Ecological Modelling 312 (2015) 239–246

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel

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

Brett A. DeGregorio[a,b,*], James D. Westervelt[b], Patrick J. Weatherhead[a], Jinelle H. Sperry[b]

[a] Department of Natural Resources and Environmental Sciences, University of Illinois at Urbana-Champaign, Urbana, IL 61801, United States
[b] Engineer Research and Development Center, PO Box 4005, Champaign, IL 61826, United States

ARTICLE INFO

Article history:
Received 7 August 2014
Received in revised form 15 May 2015
Accepted 25 May 2015

Keywords:
Activity patterns
Climate change
Forest edge
Ratsnakes
Netlogo
Predator–prey interactions

ABSTRACT

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.

Published by Elsevier B.V.

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;

* Corresponding author at: Department of Natural Resources and Environmental Sciences, University of Illinois at Urbana-Champaign, Urbana, IL 61801, United States. Tel.: +1 217 373 7253.
E-mail address: badegregorio@gmail.com (B.A. DeGregorio).

http://dx.doi.org/10.1016/j.ecolmodel.2015.05.031
0304-3800/Published by Elsevier B.V.

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,