

Tree Removal Likely Improves Thermal Quality of Basking Sites for an Imperiled Timber Rattlesnake Population at the Northern Edge of its Range

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Abstract - Lack of natural disturbance in many forests in northeastern North America has resulted in increased canopy cover and a reduction of open-habitat patches. *Crotalus horridus* (Timber Rattlesnake) in this region depends upon open basking and gestation sites, and its populations have declined markedly. We evaluated the utility of mechanical tree removal to restore potential basking habitat for a highly imperiled Timber Rattlesnake population in New Hampshire. We used a before–after, control–impact study to test for the effects of tree removal on environmental temperature and Timber Rattlesnake and other wildlife use of 3 potential basking sites. Mean temperatures were significantly higher and more variable post-treatment, while minimum temperatures were relatively unaffected. The number of temperature readings within the span of selected body temperatures of gravid female Timber Rattlesnakes (25.2–31.7 °C) increased post-treatment. Using time-lapse cameras, we detected rattlesnakes during 5 days at post-treatment sites but on only 1 day at a control site. Detections of potential rattlesnake prey species did not change following treatment, and few potential rattlesnake predators were detected pre- or post-treatment. Our results suggest that tree removal around potential basking sites likely improves thermal habitat quality for Timber Rattlesnakes.

Introduction

Disturbance regimes (e.g., fire and grazing) in temperate forests in eastern North America have been suppressed by humans over the past several decades (Nowacki and Abrams 2008, Roques et al. 2001) leading to increased shrub and tree cover (e.g., Gilliam and Platt 1999, Pringle et al. 2009). Increased vegetation cover due to lack of disturbance may have individual- and population-level consequences for ectotherms in temperate climates because of the strong effects of the thermal environment on ectotherm physiology and behavior (Angilletta 2001, Huey 1982, Peterson et al. 1993). Habitat selection by reptiles in temperate climates is strongly influenced by the thermal suitability of available habitats (Dubois et al. 2009, Reinert 1993, Row and Blouin-Demers 2006). For example, snakes in forested landscapes often select open sites for thermoregulation, particularly to facilitate thermophilic life-history functions such as ecdysis, digestion, or gestation (Blouin-Demers and Weatherhead 2001b, Harvey and Weatherhead 2010, Reinert 1984). Reduced availability of these open sites due to increased tree or shrub cover

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may increase the difficulties in fulfilling these functions, which could lead to negative population-level consequences (Lourdais et al. 2002, 2004). Multiple reptile populations in temperate regions have declined due to reduced availability of open microhabitats due to vegetation succession (Ballinger and Watts 1995, Fitch 1999, Jaggi and Baur 1999).

Crotalus horridus L. (Timber Rattlesnake) was historically widespread throughout eastern North America ranging from the Atlantic Coast to the eastern edge of the Great Plains and north from New England, southernmost Ontario, Canada, and Minnesota south to the southern Coastal Plain (Brown 1993, Martin et al. 2008). However, this species has declined throughout its range due to habitat loss and human persecution (Brown 1993, Martin et al. 2008). In particular, Timber Rattlesnakes in New England are highly imperiled, persisting in small, isolated populations in 4 of 6 New England states, where they are considered endangered (Bauder et al. 2018, Martin et al. 2008). Timber Rattlesnakes at high latitudes or altitudes experience relatively long life histories, reaching maturity at 7–9 years and reproducing every 3–7 years, with a mean fecundity of ~8–9 young per litter and an average of 1.7 litters per female over her lifetime (Brown 2016, Martin 2002, Martin et al. 2008). In these regions, Timber Rattlesnake populations will regularly congregate on open, south-facing rocky sites for ecdysis and gestation (Brown 1993). Open rocky sites may represent a limiting resource within forested landscapes and facilitate genetic connectivity among hibernacula (Clark et al. 2008). Gravid Timber Rattlesnakes spend much of the active season within open rocky sites exhibiting thermoregulatory behavior to maintain elevated and stable body temperatures (Gardner-Santana and Beaupre 2009). This behavior may be essential in seasonally extreme climates to promote embryonic development (Lourdais et al. 2004). Decreased thermal suitability of open rocky basking sites may further jeopardize already imperiled Timber Rattlesnake populations. For example, Fitch and Pisani (2006) hypothesized that vegetation succession caused the apparent extirpation of a Timber Rattlesnake population in eastern Kansas.

Mechanical removal of trees and shrubs has been used previously to successfully restore habitat for reptiles of conservation concern in temperate climates (Johnson et al. 2016, Pike et al. 2011a). In particular, this approach has been applied to open rocky sites which represent essential, yet potentially limited, habitat for many species (Pike et al. 2011a, Webb et al. 2005), including Timber Rattlesnakes. Pre- and post-treatment monitoring of vegetation removal at rocky sites is important for at least 2 reasons. The first is to determine if the treatment has indeed had the desired effects on the site's vegetation and thermal characteristics. For example, reducing canopy cover to increase the thermal suitability of a site may also increase the prevalence of extreme low or high temperatures (Currylow et al. 2012). The second reason is to document use of post-treatment sites by both the target species and potential predator and prey species (e.g., Herr et al. 2020, Pike et al. 2011b).

We used a before–after, control–impact design to evaluate the effects of tree removal on the thermal characteristics of south-facing rocky sites that could serve as potential Timber Rattlesnake basking sites for the sole remaining population of Timber Rattlesnakes in New Hampshire (Clark et al. 2011). This population declined

from ~40 individuals during 1995–2005 to ~19 individuals following an unusually wet summer in 2006, likely due to the combination of low genetic diversity and snake fungal disease (Clark et al. 2011, Lorch et al. 2016). In the years prior to this study, the population has slowly increased in response to successful reproduction (M.N. Marchand, unpubl. data). Timber Rattlesnakes in this population have access to and utilize ~5 rocky sites for basking and gestation that are characterized by low levels of canopy cover relative to the surrounding landscape. However, vegetation succession in the absence of natural disturbance over the past several decades has resulted in increased shading of some of these confirmed basking sites. Given the limited number of potential basking sites, there was particular interest in using habitat management to increase the number of potential basking sites available to this population by reducing canopy cover at additional south-facing rocky slopes to increase their thermal suitability for Timber Rattlesnakes.

We addressed 3 specific research questions: (1) how did tree removal change the thermal environment of potential basking sites?, (2) did tree removal result in increased use of potential basking sites by Timber Rattlesnakes?, and (3) did tree removal result in increased use of potential basking sites by potential predators and prey of Timber Rattlesnakes? We hypothesized that tree removal would result in warmer and more variable daily temperatures with greater extremes. We also anticipated that observations of Timber Rattlesnakes at our treatment sites would increase following tree removal. Finally, we expected that potential predators and prey would increase their use of treatment areas following tree removal because of greater foraging opportunities created by open vegetation structure and increased vegetative regrowth.

Field-site Description

We identified 3 potential basking sites in April 2014 that were accessible to rattlesnakes in our study population. Each site was characterized by south-facing rocky slopes with many rock crevices but had high canopy cover and shading in contrast to confirmed basking sites with similar substrates but relatively low canopy cover. The approximate extent of potential basking habitat at each site was 0.24 ha (Site A), 0.11 ha (Site B), and 0.10 ha (Site C). Site A included ~0.13 ha of south-facing rocky slope and ~0.11 ha of forest with multiple patches of exposed rock. We did not systematically monitor these 3 sites for rattlesnake use prior to habitat management. However, during the 9 years prior to habitat management, 2 of the authors (B.J. Clifford and M.N. Marchand) conducted multiple opportunistic visual surveys annually at these sites in addition to systematic hibernaculum surveys, rattlesnake radio-telemetry monitoring, and other field projects in the vicinity of this population. We observed no Timber Rattlesnake use of these sites prior to this study. We selected sites A and B as treatments and left site C as a control site. The vegetation community at and surrounding the sites was upland deciduous forest consisting of *Quercus alba* L. (White Oak), *Quercus velutina* (Lamarck) (Eastern Black Oak), *Betula lenta* L. (Black Birch), and *Pinus strobus* L. (Eastern White Pine). Common shrub species included *Gaylussacia baccata* (Koch) (Black

Huckleberry), *Vaccinium angustifolium* (Aiton) (Lowbush Blueberry), and *Kalmia angustifolia* L. (Sheep Laurel). The site had no recent history of logging or disturbance prior to this study.

Management personnel estimated the diameter at breast height (DBH) of all trees across the entirety of sites A and B and felled all trees greater than ~5 cm DBH approximately 15–30 cm from the ground using chainsaws during the fall of 2014 after rattlesnakes had returned to the hibernaculum. Predominant tree species felled at each site included Black Birch, White Oak, Eastern Black Oak, and Eastern White Pine. No wheeled vehicles were used within the sites. Most trees were left where they fell but some were cut into smaller pieces and removed by hand from the site to maximize solar exposure to suitable basking rocks.

Methods

Pre- and post-treatment monitoring

We measured pre- and post-treatment canopy cover on 21 August 2014 and 22 August 2015, respectively, at 16 locations within each site. Locations were arranged in a 4 × 4 grid separated by 5 m. We calculated percent canopy cover at each location with a spherical densiometer following Stricker (1959) and placed a single iButton temperature data logger (model DS1921G#F50, Maxim Integrated Products, Inc., Sunnyvale, CA) ~0.15 m off the ground. We programmed loggers to record the temperature (°C) every 2 hours daily from 0100 to 2300 for 21 weeks (14 May–7 October) during 2014 and 2015 corresponding generally to the season during which Timber Rattlesnakes in this population are active. Our iButtons received varying degrees of sunlight depending on their exact position and time of day and were also potentially subject to thermal radiation from the nearby substrate. Our temperature readings do not, therefore, represent shaded air temperature but rather a measure of the thermal environment incorporating both air temperature and direct and indirect thermal radiation. Canopy cover and temperature data were recorded at the same locations each year.

We monitored wildlife use of our sites using 2 time-lapse cameras (model LTL Acorn 5210A, Acorn Camera, Futian, Shenzhen, China) at each of the 3 sites during 19 May–6 September 2014, 11 May–17 September 2015, and 17 May–9 September 2016. We programmed cameras to take photographs every 5 min per 24-hr period. Cameras had a maximum effective range of ~20 m with the flash. We mounted cameras ~2 m above ground level on small trees that were not removed during site management to provide independent, non-overlapping vantage points that remained stationary throughout the study. We decided to monitor sites using time-lapse cameras in order to provide 24-hr monitoring independent of weather conditions and daily and seasonal variation in rattlesnake activity. We visited sites approximately every 5–7 days to replace camera batteries and memory cards.

Timber Rattlesnake radio telemetry

We captured Timber Rattlesnakes for radio telemetry opportunistically during visual searches around the hibernaculum and known basking sites from 2014 to

2016. Professional veterinarians surgically implanted radio transmitters (5-g SB-2T and 9-, 11-, and 13-g SI-2T transmitters, Holohil Systems Ltd., Carp, ON, Canada) into 12 rattlesnakes (Reinert and Cundall 1982). We monitored 4 rattlesnakes for 1 year, 7 rattlesnakes for 2 years, and 1 rattlesnake for 3 years. All telemetered rattlesnakes were >300 g, and transmitters were <3% of the body weight of each rattlesnake. Internal transmitters for some individuals were replaced prior to battery failure to extend their tracking duration across multiple years. We visually located radio-tracked rattlesnakes approximately once every 8 days and recorded their locations using a handheld GPS unit. We classified all telemetry locations as occurring in open-canopied (e.g., rocky-outcrop basking areas, wetlands, a gravel pit, and clearcuts and associated skid trails) or closed-canopied habitats using field observations. We used observations from 15 May to 15 September so as to exclude observations around the hibernaculum associated with egress and ingress and excluded any additional observation of snakes around the hibernaculum.

Data analyses

We tested for differences in canopy cover among years and sites using generalized linear models (GLM) with beta-error distributions fit using the ‘betareg’ package (v. 3.1-2; Cribari-Neto and Zeileis 2010) in program R (version 3.6.2; R Core Team 2017). Because values of 0 and 1 are not accommodated in a beta distribution, we transformed our data using the equation $(y \times (n - 1) + 0.5) / n$ (Smithson and Verkuilen 2006). We modeled the mean and precision parameter using the same parameterization to improve residual homogeneity. We fit a model with an interactive effect of site and year and conducted 15 post-hoc pair-wise tests between all combinations of site and year. We adjusted *P* values to reduce familywise error rates using sequential Bonferroni corrections with the ‘p.adjust’ function in R (Holm 1979) and used $\alpha = 0.05$ to determine statistical significance.

We tested for effects of tree removal on temperature using mixed-effects models to account for temporal autocorrelation and individual logger effects. We modeled bi-hourly temperature using a generalized additive mixed model in the ‘mgcv’ package (v. 1.8-23; Wood 2018) using a smooth term with a cubic regression spline for hour to allow for non-linear daily changes in temperature. We included logger and day of the year as nested smooth-term random effects. We modeled minimum and maximum temperature using linear mixed-effects models in the ‘nlme’ package (v. 3.1-140; Pinheiro et al. 2019) with nested random effects of logger, month, and day of the month and visually confirmed that residuals adhered to assumptions of normality and homogeneity. We modeled the coefficient of variation (CV) of daily temperature using a generalized linear mixed model (GLMM) with a gamma error distribution and log link in the ‘glmmTMB’ package (Brooks et al. 2017) with nested random effects of logger, month, and day of the month. We fit all models with an interactive effect of year and site and tested for pair-wise differences as described above.

We modeled the proportion of temperature readings by day and by logger within the min–max of selected body temperatures for free-ranging gravid female Timber

Rattlesnakes in Arkansas (25.2–31.7 °C, hereafter PropGravidTemp; Gardner-Santana and Beaupre 2009) using a Bayesian GLMM with a beta-error distribution in the ‘brms’ package (Burkner 2017, 2018) with nested random effects of logger, month, and day of the month. We transformed our proportional data as described above. We included the interactive effect of year and site as fixed effects. We used 50,000 warm-up iterations followed by 100,000 iterations retaining every 20th draw over 3 chains. We drew inferences using the mean posterior predicted values and their 95% credible intervals. Finally, we calculated the number of days where the temperature was >31.7 °C or >37.4 °C for at least 1 bi-hourly temperature reading across all loggers at a site. The latter value was the maximum observed body temperature of free-ranging adult Timber Rattlesnakes in Arkansas (Wills and Beaupre 2000). We note that while our temperatures are not operative temperatures (Bakken et al. 1985), they nonetheless should provide a closer approximation of the potential body temperatures available to Timber Rattlesnakes than air temperature.

To compare potential Timber Rattlesnake predator and prey use of treatment sites, we determined the number of sightings (hereafter events) recorded by our time-lapse cameras for potential predators and prey (Table 1). We considered small mammals (e.g., *Tamias* [chipmunks] and *Sciurus* and *Tamiasciurus* [squirrels]) and passerine birds as potential prey (Clark 2002) and medium and large mammalian carnivores and raptors as potential predators (Ernst and Ernst 2003, Herr et al. 2020). Wildlife observations were identified to species where possible. We combined multiple successive sightings of a single individual into a single event. Events were combined for the 2 cameras within each site to provide a total count of wildlife events per year per site. We used Fisher’s exact tests to test if changes in the number of recorded events of potential prey between pre- and post-treatment years (separate tests for 2015 and 2016) differed between either treatment site (A or B) and the control site. We conducted tests for all potential prey and mammals and passerine birds separately. Sample sizes were insufficient for analysis of potential predator events.

Results

Canopy cover

Mean canopy cover did not differ among any sites pre-treatment ($P \geq 0.92$) but decreased at treatment Site A from 91.8% to 10.6% and decreased at treatment Site B from 92.7% to 10.7% following canopy removal ($P \leq 0.0001$, Fig. 1). Mean canopy cover at Site C increased from 91.4% to 94.5% between 2014 and 2015 ($P = 0.0120$).

Temperature

Data loggers collected 169,344 temperature readings, and 2 loggers failed (2% failure rate). Measures of hourly temperature, daily minimum and maximum temperature, and the CV of daily temperature were all influenced by an interactive effect of site and treatment ($P < 0.0001$), such that these measures were all higher in the treated sites in the post-treatment year, 2015, with the exception of daily

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Table 1. Number of events of Timber Rattlesnakes and potential Timber Rattlesnake prey and predators recorded by time-lapse cameras at 3 potential Timber Rattlesnake basking sites in southern New Hampshire before and after canopy removal. 2014 is a pre-treatment year and 2015 and 2016 are post-treatment years. Cameras were operational 19 May–6 September 2014, 11 May–17 September 2015, and 17 May–9 September 2016 and programmed to take photographs every 5 min per 24-hr period.

Taxon	Site A (treatment)			Site B (treatment)			Site C (control)			Total
	2014	2015	2016	2014	2015	2016	2014	2015	2016	
<i>Tamias striatus</i> L. (Eastern Chipmunk)	16	19	30	15	35	19	11	22	12	179
Passerine Birds	11	23	15	3	26	22	2	2	6	110
<i>Sciurus carolinensis</i> Gmelin (Eastern gray Squirrel)	1	6	0	5	1	1	4	4	11	33
Small mammal (unknown spp.)	1	7	0	3	2	0	0	15	1	29
Raptor Birds	0	1	0	1	2	1	1	1	0	7
<i>Procyon lotor</i> L. (Raccoon)	0	1	0	1	3	1	1	0	0	7
<i>Crotalus horridus</i> L. (Timber Rattlesnake)	0	2	0	0	0	3	0	1	0	6
<i>Ursus americanus</i> (Pallas) (American Black Bear)	0	1	1	0	0	0	0	1	0	3
<i>Lynx rufus</i> (Schreber) (Bobcat)	0	0	0	2	0	0	1	0	0	3
<i>Canis latrans</i> (Say) (Coyote)	0	0	1	0	0	0	0	0	1	2
<i>Tamiasciurus hudsonicus</i> (Erxleben) (American Red Squirrel)	0	1	0	0	0	0	0	0	0	1
Potential prey	29	56	45	26	64	42	17	43	30	352
Potential prey, mammals only	18	33	30	23	38	20	15	41	24	242
Potential predators	0	3	2	4	5	2	3	2	1	22

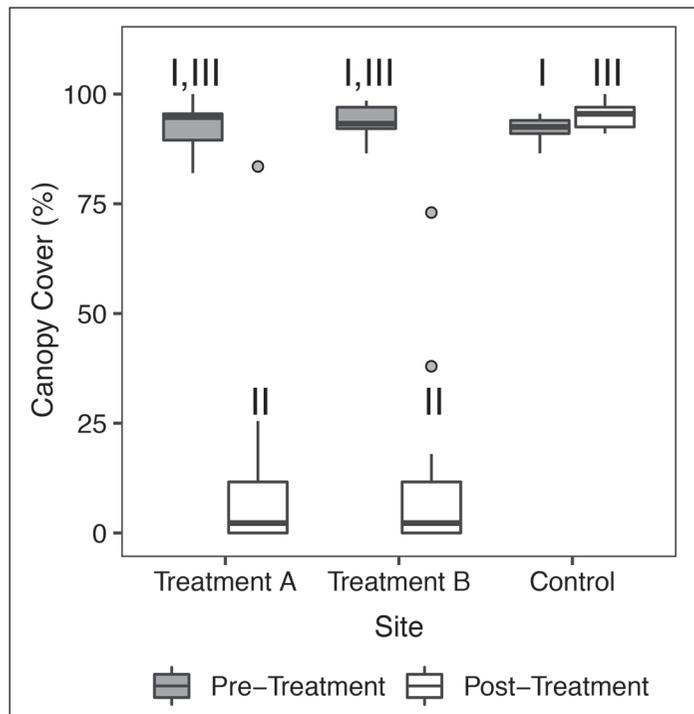
minimum temperature which showed more nuanced changes. Following canopy removal, mean temperature at treatment sites A and B increased from 18.2 °C and 18.1 °C to 20.5 °C and 20.7 °C, respectively, and was higher than mean temperature at Site C during 2015 ($P \leq 0.0001$; Fig. 2). Mean temperature at site C did not differ between years (2014 = 18.0 °C, 2015 = 18.1 °C, $P = 0.63$).

Mean predicted maximum temperature increased at treatment site A from 24.4 °C to 35.3 °C and increased at treatment site B from 24.0 °C to 35.0 °C following canopy removal. Mean predicted maximum temperature at treatment sites A and B was higher than that at Site C during 2015 ($P \leq 0.0001$; Fig. 3). There were no differences in maximum temperature between sites during 2014 ($P \geq 0.64$). Maximum temperature at site C increased from 23.9 °C to 25.4 °C between 2014 and 2015 ($P < 0.0001$).

The magnitude of change in minimum temperature between 2014 and 2015 at treatment site B (13.1 °C vs. 13.5 °C, respectively, $P = 0.0002$) and site C (13.1 °C vs. 14.1 °C, respectively, $P < 0.0001$) was relatively small. During 2015, the predicted mean minimum temperature for site C did not differ from that in site B ($P = 0.0856$; Fig. 3) nor did minimum temperature differ between 2014 and 2015 at treatment site A (13.4 °C vs. 13.3 °C, respectively, $P = 1.00$).

Following canopy removal, the mean predicted CV of temperature at both treatment sites A and B increased from 6.0% to 10.8% and was higher than the mean predicted CV of temperature at site C during 2015 (6.0%, $P \leq 0.0001$; Fig. 3). Mean predicted CV of temperature at site C during 2014 was 5.9% and was not different from that of Site C during 2015 ($P = 0.37$).

Figure 1. Mean canopy cover (%) pre- (August 2014) and post-treatment (August 2015) at 3 potential Timber Rattlesnake basking sites in southern New Hampshire before and after canopy removal. Canopy cover was measured at 16 locations at each site. Groups with different Roman numerals are significantly different ($P \leq 0.01$).



The proportion of bi-hourly readings within the min–max of observed body temperatures of free-ranging gravid female Timber Rattlesnakes (PropGravidTemp) was similar across sites during 2014 (0.07–0.08; Fig. 3). PropGravidTemp increased slightly at site C from 2014 (95% credible interval = 0.063–0.072) to 2015 (95% credible interval = 0.077–0.087). In contrast, PropGravidTemp increased

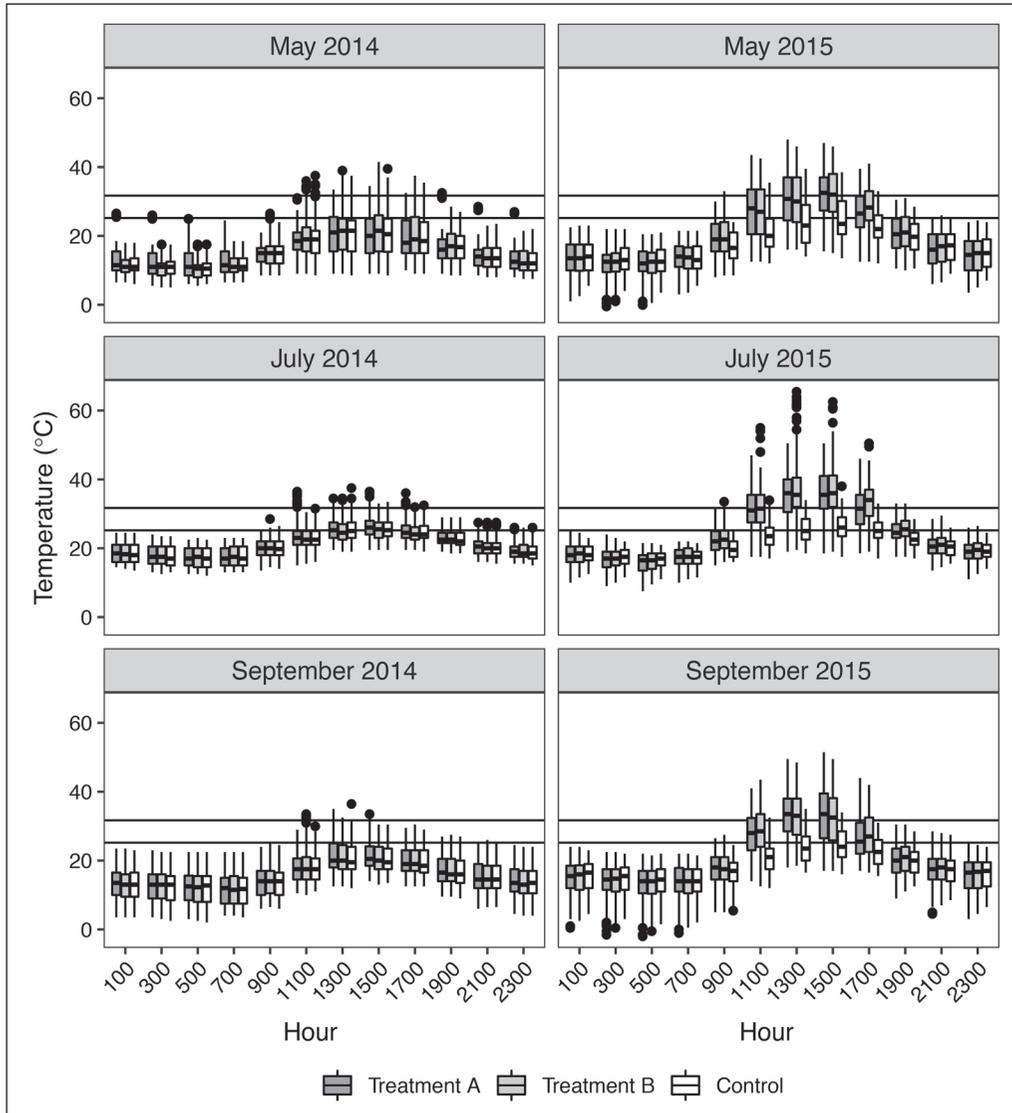


Figure 2. Distributions of bi-hourly temperatures pre- (2014) and post-treatment (2015) during 3 months (May, July, September, selected for brevity) at potential Timber Rattlesnake basking sites in southern New Hampshire before and after canopy removal. Temperature was measured at 16 locations within each site. The 2 horizontal lines represent 25.2 °C and 31.7 °C, which are the minimum and maximum, respectively, previously published selected body temperatures by free-ranging gravid female Timber Rattlesnakes (Gardner-Santana and Beaupre 2009).

markedly at both treatment sites from 0.08 and 0.07 at Sites A and B during 2014 to 0.15 at both sites during 2015 (Fig. 3).

During 2014, the site-wide bi-hourly temperature exceeded 31.7 °C for all loggers for only 1 bi-hourly reading during 1 day for site A, 2 days for Site B, and no days for the control site (Table 2). The site-wide bi-hourly temperature readings

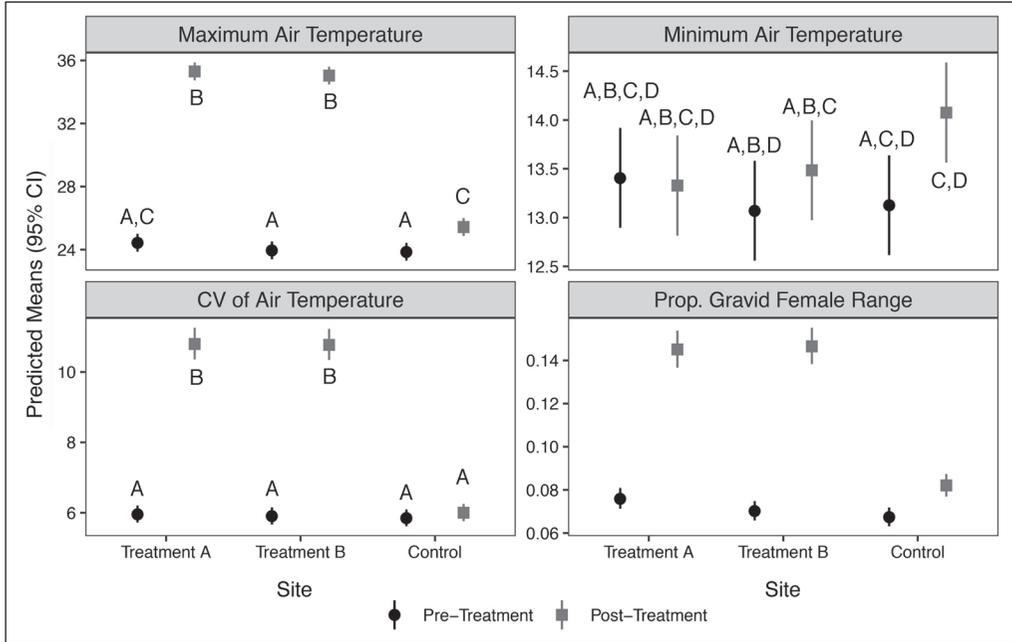


Figure 3. Predicted means and 95% CI by site and year for daily maximum temperature (°C), daily minimum temperature (°C), the coefficient of variation (CV) of daily temperature, and the proportion of bi-hourly temperature readings within the observed min–max of selected body temperatures of free-ranging gravid Timber Rattlesnakes in Arkansas (25.2–31.7 °C, Prop. Gravid Female Range) at 3 potential Timber Rattlesnake basking sites in southern New Hampshire before (2014) and after (2015) canopy removal. Bi-hourly temperature was measured at 16 locations at each site. Groups with different letters are significantly different ($P < 0.05$).

Table 2. Number of days where at least 1 bi-hourly temperature reading was >31.7 °C or >37.4 °C (parentetical values) across all 16 iButton data loggers at a site across 3 potential Timber Rattlesnake basking sites in southern New Hampshire before (2014) and after (2015) canopy removal. Temperatures are the maximum hourly mean body temperature of free-ranging gravid Timber Rattlesnakes (Gardner-Santana and Beaupre 2009) or the maximum observed body temperature of adult Timber Rattlesnakes (Wills and Beaupre 2001) in Arkansas, respectively.

Month	2014			2015		
	Control	Treatment A	Treatment B	Control	Treatment A	Treatment B
May	0	1	2	1	4	8 (2)
June	0	0	0	0	2	17 (3)
July	0	0	0	0	6	20 (8)
August	0	0	0	0	4	13
September	0	0	0	0	5	2

never exceeded 37.4 °C during 2014. During 2015, site-wide bi-hourly temperature readings for the control site exceeded 31.7 °C for a single hour (Table 2). In contrast, sites A and B had 2–20 days per month where at least 1 site-wide bi-hourly temperature reading exceeded 31.7 °C (Table 2). However, no more than 3 bi-hourly temperature readings exceeded 31.7 °C per day. These readings most often occurred at 1100, 1300, and 1500 hrs. Site-wide bi-hourly temperature readings exceeded 37.4 °C only in site B during 2015 for 2 days in May, 3 days in June, and 8 days in July and only exceeded 37.4°C for 1–2 bi-hourly readings during these days.

Wildlife camera observations

We recorded a total of 554,564 photographs across our 3 sites over 3 years ($n_{2014} = 154,619$, $n_{2015} = 210,378$, $n_{2016} = 189,567$). These photographs yielded a total of 373 unique events of potential Timber Rattlesnake predator and prey species (Table 1). *Tamias striatus* L. (Eastern Chipmunk) was the most frequently detected potential prey species ($n = 179$, 51%) followed by passerine birds ($n = 110$, 31%). We found no differences in the proportional changes of potential prey events between 2014 and 2015 and 2014 and 2016 ($P \geq 0.10$). There were few events for potential Timber Rattlesnake predators (raptors: $n = 7$; *Procyon lotor* (L.) [Raccoon]: $n = 7$; *Ursus americanus* (Pallas) [Black Bear]: $n = 3$; *Lynx rufus* (Schreber) [Bobcat]: $n = 3$; *Canis latrans* (Say) [Coyote]: $n = 2$; Table 1). Timber Rattlesnakes were not detected by camera at any sites during 2014. We detected 1 individual Timber Rattlesnake at site A during 2015 (single events with multiple photographs on 26 and 27 June). A second Timber Rattlesnake was detected at site B during 2016 (single events with multiple photographs of 25 and 28 July and 2 August; we suspected these photographs represented a single individual based on the size of the snake and the specific location in the photograph). A third Timber Rattlesnake was detected in a single photograph at site C on 23 August 2015.

Timber Rattlesnake radio telemetry

We monitored 1 male, 3 non-gravid females, and 1 gravid female during 2014; 5 males, 1 non-gravid female, and 1 gravid female during 2015; and 8 males and 1 non-gravid female during 2016. The gravid female in 2015 was also monitored during 2014 as a non-gravid female. We obtained 94 telemetry observations during 2014, 101 during 2015, and 78 during 2016 between 15 May and 15 September. The median proportion of observations across rattlesnake-years in open-canopied habitats was 0.10 (min–max = 0.00–0.80) for males ($n = 14$), 0.11 (min–max = 0.00–0.40) for non-gravid females ($n = 5$), and 0.66 (min–max = 0.52–0.80) for gravid females ($n = 2$). No telemetered rattlesnakes were detected in our sites prior to canopy removal. The only observation of a telemetered rattlesnake using a post-treatment site was a single observation of a male on site A on 25 June 2015. This individual was also detected by a time-lapse camera during the following 2 days.

Discussion

Our tree-removal treatments substantially reduced canopy cover at our treatment sites making them structurally similar to basking and gestation sites used by Timber Rattlesnakes elsewhere in northeastern North America (Brown 1993). Tree removal also resulted in warmer, yet more variable, temperatures and a greater proportion of temperature readings within the min–max of observed body temperatures of gravid female Timber Rattlesnakes. The timber cutting likely improved the thermal suitability of our treatment sites for Timber Rattlesnake basking and gestation for 2 reasons. First, snakes often maintain elevated body temperatures during ecdysis and gestation (Gardner-Santana and Beaupre 2009, Graves and Duvall 1993, Peterson et al. 1993), and warmer environmental temperatures may more easily facilitate this behavior. Herr et al. (2020) also found lower thermal suitability at Timber Rattlesnake gestation sites with higher canopy cover. Johnson et al. (2016) found that thermal conditions at plots where shrub cover was removed were similar to those at known basking and gestation sites for *Sistrurus catenatus* (Rafinesque) (Eastern Massasauga). Increasing the amount of incident solar radiation to potential retreat sites (e.g., basking rocks) also increases retreat-site temperatures (Pringle et al. 2003, Webb et al. 2005), which may increase opportunities for thermoregulation within retreat sites (Huey et al. 1989). Second, Timber Rattlesnakes in New Hampshire are at the northern edge of their range, where relatively short growing seasons (i.e., 5–6 months) result in long life histories (Brown 2016, Martin 2002, Martin et al. 2008). Warmer thermal conditions at potential basking sites may help alleviate the challenges of completing gestation within a thermally constrained activity season, particularly during cooler summers (Lourdais et al. 2002, 2004; Peterson et al. 1993).

Reduced canopy cover may exacerbate temperature extremes, and we observed higher maximum temperatures post-treatment. Daily maximum temperature readings repeatedly exceeded 37.4 °C, the maximum observed body temperature for Timber Rattlesnakes in Arkansas (Wills and Beaupre 2000), and reached as high as 65.5 °C. In contrast, minimum temperatures varied much less across sites, although the only temperature readings <0° C from May–September were at our post-treatment sites. Studies on snakes measuring operative temperatures (Bakken et al. 1985) using physical models (i.e., painted copper pipes with the same diameter and reflective characteristics of the study species) often record operative temperatures in the sun >60 °C (Peterson et al. 1993, Wills and Beaupre 2000). However, these temperature extremes do not necessarily indicate thermal unsuitability of post-treatment sites for Timber Rattlesnakes. Reptiles can use behavioral thermoregulation (e.g., moving between sun and shade, changing basking positions, etc.) to maintain body temperatures substantially cooler or warmer than the surrounding environment (Kearney and Predavec 2000, Peterson et al. 1993) as exemplified by the thermoregulatory behavior of many gravid snakes (Blouin-Demers and Weatherhead 2001a, Gardner-Santana and Beaupre 2009). Reptiles may also select thermally optimal shelter sites to maintain selected body temperatures while completely under cover (Huey et al. 1989, Shoemaker and Gibbs 2010, Webb and

Shine 1998). We did not measure the availability of potential shelter sites (e.g., basking rocks, brush piles) or the thermal characteristics of such shelter sites. However, our 3 management sites were specifically selected because of abundant rock cover, suggesting that opportunities for Timber Rattlesnakes to use behavioral thermoregulation to avoid temperature extremes were readily available.

Our camera-trap data suggest that canopy removal did not strongly affect the larger community of potential Timber Rattlesnake predator and prey species although our small number of sites limited our ability to infer broader patterns. There was a trend towards greater use of treatment sites by passerine birds relative to the control site, but the differences in year-to-year changes in events were not statistically significant. We also did not find strong evidence that tree removal increased the use of our treatment sites by potential rattlesnake predators. However, our use of 5-min photograph intervals was chosen based on rattlesnake basking behavior and may have limited our ability to detect other wildlife, particularly aerial activity of avian predators and prey. Vegetation obstruction may have also limited our ability to detect small-bodied wildlife, although we did detect multiple small-mammal taxa as well as amphibians and reptiles (B.J. Clifford, unpubl. data). Vegetative ground cover was scarce at our 3 sites prior to tree removal but increased in our treatment sites following tree removal, and small shrubs such as Lowbush Blueberry and Black Huckleberry were abundant by 2016. Increased shrub cover may provide Timber Rattlesnakes with cover from potential predators (c.f., Herr et al. 2020) and increased basking cover (Shoemaker and Gibbs 2010), although additional data are needed to test these hypotheses.

While we detected Timber Rattlesnakes at all 3 sites using time-lapse cameras, we only observed basking behavior (confirmed through multiple photographs) at our post-treatment sites. One telemetered rattlesnake was observed within a treatment site, and this same individual was detected using a camera highlighting the value of time-lapse cameras for monitoring rattlesnake basking activity. However, our small numbers of telemetered rattlesnakes, particularly gravid females, limited our ability to evaluate site use by telemetered rattlesnakes. Rattlesnake use of our treatment sites could have been in response or coincidental to tree removal. Timber Rattlesnakes in Pennsylvania did not alter their seasonal movement patterns in response to clearcut logging despite the increase in open-canopied habitats (Reinert et al. 2011). A relative lack of behavioral plasticity may, therefore, have contributed to the low number of Timber Rattlesnake observations within our treatment sites. However, we did not detect rattlesnakes at these sites prior to canopy removal in 9 years of field work at this population, which suggests that rattlesnake use of our treatments sites was a response to tree removal, although additional research is needed to more fully test this hypothesis. Other studies have reported rapid reptile colonization following canopy removal (e.g., Pike et al. 2011b). Johnson et al. (2016) found that gravid female Eastern Massasaugas selectively used basking sites within 1–4 years following mechanical shrub removal, although treated areas occurred within known Massasauga gestation sites. Additionally, the cleared sites in our study increased the availability of open basking habitat at a landscape scale. Our results suggest that

tree removal around potential basking sites likely improves the quality of the thermal environment for Timber Rattlesnakes, particularly in landscapes dominated by closed-canopy forests. Nevertheless, our observations of telemetered rattlesnakes and those from other studies (e.g., Brown 1993, Reinert 1984) also highlight the importance of forest habitats for Timber Rattlesnake foraging.

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Literature Cited

- Angilletta, M.J., Jr. 2001. Thermal and physiological constraints on energy assimilation in a widespread lizard (*Sceloporus undulatus*). *Ecology* 82:3044–3056.
- Bakken, G.S., W.R., Santee, and D.J. Erskine. 1985. Operative and standard operative temperature: tools for thermal energetics studies. *American Zoologist* 25:933–943.
- Ballinger, R.E., and K.S. Watts. 1995. Path to extinction: Impact of vegetational change on lizard populations on Arapaho Prairie in the Nebraska Sandhills. *American Midland Naturalist* 134:413–417.
- Bauder, J.M., A.G. Stengle, M. Jones, M.N. Marchand, D. Blodgett, B. Hess, B. Clifford, and C.L. Jenkins. 2018. Population demographics, monitoring, and population genetics of Timber Rattlesnakes in New England. Final report to the Northeast Regional Conservation Needs (RCN) Program. https://rcngrants.org/sites/default/files/final_reports/WMI_Timber_Rattlesnake_Report_final_2_9_18.pdf. Accessed 9 February 2018.
- Blouin-Demers, G., and P.J. Weatherhead. 2001a. Thermal ecology of Black Rat Snakes (*Elaphe obsoleta*) in a thermally challenging environment. *Ecology* 82:3025–3043.
- Blouin-Demers, G., and P.J. Weatherhead. 2001b. An experimental test of the link between foraging, habitat selection, and thermoregulation in Black Rat Snakes, *Elaphe obsoleta obsoleta*. *Journal of Animal Ecology* 70:1006–1013.
- Brooks, M.E., K. Kristensen, K.J. van Benthem, A. Magnusson, C.W. Berg, A. Nielsen, H.J. Skaug, M. Maechler, and B.M. Bolker. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal* 9:378–400.
- Brown, W.S. 1993. Biology, status, and management of the Timber Rattlesnake (*Crotalus horridus*): A guide for conservation. Herpetological Circular No. 22. Society for the Study of Amphibians and Reptiles, Lawrence, KS. 78 pp.
- Brown, W.S. 2016. Lifetime reproduction in a northern metapopulation of Timber Rattlesnakes (*Crotalus horridus*). *Herpetologica* 72:331–342.
- Burkner, P.-C. 2017. brms: An R package for Bayesian multilevel models using STAN. *Journal of Statistical Software* 80:1–28.
- Burkner, P.-C. 2018. Advanced Bayesian multilevel modeling with the R package brms. *The R Journal* 10:395–411.

- Clark, R.W. 2002. Diet of the Timber Rattlesnake, *Crotalus horridus*. *Journal of Herpetology* 36:494–499.
- Clark, R.W., W.S. Brown, R. Stechert, and K.R. Zamudio. 2008. Integrating individual behaviour and landscape genetics: The population structure of Timber Rattlesnake hibernacula. *Molecular Ecology* 17:719–730.
- Clark, R.W., M.N. Marchand, B.J. Clifford, R. Stechert, and S. Stephens. 2011. Decline of an isolated Timber Rattlesnake (*Crotalus horridus*) population: Interactions between climate change, disease, and loss of genetic diversity. *Biological Conservation* 144:886–891.
- Cribari-Neto, F., and A. Zeileis. 2010. Beta regression in R. *Journal of Statistical Software* 34:1–24.
- Currylow, A.F., B.J. MacGowan, and R.N. Williams. 2012. Short-term forest management effects on a long-lived ectotherm. *PLoS ONE* 7(7):e40473.
- Dubois, Y., G. Blouin-Demers, B. Shipley, and D. Thomas. 2009. Thermoregulation and habitat selection in Wood Turtles, *Glyptemys insculpta*: Chasing the sun slowly. *Journal of Animal Ecology* 78:1023–1032.
- Ernst, C.H., and E.M. Ernst. 2003. Snakes of the United States and Canada. Smithsonian Books, Washington, DC. 680 pp.
- Fitch, H.S. 1999. A Kansas Snake Community: Composition and Change over Fifty Years. Krieger, Malabar, FL. 165 pp.
- Fitch, H.S., and G.R. Pisani. 2006. The Timber Rattlesnake in northeastern Kansas. *Journal of Kansas Herpetology* 19:11–15.
- Gardner-Santana, L.C., and S.J. Beaupre. 2009. Timber Rattlesnakes (*Crotalus horridus*) exhibit elevated and less variable body temperatures during pregnancy. *Copeia* 2009:363–368.
- Gilliam, F.S., and W.J. Platt. 1999. Effects of long-term fire exclusion on tree species composition and stand structure in an old-growth *Pinus palustris* (Longleaf Pine) forest. *Plant Ecology* 140:15–26.
- Graves, B.M., and D. Duvall. 1993. Reproduction, rookery use, and thermoregulation in free-ranging, pregnant *Crotalus v. viridis*. *Journal of Herpetology* 27:33–41.
- Harvey, D.S., and P.J. Weatherhead. 2010. Habitat selection as the mechanism for thermoregulation in a northern population of Massasauga Rattlesnakes (*Sistrurus catenatus*). *Ecoscience* 17:411–419.
- Herr, M.W., J.D. Avery, T. Langkilde, and C.A.F. Howey. 2020. Trade-off between thermal quality and predation risk at Timber Rattlesnake gestation sites. *Journal of Herpetology* 54:196–205.
- Holm, S. 1979. A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics* 6:65–70.
- Huey, R.B. 1982. Temperature, physiology, and the ecology of reptiles. In C. Gans and F.H. Pough (Eds.). *Biology of the Reptilia. Physiology C. Physiological Ecology*. Vol. 12. Academic Press, New York, NY. 570 pp.
- Huey, R.B., C.R. Peterson, S.J. Arnold, and W.P. Porter. 1989. Hot rocks and not-so-hot rocks: Retreat-site selection by Garter Snakes and its thermal consequences. *Ecology* 70:931–944.
- Jaggi, C., and B. Baur. 1999. Overgrowing forest as a possible cause for the local extinction of *Vipera aspis* in the northern Swiss Jura Mountains. *Amphibia-Reptilia* 20:25–34.
- Johnson, B.D., J.P. Gibbs, T.A. Bell Jr., and K.T. Shoemaker. 2016. Manipulation of basking sites for endangered Eastern Massasauga Rattlesnakes. *Journal of Wildlife Management* 80:803–811.

- Kearney, M., and M. Predavec. 2000. Do nocturnal ectotherms thermoregulate? A study of the temperate gecko *Chrisinus marmoratus*. *Ecology* 81:2984–2996.
- Lorch, J.M., S. Knowles, J.S. Lankton, K. Michell, J.L. Edwards, J.M. Kapfer, R.A. Staffen, E.R. Wild, et al. 2016. Snake fungal disease: An emerging threat to wild snakes. *Philosophical Transactions of the Royal Society B-Biological Sciences* 371:20150457.
- Lourdais, O., X. Bonnet, R. Shine, D. Denardo, G. Naulleau, and M. Guillon. 2002. Capital-breeding and reproductive effort in a variable environment: A longitudinal study of a viviparous snake. *Journal of Animal Ecology* 71:470–479.
- Lourdais, O., R. Shine, X. Bonnet, M. Guillon, and G. Naulleau. 2004. Climate affects embryonic development in a viviparous snake, *Vipera aspis*. *Oikos* 104:551–560.
- Martin, W.H. 2002. Life-history constraints on the Timber Rattlesnake (*Crotalus horridus*) at its climatic limits. Pp. 285–306, *In* G.W. Schuett, M. Hoggren, M.E. Douglas and H.W. Greene (Eds.). *Biology of the Vipers*. Eagle Mountain Publishing, Eagle Mountain, UT. 580 pp.
- Martin, W.H., W.S. Brown, E. Possardt, and J.B. Sealy. 2008. Biological variation, management units, and a conservation action plan for the Timber Rattlesnake (*Crotalus horridus*). Pp. 447–462, *In* W.K. Hayes, K.R. Beaman, M.D. Cardwell and S.P. Bush (Eds.). *The Biology of the Rattlesnakes*. Loma Linda University Press, Loma Linda, CA. 606 pp.
- Nowacki, G.J., and M.D. Abrams. 2008. The demise of fire and “mesophication” of forests in the eastern United States. *Bioscience* 58:123–138.
- Peterson, C.R., A.R. Gibson, and M.E. Dorcas. 1993. Snake thermal ecology: Causes and consequences in body-temperature variation Pp. 241–314, *In* R.A. Seigel and J.T. Collins (Eds.). *Snakes: Ecology and Behavior*. McGraw Hill, Inc., NY. 414 pp.
- Pike, D.A., J.K. Webb, and R. Shine. 2011a. Chainsawing for conservation: Ecologically informed tree removal for habitat management. *Ecological Management and Restoration* 12:110–118.
- Pike, D.A., J.K. Webb, and R. Shine. 2011b. Removing forest canopy cover restores a reptile assemblage. *Ecological Applications* 21:274–280.
- Pinheiro, J., D. Bates, S. DebRoy, and D. Sarkar. 2019. nlme: Linear and nonlinear mixed effects models. R Package Version 3.1–140. Available at <http://CRAN.R-project.org/package=nlme>.
- Pringle, R.M., J.K. Webb, and R. Shine. 2003. Canopy structure, microclimate, and habitat selection by a nocturnal snake, *Hoplocephalus bungaroides*. *Ecology* 84:2668–2679.
- Pringle, R.M., M. Syfert, J.K. Webb, and R. Shine. 2009. Quantifying historical changes in habitat availability for endangered species: Use of pixel- and object-based remote sensing. *Journal of Applied Ecology* 46:544–553.
- R Core Team. 2017. R: A language and environment for statistical computing. Version 3.6.2. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>. Accessed 1 October 2017.
- Reinert, H.K. 1984. Habitat variation within sympatric snake populations. *Ecology* 65:1673–1682.
- Reinert, H.K. 1993. Habitat selection in snakes. Pp. 201–240, *In* R.A. Seigel and J.T. Collins (Eds.). *Snakes: Ecology and Behavior*. McGraw-Hill, New York, NY. 414 pp.
- Reinert, H.K., and D. Cundall. 1982. An improved surgical implantation method for radio-tracking snakes. *Copeia* 1982:702–705.
- Reinert, H.K., W.F. Munroe, C.E. Brennan, M.N. Rach, S. Pelesky, and L.M. Bushar. 2011. Response of Timber Rattlesnakes to commercial logging operations. *Journal of Wildlife Management* 75:19–29.

- Roques, K.G., T.G. O'Connor, and A.R. Watkinson. 2001. Dynamics of shrub encroachment in an African savanna: Relative influences of fire, herbivory, rainfall, and density dependence. *Journal of Applied Ecology* 38:268–280.
- Row, J.R., and G. Blouin-Demers. 2006. Thermal quality influences habitat selection at multiple spatial scales in Milksnakes. *Ecoscience* 13:443–450.
- Shoemaker, K.T., and J.P. Gibbs. 2010. Evaluating basking-habitat deficiency in the threatened Eastern Massasauga Rattlesnake. *Journal of Wildlife Management* 74:504–513.
- Smithson, M., and J. Verkuilen. 2006. A better lemon squeezer? Maximum-likelihood regression with beta-distributed dependent variables. *Psychological Methods* 11:54–71.
- Strickler, G.S. 1959. Use of the densitometer to estimate density of forest canopy on permanent sample plots. Research Note 180. United States Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, OR. 5 pp.
- Webb, J.K., and R. Shine. 1998. Thermoregulation by a nocturnal elapid snake (*Hoplocephalus bungaroides*) in Southeastern Australia. *Physiological Zoology* 71:680–692.
- Webb, J.K., R. Shine, and R.M. Pringle. 2005. Canopy removal restores habitat quality for an endangered snake in a fire-suppressed landscape. *Copeia* 2005:849–900.
- Wills, C.A., and S.J. Beaupre. 2000. An application of randomization for detecting evidence of thermoregulation in Timber Rattlesnakes (*Crotalus horridus*) from northwest Arkansas. *Physiological and Biochemical Zoology* 73:325–334.
- Wood, S. 2018. mgcv: Mixed GAM computation vehicle with GCV/AIC/REML smoothness estimation. R package Version 1.8–24. Available online at <http://CRAN.R-project.org/package=mgcv>.