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Conservation potential of prescribed fire for maintaining habitats and populations of an endangered rattlesnake *Sistrurus c. catenatus*

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ABSTRACT: Many endangered species rely on early successional habitats to complete parts of their life cycles. We examined whether prescribed fire can be used to aid in conservation of the endangered eastern massasauga rattlesnake *Sistrurus catenatus catenatus* Raf. by maintaining open-canopy early successional summer habitats that this species requires for thermoregulation (basking). Using a formal experimental design, we characterized vegetation, surface temperature, moisture, and snake occurrence in control and burned treatments before and after prescribed fire. Prescribed fire increased vegetative cover and thereby decreased ground temperature compared to pre-treatment and control conditions, whereas rattlesnake occurrence increased dramatically after the prescribed fire. A habitat suitability model indicated that snake presence was negatively affected by forb cover, which became more dominant relative to other vegetation in the absence of fire. Prescribed fire also increased the cover of legumes and maintained graminoid cover and high overall plant functional diversity — all of which decreased in the absence of fire. In conclusion, prescribed fire stimulated overall vegetation growth while promoting varied microhabitats that included greater proportions of graminoids and sufficient number of patches of bare ground, both locally associated with warmer temperatures and presence of this endangered species of rattlesnake.

KEY WORDS: Basking habitat conservation · Disturbance · Habitat management · Old field · Succession

INTRODUCTION

As humans alter natural disturbance regimes, early successional habitats are frequently being lost to natural vegetative succession toward closed-canopy communities dominated by woody plants (Smit & Olff 1998, Brown & Archer 1999, Dovčiak et al. 2005). These early successional habitats can be important for disturbance-dependent rare, threatened, or endangered species that require open post-disturbance environments characterized by increased solar radiation and warmer temperature, reduced soil moisture, or distinct early successional plant and animal communities (White & Jentsch 2001, Prach & Walker 2011, Swanson et al. 2011). The diversity of plant species and functional groups (e.g. forbs, grasses, woody species) in early successional systems provides a diversity of important microhabitats for a variety of types of wildlife, including rare reptiles (Shoemaker et al. 2009), mammals (Fuller & DeStefano 2003), birds (Thompson & DeGraaf 2001), and invertebrates (Broome et al. 2011, D'Aniello et al. 2011). Thus, anthropogenic changes in disturbance regimes (e.g. land abandonment, fire suppression)

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have led to increasing rarity of early successional habitats and related declines in wildlife species (many rare or threatened) that require such habitats for parts of their life cycles (Litvaitis 1993, Thompson & DeGraaf 2001, Wiezik et al. 2013).

One of the best examples of an endangered species threatened by land-use change and declining early successional habitats in eastern North America is the eastern massasauga rattlesnake *Sistrurus catenatus catenatus* Raf., a distinct relative of the western and desert massasaugas *S. c. tergeminus* and *S. c. edwardsii* of the southwestern USA (Johnson et al. 2000, Kubatko et al. 2011, USFWS 2012). The eastern massasauga rattlesnake is endangered in all but 1 state out of only 10 states in the USA where it occurs, and it is critically imperiled or imperiled across most of its North American range (which also includes 1 province in Canada) (Szymanski 1998, USFWS 2012, NatureServe 2013). In most of the US states where the species occurs, >50% of known eastern massasauga rattlesnake populations have been extirpated (Johnson et al. 2000), and the species thus well represents dramatic declines documented globally for several other snake species (Gibbons et al. 2000, Reading et al. 2010). As an ectothermic species, the eastern massasauga rattlesnake is negatively affected by vegetative succession because the species requires open and thus relatively warmer and drier habitat during the summer months to bask (to regulate its body temperature) and to forage (Reinert & Kodrich 1982, Seigel 1986, Harvey & Weatherhead 2006).

Many threatened and endangered wildlife species that require early successional habitats (including the eastern massasauga rattlesnake) rely increasingly on deliberate human management that uses controlled disturbance (e.g. prescribed fire, mowing, woody vegetation removal) as a conservation strategy (e.g. Johnson & Leopold 1998, Thompson & DeGraaf 2001). Prescribed fire in particular has been widely used to mimic natural disturbance regime to slow succession by removing woody plants and to create or maintain a heterogeneous mosaic of early successional plant species and environmental conditions (Peterson & Reich 2001). Woody cover tends to negatively affect habitat for ectothermic species because it decreases solar radiation at ground level and thus reduces ambient near-surface temperature (Webb et al. 2005). High habitat heterogeneity, and high diversity of plant functional groups in particular, tends to provide variable microenvironments where open and dense vegetation patches form a mosaic that can provide fine-scale thermal refugia for ectothermic species (Pringle et al 2003) as well as shelter and food for a greater variety and abundance of prey (Tews et al. 2004; important especially for generalist predators such as the eastern massasauga rattlesnake).

Although fire regime in eastern North America varies by forest type (from fire-adapted oak or pine forests to less fire-adapted northern hardwood forests), fire generally was a more common disturbance regime (frequently initiated by native Americans) prior to European settlement than it is now (e.g. Nowacki & Abrams 2008). However, the effects of fire on habitat quality can be variable, reflecting site-dependent vegetation responses to the disturbance; while more intense fire may suppress woody cover, it can increase the cover and biomass of other plant functional groups (e.g. nitrogen-fixing legumes or graminoids; Tix & Charvat 2005) and thus affect ground-level environmental conditions (e.g. temperature; Smith & Johnson 2004). Consequently, the successful application of prescribed fire in conservation of threatened or endangered species, to restore or maintain their early successional habitat, requires a detailed understanding of the ecological requirements of the target species as well as an understanding of its responses to the disturbance and post-disturbance vegetation structure and abiotic conditions.

In this study, we evaluated whether the conservation of isolated populations of the eastern massasauga rattlesnake could be enhanced by the use of prescribed fire as a vegetation (habitat) management tool. We studied 1 of only 2 known remaining populations in New York State, which has experienced a decline in its summer habitat quality due to natural successional processes (Johnson & Leopold 1998, Shoemaker & Gibbs 2010). We evaluated the impacts of prescribed fire on the suitability of summer habitat (vegetation structure and microclimate) as well as on the abundance and habitat use of the eastern massasauga rattlesnake. We hypothesized that:

(H1) Prescribed fire creates open rattlesnake basking habitat because it reduces total plant cover by decreasing the cover of woody species relative to other plant functional groups (forbs, legumes, and graminoids).

(H2) Prescribed fire enhances heterogeneity of rattlesnake basking habitat by increasing diversity of plant functional groups (plant functional richness).

(H3) Prescribed fire creates favorable basking habitat for rattlesnakes by creating warmer and drier ground surface conditions.

(H4) The eastern massasauga rattlesnake population responds positively to habitat changes caused by prescribed fire.

MATERIALS AND METHODS

Study area

This study took place in Cicero Swamp Wildlife Management Area near Syracuse, New York, USA (43°8'N, 76°2'W). Climate in the region is continental and humid, with a mean annual temperature of 8.8°C (Syracuse Hancock International Airport, 6 km from study site; NCDC 2011). The mean temperature in July is 21.8°C, and temperatures in the 3 years of the study (2010, 2009, 2006) deviated from this mean only slightly (by +1.9, −1.8, and +1.6°C, respectively). Mean annual precipitation is about 102 cm, distributed evenly throughout the year, and it was very close to the long-term mean in 2010 (105 cm), somewhat below the mean in 2009 (90 cm), and above the mean in 2006 (120 cm; NCDC 2011).

Cicero Swamp Wildlife Management Area is a mosaic of upland forest, fields, and wetlands, including the core peatland habitat for a population of the eastern massasauga rattlesnake *Sistrurus catenatus catenatus*. Although detailed long-term fire history of the area is not known, the core peatland habitat was impacted by an intense fire in 1892 that created early successional habitat appropriate for the eastern massasauga rattlesnake (LeBlanc & Leopold 1992). We focused on 2 old fields near the core rattlesnake habitat that were under active management by the New York State Department of Environmental Conservation as potential summer habitat for the eastern massasauga rattlesnake. These fields are approximately 130 m above sea level and are characterized by loam and silty loam soil (NRCS 2011). The 2 sites are <1 km apart and have similar management histories. Both fields were planted with row crops until abandonment (15 to 20 yr before this study) and have since developed old-field plant communities typical in the eastern USA (cf. Marks 1983). The New York State Department of Environmental Conservation has mowed both of these fields biannually since abandonment from farming to limit the growth of trees and shrubs and to maintain open habitat. To evaluate the effects of fire as a potential alternative management strategy in this system, a prescribed burn was applied in early April 2010 in one of the fields, while the other was left unburned to serve as a control treatment. The timing of the prescribed fire (2 April 2010) was chosen to occur outside of the active season of the eastern massasauga rattlesnakes (15 April to 15 September).

Vegetation surveys

In September 2009 (prior to the prescribed burn), we established thirty 4 × 4 m vegetation plots in the 2 old fields, with 15 plots arranged systematically along 3 transects per field. We surveyed each of these plots using four 0.5 × 0.5 m subplots (120 subplots in total) in September 2009 and 6 times during the 2010 growing season (monthly April to September) after treatments were applied. The subplots were placed systematically (2 m apart) in each plot and permanently marked with 30 cm rebar stakes at 2 diagonal corners. Surveys consisted of characterizing the vascular plant species composition in each subplot by visually estimating percent cover of each species using Daubenmire cover classes (Daubenmire 1959). From subplots, we calculated mean cover and total richness for each plot at each sampling date for further analyses. Plant nomenclature and classification into functional groups follow Gleason & Cronquist (1991).

Snake surveys

To evaluate eastern massasauga rattlesnake responses to the habitat changes caused by the prescribed fire, snakes were surveyed throughout the summer after treatment (2010) using methods and locations identical to a previous (2006) snake survey of the 2 old fields (Patrick & Gibbs 2009). In both surveys 25 cover boards (decommissioned metal road signs; 0.7 × 0.7 m) were placed in a 5 × 5 grid (70 × 500 m) in each field 2 wk before the start of surveys. Cover boards were monitored 20 times during the summer (June to August). Each survey was performed in the morning (between 06:00 h and 12:00 h), and the order of fields and the direction of cover board surveys in each field (east to west or vice versa) were randomized each time. Surveys consisted of lifting each cover board and recording the presence or absence of eastern massasauga rattlesnakes.

Environmental data collection

Ambient air temperature was monitored hourly on all vegetation plots near the soil surface (~3 cm above the soil surface) throughout the 2010 growing season (May to September, after treatments) to approximate thermal characteristics of snake basking habitat. Measurements were made using Thermochron® iButtons (Maxim Integrated Products) mounted on wooden stakes and sheltered by PVC caps (10 cm in diameter, to prevent solar radiation from directly reaching and overheating the sensors). Two temperature sensors were placed within each vegetation plot adjacent to 2 diagonal subplots (~3 m apart). Mean maximum daily temperatures were calculated monthly for each vegetation plot to approximate daytime heat load over the vegetation season for further analyses.

Soil moisture was measured in all vegetation plots immediately before and after the prescribed fire in April 2010, and subsequently every 2 wk (n = 10) throughout the growing season. Measurements were taken using a 12 cm probe attached to a Hydrosense Water Content Sensor (Campbell Scientific CS 620). The probe was inserted vertically into the soil adjacent to each corner of each vegetation subplot, for a total of 4 readings per subplot and 16 readings per vegetation plot; mean soil moisture was calculated monthly for each plot for further analyses.

Additional microhabitat characteristics were measured at each cover board in mid-September as potential predictors for the presence of eastern massasauga rattlesnakes. Vegetation height around the cover boards was measured, and ground cover was characterized as the percentage of bare ground, graminoids, and forbs following the methods of Patrick & Gibbs (2009). Four soil moisture measurements were taken under the cover boards with a Hydrosense Water Content Sensor (as described above) and averaged to characterize mean soil moisture at each cover board.

Statistical analyses

We used analysis of variance (ANOVA) to assess how continuous vegetative and abiotic environmental responses (e.g. total plant cover, cover of functional groups, functional richness, temperature, and moisture) varied across the 2 treatments (prescribed fire and control) before and after the treatments (before, after, control, impact [BACI] experimental design). The overall impact of the prescribed fire on vegetation (hypotheses H1 and H2) was assessed by comparing total plant cover (sum of individual species' covers), the cover of plant functional groups (species covers summed separately for forbs, graminoids, legumes, and woody plants), and plant functional group richness at the end of the growing seasons before and after treatments as a 2 × 2 factorial experiment. For the growing season following treatments, seasonal trends in total plant cover and functional group richness were analyzed using repeated measures ANOVA, with treatment and time as main effects (Bolker 2008).

The effects of the prescribed fire on the abiotic environment of the basking habitat — maximum daily temperature and soil moisture (H3) — were tested with repeated measures ANOVA (described above). To link changes in the vegetation structure to abiotic environment, we used linear regression to relate peak mid-season (July) maximum daily temperature and soil moisture to ground cover (bare ground, total plant cover, cover of plant functional groups).

Finally, we used ANOVA to compare post-treatment occurrence of the eastern massasauga rattlesnake to the pre-treatment levels reported by Patrick & Gibbs (2009) (H4). To determine microhabitat features influencing eastern massasauga rattlesnake responses to the prescribed fire, we created and tested several *a priori* candidate models for predicting the probability of snake occurrence from 6 relevant microhabitat variables — percentage of bare ground, graminoid cover, forb cover, plant height, soil moisture (see 'Environmental data collection'), and distance from forest edge (following Patrick & Gibbs 2009). From these variables, we created 6 univariate models and all 2-variable combinations (with 1 cover variable allowed in each model at a time to prevent collinearity). Interaction terms were not included because we expected effects to be additive, not multiplicative (Hosmer & Lemeshow 2000). The response, presence of eastern massasauga rattlesnakes under each cover board, was measured during the 20 cover-board survey periods in 2010, and rattlesnakes were considered to be present within a particular microhabitat (cover board) if they were observed there at least once (in order to eliminate temporal correlation due to observing potentially the same individual under the same cover board multiple times). We performed logistic regression (generalized linear models with binomial error distributions) to compare the candidate models to each other and to the null (intercept-only) model using the Akaike information criterion corrected for small sample size (AIC_c) to select the best model ($\Delta AIC_c < 2$; Burnham & Anderson 2010).

RESULTS

Effects of prescribed fire on rattlesnake vegetative habitat

Immediately after the prescribed fire (at the beginning of the vegetation season, in April 2010), total live vegetative cover was low (~15%) and it did not differ between the 2 treatments (Fig. 1a). The total plant cover increased to a peak in July and then

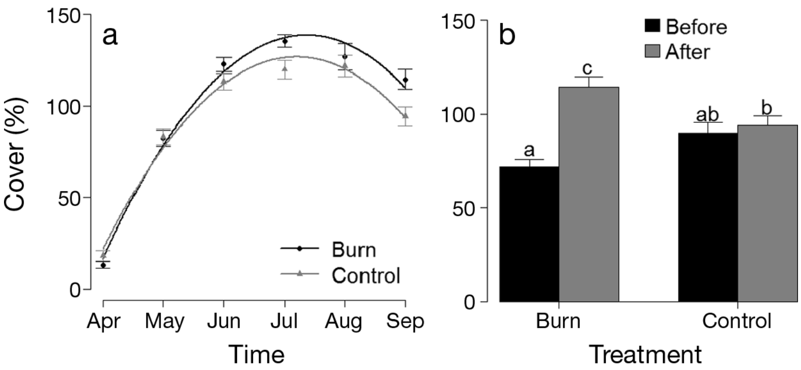

Fig. 1. Mean (±1 SE) total plant cover, measured as the sum of individual species' covers (a) during the 2010 growing season following treatments and (b) at the end of growing seasons before and after the treatments (i.e. in September 2009 and 2010) in old-field rattlesnake (*Sistrurus catenatus catenatus*) summer habitat in Cicero Swamp Wildlife Management Area, New York. Prescribed fire (burn) and control treatments were implemented in early April 2010. Values may be >100% due to overlapping canopies of neighboring plants. Quadratic polynomials were fitted for the seasonal trends in (a) based on Table 1. Significantly different means in (b) are labeled with different letters ($p < 0.05$)

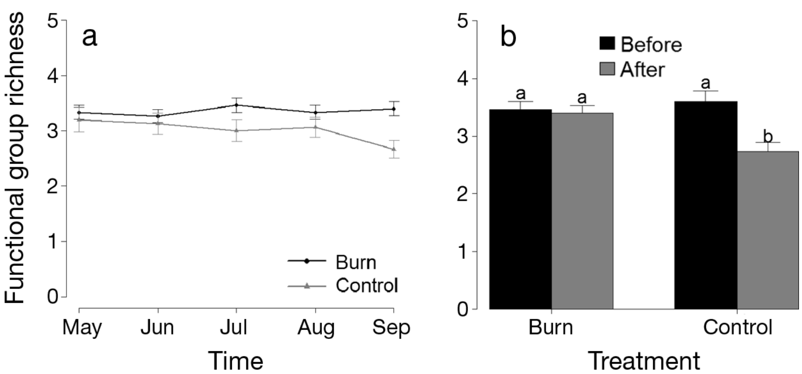

Fig. 2. Mean (±1 SE) plant functional group richness (a) during the 2010 growing season following treatments and (b) at the end of growing seasons before and after the treatments (i.e. in September 2009 and 2010) in old-field rattlesnake (*Sistrurus catenatus catenatus*) summer habitat in Cicero Swamp Wildlife Management Area, New York. Prescribed fire (burn) and control treatments were implemented in early April 2010. Significantly different means in (b) are labeled with different letters ($p < 0.05$)

decreased later in the season in both treatments, but the burned treatment reached higher peak and end-of-season cover than the control treatment (Fig. 1a, Table 1). The total end-of-season cover increased relative to the pre-treatment conditions by ~40% after the prescribed fire, but it did not change in the control ($F_{3,56}$ = 12.13, $p < 0.001$; Fig. 1b). Thus, contradictory to our hypothesis (H1), prescribed fire increased the total vegetation cover instead of reducing it.

Prescribed fire maintained the diversity of plant functional groups at pre-treatment levels (Fig. 2), in contrast with the control treatment where plant functional richness declined over time considerably between the 2 growing seasons ($F_{3,56}$ = 7.29, p = 0.0003; Fig. 2b) and less so within the single growing season following the treatments (Fig. 2a, Table 1). Thus, although prescribed fire did not increase plant functional richness as we hypothesized (H2), it did maintain a more heterogeneous early successional habitat (higher diversity of plant functional groups) than the control treatment, consistent with our hypothesis.

The decline in plant functional richness in the control treatment resulted from changes in the abundance (cover) of plant functional groups. In contrast to forbs, which increased equally in burn and control treatments over time (by ~25 to 35%; $F_{3,56}$ = 14.26, $p < 0.0001$; Fig. 3a), graminoids decreased in the control treatment (by ~20%), but they remained at pre-treatment levels in the

Table 1. Differences in total plant cover, functional richness, maximum daily temperature, and soil moisture between the control and burn (prescribed fire) treatments in the old fields at Cicero Swamp Wildlife Management Area, New York, during the 2010 growing season (after treatments) tested with repeated measures ANOVA. Temporal trends over the vegetation season were tested using linear (Time) and quadratic (Time^2) terms, and differences in temporal trends between control and prescribed fire were tested using an interaction term (Treatment × Time)

	Plant cover		Functional richness		Max. temperature		Soil moisture	
	F	p	*F*	p	*F*	p	*F*	p
Treatment	4.45	0.04	4.65	0.04	14.16	<0.001	1.16	0.29
Time	313.91	<0.0001	1.41	0.24	153.01	<0.0001	140.45	<0.0001
Treatment × Time	4.09	0.05	2.88	0.09	2.28	0.13	1.91	0.17
Time^2	379.81	<0.0001	0.60	0.44	636.85	<0.0001	120.84	<0.0001

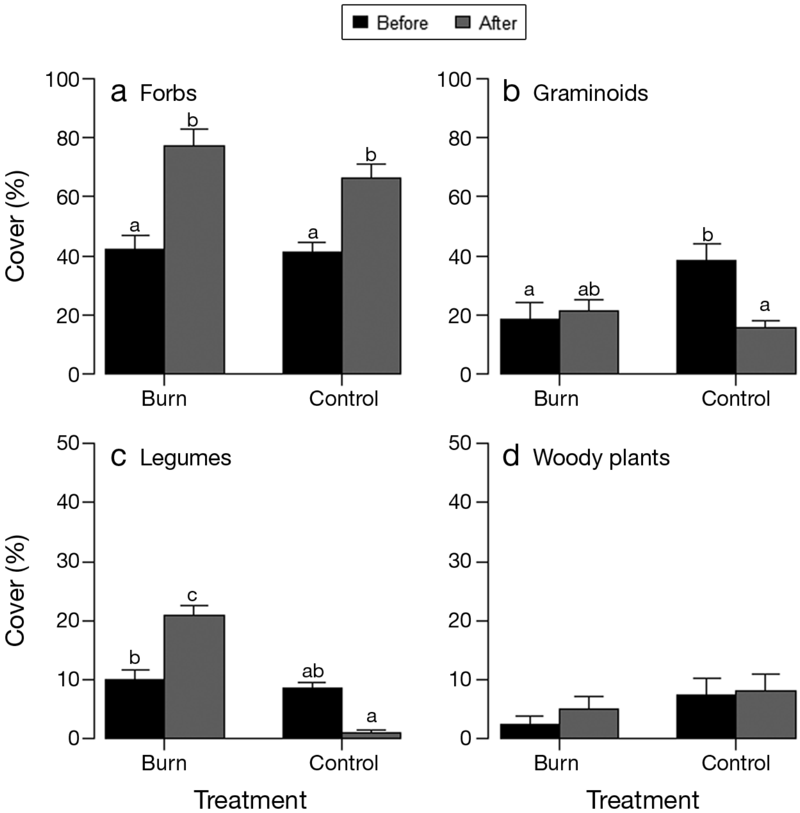

Fig. 3. Mean (±1 SE) cover of individual plant functional groups in prescribed fire (burn) and control treatments at the end of growing seasons before and after the treatments (i.e. in September 2009 and 2010) in old-field rattlesnake (*Sistrurus catenatus catenatus*) summer habitat in Cicero Swamp Wildlife Management Area, New York: (a) forbs, (b) graminoids, (c) nitrogen-fixing legumes, and (d) woody plants. Means with different letters are significantly different ($p < 0.05$). No differences were observed between years or treatments in woody plant cover ($p = 0.33$). Note that *y*-axes vary in scale

burn treatment ($F_{3,56} = 4.80$, $p = 0.005$; Fig. 3b). Moreover, prescribed fire increased the cover of nitrogen-fixing legumes, which tended to decrease without the fire ($F_{3,56} = 13.99$, $p < 0.0001$; Fig. 3c). Woody plants were the least abundant group, and their cover did not vary over time or between treatments ($F_{3,56} = 1.18$, $p = 0.33$; Fig. 3d). Thus, prescribed fire had positive effects on graminoids and legumes, no effects on forbs or woody species (contrary to H1), and it maintained heterogeneity of rattlesnake vegetative habitat (consistent with H2).

Effects of prescribed fire on rattlesnake abiotic habitat

Contrary to our hypothesis (H3), prescribed fire did not create warmer or drier basking habitat compared to the control treatment. Temperature near the ground surface was consistently lower after the prescribed fire than in the control treatment throughout the growing season, and both treatments had a similar mid-season temperature peak (Fig. 4a, Table 1) coinciding with peak vegetation cover (Fig. 1a). Soil moisture did not differ between the treatments, and it decreased over time

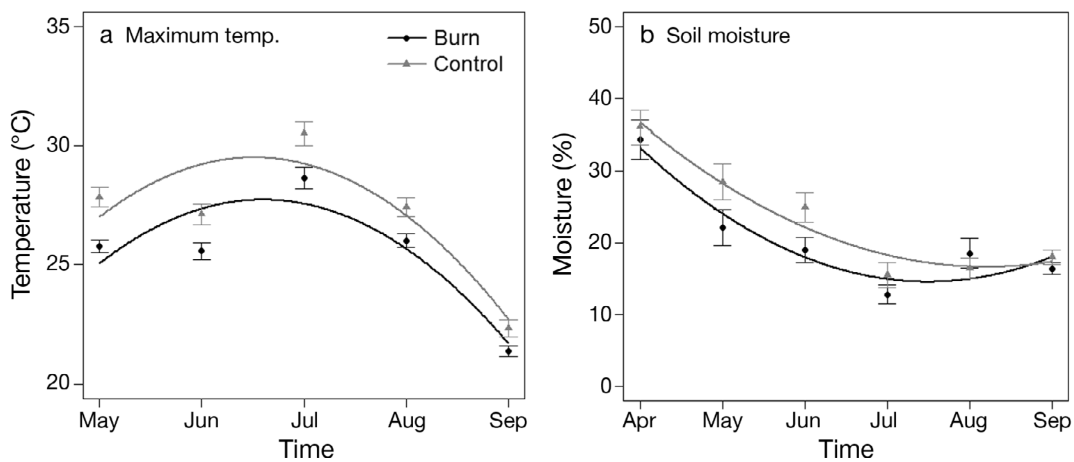

Fig. 4. Mean (±1 SE) temporal trends in (a) maximum daily temperature and (b) soil moisture in prescribed burn and control treatments in old-field rattlesnake (*Sistrurus catenatus catenatus*) summer habitat in Cicero Swamp Wildlife Management Area, New York, during the 2010 growing season. Treatments were implemented in early April 2010. Quadratic polynomials were fitted for the seasonal trends based on Table 1

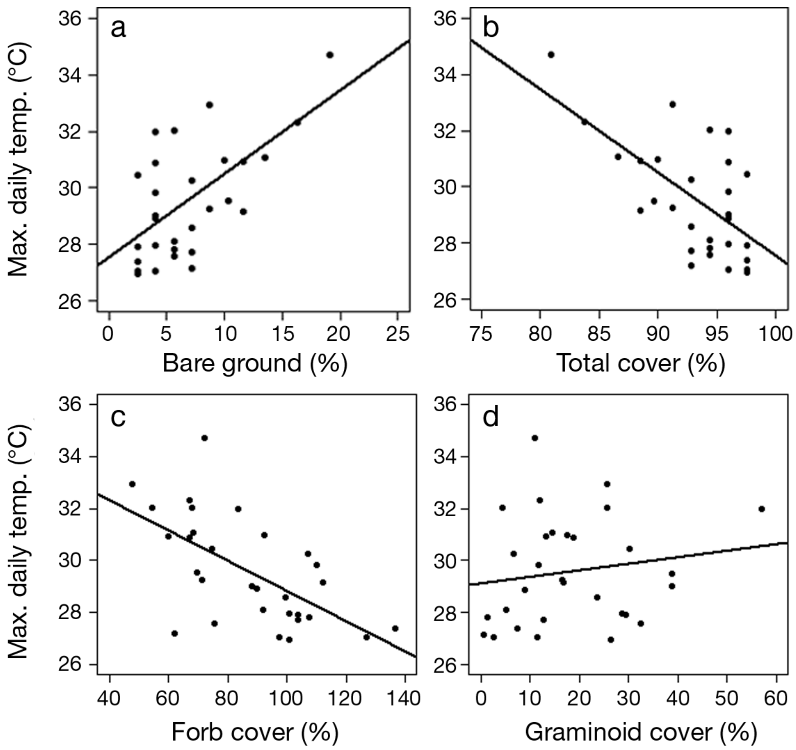

Fig. 5. Relationships between maximum daily temperature near ground surface and (a) amount of bare ground, (b) total plant cover, (c) forb cover, and (d) graminoid cover in old-field rattlesnake *Sistrurus catenatus catenatus* summer habitat in Cicero Swamp Wildlife Management Area, New York. (a to c) $p < 0.001$; (d) $p = 0.41$

equally in both treatments to the driest point in July (Fig. 4b, Table 1).

Temperature near the ground surface was mediated by vegetation; it increased with the amount of bare ground ($F_{1,28}$ = 16.05, $p < 0.001$; Fig. 5a) and decreased with total plant cover ($F_{1,28}$ = 16.05, $p < 0.001$; Fig. 5b) and the cover of forbs ($F_{1,28}$ = 17.32, $p < 0.001$; Fig. 5c), and it did not respond negatively to graminoid cover ($F_{1,28}$ = 0.69, $p = 0.41$; Fig. 5d). Although, temperatures cooler in burn than in control treatment are consistent with the increase in total plant cover after the fire, they contrast with our hypotheses that fire improves rattlesnake basking habitat by creating uniformly warmer ground surface (H3) under more open vegetation (H1).

Eastern massasauga rattlesnake responses to prescribed fire

Consistent with our hypothesis (H4), the frequency of observing eastern massasauga rattlesnakes *Sistrurus catenatus catenatus* within the old fields increased considerably after the prescribed fire, from no rattlesnake observations during the survey prior to the prescribed fire to 27 observations during the vegetation season following the fire (i.e. ~5% rattlesnake observation rate, or approximately 1 rattlesnake sighting per 20 cover-board observations) (Fig. 6). The presence of eastern massasauga rattlesnakes after the fire was consistently negatively related to forb cover, the only variable constituting the best model and occurring in the next 3 models (Table 2, Fig. 7a). Models including plant height, distance from the forest, and soil moisture in addition to forb cover also had high model weights (ranging from 0.11 to 0.18), but were much weaker than the model containing only forb cover (model weight: 0.41) (Table 2). Graminoid cover and bare ground were moderately positively related to rattlesnake presence, but were weaker predictors compared to forb cover (Table 2, Fig. 7b,c). Thus, the overall positive response of eastern massasauga rattlesnake to prescribed fire appeared to be related more to the presence of relatively rare open microhabitats with low forb cover (Table 2, Fig. 7) and warmer temperatures (Fig. 5) than to mean habitat changes (i.e. changes in mean overall plant cover; Fig. 1).

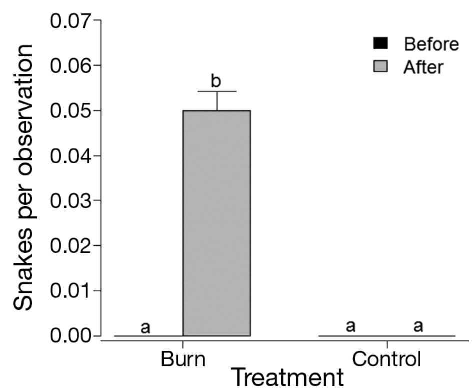

Fig. 6. *Sistrurus catenatus catenatus*. Mean (±1 SE) frequency of eastern massasauga rattlesnakes per cover-board observation (ranging from 0 to 1) in prescribed fire (burn) and control treatments in old-field rattlesnake summer habitat in Cicero Swamp Wildlife Management Area, New York, before and after treatments. Rattlesnake surveys were performed during the vegetation seasons of 2006 and 2010. Means labeled with different letters are significantly different ($p < 0.05$)

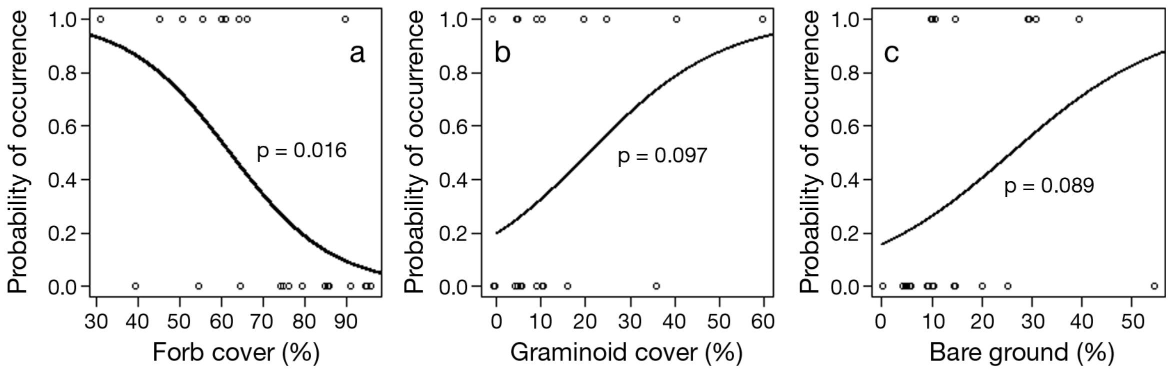

Fig. 7. *Sistrurus catenatus catenatus*. Probability of occurrence (presence) of eastern massasauga rattlesnakes relative to (a) forb cover, (b) graminoid cover, and (c) amount of bare ground after the prescribed fire (burn) treatment in 2010 in old-field rattlesnake summer habitat in Cicero Swamp Wildlife Management Area, New York

Table 2. *Sistrurus catenatus catenatus*. Candidate logistic regression models for the occurrence of eastern massasauga rattlesnakes after the prescribed burn in Cicero Swamp Wildlife Management Area, New York. Models are listed in order of increasing AIC_c values, with the best model (lowest AIC_c) listed first. Models with $\Delta AIC_c < 2$ relative to the best model are considered equivalent to the best model (Burnham & Anderson 2010). Signs indicate whether each variable had a positive (+) or a negative (–) effect on the presence of eastern massasauga rattlesnakes. *K* is the number of model parameters; all models include the intercept. ΔAIC_c is the difference in AIC_c values between the given model and the best model. w_i is the Akaike weight estimating the relative strength of each model. Forb cover includes all forbs (including legumes)

Variables included	*K*	AIC_c	ΔAIC_c	w_i
Forb cover (–)	2	28.48	0.00	0.41
Forb cover (–), plant height (+)	3	30.15	1.67	0.18
Forb cover (–), distance from forest (–)	3	30.97	2.48	0.12
Forb cover (–), soil moisture (+)	3	31.08	2.60	0.11
Graminoid cover (+)	2	33.28	4.79	0.04
Bare ground (+)	2	33.72	5.24	0.03
Null (intercept-only) model[a]	1	34.84	6.36	0.02

[a]Models with AIC_c > AIC_c of the null model are not included

DISCUSSION

Many threatened or endangered wildlife species require high-quality early successional habitats that are increasingly rare and may need to be deliberately created to compensate for their loss due to changes in disturbance regimes and land use (Litvaitis 1993, Thompson & DeGraaf 2001, Trani et al. 2001). We evaluated whether controlled disturbance, specifically prescribed fire, can be used as a conservation strategy and a habitat management tool to create an early successional summer habitat for isolated populations of the endangered eastern massasauga rattlesnake *Sistrurus catenatus catenatus*. We quantified the effects of prescribed fire on rattlesnake vegetative and abiotic habitat, as well as rattlesnake responses to these habitat changes, and found that prescribed fire can effectively improve the vegetative habitat of the eastern massasauga rattlesnake by maintaining a diverse early successional system.

Our finding of positive snake responses to prescribed burning is consistent with previous studies investigating the effect of prescribed fire on the habitat of other taxonomic groups (e.g. birds; Van Dyke et al. 2004). Since the old fields in our study were only lightly colonized by woody species (due to past management by mowing), fire did not play a major role in decreasing woody canopy short term, but it likely retarded woody colonization of the old field long term (cf. Peterson & Reich 2001). More importantly, fire stimulated increased aboveground herbaceous cover as also documented in other studies (e.g. Briggs & Knapp 1995), which could negatively affect snake thermal habitat. Webb et al (2005) show that both microclimate and snakes are very sensitive to even modest changes in vegetation canopy openness; thus, denser vegetation would negatively affect near-ground temperatures and the quality of snake basking habitat. Our results strongly suggest that dense herbaceous cover, especially the cover of forbs, can negatively affect near-ground temperatures (although graminoid cover did not, likely due to a more open canopy structure of graminoids). When prescribed fire is implemented at the beginning of a vegetative growing season to avoid active or breeding seasons of an endangered species (as in our study), it removes mainly dead plant material (litter) and enhances nutrient release, and thus it stimulates subsequent plant growth particularly well (Towne & Kemp 2003).

Early successional systems tend to be less stable than later successional systems, as plant functional groups respond differently to disturbance and associated resource fluctuations (Briggs & Knapp 1995, Dovčiak & Halpern 2010). Our results corroborate findings that prescribed fire can maintain graminoid cover (Towne & Kemp 2003) and increase the cover of nitrogen-fixing legumes (Tix & Charvat 2005), functional groups that were negatively affected by successional processes. Thus, prescribed fire in our study appeared to facilitate a heterogeneous snake habitat capable of fulfilling a broader set of ecological functions that were threatened by succession toward a more homogenous vegetation dominated by forbs (short term) or by woody species (long term). Greater habitat heterogeneity enables the development of fine-scale thermal refugia (warmer, more open microhabitats; sensu Pringle et al. 2003) that can be nested within a broader scale, less-suitable environment (cooler areas shaded by dense forb or woody cover).

The prescribed fire in our study appeared to be successful in increasing the use of old-field summer habitat by the eastern massasauga rattlesnake. Despite the overall increase in both total vegetation cover and the cover of forbs (and consequent mean changes in the thermal basking habitat), eastern massasauga rattlesnakes tended to occupy relatively rare, more open microhabitats with little forb cover (and thus warmer temperatures), suggesting that this species preferentially selects sites at the microhabitat rather than overall habitat scale (see also Harvey & Weatherhead 2006). A heterogeneous mosaic of open microhabitats embedded within dense vegetation can offer snakes better opportunities for thermoregulation than a uniformly open habitat, since snakes can bask in the more open areas and use the denser vegetation as shelter from both excessive radiation and predators (Reinert & Kodrich 1982, Wisler et al. 2008, Shoemaker & Gibbs 2010). Additionally, dense herbaceous vegetation tends to positively affect small mammal populations which are the preferred prey of the rattlesnake (Matlack et al. 2008).

In summary, our results suggest that prescribed fire can maintain or increase the heterogeneity and productivity of early successional habitat and increase its use by the eastern massasauga rattlesnake. While long-term research should determine the most appropriate frequency of prescribed fires, as well as the longer term effects of fire on the population dynamics of this species, our study suggests that prescribed fire may be a promising conservation tool for the eastern massasauga rattlesnake and likely for other disturbance-dependent threatened or endangered species. Many snake species are in decline throughout the world (Reading et al. 2010). The BACI experimental approach used in this study would be a powerful tool for studying the general response patterns of other isolated populations of the eastern massasauga rattlesnake in the USA, and of other snake species that require early successional habitats, to habitat manipulations using prescribed fire. Moreover, maintaining high-quality early successional habitats within the broader landscape could be an important conservation goal on its own, because these systems frequently supply important ecosystem services and provide habitat to species of high conservation value (Thompson & DeGraaf 2001, Swanson et al. 2011, Wiezik et al. 2013).

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