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RESEARCH ARTICLE

Fire Ecology of the
Florida Box Turtle
(Terrapene carolina
bauri Taylor) in
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Forests of the Lower
Florida Keys

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ABSTRACT: Eastern box turtles (Terrapene carolina) inhabit many fire-prone habitats in eastern North America and frequently succumb to natural and anthropogenic fires. However, little is known about the fire ecology of box turtles, and population-level effects of burning have yet to be quantified. We studied the effect of prescribed burns on a population of Florida box turtles (T. carolina bauri) inhabiting National Key Deer Wildlife Refuge, Big Pine Key, Florida. A total of 27.4 ha were burned during seven prescribed fires (1998 to 2000). We found 14 fire-killed box turtles after four wet season burns (1.04 turtles/ha); no mortality was observed following three dry season burns. Multiple regression analysis indicated that season of burning had a significant effect on the occurrence of box turtle mortality. The effect of char height (used as a surrogate measure of fire intensity in our model) was only marginally significant. Our results suggested that between 10.2% and 21.6% of box turtles per ha perished during wet season fires. Fires appeared to affect male and female turtles equally. No juvenile mortality was observed, perhaps due to their apparent rarity in the study population. If fire mortality is a concern to land managers, we recommend restricting prescribed burns to periods of the year when box turtles are dormant (dry season in south Florida; late fall, winter, and early spring in temperate regions of North America). If prescribed burns must be conducted when turtles are active, survival might be enhanced by using slower moving, less intense backfires, and burning small areas. More frequent burning might reduce fuel loads and thus fire intensity, reducing the likelihood of turtle mortality.

Index terms: box turtle, disturbance, fire intensity, fire mortality, land management, prescribed burning, *Terrapene carolina bauri*

INTRODUCTION

Disturbance is widely recognized as an important agent influencing the population dynamics of plants and animals (Sousa 1984; Pickett and White 1985). Fire is the most ubiquitous terrestrial disturbance after anthropogenic urban and agricultural activities, and studying the effects of fire on the biota of fire-prone ecosystems is an important topic in ecology and natural resource management (Sousa 1984; Pickett and White 1985; Whelan 1996; Russell et al. 1999). Moreover, restoring historical fire regimes in these ecosystems is desirable from the standpoint of conservation because many pyrogenic habitats have been significantly altered by decades of fire suppression or long-term changes in the seasonal timing of burning (Leach and Givnish 1996; Liu and Menges 2005). In some cases however, it is difficult to identify the historical fire regime (Snyder et al. 1990). Under such circumstances it is important to study the demographic response of native species to experimental fire regimes, as it is reasonable to expect a favorable response to the fire regime under which these taxa evolved (Menges and Kohfeldt 1995; Liu and Menges 2005). An experimental approach can, therefore, provide useful information on which to base land management decisions (Liu and Menges 2005).

The eastern box turtle, Terrapene caro-

lina L., has an extensive distribution in the United States, ranging from southern Maine south to the Florida Keys, and west to Michigan, eastern Kansas, Oklahoma, and Texas (Ernst et al. 1994). In many areas of its geographic range, eastern box turtles occur in habitats that are prone to natural and anthropogenic wildfires or are subject to prescribed burning for land management purposes (Russell et al. 1999). Eastern box turtles have limited locomotor abilities and live among combustible leaf litter and woody debris, making them particularly vulnerable to fires (Dodd 2001). Consequently, reports of fire-related injuries and mortality are common in the literature (Babbitt and Babbitt 1951; Carr 1952: Rose 1986: Ernst et al. 1995: Dodd et al. 1997; Russell et al. 1999; Dodd 2001; Frese 2003). However, these reports consist largely of anecdotal observations that are difficult to interpret without associated estimates of population size and density (Russell et al. 1999). Indeed, the effect of fire on any eastern box turtle population has yet to be quantitatively assessed (Dodd 2001). Moreover, nothing is known about the seasonal effects of burning on fire mortality among box turtles. Dodd (2001) speculated that conducting prescribed burns during periods when box turtles were inactive might reduce fire mortality, but noted the lack of empirical data to test this hypothesis. Because long-term studies suggest that many box turtle populations are declining (Stickel 1978; Williams and

Parker 1987; Schwartz and Schwartz 1991; Hall et al. 1999), understanding the various causes of mortality among populations has been accorded high priority (Maret et al. 2004).

The Florida box turtle, Terrapene carolina bauri Taylor, one of six extant subspecies of T. carolina in North America (Dodd 2001), is especially abundant in pine habitats of southern Florida (Carr 1952), where historically fires were a frequent form of disturbance (Taylor 1980; Snyder 1991; Carlson et al. 1993). The fire regime that existed in pine habitats of south Florida prior to Euro-American settlement is problematic and the seasonal timing of burning remains unclear (Robertson 1955; Alexander 1967; Snyder et al. 1990). Lightning was probably the primary ignition source before European settlement and lightningcaused fires generally occurred during the wet season (Snyder 1991; Liu and Menges 2005). However, Native Americans inhabited the region for thousands of years (Carr and Beriault 1984), and may have burned extensively during the dry season (Snyder 1991; Spier and Snyder 1998). Studies of endemic pine rockland vegetation suggest a fire regime of lightning-caused early wet season burns and non-lightning fires during the dry season (Spier and Snyder 1998; Liu and Menges 2005).

Here, we compare fire mortality of Florida box turtles resulting from prescribed burns conducted during the wet and dry seasons in pine rockland forests on Big Pine Key, Florida. We relate our observations of fire mortality to a published estimate of population density (Verdon and Donnelly 2005), suggest management practices that might reduce fire mortality among Florida box turtles, and make inferences regarding the historic fire regimes in the lower Florida Keys.

Study Area

Our study was conducted on National Key Deer Wildlife Refuge (NKDWR; 24°42'N, 81°22'W), Big Pine Key, Monroe County, Florida. NKDWR (3110 ha) was established for the protection of the Florida Key deer, *Odocoileus virginianus clavium* Barbour and Allen, a federally endangered subspecies of white-tailed deer endemic to the lower Florida Keys. The refuge is characterized by extensive pine rockland forest with smaller areas of hardwood hammock and coastal mangrove forest. Pine rockland forest is a globally endangered ecosystem occurring on limestone outcrops in extreme southern Florida (Snyder et al. 1990). This ecosystem is dominated by a relatively open canopy of slash pine (Pinus elliottii Engelm.) with a diverse and often dense understory of shrubs, vines, herbs, and several species of palms (Snyder et al. 1990). The climate of the region is subtropical with a pronounced wet (May to October) and dry (November to April) season. Wet and dry season rainfall averages 743 and 265 mm, respectively, while the mean dry season temperature (22 °C) is considerably less than that of the wet season (29 °C) (Verdon and Donnelly 2005).

Pine rockland forest is a fire-dependent ecosystem; long periods (several decades) of fire exclusion reduce herb diversity and allow succession to proceed towards hardwood hammock vegetation (Robertson 1955; Alexander 1967; Snyder et al. 1990). Pine rockland forest on NKDWR consists of a mosaic of open and shrubby pinelands, probably resulting from the past occurrence of fires (Liu and Menges 2005). Open pinelands have a relatively sparse shrub layer and a well-developed herb layer, due to fairly frequent burning (Liu and Menges 2005). In contrast, shrubby pinelands have a dense shrub layer and poorly developed herb layer that results from less frequent burning (Liu and Menges 2005).

Field Sampling and Data Analysis

Our study of fire mortality among Florida box turtles took advantage of the experimental design of a larger investigation into the development of ecological criteria for prescribed burning in pine rockland forests on Big Pine Key (Liu et al. 2005a,b; Snyder et al. 2005). As part of that investigation, a block was established in each type of pineland (open and shrubby) on NKDWR during each of two years (1998 and 1999) for a total of four blocks (Dogwood, Iris, Orchid, and Poisonwood). The time elapsed since these blocks last burned ranged from

8 to 30 years (Table 1). Each of the four blocks was divided into three treatment units of 2 to 10 ha each: wet season burn, dry season burn, and unburned control. Wet season and dry season prescribed fires were replicated within and between years; however, for logistical reasons the dry season burn in Dogwood could not be conducted and the winter burn in Iris was delayed. The location and a detailed description of each block are provided elsewhere (Snyder et al. 2005). Prescribed fires occurred within 1 to 3 days of a significant rainfall event, during periods of little or no wind, and consisted of backfires and flanking fires with recorded flame lengths ranging from 0.3 to 4.5 m (Snyder et al. 2005). The maximum height of charred bark on the trunk of each canopy tree was measured in the seven treatment units following prescribed burns and used as a surrogate measure of fire intensity (Menges and Deyrup 2001; Snyder et al. 2005) in our analysis (see below).

We intensively searched seven burned areas for turtles during and immediately after prescribed fires, and conducted additional searches for dead turtles and shells during numerous post-burn visits to sample vegetation in the burned areas. Concurrent to this study, we searched control units and other unburned areas of NKDWR (1999-2000) for box turtles as part of a larger investigation into seed dispersal and wet season food habits (Liu et al. 2004; Platt et al. 2009). The straightline carapace (CL) of each living and dead turtle was measured with calipers (± 0.1 cm). We followed Dodd et al. (1994) and considered turtles with a CL > 11.0 cm as adults. Sex was determined based on plastral morphology; males exhibit a deep concavity that is absent in females (Dodd 2001). Living turtles were permanently marked by notching a unique series of marginal scutes (Cagle 1939) and released at the capture site within 24 to 48 hours. Dead turtles were dissected and stomach contents removed as part of a concurrent study on seed dispersal (Liu et al. 2004) and wet season diet (Platt et al. 2009). If salvageable, dead turtles were deposited in the Campbell Museum, Clemson University, Clemson, South Carolina (CUSC 1750-51, 1783, 1785-86).

Table 1. Treatment unit, area burned, date of burning, mean char height, month and year of most recent previous burn, years since last burn, and the number of fire-killed Florida box turtles (*Terrapene carolina bauri*) recovered from wet and dry season burn units on National Key Deer Wildlife Refuge, Big Pine Key, Florida. Treatment units classified as open (OP) or shrubby (SH) pineland. Previous burns categorized as prescribed fire (Rx) or wildfire (WF). Fire history data are from Liu (2003).

	Area			Month/year of previous	Years since	Dead
Treatment unit	burned (ha)	Date burned	Char height (m)	burn (Rx or WF)	last burn	box turtles
Wet season burn uni	ts					
Orchid (OP)	5.3	16-Aug-98	2.50	September 1990 (Rx)	8	3
Poisonwood (SH)	3.6	17-Aug-98	2.80	July 1986 (WF)	12	1
Dogwood (SH)	1.8	22-Jun-99	2.62	1969 (?)	30	2
Iris (OP)	2.5	18-Jul-99	2.07	September 1991 (Rx)	8	8
Total	13.4					14
Dry season burn unit	s					
Orchid (OP)	2	15-Dec-98	1.70	September 1990 (Rx)	8	0
Poisonwood (SH)	2	15-Dec-98	1.09	July 1986 (WF)	12	0
Iris (OP)	10	12-Dec-00	1.29	September 1985 (WF)	15	0
Total	14					0

We used a backward stepwise multiple regression model (SPSS 13.0, Chicago, Illinois) to determine if pineland type (open vs. shrubby), average char height on canopy trees, and fire season (wet season vs. dry season) had a significant effect on the occurrence of fire mortality among Florida box turtles. We did not include time elapsed since the most recent previous burn as an independent variable in our model because this variable is partially reflected in pineland type. The latter is a more comprehensive independent variable that results from both the time elapsed since the most recent previous burn and fire frequency over the last several decades. We square root transformed ($\sqrt{\text{count}} + 1$ $\sqrt{\text{count}+1}$ the dependent variable (number of dead turtles on each burn unit) to meet the assumptions of parametric analysis (Littell et al. 2002).

RESULTS

A total of 27.4 ha were burned during four wet season and three dry season prescribed fires on NKDWR (Table 1). We found 14 fire-killed Florida box turtles (five males, nine females) after wet season burns on 13.4 ha (1.04 turtles/ha), but no mortality was observed following the dry season fires (Table 1). We expended approximately

78 person-hours searching for turtles in burned areas. The final model generated by backward stepwise multiple regression included both fire season and mean char height as explanatory variables (adjusted $r^2 = 0.73$, $F_{2.4} = 9.45$, P = 0.03). Among these explanatory variables, coefficient of fire season was statistically significant (t = 3.7, P = 0.02), while mean char height was only marginally so (t = -2.4, P = 0.07). The number of fire-killed turtles found on each wet season treatment unit ranged from one to eight (Table 1). Eleven fire-killed turtles were recovered on the same day as the prescribed burn, and two and one were recovered two and five days, respectively, post-burn. All fire-killed turtles were adults (mean CL = 14.2 cm; SE = 0.2; range = 13.0to 15.4 cm). During wet season fires, we observed four box turtles moving across fuel breaks to escape approaching flames and three others sheltering in small wetlands within the treatment unit as it was being burned. We found 217 adult and a single juvenile box turtle during approximately 68 person-hours of searching control units and other unburned habitat on NKDWR (Liu et al. 2004; Platt et al. 2009; S. Platt and H. Liu, unpubl. data).

DISCUSSION

There is little doubt that dead box turtles we recovered following prescribed burns were killed by fire. Turtle carcasses were intact, fresh, and heavily charred, strongly suggesting that burning was the cause of death. Moreover, with the exception of several weathered shells, dead box turtles were not found during an intensive search of unburned habitat on NKDWR (Platt et al. 2009; S. Platt and H. Liu, unpubl. data). Fire-killed box turtles were generally quite obvious during our immediate post-burn searches because fires removed ground vegetation, leaf litter, and clumps of dead palm fronds where turtles often shelter. Owing to the time spent intensively searching each plot immediately after burning, coupled with our later visits to sample vegetation, we believe that few if any fire-killed turtles escaped detection. Although not subjected to fire, the shells of several species of turtles remained intact for over two years under similar environmental conditions in north-central Florida (Dodd 1995). Therefore, it is likely that any fire-killed turtle we initially overlooked would have been found during our many subsequent visits to the burn units.

Our results indicate a strong seasonal ef-

fect on fire mortality among Florida box turtles; mortality only resulted from wet season fires, and dry season fires seemingly posed minimal risk to turtles. This is likely due to the seasonal activity patterns of Florida box turtles, which are most active from late April through October, but dormant and rarely found above-ground during other times of the year (Verdon and Donnelly 2005). Almost nothing is known concerning the dry season refugia used by Florida box turtles on NKDWR; but in central Florida, Dodd (2001) found dormant box turtles buried beneath leaf litter and in depressions created by decaying palm stumps. In addition to affording protection from fires, dry season retreats provide cool, moist microsites that prevent box turtles from desiccating during prolonged periods of drought (Dodd et al. 1994; Dodd 2001). Burn characteristics probably also influence turtle mortality on NKDWR; dry season burns are less intense than wet season burns, and consume less of the surface litter layer (Liu et al. 2005b; Snyder et al. 2005) where turtles are buried (Verdon and Donnelly 2005).

The estimated density of Florida box turtles on NKDWR ranges from 4.8 to 10.1 turtles/ha (Verdon and Donnelly 2005). A comparison of these densities with our estimate of fire mortality (1.04) turtles/ha) suggests that between 10.2% and 21.6% of Florida box turtles per ha perished during wet season burns. To our knowledge, this is the only population-level estimate of fire mortality available for T. carolina. However, our estimate of fire mortality must be interpreted with caution because of the large variance associated with the population estimate of Verdon and Donnelly (2005). Owing to the small number of recaptures and the sensitivity of their model to this parameter, Verdon and Donnelly (2005) concluded the actual population size of box turtles on NKDWR may be somewhat larger than estimated. In that case, our estimate of population-level fire mortality would be correspondingly lower.

Given the current lack of demographic models (Seigel 2004), it cannot be determined how these estimated levels of mortality influence the long-term viability of

Florida box turtle populations on NKDWR. Owing to a suite of life history characteristics such as delayed sexual maturity, high adult survivorship, long reproductive lifespan, and low fecundity, the viability of most turtle populations is sensitive to even small increases in mortality among older juveniles and adults (Congdon et al. 1993). Furthermore, fire losses are additive to other causes of adult mortality (e.g., roadkill, predation) and the apparently low annual recruitment of smaller size classes into this population (Verdon and Donnelly 2005). For example, our anecdotal observations suggest that the annual roadkill of adult Florida box turtles on Big Pine Key constitutes a chronic, additive, and probably significant source of mortality. Obviously, developing viability models for Florida box turtle populations is an urgent and necessary prerequisite for evaluating prescribed burning strategies on NKDWR and elsewhere. Finally, it is important to note that the prescribed burns we studied on NKDWR were limited in scale; larger burns might result in a greater proportion of the population succumbing to fire if the distance to a fuel break exceeds the locomotor abilities of turtles. Likewise, low intensity fires often produce a mosaic of burned and unburned patches, and the latter could serve as easily accessible refugia for box turtles during prescribed burns.

Previous studies of the incidence of firescarring among box turtle populations (Ernst et al. 1995; Dodd et al. 1997) suggest that fires do not randomly affect adults with respect to sex. Dodd et al. (1997) found fire-scarred males were larger (and probably older) than fire-scarred females, and speculated males have an increased likelihood of being burned during their longer lifespan. Female box turtles were more likely to exhibit fire-scarring than males, although the sex ratio of burned turtles did not significantly differ from the population sex ratio (Dodd et al. 1997). In contrast, Ernst et al. (1995) found no significant differences in the size of burned males and females; however, this study was based on museum specimens and may not be representative of wild populations (Dodd et al. 1997; Dodd 2001). The sex ratio of our sample of fire-killed turtles (1 male: 1.80 females) was similar to the moderately female-biased sex ratio (1 male: 1.74 females) reported for Florida box turtles on NKDWR (Verdon and Donnelly 2005), suggesting that fires affected male and female turtles equally.

Ernst et al. (1995) stated that hatchling and juvenile box turtles are more likely than adults to perish due to their habit of hiding among leaf litter, but we found no fire-killed juveniles on NKDWR. While it is possible that smaller turtles were overlooked during post-burn searching, we attribute this finding to the apparent rarity of juveniles in our study population. Verdon and Donnelly (2005) reported only six juveniles (7.5%) in a sample of 80 Florida box turtles marked on NKDWR, and there was only one juvenile among the 217 turtles (0.004%) we found on the refuge (S. Platt and H. Liu, unpubl. data).

Fire avoidance behaviors among eastern box turtles are poorly documented. Carr (1952) stated that box turtles "appear to have no notion of how to escape an advancing blaze". Others suggest that box turtles passively escape fires by burrowing into shallow forms, leaving the carapace partially exposed above-ground (Babbitt and Babbitt 1951; Frese 2003), a behavior that might explain the prevalence of fire damage on neural and costal bones (Ernst et al. 1995). Florida box turtles occasionally inhabit gopher tortoise (Gopherus polyphemus) burrows (Jackson and Milstrey 1989; Dodd 2001), but it is unclear if these subterranean retreats are used to escape fires. Our observations of box turtles moving across fuel breaks and sheltering in small wetlands appear to be the only examples of active fire avoidance behaviors yet reported. These observations are not unexpected; because fire mortality is a potentially strong selective force, animals associated with pyrogenic vegetation will almost certainly evolve a suite of adaptive fire avoidance behaviors (Means and Campbell 1981; Russell et al. 1999).

Based on studies of endemic pine rockland plants, Liu and Menges (2005) suggested that the biota of the lower Florida Keys evolved under a regime of early wet season burns caused by lightning strikes coupled with non-lightning caused dry

season fires. Both pineland clustervine (Jacquemontia curtisii Peter ex Hallier f.) and pineland partridge pea (Chaemacrista keyensis Pennell) exhibited a positive demographic response to dry season, but not wet season burning that was attributed to their dormancy during the dry season (Spier and Snyder 1998; Liu and Menges 2005). Furthermore, Chaemacrista keyensis exhibited a more favorable response to early wet season fires (prior to July) when compared to mid- or late-wet season fires (Liu and Menges 2005). In contrast, annual box turtle activity peaks early in the wet season (Verdon and Donnelly 2005) and, although only one of our burns occurred prior to July, fires during this period are expected to result in high levels of fire mortality. Clearly, research on additional taxa inhabiting these fire-prone ecosystems is needed to further elucidate the historic fire regime of the lower Florida Keys.

MANAGEMENT IMPLICATIONS

The results of our study lend support to an earlier recommendation for reducing fire mortality by conducting prescribed burns during periods when box turtles are inactive (Dodd 2001). Throughout most of their range in temperate North America, eastern box turtles are active only during the warmer months, generally from mid-March to early November (Neill 1948; Schwartz and Schwartz 1974; Dodd 2001). In Florida, ambient temperature is less important in determining seasonal activity patterns, which instead coincide with the annual cycle of wet and dry seasons (Dodd 2001; Verdon and Donnelly 2005). During inactive periods, eastern box turtles occupy a variety of retreats that are partially or wholly underground (Dodd 2001) and provide protection from fires. Therefore, if fire mortality of box turtles is a concern to land managers in south Florida, we recommend conducting prescribed burns during the dry season; elsewhere in eastern North America burning in the late fall, winter, and early spring would probably result in little mortality. Dry season prescribed burning is also consistent with management objectives on NKDWR that favor endemic understory herbs and forage production for Key deer (Taylor 1980; Carlson et al.

1993; Liu and Menges 2005; Liu et al. 2005a,b). Whereas the mixed fire regime of dry season and early wet season burns recommended by Liu and Menges (2005) will maintain populations of endangered endemic plants, the effects on box turtle populations are less clear and considerable mortality could result.

If burning is to be conducted during the active season, box turtle survival might be enhanced through careful fire management. For instance, our behavioral observations of box turtles during prescribed burns suggest that slower moving, less intense backfires are preferable to faster moving, more intense head fires because backfires give turtles time to move away from advancing flames and are more likely to leave unburned patches that could serve as refuges for fleeing turtles. Fast moving head fires may overtake and kill box turtles before they are able to reach safety. Furthermore, because prescribed burns reduce fuel loads and thus fire intensity (Wright and Bailey 1982; Wade and Lewis 1987), more frequent burning might reduce fire mortality among turtles. Prescribed burning can also affect wildlife abundance by altering the availability of preferred food plants (Leopold 1933; Perkins 1968; Russell et al. 1999). However, box turtles on NKDWR consume a diversity of plants (Platt et al. 2009) that respond differently to burning (Snyder et al. 2005), making generalizations regarding fire management practices difficult.

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Hong Liu was educated in China before attending Clemson University in 1994 for her first post graduate degree in Botany. She then attended Florida International University and studied the fire ecology of rare and endangered plants in the Florida Keys as her dissertation project. She is currently an Assistant Professor in the Department of Earth and Environment at Florida International University. Her current research includes conservation of endangered plants in China as well as weed risk assessment of horticultural plants in Florida.

Christopher Borg received his MS degree from the University of New Mexico in 1997 and soon after took on a job as a coordinator of a multi-year fire and vegetation research project in the Florida Keys. He is currently a land conservation biologist at the Tall Timbers Research Station and Land Conservancy.

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