RESPONSES OF TIMBER RATTLESNAKES TO FIRE: LESSONS FROM TWO PRESCRIBED BURNS

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Abstract.—Timber rattlesnakes (*Crotalus horridus*) are excellent model organisms for understanding the effects of large scale habitat manipulations because of their low-energy lifestyle, rapid response to changes in resource environment, uniform diet (small mammals), and simple behaviors. We present two case studies that illustrate interactions between timber rattlesnakes and fire in a single large population. Case 1 describes the decimation and subsequent 11 year recovery of a timber rattlesnake subpopulation associated with a fire during a particularly vulnerable time of year. In Case 2, four control plots, three cut (thinned) plots, three burned plots, and three plots that were both cut and burned were studied. Our primary goals were to monitor responses of the food chain to the above four treatments and to assess timber rattlesnake responses as potential indicators for the relative success of manipulations. Although plant communities did not initially differ among treatment plots, manipulated sites experienced increases in early-successional annual vegetation after thinning and burning. Biannual live-trapping sessions indicated an increase in abundance of principal prey species after manipulations, although this increase was not uniform among treatments. Timber rattlesnakes that utilized manipulated sites exhibited enhanced growth and body condition relative to snakes that foraged solely in control areas. Snake physiological responses were more rapid and well-defined than measurable small mammal population responses suggesting that these top predators may potentially serve a role as indicator species for restoration ecology. Our case studies illustrate both direct and indirect effects, as well as dramatically divergent outcomes resulting from minor changes in the timing of fire application.

BACKGROUND

Although the practices of thinning and fire application have become important tools for forest habitat management, relatively little is known about the responses of large-bodied ground-dwelling reptiles to large-scale habitat manipulations (however see Reinert and others 2011b). Most studies of the effect of fire on reptiles in eastern oak-dominated ecosystems have found little to no effect on diversity, species composition, and abundance (Ford and others 1999, Greenberg and Waldrop 2008, Renken 2006). Frequently, in some treatments (typically thinned and burned plots) some reptiles show increases in abundance (Kilpatrick and others 2004, Matthews and others 2010), suggesting beneficial effects of fire. The few studies that have examined seasonal burn timing (Keyser and others 2004, Renken 2006) suggest that reptile communities may be resilient to both dormant and growing season burns (for a counter-example, see Griffiths and Christian 1996).

Most of the afore-mentioned studies use similar methods. Specifically, reptile populations are sampled using one or more methods, including drift fences with funnel traps or pitfall traps. Both funnel and pitfall traps are subject to sampling biases since not all reptiles can be equally caught using these methods (Crosswhite and others 1999, Enge 2001, Greenberg and others 1994, Jenkins and others 2003). In eastern oak-dominated ecosystems, pitfall traps tend to capture small mobile species such as fence lizards (*Sceloporus undulatus*), members of the five-lined skink group (*Plestiodon* spp.), ground skinks (*Scincella lateralis*), Anoles (*Anolis carolinensis*), small snakes such as garter snakes (*Thamnophis* spp.), and fossorial species such as worm snakes (*Carphophis* sp.) and ring-necked snakes (*Diadophis* spp.). Indeed, members of this short list tend to be the primary species upon which assessments of the effects of fire are made (but see Steen and others 2010). Funnel or box traps seem more effective at sampling larger snakes (Burgdorf and others 2005, Crosswhite and others 1999, Enge 2001, Greenberg and others 1994, Jenkins and others 2003, Sutton and others 2010). We note that many larger reptiles (e.g., box turtles, larger snakes) or those that are less mobile (e.g., ambush foragers such as the timber rattlesnake; Beaupre and Montgomery 2007) typically occur in low density and are relatively poorly sampled by funnel traps and pitfalls, and thus, their responses to fire may be under-represented in the literature. Whereas we acknowledge the importance of a variety of trapping methods for quantifying community dynamics, significant information regarding response to environmental perturbation can be obtained through radio telemetry in appropriate target species (Beaupre 2008, Durbian 2006, Reinert and others 2011b).

Long-lived vertebrates with slow life-histories (e.g., long life spans, low growth rates, late age at maturity, infrequent reproduction with small litter size) such as the timber rattlesnake (*Crotalus horridus*) that forage by ambush in the leaf litter (Brown 1993), may be especially susceptible to fire, depending on their evolutionary interaction with fire. Timber rattlesnakes are of special conservation concern throughout much of their geographic range as documented by their legally protected status throughout the northeast (Brown 1993). Thus, knowledge of their response to logging and fire may be of great value to habitat managers. It has been suggested that the behavior and physiology of top predators may be effective monitoring tools for assessing the outcomes of habitat manipulations (Beaupre 2002, Beaupre and Douglas 2009, DeAngelis and others 1991, Dunham and others 1989). With training, rattlesnakes may be easy to find (depending on species and locality), easy to measure and manipulate, and may provide a time- and cost-effective monitoring approach. Herein, we describe and discuss two case studies of the response of timber rattlesnakes to the application of fire in a habitat management context. Both cases illustrate potential benefits and costs associated with application of fire.

STUDY SITES

We conducted studies on the McIlroy Madison County Wildlife Management Area (MMCWMA) in Madison County, northwest Arkansas. The MMCWMA is a public holding with a primary function as a public hunting ground. The MMCWMA and adjacent lands including Bear Hollow Natural Area (BNHA) and Ozark Natural Science Center (ONSC) comprise over 6,000 ha managed for multiple uses. Topography can be rugged with permanent and intermittent streams, steep rock walls along ridgelines, periodically maintained food plots, and artificial ponds for game management. We have been continuously engaged in studies of the ecology and physiology of timber rattlesnakes at these sites since the fall of 1995 (e.g., Beaupre 2002, 2005, 2008; Beaupre and Montgomery 2007; Beaupre and Zaidan 2001; Browning and others 2005; Wills and Beaupre 2000).

In general, forests at the MMCWMA are typical of disturbed Ozark hardwood forests and could be described as closed-canopy, dense, even-aged stands of mixed hardwoods and pine resulting from long-term fire suppression (Spetich 2004). Aggressive tree harvesting in the late 19th century followed by roughly 100 years of fire suppression (Guyette and others 2006, Smith and others 2004, Stambaugh and Guyette 2006) dramatically altered species dynamics, causing an increase in recruitment of shade tolerant species (Burns and Honkala 1990) while oaks and hickories, which once dominated these forests, had low establishment rates (Spetich 2004). The system became an even-aged, closed-canopy forest with relatively little herbaceous understory growth (Spetich 2004). Canopy closure and decreased herbaceous growth has reduced ground-level productivity resulting in mast-crop (primarily acorns) dependence of wildlife (Fralish 2004, Spetich 2004).

The timber rattlesnake is a low-energy adapted ambush forager that feeds on small mammals, primarily including squirrels, chipmunks, and deer mice (Clark 2002, Montgomery 2005, Reinert and others 2011a, Wittenberg 2009). Previous studies have suggested that annual variation in acorn mast crop affects small mammal densities, which in turn rapidly affect feeding rates, growth dynamics, and body condition of timber rattlesnakes (Beaupre 2008). The population dynamics of timber rattlesnakes at MMCWMA can be described as “boom and bust” with periods of extended starvation punctuated by bursts of growth and reproduction associated with resource availability (Beaupre 2008). Their simple and narrow diets leave little ambiguity regarding the structure of their food chain. Studies of timber rattlesnakes have been facilitated by highly developed radio telemetry techniques (Reinert 1992). Their relatively small home ranges (as compared with predatory mammals or birds) and their tolerance to close approach by humans allows them to be repeatedly tracked on foot and relocated with high precision (Beaupre 2008, Reinert 1992). The extreme sensitivity and rapid physiological responses of timber rattlesnakes to variation in the food resource environment coupled with ease of measurement and estimation of body condition potentially make them excellent bioindicators for assessing changes in small mammal populations as a result of habitat management practices that affect ground level seed production. Similarly, timber rattlesnake populations are highly sensitive to the effects of short-term mortality events (Brown 1993, Sealy 2002) and disturbances that undermine their food chain (Beaupre 2008).

CASE 1: DECIMATION AND RECOVERY AT SITE K

Background

Site K is a timber rattlesnake den complex (defined as an association of several independent hibernacula located on the same rocky outcrop) centrally located in our study area. The complex consists of at least five unique cracks that are occupied by one or more hibernating snakes distributed north to south along a 450 m west-facing ridgeline. Timber rattlesnakes typically emerge from hibernation in early April and rapidly disperse from the immediate hibernation area to take shelter under transitional rocks, logs, or leaf litter. In the weeks that follow emergence the snakes usually remain concealed, using cover to insulate them from temperature extremes while physiologically acclimatizing to warmer temperatures outside the den crevice. Prior to emergence, while in the den, snakes are likely insulated from damage due to surface fires. During a posthibernation fire, however, snakes are directly exposed to heat, oxygen deprivation, and desiccation, as they are physically located in the flammable substrate.

Since the inception of our studies in 1995, sections of the MMCWMA have been periodically burned either as part of a formal management plan, accidentally, or as a result of arson. Fire management plans at MMCWMA have historically been directed at fuel reduction, but more recently have been designed for wildlife habitat improvement (see Case 2). In spring of 1999 (between April 6 and April 15), a management-related fire swept through Site K involving all known hibernacula and transitional habitats associated with snakes that used the site. The fire encompassed approximately 10 ha and was of sufficient intensity to completely consume ground cover (leaf litter) and structure (logs) in the immediate vicinity of Site K. The fire occurred after emergence and during the period when snakes had taken refuge in transitional habitat, but before snakes had moved to summer foraging ranges.

Methods

Site K has been visually surveyed during spring emergence (March 20-April 20, depending on weather) in every year since spring 1996. Although some variation in search effort among years is unavoidable, the site has been consistently surveyed (two to four visits per year during peak emergence) by the primary author. All captured snakes were transported to the laboratory at the University of Arkansas where they were individually marked (by PIT tag), sexed (by caudal probe), weighed (±0.01 g), and measured (snout-vent length [SVL], head length [HL], head width [HW], and tail length [TL]) in a squeeze box (Beaupre 2008, Quinn and Jones 1974). After processing, all snakes were released at their point of capture.

Results and Discussion

In 4 years of spring sampling (1996-1999) prior to the fire, 20 individual timber rattlesnakes were captured from Site K, processed, and released. The fire occurred between April 6 and April 15, 1999, immediately postemergence when most snakes had entered vulnerable transition sites. Two snakes had been captured at the site in 1999 on April 6 and were safe in the laboratory when the fire struck. These two snakes were released on Site K after the fire, but no additional snakes were captured in 1999 at the site after the fire. In the years immediately following the fire, no snakes were found in spring surveys (Fig. 1). Snakes were not captured again until 2002 (n=2) with relative abundance increasing in 2005-2011 (Fig. 1). In the 12 years since the fire, 16 individual timber rattlesnakes have been captured at the site. The fire had a pronounced effect on the body size distribution of snakes that resided at the site (Fig. 2). Prior to the fire, the SVL distribution was relatively evenly distributed with some snakes present in all size classes, including several very large adult males and a large number of reproductively mature females near 75 cm SVL (Fig. 2). Furthermore, active reproduction was known to be ongoing, as we observed pregnant females there in 1998. In the years after the fire, there was an apparent complete loss of snakes in the two largest size classes and a shift of the most frequent size class from 75 cm to the bin centered on 55 cm SVL (Fig. 2). This size class is typical of snakes roughly 3 to 5 years old that have not yet reached the age and size of first reproduction. Because timber rattlesnakes exhibit high den site fidelity (Agugliaro 2011, Browning and others 2005) and highly repeatable home ranges (Beaupre, per obs.), we interpret this result as a near total loss of snakes at the site due to the effects of fire. The site was then slowly repopulated by dispersing young (Cobb and others 2005) over the 12 postfire years from adjacent unaffected sites.

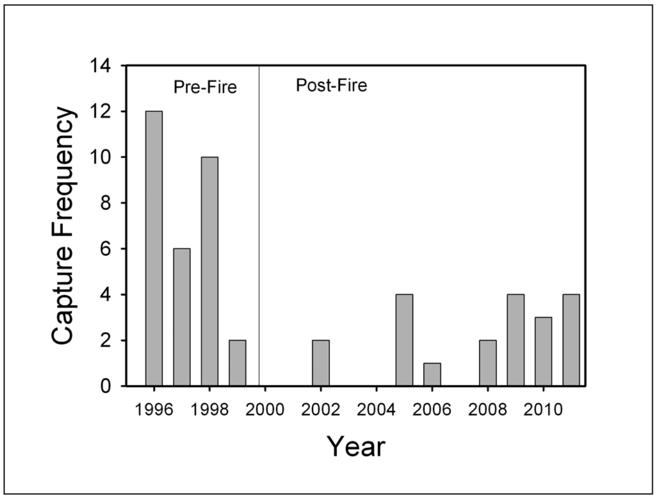

Figure 1.—Timber rattlesnake capture frequencies at Site K before (pre-spring 1999) and after (post-spring 1999) a destructive fire swept through the den area in the days just after spring emergence. Note: the two snakes captured in 1999 were captured prior to the fire.

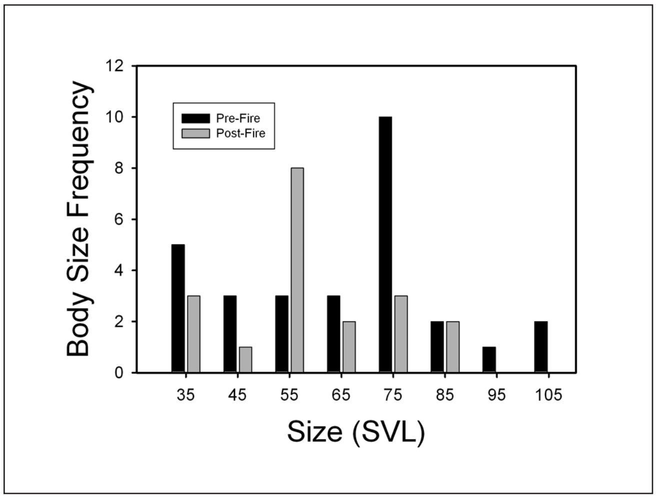

Figure 2.—Site K timber rattlesnake body size (snout-vent length: SVL in cm) distribution before fire (black bars) and after fire (gray bars). Each bin represents a 10 cm range centered on the tick label value.

Capture records before and after burns and from adjacent sites have revealed that 2 of the 16 snakes captured in later years (one male, one female) were present at Site K prior to the fire. We interpret these individuals to be persistent survivors of the fire. No other individuals present prefire at Site K were captured there or elsewhere in the study site after the fire. Notably, one of the two recaptured individuals (the male) was safely in the lab during the fire. A third individual of the 16 was a known migrant, captured and marked as a neonate on September 12, 1999 at an adjacent site (ca. 1150 m distant) and next appeared on Site K on April 9, 2005 as a small (79.6 cm SVL, 336.94 g) adult male. The remaining 13 snakes were marked as new captures on Site K. One of these new individuals was large enough to be considered an adult, the remaining 12 were sub-adults, all having SVL of less than 60 cm. These young snakes were unlikely to have been present at the site prior to 2009 and were probably either born at Site K or migrated from one of roughly 40 nearby areas (Browning and others 2005) in the years following the fire. Radio telemetry observations on neonate timber rattlesnakes in Tennessee support the contention that at least some neonates disperse to nonmaternal hibernacula (Cobb and others 2005). The persistent postfire paucity of adult (SVL = 65 cm) reproductive females suggests that most if not all of these young snakes have dispersed to Site K from adjacent den areas.

The preceding data led us to the following interpretation. A healthy population of rattlesnakes hibernating at Site K was decimated (only 2 of 20 known snakes survived) by a fire that struck after spring emergence when the snakes were particularly vulnerable. In the 12 years postfire, the site has been repopulated mostly by juvenile migrants from adjacent areas of higher timber rattlesnake density. We note that the site continues to recover and predict that in the coming years as sub-adults mature, reproduction will resume and a more typical size distribution will be reestablished. However, due to the long intervals between reproductive events and late female age at maturity in this species (Brown 1993), full recovery may take many more years. With respect to timber rattlesnakes, the severity of this fire was due primarily to the posthibernation timing of its application. It is also fortunate that the size of the fire was small, leaving surrounding hibernacula relatively undisturbed to serve as source populations for juvenile migrants.

CASE 2: CAN FIRE ENHANCE TIMBER RATTLESNAKE HABITAT?

Background

In 2004, we were approached by the Arkansas Game and Fish Commission (AGFC) and were informed that sections of our study site would be selectively thinned of timber and/or burned in an effort to enhance habitat quality for wildlife. Subsequent planning led to establishment of a detailed experimental design (described below). The AGFC sought to enhance habitat for game species, of which white-tailed deer (*Odocoileus virginianus*) and turkey (*Meleagris gallopavo*) were of primary interest. Thinning and burning were applied with the ultimate goal of opening habitat to approximate the historically present oak savanna or shortleaf pine forest system (Dey and others 2004, Guyette and others 2006).

Like white-tailed deer and turkey, small mammal populations (e.g., squirrels, chipmunks, and other rodents) are also dependent on acorn mast crop. These small mammals comprise over 90 percent of the diet of timber rattlesnakes. We hypothesized that small mammals would respond to increases in ground level food production much as deer and turkey would, and that rattlesnakes would in turn respond to increasing prey availability. Because of the ease of capture and measurement of timber rattlesnakes, we also hypothesized that they might be effective organisms to monitor changes in food productivity at the ground level. Thus, we measured changes in vegetation structure associated with forest manipulations, changes in small mammal populations, and changes in growth and body condition (both indicative of changes in resource availability) of timber rattlesnakes. Herein, we review the major findings of our study. A more detailed account can be found in Douglas (2010), and forthcoming publications.

Methods

In 2005, areas on ridge tops intended for timber harvest were identified by AGFC managers, and trees slated for removal were marked. Six plots ranging in size from 4 to 26 ha were chosen for timber harvest. Low-impact logging occurred during the summer of 2007 and was accomplished by two to three individuals on foot with chainsaws. Logs were skidded to existing forest roads and removed without major habitat disruption. Fire was applied on March 12, 2008, prior to rattlesnake spring emergence. The net result of these management activities was 13 experimental plots, including 3 plots that were only harvested (cut-only), 3 plots that were both harvested and burned (cut-burn), 3 plots that were burned but not harvested (burn only), and 4 plots (control) that were not manipulated. Our experimental design approximated a BACI (before, after, control impact) design (Williams and others 2001). However, manipulated plots were located on ridge tops only and were chosen based on accessibility and suitability for harvest and the ability to control application of fire. Thus, plots were not chosen at random, a normal assumption of BACI design, weakening inferences about the effects of manipulations by potential interactions related to the geographic proximity of certain site types (Bennett and Adams 2004). All experimental and control plots were located within known home ranges of several timber rattlesnakes, and plots were sized and located such that several snakes could occupy a plot simultaneously, but all snakes could easily avoid all manipulated plots.

Vegetation

We monitored plant diversity and community composition at all sites beginning in summer 2005 and continued throughout the study (Douglas 2010). Circular quadrat surveys (Cox 1980, Lindsey and others 1958, Patterson and James 2009) were employed at three spatial scales (1 m^2, 15 m^2, and 0.04 ha) three times per year to examine herbaceous plants, understory saplings and shrubs, and mature trees. Species were identified on site using field guides (Hunter 2004, Little 1980). Problematic identifications were confirmed with the help of ONSC field staff, Professor Doug James at the University of Arkansas, or University of Arkansas Herbarium staff. Data were analyzed by a variety of techniques, including MANOVA and principal components analysis.

Small Mammals

Small mammals at all 13 plots were sampled biannually (spring, late summer) from 2005 to 2009 using Sherman live traps (3” x 3.5” x 10” LFAHD Folding Trap and 3310A Non Folding Trap, H.B. Sherman Traps, Tallahassee, FL), with populations assumed to be open between trapping periods. Each trapping session lasted five nights (after five nights of prebaiting), a brief period through which the population was treated as closed. Fifty traps were set per site per night, with 4 of the 13 sites sampled per night. Trapped animals were marked with a unique ear tag (Self Piercing Fish Tag, National Band and Tag Company, Newport, KY) and released, and marks were used to identify recaptured individuals. Trap data were analyzed by Lincoln-Peterson estimator and by trap success rates which can be adjusted for trap disturbance and, in this case, provided qualitatively similar results to more formal population density estimators (Douglas 2010).

Rattlesnake Physiological Responses

Snakes were captured between 2006 and 2009 during routine den and gestation site surveys and incidentally during random walks through study areas. We surgically implanted radio transmitters (Holohil SI-2T, Holohil Systems, Ltd., Carp, Ontario) in the coelomic cavity of adult snakes (minimum 300 g) under anesthetic (Beaupre 2008, Reinert and Cundall 1982, Wills and Beaupre 2000). Depending on year, 20 to 30 snakes were tracked approximately three times weekly using portable receivers (Wildlife Materials TRX 1000s, Murphysboro, IL or Communication Specialists Inc. R1000 receiver, Orange, CA) and hand-held antennae (Yagi three-element directional antenna). Snake locations were recorded using a Garmin GPS III Plus (Olathe, KS). At least twice per active season, snakes were captured and brought to the lab for morphometric measurements (SVL, HL, HW, TL, and body mass) as described above (Case

1). All measurements were made by the first author to minimize observer bias. Morphometric measurements were used to estimate growth rates in SVL (cm/year) and body condition (residuals from a nonlinear mass-length regression; a measure of fatness relative to length) (Beaupre and Douglas 2009). Snakes that spent more than a week of the active season foraging in manipulated areas were classified as manipulated (man). Snakes that spent their entire active season away from manipulated areas were classified as controls (con). Thus, statistical comparisons (repeated measures analysis of variance) were possible among treatments both before and after the habitat manipulations (Douglas 2010).

Results and Discussion

Major shifts in vegetation occurred from 2005 to 2009 in association with both experimental manipulations and natural events that affected canopy density and dynamics. The most significant component of habitat change was associated with increases in sun grasses, early annuals, early perennials, shade perennials, sassafras, blackberry, and sedges. Most of these groups are associated with invasions of forest openings and are seed-producing. In addition to planned forest treatments, all sites including control sites were also affected by natural events between 2005 and 2009. In 2005, all sites clustered closely to the grand mean of pre-manipulation sites, suggesting that sites were quite similar prior to manipulations. However, each plot type exhibited a different response to manipulation with burn and cut-burn sites exhibiting increases in seed-producing sun-tolerant species, and control and cut sites exhibiting increases in tree recruitment (Douglas 2010). Application of logging and fire caused significant shifts in vegetation communities observed at our 13 sites. Paradoxically, control sites exhibited large shifts in vegetation, although in a slightly different multivariate direction than burned sites. We attribute this shift in control sites to a severe ice storm in February of 2009 that caused a significant canopy opening event, subsequently changing incident sunlight on the ground and affecting vegetation assemblages. Thus, control sites responded in a similar multivariate direction as thinned (cut-only) sites, but to a lesser degree. Burn-only and cut-burn sites shifted significantly toward greater density of ground level seed producing annuals and perennials. All manipulated sites showed increases in ground level seed producing plants, thus cutting and burning did achieve, to some measure, intended management objectives at the MMCWMA.

Small mammal trapping data were collected for a total of 25,750 trap-nights, adjusted to 21,596 when disturbance by larger mammals (e.g., raccoons, skunks, opossums) was accounted for. During this time, there were 1016 total captures of 463 individuals. Capture rates varied from 0 to 45 captures per 100 trap-nights, with a mean of 5.58 captures per 100 trap-nights. Eight potential snake prey species were captured, although the vast majority of all mammals captured (92.7 percent) were either deer mice (*Peromyscus maniculatus*) or white-footed mice (*Peromyscus leucopus*). After adjusting for high trap disturbance rates and using different approaches to cope with departures from normality in trapping data, we are confident that there were significant changes in small mammal capture success over time and that the responses were dependent on treatment (Douglas 2010). Our data suggest that small mammal trapping success increased in cut, cut-burn, and control sites, while staying relatively unchanged at burn-only sites. The degree of increase in trapping success was greatest at cut-burn sites. Together with vegetation data, these results are consistent with the hypothesis that manipulations improved food availability in manipulated plots, and a numerical response of small mammals resulted. Enigmatically, burn-only sites exhibited some shift in vegetation but did not result in increased small mammal abundance. One possible explanation is that continued presence of closed canopy and reduction of ground level complexity did not favor small mammals. Also, snakes foraged in burn-only sites, and the lack of structural complexity compared to cut and cut-burn sites may have enhanced their prey capture success by reducing obstructions to sensory reception and strike mechanics. There is also evidence (Douglas 2010) that burn-only sites are thermally extreme (hotter than other treatments), which may adversely affect small mammals. Surprisingly, control sites also exhibited small but significant increases in small mammal abundance, which we attribute to increases in ground level seed production after a canopy-opening ice storm. In our more complete analyses (Douglas 2010), Lincoln-Peterson abundance estimates were highly correlated with capture success estimates, and both methods yield similar conclusions regarding increases in small mammals that serve as prey species for timber rattlesnakes. Thus, we concluded that snake prey abundance increased at cut-only and cut-burn sites relative to control and burn-only sites.

Prior to habitat manipulations, the growth rates of snakes that used areas planned for manipulation were not statistically distinguishable from snakes using control areas (Douglas 2010). However, after application of thinning and fire, snakes that used manipulated sites exhibited statistically significant increases in growth rates (Douglas 2010). Body condition in snakes using control areas appeared to decrease from 2005 to 2009, whereas body condition for snakes using manipulated areas did not change and was maintained at healthy levels. Thus, control areas were poor sites for snake mass gain throughout the duration of the study, whereas the best plots were the manipulated sites. Furthermore, a regression of body condition on proportion of time spent in manipulated plots was significant suggesting increased foraging success in manipulated plots (Douglas 2010).

Growth rates and body conditions of timber rattlesnakes were improved for snakes that used manipulated areas after manipulations occurred. This was consistent with expectations from previous studies of the effects of elevated resource levels on rattlesnakes (Beaupre 2008, Taylor and others 2005). Also, use of manipulated habitat for a greater proportion of a snake's active season was associated with higher body condition index (Douglas 2010). Therefore, increased use of manipulated habitats appears to result in healthier snakes. In light of these data, we suggest that not only does habitat manipulation enhance habitat quality for timber rattlesnakes, but also that both body condition and growth rates of timber rattlesnakes may be viable indicators of the effectiveness of large-scale habitat manipulations. Timber rattlesnakes responded rapidly to changes in resource environment, and their physiological responses were more immediately and unambiguously measured than changes in small mammal abundance or capture success which is highly variable and requires very large allocation of resources and effort.

CONCLUSIONS

Our two case studies located in the same experimental system offer dramatically different lessons regarding the response of timber rattlesnakes to the application of fire in an Ozark oak ecosystem. We offer several caveats regarding our observations and the quality of our experimental data. Results obtained are clearly specific to our sites and our general approach. The effects of logging and fire application on reptiles in general are likely highly variable, and dependent on a number of relevant conditions. For example, as demonstrated by Case 1, the severity and timing of fire application will likely have a profound effect on outcomes for ground-dwelling reptiles. Application of fire immediately after emergence had a local but devastating effect on ground-dwelling, leaf-litter hiding timber rattlesnakes. For Case 2, prior knowledge of the pending manipulation allowed us to negotiate with AGFC to apply fire to the system prior to spring emergence of most large-bodied reptiles present in our system. Foreknowledge and planning resulted in dramatically different outcomes than those seen at Site K. Thus, timing is critical, and at least for the preservation of timber rattlesnakes, fire is probably best applied during their natural dormant season.

The vulnerability of timber rattlesnakes and other large-bodied snakes to fire during the growing season is unknown. Aside from post-spring emergence, snakes in particular may also be vulnerable during ecdysis, when eyesight and other senses are impaired as old skin lifts and separates from new tissue in preparation for shedding (Means and Campbell 1981, Russell and others 1999). Clearly, the ability of a species to endure fire will depend upon its evolutionary history and the frequency and intensity of fires in its native habitat. Nevertheless, some accounts in the literature suggest that rattlesnakes can survive low intensity growing season fires in nature. For example, only 2 of 68 marked eastern diamondback rattlesnakes (*Crotalus adamanteus*) succumbed to direct effects of prescribed fire in a Florida scrub ecosystem (Means and Campbell 1981). Likewise, low intensity fires in desert island systems can be survived by montane rattlesnake species (Smith and others 2001). However, in the French Alps, an autumn grassland burn (while snakes were still active) doubled the mortality rate of the highly endangered Orsini's viper (*Vipera ursinii*), and surprisingly, the snakes showed no improvement in body condition in the postfire environment (Lyet and others 2009). It is also clear that intense growing season fires can be catastrophic for rattlesnakes in some systems. The first author witnessed such an event in the Sonoran Desert in July 1995 when a thriving population of western diamondback rattlesnakes (*Crotalus atrox*) was locally extirpated, mostly by indirect effects, in the aftermath of the Rio Verde fire which consumed over 20,000 acres (Beaupre 1995). In any event, growing season fires should be expected to produce some mortality and possibly high mortality under some conditions. For healthy populations of common species, this mortality may be tolerable. For small relict populations of sensitive or threatened species, dormant season burns or alternatives to fire should be considered.

We also suggest that initial conditions of the manipulated forest will profoundly influence outcomes. Degraded forests are likely to benefit through increases in heterogeneity, and associated food production. Healthy climax forests would likely be adversely affected. Furthermore, maintenance of a healthy disturbance-dependent state requires not only the initial manipulation, but frequent return of fire to the system. However, optimal intervals of fire return for most vertebrates are unknown. In addition, climate-related weather events (e.g., ice storms, late freezes) have the capacity to impact experimental data, providing less than perfect confidence in all interpretations.

Finally, we caution the reader by reminding of some shortcomings in our Case 2 experimental design. In violation of the assumptions of a formal BACI design (Williams and others 2001), our sites were not chosen at random but were restricted to ridge tops and areas with sufficient logging access to saleable timber. This is less an admission of flawed experimental design and more of an acknowledgment of reality and the need to seize opportunities to forward our understanding, however imperfect they may be. Furthermore, all of our postmanipulation observations were made under transient successional dynamics. A critical question is whether differences in vegetation, small mammal abundance, and indicators of rattlesnake health will persist as the system settles into a long-term disturbance-dependent state.

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