 3 % additional annual mortality likely to result in population declines, assuming no density-dependent compensation or immigration (Brooks 1991, Congdon et al. 1993, 1994, Dodd et al. 2016). The 4.9 % greater mortality rate at the fire-maintained site is above this threshold, which is at first concerning for population declines. However, overall annual survivorship at the fire-maintained site (86 – 90 % for females and males, respectively) was similar to stable *T. carolina* populations elsewhere (87 – 89 % for females and males, respectively, Dodd et al. 2006), and concurrent population estimates from capture-mark-recapture data at the fire-maintained site indicate a stable population as well (J. Roe, unpubl. data). We hypothesize that selection of mesic habitats provides *T. carolina* some refuge from fire at our site. The mosaic of fire-exclusion zones and small-sized burn units may also give turtles opportunities to escape approaching fire fronts by entering wet areas or moving into neighboring unburned

habitats, both of which could also minimize fire-related mortality (Platt et al. 2010). *Terrapene carolina* populations elsewhere have demonstrated some resilience in response to disturbance events (Dodd and Dreslik 2008, Currylow et al. 2012, Dodd et al. 2012). As long as suitable resources remain available in nearby habitats and mortality is not high, long-lived turtles may be able to withstand some forms of natural and anthropogenic disturbance.

We caution that management targets for burn extent and frequency were not met in most years of our study (Fig. 7), and a return to a more frequent burn schedule that reflects both historic management and natural fire regime would likely increase fire-related mortality. An additional limitation is that only subadult and adult turtles were included in our study, yet juvenile turtles have been identified as especially vulnerable to fire (Hailey 2000, Sanz-Aguilar 2010). The juvenile life stage is notoriously difficult to study in *T. carolina* and other turtles due to their small size and differences in habitat use and activity from larger individuals (Jennings 2007), yet examination of this life stage in response to fire is critical. Future studies could also take a more controlled approach where researchers and burn managers collaborate to test various burn plans to answer specific questions about fire seasonality, fire strategies (e.g., head fire vs. backing fire), fire frequency, and other modifications that could influence risks and responses of both target and non-target biota. Nonetheless, this study together with Roe et al. (2017) provides a detailed example of turtle responses to fire that could serve as a model for examining animal responses to fire elsewhere.

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Highlights

- Box turtle survival decreased with increasing fire extent and frequency in longleaf pine forests
- Disease resulted in more deaths in box turtles than direct interactions with fire
- Fire did not affect turtle growth rates or body condition
- Mortality peaked in winter and spring in both fire-maintained and unburned forests
- Females had higher mortality rates than males in both fire-maintained and unburned forests

Figure 1.
Prescribed fire in an upland Longleaf Pine forest at Weymouth Woods Sandhills Nature Preserve, North Carolina.

Figure 2.

Map of turtle locations, burn units, and the frequency of burning during the period of study (2012 – 2017) at Weymouth Woods Sandhills Nature Preserve, North Carolina. Fire-excluded units have not been burned since the park initiated prescribed fire management in 1975, while fire-managed units were burned between 0 – 3 times during the study period. Larger points indicate locations of observed turtle-fire interactions.

Figure 3. Seasonal and sex-specific variation in survival of Eastern Box Turtles, *Terrapene carolina* in south-central North Carolina. Values are mean $\pm$ 1 SE.

Figure 4. Variation in survival across a gradient of fire extent and frequency (fire index) for Eastern Box Turtles, *Terrapene carolina*, at a site that uses prescribed fire in forest management. The black line is mean seasonal (i.e., quarterly) survival probability with upper and lower 95% confidence intervals as gray lines. See methods for a description of the fire index.

Figure 5. Annual growth rates for subadult and adult Eastern Box Turtles, *Terrapene carolina*, from fire-managed (Weymouth Woods) and unburned (Lumber River) sites.

Figure 6.

Relationships between body mass and carapace length for subadult and adult Eastern Box Turtles, *Terrapene carolina*, from fire-managed (Weymouth Woods) and unburned (Lumber River) sites.

Figure 7.

History of use of prescribed fire at Weymouth Woods Sandhills Nature Preserve. The dashed line indicates the targeted amount of area to be burned each year if a five-year fire rotation is to be maintained for all burn units.

Table 1.

Model comparisons of survival probability (S) for Eastern Box Turtles, *Terrapene carolina*, depending on season^a, sex, and site in fire-managed and unburned forests of south-central North Carolina.

Model	AICc	AICc	Weight	n	Deviance
$S(\text{sex})$	128.5	0.00	0.241	2	124.5
$S(\text{season})$	128.9	0.41	0.196	4	120.9
$S(\cdot)$	129.2	0.69	0.171	1	127.2
$S(\text{season} \times \text{sex})$	129.6	1.05	0.143	8	113.3
$S(\text{site})$	129.8	1.27	0.128	2	125.8
$S(\text{site} \times \text{sex})$	130.9	2.38	0.074	4	122.8
$S(\text{season} \times \text{site})$	131.9	3.40	0.044	8	115.7
$S(\text{season} \times \text{site} \times \text{sex})$	138.1	9.59	0.002	16	105.2

^a winter (Jan – Mar), spring (Apr – Jun), summer (Jul – Sep), fall (Oct – Dec)

Table 2.

Site- and sex-specific annual survival probability estimates for Eastern Box Turtles, *Terrapene carolina*, in fire-managed (Weymouth Woods) and unburned (Lumber River) forests of south-central North Carolina.

Site	Sex	Annual survival ($\pm$ SE) ^a
Weymouth Woods	Female	0.858 (0.809 – 0.910)
	Male	0.903 (0.864 – 0.944)
Lumber River	Female	0.871 (0.824 – 0.920)
	Male	0.913 (0.875 – 0.953)

^aValues are model averages using known-fate models in the program MARK.

Table 3.

Model comparisons of survival probability (S) for Eastern Box Turtles, *Terrapene carolina*, depending on sex, season, and use of areas managed with prescribed fire (fire index^a) in forest management.

Model	AICc	AICc	Weight	n	Deviance
$S(\cdot)$ fire index	83.4	0.00	0.302	2	79.4
$S(\text{sex})$ fire index	84.0	0.58	0.226	3	77.9
$S(\cdot)$	85.2	1.82	0.122	1	83.2
$S(\text{sex})$	85.4	1.99	0.111	2	81.4
$S(\text{season})$ fire index	86.0	2.52	0.086	5	75.8
$S(\text{season} \times \text{sex})$ fire index	86.0	2.57	0.084	9	67.5
$S(\text{season} \times \text{sex})$	87.6	4.14	0.038	8	71.1
$S(\text{season})$	87.9	4.50	0.032	4	79.8

^a fire index was used as an individual covariate, reflecting the extent of use of areas burned and the frequency of burning during the study period