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CONSERVATION ECOLOGY - ORIGINAL RESEARCH

Isolating weather effects from seasonal activity patterns of a temperate North American Colubrid

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Abstract Forecasting the effects of climate change on threatened ecosystems and species will require an understanding of how weather influences processes that drive population dynamics. We have evaluated weather effects on activity patterns of western ratsnakes, a widespread predator of birds and small mammals in eastern North America. From 2010–2013 we radio-tracked 53 ratsnakes in the fragmented region of central Missouri. We relocated each snake 4× per week and used movement frequency as an index of activity. We used generalized linear mixed models within an information–theoretic approach to evaluate temporal and weather variables as potential predictors of snake activity. While snakes were generally sedentary, activity showed a linear response to relative humidity and a quadratic response to air temperature, peaking near 30 °C. Seasonal activity patterns differed between sexes and among years, but snakes were generally least active in mid-summer, regardless of weather. Our findings provide strong evidence that air temperature and relative humidity differentially affect activity patterns of an important predator and are the mechanism explaining increased nest predation rates with warmer temperatures.

Keywords Climate change · *Elaphe obsoleta* · *Pantherophis obsoletus* · Thermal ecology · Western ratsnakes

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Introduction

Global climate change is widely regarded as a major conservation challenge because of its far-reaching effects on ecosystems (Bellard et al. 2012; McCarty 2001). Shifts in temperature and precipitation patterns can affect plants and animals by disrupting trophic interactions, for example, by decoupling the phenology of interdependent species (Traill et al. 2010; Van der Putten et al. 2010). Effects of climate change are often synergistic and act in conjunction with other factors known to affect populations. For example, temperature fluctuations associated with climate change can interact with landscape composition or predator behavior to limit productivity of prey (Cox et al. 2013b; Morrison and Bolger 2002; Skagen and Yackel Adams 2012). Accurately predicting and mitigating effects of climate change on threatened ecosystems will require an understanding of how proximate climate factors affect individual species that perform key ecosystem functions (Bellard et al. 2012; Traill et al. 2010).

Although generally understudied, snakes make an ideal model organism for understanding the effects of climate change on predator–prey interactions. Because snakes are ectotherms, their physiology and behavior are constrained by environmental conditions that are subject to climate warming (e.g., Aubret and Shine 2009; Weatherhead et al. 2012). Where snakes are abundant they can potentially exert strong top–down effects on the behavior, population demographics, and evolution of prey species (Bouskila 1995; Brodie et al. 2005; DeGregorio et al. 2014; Savidge 1987). For example, in eastern North America, snake behavior has been recognized as a potential mechanism linking climate warming to songbird productivity (Cox et al. 2013a, b; Reidy et al. 2009; Sperry et al. 2013). Furthermore, there is evidence that many snake species are

undergoing population declines, in part because of climate change, which may in turn affect ecosystem functioning in regions where snakes are the predominant predators (Gibbons et al. 2000; Reading et al. 2010).

Snake activity patterns are widely presumed to be influenced by seasonal temperature changes in temperate regions (Gibbons and Semlitsch 1987). Virtually all aspects of ectotherm physiology are constrained by body temperature, and snake behavior is therefore affected by ambient temperatures (Lillywhite 1987; Peterson et al. 1993). Snake activity patterns also reflect seasonal changes in reproductive behavior, predator avoidance, or resource selection (Gibbons and Semlitsch 1987). Seasonal or daily activity patterns have been documented for many snake species, but studies that isolate specific environmental factors from temporal patterns have been surprisingly sparse. This paucity of information has resulted in part from the difficulty of studying snakes in the field; most information is based on anecdotes, museum collections, or capture rate data (e.g., Dalrymple et al. 1991; Krysko 2002). Radio-telemetry has permitted more rigorous analyses of snake movements and thermoregulation, but few studies have specifically linked activity patterns of individual snakes to ambient weather conditions (Howze and Smith 2012; Sperry et al. 2013; Whitaker and Shine 2002).

Thermoregulation in snakes has been well studied in laboratory and field experiments (Blouin-Demers and Weatherhead 2001b; Lelièvre et al. 2011; Peterson et al. 1993; Weatherhead et al. 2012). Thermal preferences for most species are close to 30 °C, although snakes in temperate regions can tolerate a wider range of temperatures than those in tropical regions (Lillywhite 1987). The availability of optimum environmental temperatures affects how much time and energy a snake must invest in actively thermoregulating compared to other activities. A snake must either thermoregulate more or become sedentary as temperatures depart from the optimum. A lowered metabolism may require less food and therefore less time hunting. Snakes can invest more in hunting or reproductive behavior when optimal environmental temperatures are more readily available (Peterson et al. 1993). Therefore, the availability of optimal environmental temperatures should affect snake activity patterns, with snakes moving more frequently when environmental temperatures permit them to achieve a body temperature near 30°.

Water balance is an important but often overlooked aspect of snake physiology. Snakes are susceptible to desiccation under dry conditions, and activity during warm periods can expose snakes to increased evaporative water loss (Guillon et al. 2013; Winne et al. 2001). Snake activity should therefore be positively related to precipitation or relative humidity, with less frequent movements when moisture levels are low, including under optimal thermal conditions (e.g., Daltry et al. 1998).

We used radio-telemetry and local weather data to model temporal activity patterns of western ratsnakes (*Pantherophis obsoletus*), a regionally important predator. Our goal was to investigate the relationship between snake behavior and weather variables that will be affected by climate warming. We tested various competing hypotheses regarding weather effects on ratsnake activity patterns. Specifically, we predicted that movement frequency would increase with temperature and environmental moisture, and that weather conditions could be used to predict snake activity independently of temporal patterns.

Materials and methods

We used radio-telemetry to track 53 western ratsnakes from 2010–2013 at the Thomas S. Baskett Wildlife Research and Education Center (38°44′N, 92°12′W) and Three Creeks Conservation Area (38°49′N, 92°17′W) in central Missouri. This region has been the focus of several long-term bird nest predation studies, and the western ratsnake has been identified as the predominant nest predator (e.g., Cox et al. 2012; Robinson et al. 1995; Thompson and Burhans 2003). Both study sites consist of mixed-hardwood forest interspersed with early successional red cedar (*Juniperus virginiana*) stands and old fields.

We captured snakes opportunistically or as they emerged from previously located hibernacula and surgically implanted radio-transmitters following standard methods, with isoflurane as the anesthetic (Blouin-Demers et al. 2000; Reinert and Cundall 1982). Transmitters [Advanced Telemetry Systems (ATS) models R1530, R1680] were always <3 % of the snake's body mass. Snakes were given meloxicam (0.1 mg/kg) and enrofloxacin (5 mg/kg) and released within 3 days of surgery. With one exception, all snakes recovered from surgery and continued to exhibit apparently normal feeding and reproductive behavior during the study (George et al. unpublished data). While it is likely that the transmitters affected the snakes, our methods were consistent with other snake telemetry studies (Weatherhead and Blouin-Demers 2004a). All methods were approved by the University of Missouri Animal Care and Use Committee (Protocol #6605). We located snakes with a handheld receiver and antenna (ATS models R410, R2000, 13562, 13863) 4× per week during the morning, afternoon, evening, and after dark from April through September. Tracking times typically rotated on a weekly basis, and the order of snakes tracked rotated on a daily basis. We tracked snakes to within 1 m of their actual locations (i.e., we did not triangulate). We recorded UTM coordinates at each location (GPS error <10 m) and whether the snake was in a new location, the same location as when last located, or had returned to a previously used location. To avoid possible

GPS error in determining each snake's movement status, the same field technicians typically tracked the same individual snakes throughout a given field season. Therefore, technicians could visually confirm each snake's movement status independently of the GPS coordinates. In cases where snakes moved <10 m, we only classified snakes as having moved if they were located in a substrate different from the former location. For example, a snake using different branches of the same tree for 2 consecutive days would be classified as not moved, whereas a snake that moved to an adjacent tree would be classified as moved. We calculated the linear distance moved and the elapsed time from the previous location. We only used locations <36 h apart in our analysis to minimize the likelihood of underestimating movements. Automated telemetry studies have demonstrated that ratsnakes occasionally move and return to within tens of meters of their initial location within a short time period (Ward et al. 2013). Therefore, our distance per movement estimates may have underestimated actual distances moved by snakes. However, our tracking methodology permitted greater location accuracy than automated telemetry (<10 m) and therefore a lower error rate for short distances and of whether a snake changed locations. Moreover, we tracked snakes more frequently than has been done in most other non-automated snake telemetry studies.

We obtained weather data collected from the Missouri Ozark AmeriFlux site (MOFLUX; http://ameriflux.ornl.gov/), which was located within 12 km of all snake locations. Measurements included air temperature at 1 m above ground, relative humidity, and total precipitation; all measurements were taken every 30 min. For each snake we calculated the mean air temperature, temperature range, mean relative humidity, and total precipitation for each time interval between snake locations. Whereas modeling operative temperature (T_e; Peterson et al. 1993) can provide a more accurate index of the local conditions available to a snake than air temperature, our goal here was to examine weather patterns rather than microhabitat variation.

We used generalized linear mixed models within an information–theoretic approach to evaluate relationships between weather and temporal variables and snake movements (Bolker et al. 2009; Burnham and Anderson 2002). Ratsnakes have distinct home ranges and frequently return to specific locations throughout the active season and across years (Blouin-Demers and Weatherhead 2001a; Durner and Gates 1993). Thus, distance moved between relocations may be partially dependent on the spatial arrangement of habitat features within each snake's home range. Therefore, we used frequency of movement rather than Euclidean distance as an index of activity in our models. We treated snake movement as a binary response variable (moved = 1, did not move = 0) and used a binomial distribution with a logit link function in our models. We included day of year and individual snake within year as random effects to account for non-independence of individuals' movements in time. Elapsed time between each snake location was included as an offset term in the model. A multicollinearity test prior to model fitting indicated weak pairwise correlations between all covariates ($r < 0.6$). An initial comparison of the global model without year, with year as an additive effect, and a day of year × year interaction indicated strong support for the interaction term. Therefore, day of year × year was included in all candidate models to account for these seasonal and annual effects. The 36 candidate models included mean air temperature and different combinations of temperature range, total precipitation, mean relative humidity, sex, and snout–vent length (SVL) as additive fixed effects. In addition, we evaluated interactions between day of year and sex, and linear as well as quadratic responses to air temperature and day of year. We included a global model that contained all variables, as well as a null model with only the intercept. Candidate models were developed a priori based on plausible hypotheses, and models were then fit and ranked using Akaike's Information Criteria (AIC) and model weights. We tested for overdispersion by calculating the ratio of the sum of squared Pearson residuals by the residual degrees of freedom and used the area under the receiver operating characteristic curve (AUC) to assess overall fit of each model (Fielding and Bell 1997). We based inference on the top model because the next ten models added uninformative parameters that did not sufficiently contribute to the model likelihood to overcome the 2-point penalty for an additional parameter (ΔAIC < 2; Arnold 2010; Burnham and Anderson 2002). Statistical analyses were conducted in R version 3.0.1 on z-transformed data and with package lme4 (Bates et al. 2014; R Core Team 2014).

Results

We obtained 2130 locations from April to September across 4 years from 36 male and 17 female snakes. SVL was 112.8 ± 2.7 cm ($\bar{X}$ ± standard error) for males and 109.5 ± 2.0 cm for females. The total number of locations per individual was 47.2 ± 26.3 ($\bar{X}$ ± standard deviation) and ranged from 6 to 128. We tracked 33 individual snakes during 2 years and seven snakes during at least 3 years. The number of snakes tracked per year ranged from seven in 2010 to 41 in 2012. Snakes were often sedentary and did not change locations on 51 % of the occasions they were tracked. When snakes did move, the mean distance moved per day was 120 m but ranged between 1.1 and 776.7 m.

The monthly mean temperature during the study period was 21.7 °C but ranged from 12.3 °C in April 2013 to 28.9 °C in July 2012. Total precipitation was 67.8, 29.9,

Table 1 Summary of model-selection results from the best-ranked a priori candidate models of the effects of sex, body size, and temporal and weather variables on the probability of snake movement in Missouri, 2010–2013

Model	K	ΔAIC	w_I
$Temp^2 + RH + Sex \times DOY^2 + Year \times DOY^2$	20	0	0.1
$Temp^2 + Range + RH + Sex \times DOY^2 + Year \times DOY^2$	21	0.27	0.09
$Temp^2 + Range + Precip + Sex \times DOY^2 + Year \times DOY^2$	21	0.38	0.08
$Temp^2 + RH + Sex \times DOY^2 + Year \times DOY^2 + SVL$	21	0.61	0.07
Null	3	68.23	0

Quadratic terms and interactions include their constituent additive terms. The null model is also included for comparison. See "Appendix" for the complete model set

AIC Akaike's Information Criteria, *Temp* air temperature, *RH* relative humidity, *DOY* day of year, *Precip* precipitation, *SVL* snout-vent length

Table 2 Estimated coefficients for the best supported model of the effects of sex, body size, and temporal and weather variables on the probability of snake movement in Missouri, 2010–2013

Parameter	Coefficient	Standard error	Lower 95 % CI	Upper 95 % CI
Intercept	−1.21	0.27	−1.74	−0.68
Temp	0.35	0.08	0.20	0.51
$Temp^2$	−0.11	0.05	−0.20	−0.02
RH	0.17	0.08	0.01	0.33
Sex[a]	0.25	0.16	−0.07	0.57
DOY	0.93	0.51	−0.06	1.93
DOY^2	−0.80	0.41	−1.62	0.01
Sex × DOY	−0.68	0.16	−0.99	−0.37
Sex × DOY^2	−0.05	0.09	−0.23	0.12
Year 2011	−0.69	0.31	−1.29	−0.09
Year 2012	−0.17	0.28	−0.71	0.37
Year 2013	0.04	0.26	−0.48	0.56
Year 2011 × DOY	−0.25	0.53	−1.29	0.78
Year 2012 × DOY	−0.95	0.50	−1.93	0.03
Year 2013 × DOY	−1.24	0.52	−2.25	−0.23
Year 2011 × DOY^2	1.51	0.48	0.57	2.46
Year 2012 × DOY^2	0.88	0.41	0.07	1.69
Year 2013 × DOY^2	1.33	0.45	0.45	2.22

CI Confidence interval

[a] Male = 1; female = 0

24.5, and 46.0 cm during the period April–August in 2010, 2011, 2012, and 2013, respectively. The study region underwent a severe drought in 2012, with mean temperatures 2.8° above and precipitation 14.5 cm below the long-term average for the study period (Missouri Climate Center 2014).

The best-supported model included the variables mean air temperature, mean relative humidity, day of year × sex, and day of year × year interactions and had an AIC model weight of 0.1 (Tables 1, 2). The AUC was 0.71, which is commonly interpreted as "fair" model performance (0.5 = indistinguishable from random, 1.0 = perfect; Swets 1988). The next ten models added total precipitation, temperature range, and SVL, but these models were not well supported. Snake activity showed a quadratic response to temperature, increasing with temperature to approximately 30 °C, and showed a linear increase with relative humidity (Fig. 1). The response to day of year differed among years and between sexes (Fig. 2). Males were more likely to move earlier in the season than females, whereas females were more likely to move later in the season. In contrast to other years, snake activity was greatest in mid-summer in 2010; in 2011–2013 snake activity declined from spring to summer, and in 2011 and 2013, it increased in late summer.

Discussion

We evaluated the relationship between western ratsnake activity patterns and weather and temporal variables. While the snakes in our study were generally inactive, individual snakes showed wide variation in daily movements. We found support for relationships between snake activity and air temperature, relative humidity, and day of year.

Seasonal activity patterns have been described in multiple temperate snake species, including ratsnakes (Carfagno and Weatherhead 2008; Durner and Gates 1993; Gibbons and Semlitsch 1987; Sperry et al. 2008). However, previous studies did not attempt to isolate temporal patterns from other effects in a model-selection framework. We found support for both temporal and weather effects and demonstrated the effect of each factor while holding the effects of other factors constant. Seasonal activity varied between sexes and among years, regardless of weather, but was generally highest in spring for males and highest for females in late summer. Seasonal differences between sexes likely reflect changes in mating behavior, which peaks in late May in Missouri. For example, male ratsnakes may exhibit longer or more frequent movements associated with mate searching in spring, whereas gravid females may remain sedentary (Bozinovic and Rosenmann 1988; Carfagno and Weatherhead 2008). The fact that tracking began in June in 2010, after the peak in breeding activity, may explain the divergent activity pattern observed in this year. In addition to reproductive behavior, seasonal activity patterns could reflect changes in food resources or dietary patterns as snakes restore depleted energy reserves. For example, snakes might require less frequent movements after initially regaining mass lost during winter, or if prey populations

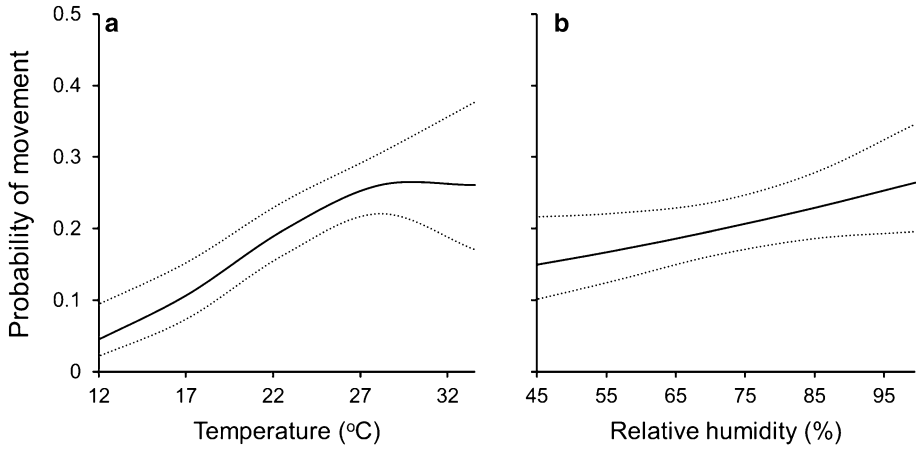

Fig. 1 Predictions of the best supported model showing the effects of air temperature (**a**) and relative humidity (**b**) on the probability of snake movement. Estimates are reported for the range of temperatures recorded. For model predictions, year is held constant at 0.25, sex is held constant at 0.5, and other variables are held constant at their means. *Dotted lines* 95 % Confidence intervals (CIs)

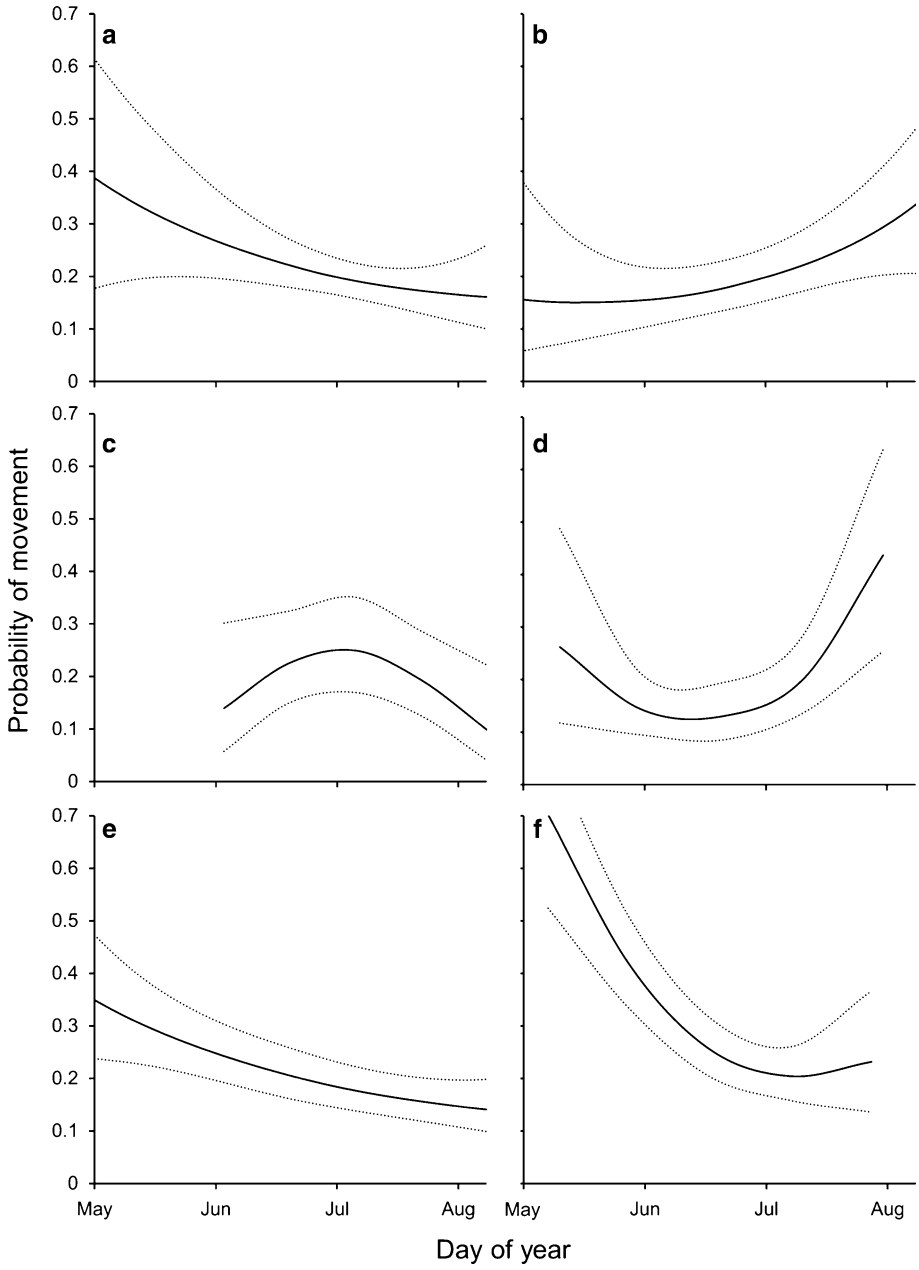

Fig. 2 Predictions of the best supported model showing the effect of day of year on the probability of snake movement. *Panels* show estimates for males (**a**), females (**b**), and each of the 4 years of the study (**c**, **d**, **e**, **f** 2010, 2011, 2012, 2013, respectively). For **a** and **b**, year is held constant at 0.25; for **c**–**f**, sex is held constant 0.5. All other variable are held constant at their means. *Dotted lines* 95 % CIs

increase as the season progresses (Aleksiuk and Stewart 1971; Luis et al. 2010). The different response to day of year among years likely reflects environmental factors that vary seasonally among years. For example, the longest seasonal decline in activity occurred in 2012, when the study region underwent abnormally high temperatures and a severe drought. While we did not find strong support for models that included precipitation, weather variables were measured during the time period of each snake movement. In contrast, day of year likely encapsulates broader phenological patterns, such as seasonal changes in soil moisture that affect prey populations via ecosystem productivity.

Snakes were twice as likely to move during periods of high humidity as in periods of low humidity. Water balance in temperate snakes has received sparse attention, despite evidence that moisture can affect activity patterns and habitat selection (Daltry et al. 1998; Howze and Smith 2012; Moore and Gillingham 2006). Movement during dry conditions can increase evaporative water loss, potentially leading to desiccation (Guillon et al. 2013). Future studies of climate effects on temperate snake activity patterns and thermal ecology should likewise consider moisture availability, especially given that drought conditions are expected to increase in many temperate regions during the next century (IPCC 2013).

As predicted, we found a quadratic relationship between temperature and snake movements. Snakes were more likely to move as temperatures increased, with the maximum probability of movement occurring near 30 °C. This result is consistent with findings from previous studies, including the optimal temperature range reported for most snake species (Lillywhite 1987; Weatherhead et al. 2012). Surprisingly, other researchers did not find a strong or consistent relationship between temperature and ratsnake activity (Sperry et al. 2008, 2010). However, these latter studies used the mean distance traveled per day across all individuals as a measure of snake activity, or mean temperature across longer time intervals as a temperature index. In contrast, we located snakes more frequently (<36 h between locations) and calculated weather variables for the exact time interval between each location for each individual. In addition, our modeling approach provided a more robust analytical framework, permitting us to account for variation among individual snakes while isolating the effects of individual weather variables on snake activity.

While we found support for models that included temperature, humidity, and day of year, our goodness-of-fit tests indicated a fair amount of variation that was not explained by our analysis. Snake activity is influenced by additional biotic and abiotic factors that were beyond the scope of our study. For example, we measured temperature at a single weather station, but operative temperatures available to individual snakes can vary widely based on local geography and habitat features, and individual snakes might have differing thermal requirements depending on body size or condition (Blouin-Demers and Weatherhead 2001b; Peterson et al. 1993). Moreover, the frequency of movement of individual snakes is likely to be dependent on prey availability and satiation levels (Mushinsky 1987; Wasko and Sasa 2012).

Snakes are regionally important bird nest predators, being in some cases responsible for more nest failures than any other cause (DeGregorio et al. 2014; Thompson 2007). The potential of ratsnakes to affect bird demography has prompted researchers to study ratsnake behavior in order to understand and potentially mitigate bird population declines (e.g., Stake et al. 2005; Weatherhead and Blouin-Demers 2004b). Bird nest predation rates are high when snakes are more active or when air temperatures are hotter (Cox et al. 2013b; Sperry et al. 2008, 2012; Weatherhead et al. 2010), and snakes become more frequent nest predators when air temperatures increase (Cox et al. 2013a). Albeit indirectly, our study provides a possible mechanism by which climate change could affect the demographics of birds and other prey species. However, in light of the inherent variability of seasonal snake activity, we caution against specific long-term predictions.

Air temperatures in North America are projected to increase during the next century, and there is evidence that temperate snake populations can respond positively by adjusting activity patterns to optimize available temperatures (IPCC 2013; Weatherhead et al. 2012). Future studies that incorporate spatiotemporal temperature and moisture variation as it relates to snake space use and resource selection could enhance our understanding of climate effects on snake ecology. Nevertheless, here we provide strong evidence that temperature and relative humidity differentially affect the movements of an important predator.

Author contribution statement ADG and JF designed the project and oversaw data collection. ADG and FRT developed computer models and analyzed the data. ADG wrote the manuscript. JF and FRTprovided editorial advice.

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Appendix

See Table 3.

Table 3 Model-selection results from a priori candidate models of the effects of sex, body size, and temporal and weather variables on the probability of snake movement in Missouri, 2010–2013

Model	K	AIC	ΔAIC	w_I
Temp + Temp^2 + RH + Sex + DOY + DOY^2 + Year + Sex × DOY + Sex × DOY^2 + Year × DOY + Year × DOY^2	20	2798.52	0	0.1
Temp + Temp^2 + Range + RH + + DOY + DOY^2 + Year + Sex × DOY + Sex × DOY^2 + Year × DOY + Year × DOY^2	21	2798.79	0.27	0.09
Temp + Temp^2 + Range + Precip + Sex + DOY + DOY^2 + Year + Sex × DOY + Sex × DOY^2 + Year × DOY + Year × DOY^2	21	2798.9	0.38	0.08
Temp + Temp^2 + RH + SVL + Sex + DOY + DOY^2 + Year + Sex × DOY + Sex × DOY^2 + Year × DOY + Year × DOY^2	21	2799.13	0.61	0.07
Temp + Temp^2 + Range + Sex + DOY + DOY^2 + Year + Sex × DOY + Sex × DOY^2 + Year × DOY + Year × DOY^2	20	2799.17	0.65	0.07
Temp + Temp^2 + Range + RH + SVL + Sex + DOY + DOY^2 + Year + Sex × DOY + Sex × DOY^2 + Year × DOY + Year × DOY^2	22	2799.37	0.85	0.07
Temp + Temp^2 + Range + Precip + SVL + Sex + DOY + DOY^2 + Year + Sex × DOY + Sex × DOY^2 + Year × DOY + Year × DOY^2	22	2799.41	0.89	0.07
Temp + Temp^2 + Range + SVL + Sex + DOY + DOY^2 + Year + Sex × DOY + Sex × DOY^2 + Year × DOY + Year × DOY^2	21	2799.66	1.14	0.06
Temp + Temp^2 + Range + Precip + RH + Sex + DOY + DOY^2 + Year + Sex × DOY + Sex × DOY^2 + Year × DOY + Year × DOY^2	22	2799.85	1.34	0.05
Temp + Temp^2 + Precip + RH + Sex + DOY + DOY^2 + Year + Sex × DOY + Sex × DOY^2 + Year × DOY + Year × DOY^2	21	2800.03	1.51	0.05
Temp + Temp^2 + Range + Precip + RH + SVL + Sex + DOY + DOY^2 + Year + Sex × DOY + Sex × DOY^2 + Year × DOY + Year × DOY^2	23	2800.42	1.9	0.04
Temp + Temp^2 + Sex + DOY + DOY^2 + Year + Sex × DOY + Sex × DOY^2 + Year × DOY + Year × DOY	19	2800.64	2.12	0.04
Temp + Temp^2 + Precip + RH + SVL + Sex + DOY + DOY^2 + Year + Sex × DOY + Sex × DOY^2 + Year × DOY + Year × DOY^2	22	2800.64	2.12	0.04
Temp + Temp^2 + Precip + Sex + DOY + DOY^2 + Year + Sex × DOY + Sex × DOY^2 + Year × DOY + Year × DOY^2	20	2800.7	2.18	0.03
Temp + Temp^2 + SVL + Sex + DOY + DOY^2 + Year + Sex × DOY + Sex × DOY^2 + Year × DOY + Year × DOY^2	20	2801.16	2.64	0.03
Temp + Temp^2 + Precip + SVL + Sex + DOY + DOY^2 + Year + Sex × DOY + Sex × DOY^2 + Year × DOY + Year × DOY^2	21	2801.23	2.71	0.03
Temp + RH + Sex + DOY + DOY^2 + Year + Sex × DOY + Sex × DOY^2 + Year × DOY + Year × DOY^2	19	2802.41	3.9	0.01
Temp + Range + RH + Sex + DOY + DOY^2 + Year + Sex × DOY + Sex × DOY^2 + Year × DOY + Year × DOY^2	20	2802.8	4.28	0.01
Temp + RH + SVL + Sex + DOY + DOY^2 + Year + Sex × DOY + Sex × DOY^2 + Year × DOY + Year × DOY^2	20	2803.13	4.61	0.01
Temp + Range + RH + SVL + Sex + DOY + DOY^2 + Year + Sex × DOY + Sex × DOY^2 + Year × DOY + Year × DOY^2	21	2803.49	4.97	0.01
Temp + Range + Precip + RH + Sex + DOY + DOY^2 + Year + Sex × DOY + Sex × DOY^2 + Year × DOY + Year × DOY^2	21	2803.95	5.43	0.01
Temp + Precip + RH + Sex + DOY + DOY^2 + Year + Sex × DOY + Sex × DOY^2 + Year × DOY + Year × DOY^2	20	2803.97	5.45	0.01
Temp + Range + Precip + Sex + DOY + DOY^2 + Year + Sex × DOY + Sex × DOY^2 + Year × DOY + Year × DOY^2	20	2804.15	5.63	0.01
Temp + Range + Precip + RH + SVL + Sex + DOY + DOY^2 + Year + Sex × DOY + Sex × DOY^2 + Year × DOY + Year × DOY^2	22	2804.62	6.1	0
Temp + Precip + RH + SVL + Sex + DOY + DOY^2 + Year + Sex × DOY + Sex × DOY^2 + Year × DOY + Year × DOY^2	21	2804.68	6.16	0
Temp + Range + Precip + SVL + Sex + DOY + DOY^2 + Year + Sex × DOY + Sex × DOY^2 + Year × DOY + Year × DOY^2	21	2804.75	6.23	0
Temp + Range + Sex + Sex × DOY + Sex × DOY^2 + Year × DOY + Year × DOY^2	19	2804.95	6.43	0
Temp + Range + SVL + Sex + DOY + DOY^2 + Year + Sex × DOY + Sex × DOY^2 + Year × DOY + Year × DOY^2	20	2805.54	7.02	0
Temp + Precip + Sex + DOY + DOY^2 + Year + Sex × DOY + Sex × DOY^2 + Year × DOY + Year × DOY^2	19	2806.41	7.89	0
Temp + Sex + DOY + DOY^2 + Year + Sex × DOY + Sex × DOY^2 + Year × DOY^2 + Year × DOY^2	18	2806.85	8.33	0
Temp + Precip + SVL + Sex + DOY + DOY^2 + Year + Sex × DOY + Sex × DOY^2 + Year × DOY + Year × DOY^2	20	2807.05	8.53	0
Temp + SVL + Sex + DOY + DOY^2 + Year + Sex × DOY + Sex × DOY^2 + Year × DOY + Year × DOY^2	19	2807.47	8.95	0
Sex + DOY + DOY^2 + Year + Sex × DOY + Sex × DOY^2 + Year × DOY + Year × DOY^2	17	2821.37	22.85	0
SVL + Sex + DOY + DOY^2 + Year + Sex × DOY + Sex × DOY^2 + Year × DOY + Year × DOY^2	18	2821.91	23.39	0
DOY + DOY^2 + Year + Year × DOY + Year × DOY^2	14	2832.47	33.95	0
SVL + DOY + DOY^2 + Year + Year × DOY + Year × DOY^2	15	2833.75	35.23	0
Null	3	2866.74	68.23	0

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