Indirect effect of climate change: Shifts in ratsnake behavior alter intensity and timing of avian nest predation

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A B S T R A C T

Understanding how climate change will affect the abundance, distribution, and behavior of wildlife has garnered substantial attention, but predicting how climate change may alter interspecific relationships is more challenging and has received less attention. Here, we use agent-based modeling to explore how climate warming may alter activity patterns and habitat use of ratsnakes and how this will change their interactions with nesting birds. Overall nest predation by ratsnakes increased with warming environmental temperatures, with a 7% increase in daily nest predation as temperatures warmed by 2 °C. Modest increases in ambient temperature (0.5 °C) caused nocturnal predation by ratsnakes to increase by 15%, particularly in the early spring (200% increase in nocturnal nest predation in March) when nocturnal snake activity is currently limited. Increased nocturnal nest predation can have important demographic consequences beyond nest failure when adult birds on the nest are vulnerable to snakes. Increased temperatures also caused nest predation to increase substantially in forest and forest edge habitats. In a warming world ratsnakes are predicted to use forested habitats more because the thermal heterogeneity of forests buffers snakes against potentially lethal environmental temperatures. If ratsnakes become more concentrated in small forest patches and edges, nest survival in these patches may fall below a sustainable level. Conversely, as temperatures increase, ratsnakes will be less likely to prey on nests in open habitats such as shrublands, which may provide refuges for some nesting birds. Species conservation in a warming world requires understanding how the behavior of both the focal species and its predators are affected.

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1. Introduction

The potential consequences of global climate change on the abundance, distribution, and behavior of wildlife are a growing concern (Thomas et al., 2004; Malcolm et al., 2006; Robinson et al., 2009). To date, most research on animals has focused on species-specific responses to climate change, with relatively little consideration of alterations to community level interactions and the underlying mechanisms. Although more difficult to predict, climate-mediated changes to interspecific relationships could have profound ecological effects. For example, shifts in the onset of avian migration in response to climate change (Parmesan, 2007; Robinson et al., 2009) potentially decouples the timing of breeding

by birds and the availability of their insect prey, thereby lowering nestling survival (Visser and Both, 2005). Similarly, because nest predation is the primary cause of nest failure in temperate songbirds (Ricklefs, 1969; Martin, 1988), climate-mediated changes in predator abundance, distribution or behavior could profoundly affect bird reproductive success, although this hypothesis has yet to be tested. Here, we use ecological modeling to test the hypothesis that changes in snake behavior due to warming temperatures will affect the timing and intensity of predation by ratsnakes (*Pantherophis* spp.; formerly *Elaphe obsoleta*) on songbird nests.

A growing body of evidence has identified snakes as primary predator of many birds' nests (Weatherhead and Blouin-Demers, 2004; Carter et al., 2007; Reidy and Thompson, 2012; DeGregorio et al., 2014a). As ectotherms, it is likely that snakes will be strongly affected by climate warming (Deutsch et al., 2008; Kearny et al., 2009; Sinervo et al., 2009). Recent studies examined snake activity across a latitudinal gradient, using thermal differences associated with latitude as a surrogate for climate change (Sperry et al., 2010;

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Weatherhead et al., 2012). This work predicts both an expansion of seasonal snake activity in response to warmer climates, with snakes becoming active earlier in the spring and continuing later in the fall, and a shift in diel patterns, with snakes in warmer climates switching from diurnal to nocturnal activity at the warmest time of the year. Because snake activity and behavior can be directly linked to songbird nest predation risk (Sperry et al., 2008; Klug et al., 2010; Weatherhead et al., 2010; Cox et al., 2013; DeGregorio et al., 2014b), this shift in seasonal and nocturnal activity is likely to alter the predator-prey interactions between snakes and birds, most likely to the detriment of bird populations.

Nest survival rates often vary seasonally, with nests initiated earlier in the season contributing more to population growth than those initiated later (Borgmann et al., 2013). Nests initiated early in the nesting season often contain more and larger eggs than later nests, indicating that birds invest more in early-season nests (Perrins, 1970; Daan et al., 1990; Nager and Noordwijk, 1995). In areas where snakes are primary nest predators, nest survival rates can vary with snake activity, with high nest survival early in the season before snakes are active and declining as snakes become active during the hotter months (Sperry et al., 2008; Weatherhead et al., 2010). If climate warming allows snakes to become active earlier in the nesting season, nests initiated early in the season may no longer be safe and overall reproductive output for birds may decline.

Nocturnal snake predation on avian nests has been extensively documented across a wide range of ecosystems (e.g., Thompson et al., 1999; Thompson and Burhans, 2003; Reidy et al., 2009; Reidy and Thompson, 2012) and has been implicated as a conservation concern for several imperiled bird species (Carter et al., 2007; Reidy et al., 2009). There is evidence that nocturnal predation by snakes is more successful because most birds cannot defend their nests at night, whereas they might during the day (Hensley and Smith, 1986; Carter et al., 2007). Additionally, for at least one imperiled passerine species, the golden-cheeked warbler (*Dendroica chrysoparia*), nocturnal snake predation may result in the predation of the incubating or brooding female in up to 75% of encounters, resulting in the loss of 14% of breeding females (Reidy et al., 2009). In contrast, the same study found that no incubating or brooding adults were preyed on during the day. If this phenomenon occurs generally for birds, an expansion of nocturnal snake behavior could have severe detrimental impacts on nesting birds, including reduced nest survival, increased adult mortality, and skewed sex ratios resulting from a disproportionate loss of breeding females. A deeper exploration of the link between snake activity patterns (diel and seasonal), temperature, and nest predation is needed to better understand the potential implications of increased nocturnal snake predation on nesting birds.

Snakes preferentially occupy particular habitat patches to facilitate efficient thermoregulation (e.g., Shine, 1987; Charland and Gregory, 1995; Blouin-Demers and Weatherhead, 2001a; Harvey and Weatherhead, 2010). In response to warming temperatures, snakes may not only change the time of day they are active, but also alter the habitats they occupy. Nesting birds may select thermally inhospitable nest sites to minimize predation risk by snakes (Weatherhead and Blouin-Demers, 2004). If climate change results in snakes altering their habitat use, however, nest sites that were once thermally protected from predation by snakes may become vulnerable. Using spatially explicit agent-based modeling (Railsback and Grimm, 2011), we explore how different climate warming scenarios will affect ratsnake activity and habitat use and subsequently avian nest survival. We test the hypothesis that higher ambient temperatures will increase ratsnake predation on nests during cooler periods (night and early season). We also test the hypothesis that warming temperature will cause snakes to occupy different habitats, thus altering habitat-specific nest predation rates. Specifically, we predict that warmer temperatures

will cause snakes to use habitat with more moderate temperatures (mature forests), increasing nest predation rates in this habitat. Similarly, we predict that snakes will reduce their use of open and warmer habitat (shrublands or clear cuts) as they become thermally inhospitable, resulting in less nest predation by snakes in these habitat patches. Further, we expect increasing temperatures will alter the intensity, timing, and location of ratsnake predation on bird nests. In addition to testing our hypotheses, our goal is to use the model to evaluate which of these changes are expected to be most pronounced and to interpret how these changes may affect avian ecology and conservation.

2. Methods

2.1. Study site

Data for our model were collected at and around the Ellenton Bay Set Aside Research Area on the Department of Energy's Savannah River Site, South Carolina (http://srel.uga.edu/set-asides/area1.html). Our model focused on an approximately 450 ha area at the center of the set aside area. For the model, this irregularly shaped area was gridded into 5 m resolution cells and enclosed in a minimal bounding box of 760 ha (609 cells east-to-west and 497 cells north-to-south). Snakes were bound within the closed study area such that they were not allowed to leave or enter. The study area contained a mix of habitat types from mature, closed-canopy forests to younger open forests, and shrublands and clear-cuts. The area was once used for row-crop agriculture and pasture, but since 1951 has been allowed to regenerate naturally. The site is primarily wooded, with mixed forests of laurel oak (*Quercus laurifolia*), loblolly pine (*Pinus taeda*) and slash pine (*Pinus elliottii*) interspersed with open shrubland areas of Chicasaw plum (*Prunus angustifolia*) and blackberry (*Rubus* sp). Areas of the site have been clear-cut. In some areas, long-leaf pine seedlings are present (*Pinus palustris*) and in others shrubby laurel oaks are sprouting from stumps. All clear cut habitats are hot, dry, devoid of canopy cover and have piles of woody debris present. The site also has four utility right-of-ways bisecting the site from East to West. These corridors are maintained by the state utility company and are surrounded by shrubland. Since May 2011, predator–prey interactions between ratsnakes and shrubland bird nests have been studied via nest monitoring, nest cameras, and radiotelemetry of snakes (DeGregorio et al., 2014b).

2.2. Model description and entities

We incorporated three types of individual-based entities in our model: ratsnakes (predators), bird nests (prey), and dynamic thermally variable habitat patches. The model was designed to represent a generic songbird species based on the nesting patterns of the most common local nesting bird (Northern Cardinal [*Cardinalis cardinalis*]) and predation by the ratsnake, the locally dominant nest predator (DeGregorio et al., 2014b). Cardinals are ideal "generic" birds for this study because they nest in a broad range of habitats. We used open-source, agent-based simulation modeling software (NetLogo 5.0: Wilensky, 1999) to investigate how thermal heterogeneity of a patchy landscape and different climate change scenarios will influence the predator–prey interactions between ratsnakes and bird nests. We followed the overview, design concepts, details, and protocol for describing individual-based models suggested by Grimm et al. (2006, 2010). We provide a complete ODD protocol of the model as supplementary material (Appendix A). Additionally, the entire NetLogo model is available upon request. Several previous agent-based models have simulated predator "agents" to explore foraging behavior according to various behavioral rules (e.g., Fronhofer et al., 2012; Ringelman,

2014). Our model differs from previous studies in that snake behavioral decisions are based on the dynamically changing thermal qualities of the environment, with nest predation a byproduct of snake activity and habitat use. Additionally, we use the model to explore plausible climate-warming scenarios for the study region to predict snake behavior and nest predation. The inherent assumptions of our model make it likely that increased ambient temperature will alter the intensity, timing, and location (habitat shifts) of nest predation by ratsnakes. Thus, our goals with this model are to quantify how extensive these changes may be, which changes are likely to be most pronounced, and to evaluate the ramifications of the observed changes.

2.3. Thermal landscape and inputs

Using aerial photographs and extensive ground truthing, we used GIS software (ArcMap 10.0: ESRI Inc., Redlands, CA, USA) to delineate boundaries of the six major habitat types available at the site: deciduous forest, mixed forest, clear cuts, shrublands, forest edge, and wetland. Deciduous forests had a continuous tree canopy greater than 25 m in height and were dominated by laurel oak, live oak (*Quercus virginiana*), and in wetter areas, sweet gum (*Liquidambar styraciflua*). Conversely, mixed forests were drier habitats, lacked a continuous canopy composed of laurel oak and pine, and often had a dense understory of herbaceous vegetation, shrubs, and vines in all areas where sunlight reached the forest floor. Mixed forests were more structurally complex and thermally heterogeneous relative to deciduous forests. Clear cuts were areas that had been logged and were being regenerated by planted long-leaf pine seedlings or laurel oaks sprouting from stumps. All clear cuts were devoid of canopy and often had large amounts of fine and coarse woody debris on the ground. We considered any habitat lacking an overstory canopy (continuous or scattered) and with primarily shrubby or grassy vegetation as shrubland. It should be noted that shrublands often contained scattered, mature laurel oaks that provided cooler micro-sites that were often used by snakes and nesting birds. Finally, we considered forest edge as the 30 m strip of habitat occurring where one of the two forest types abutted any of the other habitat types. Thus, forest edge extended 15 m into the forest and 15 m out from the forest. We chose 30 m as the definition of edge to be consistent with studies of snake habitat use (e.g., Carfagno et al., 2006). Although wetlands occurred at our study site, they were not used by ratsnakes and were excluded from analyses. However, the forest edges at the wetland–forest interfaces were included in analyses. The resulting vector ESRI shapefile map, which delineates the six habitat types and forest edges, provided input to the NetLogo model to establish a habitat type for each 5 m resolution grid cells over the entire study site.

Each macrohabitat type has unique thermal qualities based on its vegetative composition and structure. Our goal was to measure the full range of body temperatures snakes could experience in each habitat (hereafter "operative environmental temperatures": Hertz et al., 1993). To measure operative environmental temperatures we used biophysical models that had the same thermal characteristics as ratsnakes. Each model consisted of a 40 cm length of 1.5 cm diameter copper pipe, filled them with water, painted glossy black and gray to approximate the reflectance of ratsnakes. We suspended a thermocouple in each model and capped the ends with rubber caps and silicone. The thermocouples were attached to miniature temperature loggers (HOBO Temp, ONSET Computer Corp., Pocasset, MA, USA). We programmed temperature loggers to record at 10 min intervals. Similar models have been calibrated with the carcasses of ratsnakes by Blouin-Demers and Weatherhead (2001c) and were found to accurately reflect the internal body temperatures experienced by snakes under a wide range of

Table 1
Regression equations for calculating the body temperature of a resting snake.

Habitat type	Regression equation for calculating the body temperature of a snake
Clear cut	$-1.45 + 0.477 * T + 0.019 * R + 0.151 * Rh + 0.203 * Rain$
Deciduous forest	$0.699 + 0.947 * T - 0.002 * R + 0.008 * Rh + 0.166 * W$
Forest edge	$-10.694 + 0.949 * T + 0.011 * R + 0.153 * Rh$
Mixed forest	$-4.964 + 0.855 * T + 0.007 * R + 0.104 * Rh - 0.381 * W$
Shrubland	$0.11 + 0.889 * T + 0.008 * R + 0.02 * Rh$

where T = temperature (°C), R = solar radiation (W/m^2), Rh = relative humidity (%), and W = wind speed (m/s).

temperatures, humidity, wind, precipitation, and solar radiation conditions.

We placed models in each of the major macrohabitat types at the site and situated models in locations representing the microsites used by ratsnakes (e.g., brushpiles, hollow logs, vine tangles). We placed models to establish the general thermal properties of each habitat type. We left models in place for 2–3 weeks at a time (48 total sites) before retrieving their recorded data. We acquired meteorological data recorded during the same time period at a nearby (~7 km) weather station (courtesy of Savannah River National Laboratory). Using backwards step-wise linear regression we derived a regression equation for each habitat type that related air temperature, relative humidity, solar radiation, rainfall, and wind speed to temperatures recorded by the biophysical models (Table 1). Thus, using local weather station data we were able to calculate operative environmental temperatures for each of the habitat types for each weather record (at 15 min intervals) throughout the bird nesting seasons of 2011–2013. We used these data in our model to calculate a temperature at each patch at each 15-min time step using the regression equations in Table 1 to generate a dynamic thermal landscape, to which the snakes responded.

2.4. Ratsnake movement

Ratsnakes are often associated with forest and forest edge habitat (Weatherhead and Charland, 1985; Durner and Gates, 1993) and appear to use different habitat patches for their thermal properties (Blouin-Demers and Weatherhead, 2001a,b). Ratsnakes placed in thermal gradient chambers preferentially maintain body temperatures of 28 °C (Blouin-Demers and Weatherhead, 2001c). In our dynamic thermal model, ratsnakes are motivated to find and occupy grid cells with a temperature of 28 °C. Similarly, ratsnakes are most likely to move when their body temperature is 28 °C (J.H. Sperry, unpublished data). Based on snake movement data collected through radio-telemetry in Texas (J.H. Sperry, unpublished data) and South Carolina (B.A. Degregorio, unpublished data), modeled snake movement increases linearly with temperature, starting at 0 m per hour at 11 °C to a maximum of 52 m per hour at 28 °C and decreases linearly from that maximum to 0 m per hour at 34 °C. Accordingly, for each 15-min time-step, the distance each snake travels is established. To ensure that a snake would not "jump" over a cell, the total movement was divided into 5-m movement steps. It should be noted that there are three components to "steps". There is the time step, the distance to be moved, and the steps taken to achieve that distance. For instance, if the distance for a snake to move in a time step is 13 m, then steps of 5 m, 5 m, and 3 m will be taken. Before each of those steps, each snake would inspect all of the grid cells within 15 m and ±45 degrees of the direction it was currently facing and then face the grid cell that would provide the temperature closest to the preferred body temperature. To reflect the notion that not all movement decisions in nature are optimal, a degree of randomness was added by having the snake turn a random amount to the right between 0 and 10 degrees, and then back to the left 0–10 degrees, a movement often called a

"wiggle". If a snake is occupying an optimal cell and is surrounded by suboptimal cells, the current heading is not affected by the location of surrounding cells. The "wiggle" move can still alter the heading, and the snake moves in the resulting heading, leaving the current optimal cell. If a snake hits the edge of the map, the wiggle routine is run until the patch ahead is not an edge. Finally a check was made to ensure that a movement ahead was onto a space with an appropriate vegetation type. If this were not true, the snake would repeat the above random turn until true, and finally move forward. Steps were repeated until the required distance was achieved. Snakes could occupy any location within a cell; they were not constrained to the "center" of a cell. Because ratsnakes maintain home ranges, snakes in our model would not move more than 1000 m from their hibernation location, which were typically located in the center of their home ranges at our site (B.A. DeGregorio, unpublished data). The probability of turning toward the home range center increased with distance from that center, such that at 1000 m the probability of turning toward the center of their home range was 100%. Once per day, at noon, snakes made the choice whether to turn back toward center or remain going the way they were going. The probability of turning toward the home-range center increased linearly from 0 to 100% as the snake reached the 1000 m limit. Because our study site was relatively small (460 ha), a 1000 m home range ensured that any individual snake was able to reach and explore a large percentage of the study area comprised of a mix of habitat patch types. Consistent with the reported range of rat snake densities (Fitch, 1963; Stickel et al., 1980), for our model we assumed there were 100 ratsnakes at the site. All snake movements were independent of other snakes on the landscape.

2.5. Bird nests

We used empirically derived data from our field sites (DeGregorio et al., 2014a,b, unpublished data) to estimate timing and placement of nests in our model. Cardinals begin nesting at our site in early March, peak in May, and taper off in July and early August. Therefore we limited our model to 1-March to 1-August. Consistent with observed nesting intensity, we placed 15% of the nests on the landscape in March, 75% in April, and 100% in May. Beginning in June, the number of nests was allowed to decrease to 75% as nests fledged or were destroyed by a snake, and to 45% beginning in July. A subset of nests was initiated on 1 March based on empirical data. When a nest was preyed on or fledged, a 3-day wait period occurred before a nest could be regenerated, which happened if the total number of active nests was below the current monthly number needed. We placed 38% of model nests in shrublands, 10% in open forest, 8% in mature forest, 17% in clear cut, and 27% in forest edge. Each nest existed for a maximum of 22 days (the mean time for a cardinal clutch to hatch and fledge; Poole, 2005) unless a snake moved into the same grid cell, in which case there was a probability of the snake detecting and preying on the nest, which caused the nest to be removed.

Evidence suggests that ratsnakes are more likely to find nests during the nestling stage when more adult activity occurs around the nest and nestlings are presumed to provide odor cues. Thus, if a snake moved into a grid with a nest older than 12 days (presumed to have nestlings), the probability of the snake finding and eating the nest contents was set at 0.8. Nests younger than 12 days (incubation stage) were presumed to be found and eaten by snakes at a probability of 0.2, because much less adult activity occurs around incubating nests, providing fewer clues for predators. Similarly, because adult birds are less likely to actively defend their nest at night (Hensley and Smith, 1986), we assumed that nests located at night were preyed on with a probability of 1.0 whereas nests encountered by snakes during the day were preyed on with a probability of 0.75. Thus, nests >12 days of age encountered during the

day had a probability of being preyed on of 0.6 (0.8 * 0.75), nests encountered during the night with contents <12 days of age were preyed on with a probability of 0.5 (1.0 * 0.2), etc. Although these values are not available in the literature, based on our understanding of rat snake behavior and foraging, we believe these values are realistic. If a nest was not encountered by a snake in 22 days, it was considered successful. The habitat the nest was in, the time the snake encountered the nest, and the number of days the nest had survived until being located by the snake (observation days) were recorded. After a nest had been "preyed on" it was removed from the landscape and a new nest was regenerated at the same location 72 h later, simulating a re-nesting attempt to maintain a constant source of nests available to foraging snakes. Our data suggest that cardinals at this site will attempt to nest in excess of six times per season, often initiating a new nest only days after a nest has failed or fledged.

2.6. Analyses

We conducted 36 simulations of five climate-warming scenarios in which ambient temperatures (based on weather data recorded in 2011, 2012, and 2013) were elevated 0, 0.5, 1, 1.5, and 2 °C for a total of 180 simulations. All ambient temperatures from the weather station were then adapted for each habitat patch based on the regression equations derived from biophysical models. To initiate a simulation we placed ratsnakes on the landscape at randomly determined locations in mature forest (75% of snakes) and open forest (25% of snakes), reflecting the observed distribution and habitats in which this species overwinters at our site based on four years of radio tracking more than 45 individual rat snakes (B.A. DeGregorio, unpublished data). Ratsnakes were randomly initiated within 200 m of the forest edge to represent hibernation locations observed in the field. During the simulation all snakes were able to leave hibernation patches and reach all other available habitat types. For each climate scenario, habitat type, and each month of the active season (March–July) we calculated daily nest predation rates (Mayfield, 1961), defined as:

"(The number of failed nests/Total number of nest observation days)"

We qualitatively compared results from model simulations of contemporary conditions (0 °C increase) to field-collected seasonal nest predation patterns. Additionally, we compared habitat-specific predation-rates generated by the model to those documented in the field. To examine the influence of climate change scenarios on overall nest predation rate we used a univariate general linear model with temperate change scenario as our fixed factor and daily predation rate as our response variable. If differences were detected, we used least significant difference (LSD) post hoc tests to examine differences between the temperature scenarios.

We used a two-way general linear model to examine the influence of month and habitat type on daily predation rate. We used month and habitat as fixed factors and daily predation rate as our response variable. We then used LSD post hoc tests to explore differences between the groups.

To explore how increasing temperatures might alter the timing of predation by snakes on bird nests, we summarized the proportion of predation events occurring during the day (>0600 and <2030 h) relative to during the night. We first examined whether temperature warming scenarios would alter overall timing of nest predation using a general linear model with temperature scenario as a fixed factor and proportion of nests preyed on at night as our response variable. We then used LSD post hoc tests to explore differences between the five temperature change scenarios. To explore how nocturnal nest predation varied by month and

temperature scenario, we used a two-way general linear model with temperature scenario and month as fixed factors and LSD post hoc tests to examine differences between groups.

3. Results

3.1. Model validation

Model and field results were strongly aligned. Overall intensity of daily nest predation rate was similar between the model (0.056) and field results (0.05). Seasonal patterns of predation in the model varied significantly by month ($F = 444.728$, df = 4, $P < 0.001$) and conformed to the pattern expected in the field, with daily predation rate being lowest in March, greatest in April and May and declining slightly later in the summer. These trends align well with reported trends in seasonal ratsnake movement, with ratsnakes moving less later in the summer as temperatures exceed preferred snake body temperatures (e.g., Sperry et al., 2008, 2010). At our field site, daily predation risk from ratsnakes is greatest in forest edge and forested habitats and lowest in open habitats (shrubland and clear cuts). Under contemporary conditions, the model predicted an identical trend, with daily predation rate highest in forest edge followed by deciduous forest then mixed forest and lowest in shrubland and clear cut. Similar trends between field and model predation intensity, seasonality, and habitat-specific rates provide confidence in the model's future projections.

3.2. Seasonal and habitat-specific nest predation

Overall, daily nest predation rate was significantly influenced by increasing ambient temperature ($F = 3.874$, df = 4, $P = 0.004$: Fig. 1). In general, daily nest predation rate increased in a stepwise manner as temperatures increased, with daily predation rate at the 2 °C increase scenario being higher than in all other scenarios ($P < 0.050$) except 1° increase ($P = 0.292$). However, daily predation rate decreased in the 1.5° scenario and it is unclear why this was the case. When ambient temperatures were elevated by 2 °C, overall mean daily nest predation rate increase by 7% relative to contemporary conditions.

Increasing temperatures did not alter the observed seasonal trend in daily nest predation rate reported earlier. However, increases in nest predation rate corresponding to warming temperatures were not equal throughout the nesting season, with daily predation rate during the spring months (March and April) increasing most dramatically, while nest predation in July actually decreased (Fig. 2). A temperature increase of 2 °C caused nest predation in March to increase by 43% relative to contemporary conditions ($P < 0.001$). Similarly, daily nest predation rate in April increased by 10% as temperature warmed by 2 °C ($P = 0.019$). Very

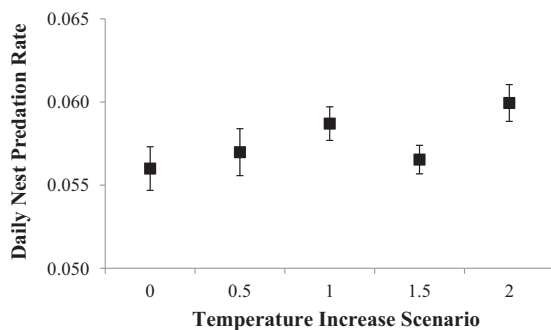**Fig. 1.** Daily nest predation rate (±SE) of songbird nests by ratsnakes (*Elaphe obsoleta*) as a function of five temperature increase scenarios (0–2 °C increments) derived from 180 simulations of an agent-based model.
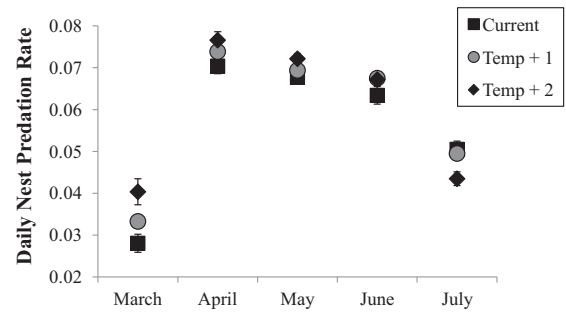
Fig. 2. Monthly mean daily nest predation rates during contemporary temperature conditions and 1° and 2° temperature increase scenarios derived from an agent-based model.
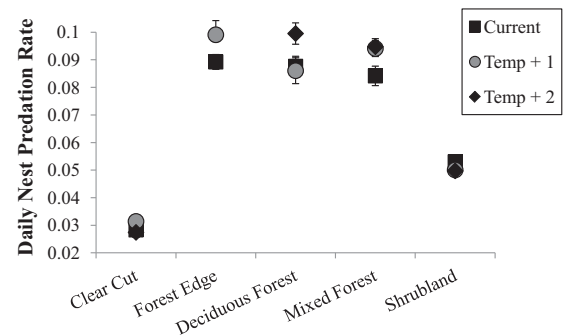
Fig. 3. Habitat-specific daily nest predation rates under contemporary climate conditions and ambient temperature increases of 1 and 2 °C derived from an agent-based model.

little change was detected in daily predation rate in May and June as temperatures increased ($P > 0.093$ and $P > 0.079$, respectively). In July, daily nest predation rate decreased by 16% with 1.5 and 2 °C temperature increases relative to contemporary conditions ($P = 0.005$ and $P = 0.008$, respectively).

Daily nest predation rate also varied among habitats ($F = 552.079$, df = 4, $P < 0.001$), with the highest predation rate occurring in forest edge and forest and the lowest rates in open habitats such as shrublands and clear cuts (Fig. 3). There was also evidence that habitat-specific predation rates would be affected by warming temperatures ($F = 2.738$, df = 4, $P = 0.001$). Relative to contemporary conditions, a 2 °C increase in temperature resulted in 8%, 13%, and 15% increases in predation in deciduous forest, mixed forest, and forest edge ($P = 0.004$, 0.011, 0.003, respectively). Daily predation rate was higher in forest edge for all temperature treatments relative to contemporary temperature conditions ($P < 0.018$). Anecdotally, snakes were observed to use forest edge habitats to a very high degree during model runs. Increased predation in deciduous forest was only significant when temperature increased by 2 °C ($P = 0.004$). Daily nest predation rate in mixed forest was significantly higher when temperature was increased by 1, 1.5 or 2 °C. Increasing temperatures did not increase predation rates in shrubland ($P > 0.251$) or clear cut habitat ($P > 0.459$), because snake activity in these habitat was limited by thermal constraints.

3.3. Nocturnal nest predation by ratsnakes

The proportion of nests preyed on at night varied by both temperature change scenario ($F = 48.718$, df = 4, $P < 0.001$) and month ($F = 2236.441$, df = 4, $P < 0.001$). The proportion of nests preyed on at night increased from 34% at current conditions to 40% in the 2 °C increase scenario (Fig. 4). Even at modest temperature increases (0.5°), nocturnal predation increased by 7% relative to
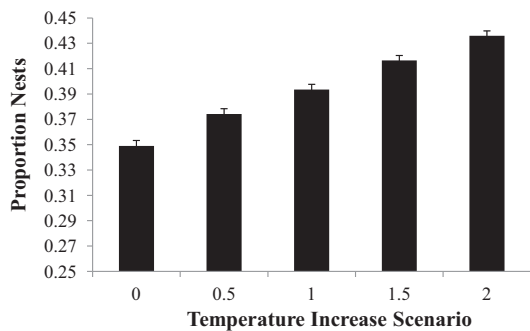
Fig. 4. Proportion of songbird nests (±SE) preyed on at night by ratsnakes (*Elaphe obsoleta*) under five climate warming scenarios derived from an agent-based model.
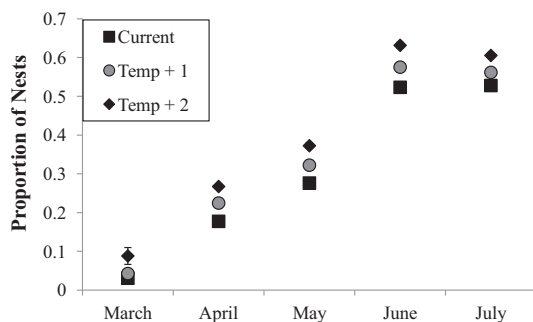

Fig. 5. Proportion of nests preyed on at night as a function of month and ambient temperature increase derived from an agent-based model.

contemporary conditions. Nocturnal predation increased by 15% with a 2 °C increase in temperature relative to contemporary conditions ($P < 0.001$). In general, nocturnal predation was infrequent in March (3%), and increased throughout the summer, with the most nocturnal predation occurring in July (>52% for all temperature scenarios; Fig. 5). Under contemporary conditions, nocturnal predation was less frequent in March relative to all other months ($P < 0.001$). Nocturnal predation in April was also less frequent than in May ($P < 0.001$), June ($P < 0.001$), and July ($P < 0.001$). A 2 °C increase in temperature caused the proportion of nocturnal nest predation in March to increase by nearly 200% ($P < 0.001$). Nocturnal nest predation also increased in April (51%), May (35%), and June (19%: $P < 0.02$).

4. Discussion

Species conservation in a warming world will rely on understanding not only how the behavior of the focal species is influenced by climate change, but by how their predators and prey are affected. Using agent-based modeling, we predicted that warming temperatures would cause ratsnakes, a major ectothermic predator of bird nests (Thompson et al., 1999; DeGregorio et al., 2014a), to shift activity patterns and habitat use, thereby altering patterns of nest predation risk. Our model predicts that a 2 °C increase in ambient temperature will increase overall predation risk by up to 7% and that temporal (seasonal and diel) and spatial patterns of predation risk will also change, and in some instances the predicted change is substantial. Thus, if we assume there are 310 cardinal nests annually at our site, under contemporary conditions we should expect 87 to be successful. However, with a 2 °C increase in temperature only 79 are expected to be successful.

Although the predicted increases in nest predation were relatively modest and seem likely to have limited effects at bird populations, the timing (daily and seasonally) of these increases may have greater implications for avian nesting ecology. Increasing temperatures led to a shift in seasonal snake activity such that snakes were active earlier in the spring and became less active in late summer when it became too warm. This is similar to what would be predicted based on latitudinal comparisons of snake seasonal activity patterns (Sperry et al., 2010). Under current temperature conditions, both empirically derived nest data from our site (B.A. unpublished data) and our model indicate that nest survival is highest in the spring and then declines later in the nesting season, a pattern reported for many bird species (Borgmann et al., 2013). Ectothermic nest predators are relatively inactive when temperatures are suboptimal, but as temperatures increase these predators become more active, thus increasing the possibility of interaction with nests (Sperry et al., 2008; Cox et al., 2013). Avian population viability may rely on the production of offspring in the early part of the season when predation rates are lowest and clutch sizes are largest (Perrins, 1970; Daan et al., 1990; Nager and Noordwijk, 1995). If climate warming causes predation by snakes to increase in the early part of the season, as predicted by our model, this may counteract the benefit to birds of having larger clutches early in the season (Borgmann et al., 2013). However, our model does not take into account climate-induced shifts in avian breeding phenology. As climate change allows ratsnakes to become more active in the spring, birds may be able to nest earlier in response (Crick et al., 1997). Initiation of avian breeding can be dependent on a wide variety of factors (e.g., migration, leaf phenology, insect emergence), so earlier nesting in response to warming temperatures may not always occur. Given the importance of temperature for snake activity, however, warming temperatures seem likely to cause snakes to become active earlier in the spring. Conversely, as snake activity is constrained during the later, hotter months, birds may be able to invest more heavily in these nests to offset early losses.

In additional to shifts in seasonal activity, our model predicted interesting patterns of diel activity shifts with increasing temperatures. Ratsnakes, like many snake species, are facultatively nocturnal (Gibbons and Semlitsch, 1987; Abom et al., 2012). Ratsnakes alter their activity patterns to take advantage of optimal environmental temperatures (DeGregorio et al., 2014c). Our model indicated that even modest temperature increases (0.5 °C) were enough to cause substantial increases (7%) in the amount of nocturnal nest predation by ratsnakes and that substantial temperature elevations (2 °C) increased nocturnal predation by 30%. Increased nocturnal predation was especially prevalent during the early spring (200% increase in nocturnal predation in March), which, under contemporary conditions, is a time when ratsnakes are primarily diurnal (Sperry et al., 2013; Ward et al., 2013). Increased nocturnal predation is a cause for concern because snake predators are more successful due to the inability of most birds to defend their nests at night (Hensley and Smith, 1986; Carter et al., 2007). Additionally, nocturnal snake predation may result in the predation of the incubating or brooding adult (Reidy et al., 2009). Although we have not documented ratsnakes capturing incubating or brooding adults at night at our site (unpublished data), more research is needed to identify which bird species or nesting characteristics (e.g., nest height, diameter of supporting tree limb) make nesting birds vulnerable to snakes at night.

Nest predation by ratsnakes varied by habitat and model results of contemporary temperature conditions produced a pattern similar to that observed in the field. Ratsnakes are generally associated with forests and forest edges and accordingly, predation by ratsnakes in both the model and field were highest in these habitats relative to open, canopy-free habitats. We predicted that as temperatures increased, open habitats such as shrubland and clear cuts would become unsuitable for ratsnakes, causing nest predation in these patches to decrease. Conversely, as temperatures

increased, ratsnakes would use cooler, more forested habitats causing nest predation in these patches to increase. Results from the model support our hypotheses, with marked increases in predation rates within forest and forest edges (Fig. 3). Ratsnakes are an edge-associated species (Durner and Gates, 1993; Blouin-Demers and Weatherhead, 2001a,b; Carfagno et al., 2006) and appear to use edges for the thermoregulatory heterogeneity that they provide (Blouin-Demers and Weatherhead, 2001b; Carfagno et al., 2006). As climate warms, edges may continue to provide thermal refugia for ratsnakes. Edge effects on avian nesting survival have been debated in the literature for decades and appear to be context and species-specific (Gates and Gysel, 1978; Hanski et al., 1996; Flaspohler et al., 2001). Studies documenting edge effects attribute them to increased predation rates from edge-associated predators such as brown-headed cowbirds (*Molothrus ater*), snakes, and mammalian mesopredators such as raccoons (*Procyon lotor*). Although our model results indicate that nest predation in edges by ratsnakes will increase as temperatures warm, predicting how overall nest predation in edges will change requires knowing how edge use by other nest predators will change in warmer climates. However, increased nest predation by ratsnakes alone in forest edges under warming temperatures could cause these habitats to become sinks for many nesting birds (Gates and Gysel, 1978; Battin, 2004).

Our results provide an important step in exploring how climate change may affect behavior of a predator species and thereby affect survival of one of its prey species. Our research indicates that although the overall intensity of nest predation is expected to increase, the most pronounced effect of climate change on predation may be changes in when and where nest predation occurs, such as increases in early-season and nocturnal predation or increases in specific habitats. Understanding how a predator is likely to respond to a changing climate provides an important platform to begin to explore the scope that the prey species has for countering these effects, such as shifts in nesting phenology or nesting habitats.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmodel.2015.05.031

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