Phenology and predictors of spring emergence for the Timber Rattlesnake (*Crotalus horridus*)

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Abstract

Many temperate reptiles survive winter by overwintering in subterranean refugia until external conditions become suitable for above-ground activity. Determining when to emerge from refugia relies on a reptile's ability to interpret when above-ground environmental conditions are survivable. If temperate reptiles rely on specific environmental cues such as temperature to initiate egress, we should expect emergence phenologies to be predictable using available local climatic data. However, specific predictors of emergence for many temperate reptiles, including the Timber Rattlesnake (*Crotalus horridus*), remain unclear, limiting our understanding of overwintering phenologies and restricting effective conservation and management. Our objectives were to identify potential environmental cues of spring egress for *C. horridus* to determine the species' emergence phenology and to examine the applicability of identified cues in predicting the emergence phenology across the species' range. We used wildlife cameras and weather station-derived environmental data to observe and predict the daily surface presence of *C. horridus* throughout the late winter and early spring at communal refugia in Jersey and Jo Daviess Counties, Illinois. The most parsimonious model for predicting surface presence included the additive effects of maximum daily temperature, accumulated degree days, and latitude. With a notable exception in the southeastern U.S., the model accurately predicted the average egress day for other populations range wide, emphasizing the role of temperature in influencing the substantial phenological plasticity observed across the species' range. The apparent broad applicability of the model to other populations suggests it can be a valuable tool in predicting spring egress phenology. Our results provide a foundation for further ecological enquiries and effective management and conservation strategies.

Introduction

Seasonally colder periods in temperate regions expose reptiles to temperatures exceeding critical thermal minima (Ganz and Pough, 1982). A common strategy to survive such critically low temperatures is to retreat into subterranean refugia until external conditions become suitable for above-ground activity. Though buffered from external conditions, occupants of refugia are often still subject to thermal regimens lower than preferred (Brown, 1982; Claussen et al., 1991; Firth, 1998), resulting in a cold-induced dormancy characterized by restricted physiological, behavioral, and cellular-level functions (Angilletta and Angilletta, 2009). Cold-induced dormancy poses several challenges to reptiles. Despite highly depressed metabolic rates, cold

If spring emergence in temperate reptiles is prompted by specific environmental cues such as temperature, we should expect emergence phenologies to be predictable using available local climatic data. Wide-ranging species subject to latitudinal and altitudinal clines might exhibit phenological plasticity, similar to what is observed for insects (Cayton et al., 2015; Herms, 2004; Uelmen et al., 2016), plants (Aslam et al., 2017) and mammals (Boutin and Lane, 2014). However, local adaption or study methodologies have often confounded the identification of such spatial patterns (Andrews and Waldron, 2017; Blouin-Demers et al., 2000). While environmental variables, primarily temperature, likely dictate the timing of emergence, specific predictors of egress for many temperate reptiles remain unclear. Furthermore, to our knowledge, no study has examined the applicability of their results across populations, particularly for wide-ranging species exhibiting a high degree of phenological plasticity (Blouin-Demers et al., 2000; DeGregorio et al., 2017; Gregory, 1982; Martin, 1992). The lack of phenological schedules for such species limits our understanding of overwintering ecology and restricts effective conservation and management (e.g., defining date cutoffs for management), particularly for species of conservation concern.

The Timber Rattlesnake (*Crotalus horridus*) is a wide-ranging terrestrial pitviper dependent on subterranean refugia for overwinter survival exhibiting population declines. Dependency on refugia throughout higher latitude within its distribution dictates the species' ecology – exemplified by communal overwintering of up to 200 individuals (Brown, 1993) and seasonal movements between refugia and summer habitat in the fall and spring (Brown, 1992; MacGowan et al., 2017; Sealy 2002). Having the largest geographic range of any rattlesnake, *C. horridus* exhibits considerable phenological plasticity in its overwintering ecology (Andrews and Waldron, 2017; Brown, 1992; Martin, 2002; Reinert, 2002). Southern populations in warmer dormancy creates an energy deficit, and reptiles must survive solely on stored energy reserves. Cold-induced dormancy also restricts a reptile's ability to conduct vital active-season processes such as foraging, reproduction, or basic physiological maintenance (Blouin-Demers et al., 2000; Gregory, 1988; Macartney and Martin, 1993; Smits and Yorke, 1980; Viitanen, 1968). It is, therefore, advantageous for reptiles to limit the duration of cold-induced dormancy and balance the inherent risks of emerging too early and being subject to lethal thermal regimes with the advantage of maximizing active duration out of the refugia.

Determining when to emerge from refugia relies on a reptile's ability to interpret when above-ground conditions are survivable. Such a decision is particularly complicated in temperate climates subject to stochastic environmental conditions. While studies have proposed several cues for egress, including physiological thresholds (Angilletta and Angilletta, 2009), endogenous rhythms (Lutterschmidt, 2006; Weatherhead, 1989), rainfall/humidity (Viitanen, 1967), and photoperiod (Rismiller and Heldmaier, 1982), the most prevalent for temperate reptiles is temperature. Reptiles generally emerge as air temperatures rise in the spring, a phenomenon correlated with several covariates, including maximum, minimum, and mean daily temperatures (Bishop and Echternacht, 2004; Brown, 1992; Graves and Duvall, 1990), accumulated degree days (ADD; Hoffman, 2021; Turner and Maclean, 2022;) and moving "lagged" average temperatures (DeGregorio et al., 2016). Many species emerge only when specific threshold temperatures are surpassed (Blouin-Demers et al., 2000; Burger, 2019; DeGregorio et al., 2017; Sexton and Marion, 1981), although significant inter-individual variation has often confounded the identification of a reliable thermal trigger. Such thresholds likely reflect the thermal dependency of many physiological, behavioral, and cellular-level functions, which dictate the lower thermal limits of surface activity (Angilletta and Angilletta, 2009).

climates emerge up to 3 months earlier (March/April in South Carolina; Andrews and Waldron, 2017) than northern populations (May/June in New York; Brown, 1992).

Despite studies identifying various temperature-related drivers of egress (Andrews and Waldron, 2017; Brown, 1992; Martin, 1992), the range-wide applicability of specific cues remains unknown. Consequently, the timing of spring egress for most populations, such as in Midwest states, including Illinois, remains undefined. Such inquiries are particularly relevant for *C. horridus* throughout northern regions where philopatric individuals congregate at refugia during spring egress and are consequently susceptible to threats including human persecution (Galligan and Dunson, 1979) and management activities such as prescribed burns (Beaupre and Douglas, 2012). As a slow-maturing species with infrequent reproductive events (Aldridge and Brown, 1995; Bielema, 2022; Brown, 1991), *C. horridus* lacks the demographic plasticity to recover from population declines rapidly (Brown, 1993), leaving mortality events detrimental to population viability. Therefore, knowledge of spring egress phenology is invaluable for management and conservation purposes.

Thus, our objectives were to: 1) identify potential environmental cues of spring egress for *C. horridus* to determine emergence phenology; and 2) examine the applicability of identified cues in predicting the emergence phenology across the species' range. We used wildlife cameras and weather station-derived environmental data to construct a predictive model for the daily surface presence of *C. horridus* during spring egress at refugia across Illinois. Using our model, we predicted the surface presence and egress phenology of other populations reported in other studies and throughout Illinois. Our results detail the overwinter ecology of *C. horridus,* which provides a foundation for further ecological enquires and effective management and conservation strategies.

Materials & Methods

Study Site and Data Collection. — We conducted research at two over-wintering sites located ~350 km (>3° latitude) apart in western Jo Daviess County and Principia College in Jersey County (Fig. 1). We performed all research under an approved Illinois Department of Natural Resources Endangered and Threatened Species Permit (#05-11S) and approved University of Illinois Animal Care and Use Protocols (#22167, #22168). Knowledge of *C. horridus* at Jo Daviess County dates to the 1930s, with locations of refugia discovered via visual encounter surveys in 1991 (Bielema, 2022). Known occupancy at Principia College also dates to the 1930s with the acquisition of the land for the College, with specific entrances identified and reconfirmed via visual encounter surveys and VHF-radiotelemetry of individuals beginning in 2010 (S. Eckert, Pers. Coms). Both sites consist of upland mesic forest bounded to the south (Jersey County) and southwest (Jo Daviess County) by Mississippi River limestone-dolomite bluffs, covered with a vegetational matrix of remnant hill prairies and oak-hickory dominated woodlands. Crevices, talus, and holes along the bluff fronts at both sites provide overwintering refugia for *C. horridus*.

Are there other refugia known in Illinois? Some context here would be good (briefly).

We monitored *C. horridus* activity at all identified refugia entrances using Bushnell HD Trophy Cameras (Model #119736) fitted with external 12V batteries for extended life. Our cameras were in remote, topographically rugged locations away from local communities, and thus no people, apart from the researchers ~~involved in data collection (the authors),~~ visited the sites or were photographed. Each camera's position depended on substrate and habitat but was generally set ~1–2 m from ~~the~~ refugia and at the same elevation as the main entrance to afford a satisfactory field of view. Preliminary investigation revealed cameras occasionally failed to photograph ~~the~~ slow-moving *C. horridus* because the passive infrared sensors (PIR) did not detect the snakes.

Therefore, we supplemented PIR-triggered photos with the camera's time-lapse feature to take date/time-stamped photographs at 5 min intervals for the deployment periods; a 5 min photo interval provided high-resolution monitoring of refugia while also maximizing battery life and camera uptime. One exception to our camera schedule occurred at Jo Daviess County during spring 2018, where cameras photographed the entrances at 1 hr intervals alongside PIR-triggered photos.

Data Analysis. — We visually inspected all photographs for *C. horridus* and recorded the dates and times of surface presence. We then converted the surface presence of each refugia-year combination into a binomial response variable representing daily surface presence (1 = snake present, 0 = no snake present), omitting days where cameras malfunctioned, and deployment/retrieval days. We determined differences between the days of presence for each refugia-year combination using bootstrapped means and 95% confidence intervals (CIs). Specifically, we resampled the ordinal days of presence for each refugia-year combination with replacement 10,000 times, calculated the mean for each resample, and then determined the mean and 95% CIs based on the resulting bootstrapped resampling distributions (2.5% quantile = lower CI limit; 97.5% quantile = upper CI limit). Non-overlapping CIs indicated informative differences in the effects between refugia-year combinations.

We used Generalized Logistic Mixed Effects Models (GLMMs) in the R package 'lme4' (Bates et al., 2014) to examine the effects of environmental variables (Table 1) on the probability of surface presence; the probability of one or more *C. horridus* being surface active on a given day. For our study, we limited our analysis to variables derived from weather stations <= 30 km from each site, allowing for relative comparisons across different spatial and temporal extents. Due to the prevalence and apparent importance of temperature as a cue for egress within the literature, we focused primarily on temperature-derived variables found to be important drivers of surface presence for *C. horridus* and other temperate reptiles: maximum, minimum, and mean daily temperatures, five-day rolling minimum and maximum daily temperature, day of year, latitude, and accumulated degree days of base 5 °C (ADD). ADD is a phenological measure of seasonally increasing cumulative mean daily temperature above a selected threshold temperature, frequently used to predict phenological events and organismal developmental stages for a variety of taxa (Boutin and Lane, 2014; Cayton et al., 2015; Herms, 2004; Uelmen et al., 2016; Hoffman, 2021). We calculated degree days for each day using the formula: $((T_{\text{max}} + T_{\text{min}})/2) - T_{\text{base}}$, where T_{max} and T_{min} are the maximum and minimum temperature for a given day, and T_{base} is a selected threshold (base) temperature. The selection of the base temperature of 5 °C represented the lowest temperature we observed snake surface activity throughout our study. We then summed ("accumulated") the degree day values for each sequential day, starting from 1 January, to calculate ADD over the study period. Before modeling, we Z-transformed (centered and scaled) all variables and tested them for multicollinearity using Variance Inflation Factor analysis, removing highly correlated (VIF >= 5) covariates from the same model.

We created a suite of candidate models (Table 2), including a null model (intercept and random effect only) and a fully additive global model based on *a priori* hypotheses of drivers of surface presence. The dependent variable for each model was the daily presence, the random effect structure was refugia nested within the year, and the fixed effects were a combination of the environmental variables. We included latitude as a fixed effect in all models, serving as a numerical proxy for the site, to examine potential differences between the two populations. Our candidate set also included additive and two-way interactive models (sample size limitations precluded examining models with higher-level interactions) of the same fixed effect configurations to account for different hypotheses. For example, a significant interaction between latitude and a temperature-related variable might imply the effect of temperature on surface presence depended on latitude (Jersey County snakes might be surface active at different temperatures than Jo Daviess County). In contrast, an additive model might imply both populations responded equally to temperature, although the probability of surface presence between the two sites might differ. Finally, as demonstrated by other studies, we specified all continuous variables as quadratic terms to account for potential curvilinear relationships (Hoffman, 2021).

Examination of candidate models using the R package 'aer' (Kleiber and Zeileis, 2020) revealed no overdispersion, and therefore we ranked all models using Akaike's Information Criterion adjusted for small sample sizes (AICc) in the R package 'AICcmodavg' (Mazzerole and Mazerolle, 2017), and then examined the marginal and conditional effects of the most parsimonious model(s) using the R package 'effects' (Fox and Hong, 2009). Parameters with 95% CIs, not broadly overlapping zero indicated informative predictors of daily presence. We back-transformed the top model for interpretation and graphed the predicted values and 95% CIs using the R package 'ggplot2' (Wickham, 2011). We examined model fit via marginal and conditional coefficients of determination using the R package 'MuMin' (Barton and Barton, 2015).

We examined the applicability of the top-ranked AIC_c model in correctly determining the spring egress of other *C. horridus* populations by comparing our predictions with the average egress dates reported by other studies. Examination of other studies also allowed us to examine the extent of phenological plasticity in spring egress across the species' geographic range. We limited our comparisons to studies providing a detailed assessment of *C. horridus* egress (Andrew and Waldron, 2017; Brown, 1992; Martin, 2002) instead of briefly mentioning general

Expand this a little. Where were these studies? List the locations.

dates with little empirical evidence. For each study, we used our top-ranked AIC_c model to calculate predicted probabilities of surface presence for each ordinal day from day 1 to 243, comfortably spanning the entire egress period at each site, using environmental data gathered from National Oceanic and Atmospheric Association (NOAA) weather stations nearest to the study sites. Because missing data was present in the NOAA datasets, we calculated 15 year "normals" (averages) for estimation using the top model parameters. Doing so afforded complete datasets and determined the typical climatic conditions and probability of surface presence on a given day for each site. Because we were interested in population-level predictions, we held the fixed effect "latitude" at its mean and set the random effects of den and year to zero. If our model predictions were accurate, we expected the day of year with the highest (peak) probability of surface presence at each site to correspond to the average egress day reported by each study. To aid interpretation, we performed a simple linear regression between each study's reported average egress day and latitude and graphed the results with our model predictions.

Given our model predictions were accurate, we also used the top-ranked AIC_c model to predict surface presence across the latitudinal gradient of Illinois for each year of the study period (2018–2020), allowing examination of the intra- and inter-annual differences in predicted surface presence across a finer latitudinal scale. We derived the same environmental variables as before from weather stations within each degree of latitude in Illinois (37–42°) and used the top model to generate predicted probabilities of surface presence for each latitude-year combination. As before, because we were interested in population-level predictions, we held the fixed effect latitude at its mean and set the random effects of den and year equal to zero. We determined predicted values and 95% confidence intervals using the R package 'lme4'. Using the 'bootMer' function, we refit the model by resampling the dependent variable, daily presence, with replacement 10,000 times, and calculated the predicted values and 95% CIs based on the resulting bootstrapped resampling distributions (2.5% quantile = lower CI limit; 97.5% quantile = upper CI limit). We present graphs of the daily predictions and 14 day moving averages (for examination of general phenological patterns) against ordinal date for each latitude-year combination and averaged across all three years.

Results

We deployed cameras at six overwintering refugia (three in Jersey County and three in Jo Daviess County) for one or more years from 2018–2020 (Table 3), accumulating ~473,000 photos throughout the study. In Jersey County, cameras monitored two refugia for three years and a third den for two years after being discovered in 2019. All refugia in Jersey County were <1km apart and situated on tree-covered talus slopes near bluff prairies. In Jo Daviess County, cameras monitored all three refugia for two years in 2018 and 2019, although we removed all omitted data from one refugium in 2019 because vegetation restricted the cameras' view and obscured observations. Jo Daviess County refugia were < 0.5 km apart and were located on open-canopy outcrops.

The dates and durations of camera deployment varied between refugia and years (Table 3), but all deployments successfully spanned the snake emergence periods at their respective sites. Generally, most camera records showed several weeks of no snake presence on either end of the camera deployment periods, although some cameras in Jo Daviess County photographed several post-emergent *C. horridus* remaining near refugia entrances at the tail-end of the emergence periods. The individuals typically coiled in crevices within the camera's field of view and often occupied the same location daily. We suspect snakes were gravid females who frequently remain near refugia after spring emergence until parturition. Because we were interested only in activity related to refugia use, we removed these observations from further analysis (Table 3; Fig. 2).

Examination of bootstrapped 95% means and CIs revealed the daily presence of *C. horridus* at all refugia in Jo Daviess County occurred later in the spring than in Jersey County (Fig. 2). The mean county-level presence day for Jo Daviess County occurred on day 136 (16 May) compared to day 103 (13 April) for Jersey County. The 95% CIs also indicated intra-county differences in presence days between some, but not all, refugia-year combinations in Jersey County (Fig. 2). Early "one-off" surface presence occurred at all refugia in Jersey County in most years (Fig. 2), with the earliest activity occurring on day 55 (24 February). Cameras observed no such early surface presence in Jo Daviess County. Despite early activity, refugia in Jersey County usually exhibited fewer days of surface presence each year (range = 13–27) than in Jo Daviess County (range = 20–41) (Table 3).

We used 1525 camera-deployment days in our analysis to predict the surface presence of *C. horridus* during the late fall and spring from the six refugia (Table 3). Three candidate models received 100% of the AIC_c weights and included additive or two-way interactive effects between ADD, maximum daily temperature, and latitude (Table 4). The most parsimonious model included the additive effects between model covariates, accounted for 72% of model weights, and was used for all further analyses. The 95% CIs of ADD and maximum daily temperature in the top model did not span zero, signifying they had strong explanatory power and were strongly related to the surface presence (Table 5). Conversely, latitude narrowly spanned zero, indicating the parameter had weaker explanatory power.

The additive-only top model, as opposed to the interactive, implied *C. horridus* responded equally to maximum daily temperature and ADD. However, the probabilities of surface presence were higher in Jo Daviess County than in Jersey County for both variables (Fig. 3). The marginal effects of ADD (holding maximum daily temperature constant; Fig. 3A) revealed an increase in the probability of surface presence to a peak at 277.24 °C, decreasing thereafter, with the high value of ADD reflecting the accumulation of degree days from day of year 1 (1 January). The marginal effects of maximum daily temperature, holding ADD constant (Fig. 3), revealed that the probability of surface presence increased with increasing. Snakes were not observed in Jo Daviess County when the maximum daily temperature fell below 11°C. In Jersey County, snakes remained present on the surface at temperatures of 5 °C; however, such occurrences represented only 2.5% (4/155) of all days occurring below 11 °C. Therefore, the combined effect of both variables implies the probability of surface presence increases with higher ADD and temperatures (Fig. 3C and 3D).

We used seven other studies to examine the applicability of the top AIC$_c$-ranked model in accurately determining spring egress in other *C. horridus* populations (Table 5). The studies reported the average day of spring egress spanning latitudes from ~32.4° to ~43.8° (Table 5; Fig. 6). Simple linear regression (Fig. 6) revealed a later date of spring egress as latitude increased (r^2 = 0.81). Our model predicted the average egress day at each site within 10.2 (SD = 13.1) days. Closer inspection revealed our model failed to accurately predict two sites in Hampton (–23 day difference) and Beaufort Counties (–42 day difference), South Carolina (Andrews & Waldron, 2017), which inflated prediction error (Fig. 6; Table 6). If we removed the two sites, our model predicted the day of peak egress within 4.6 days (SD = 4.2).

We also predicted the probability of surface presence across each latitude-year combination of Illinois (Fig. 6). Visual inspection of each latitude-year subplot suggests the probability of surface presence is highly stochastic throughout late winter and spring, with intra- and inter-year phenological differences within each degree of latitude, particularly in more southerly regions. However, a general unimodal trend is apparent, characterized by a steady increase in the probability of surface presence to a peak as individuals egress from refugia and then declining after that as snakes disperse to summer habitats. The peak probability of surface presence between the southernmost (37°; peak probability = day 95) and northernmost Illinois (43°; peak probability = day 137), averaged over the three study years were approximately 42 days apart. Thus, our model suggests a 1° increase in latitude shifts the predicted peak probability of surface presence approximately seven days later into the spring, although substantial annual differences in peak surface presence occurred across latitudes, likely dependent on local climatic variation (Fig. 6). Additionally, comparison between subplots suggests an increased probability of daily surface presence earlier in the season at progressively lower latitudes with early spikes of probability on warmer days, perhaps indicating the greater potential for early "midwinter" emergences (longer left tails and probability spikes; Fig. 6).

Discussion

We used wildlife cameras and weather station-derived environmental data to successfully observe and predict the daily surface presence of *C. horridus* throughout the late winter and early spring at communal refugia in Jersey and Jo Daviess Counties, Illinois. The most parsimonious model for predicting surface presence included the additive effects of maximum daily temperature, accumulated degree days (ADD), and latitude. With a notable exception in the southeastern U.S., the model accurately predicted the average egress day for other populations range wide, emphasizing the role of temperature in influencing the substantial phenological plasticity observed across the species' range. The apparent applicability of the model to other populations suggests it can be a valuable tool in predicting the spring egress phenology of unknown populations across much of the species' geographic range, as demonstrated across Illinois.

Our results suggest temperature-related variables are strong drivers of spring emergence of *C. horridus*. ADD allowed our model to capture the general increase in temperature occurring at refugia sites throughout the late winter and early spring. ADD have a long history in phenological predictions of plants (Boutin and Lane, 2014), invertebrates (Cayton et al., 2015; Herms, 2004; Uelmen et al., 2016), and to a lesser extent, reptiles (Hoffman, 2021; Turner and Maclean, 2022). Unlike other time-related variables such as ordinal date and photoperiod (Martin, 1992), ADD allow for flexible predictions of surface presence by accounting for temperature variation across spatial (latitude and altitude) and temporal (years) extents. For example, degree days will accumulate faster in years and regions exhibiting earlier spring warming. Incorporating such climatic variation in phenological studies is particularly important for species occupying large geographic ranges subject to varying thermal regimes and exhibiting substantial phenological plasticity.

Including maximum daily temperature with ADD allowed our model to capture the highly stochastic thermal regimes characteristic of temperate climates during gradual spring warming. Other studies have implied daily air temperatures are highly influential and suggest surface activity occurs only once thermal thresholds are surpassed. Spring egress was associated with a maximum air temperature of ~15 °C in New York, South Carolina, and Virginia (Andrews and Waldron, 2017; Brown, 1992; Martin, 1992). Our results concur with the findings, suggesting 15 °C corresponds to a 50% probability of surface presence, above which surface presence was more likely than not.

It is apparent *C. horridus* only remains surface active until ~11 °C, with some exceptions, perhaps indicating the lower thermal limits of the species and the onset of physiological changes which inhibit surface activity. Agugliaro (2011) showed temperature-dependent metabolic rate depression in *C. horridus* occurred at 5 °C and 9 °C, with a steep temperature sensitivity in metabolic rate between 9 °C and 13 °C. Similar metabolic sensitivity was found in Red-sided Garter Snakes (*Thamnophis sirtalis parietalis*) at ~10 °C (Aleksiuk, 1971a, 1976b). Such metabolic responses likely promote energy conservation during cold-induced dormancy and serve as a mechanism to rapidly return to activity with increasing temperatures (Agugliaro, 2011). Snakes tend not to exhibit activity close to their critical thermal limits because of the risks associated with lower performance (Gregory, 1982; Angilletta and Angilletta, 2009). Thus, the warmer temperature of 15 °C may represent the species' voluntary thermal minima, below which most snakes remain within refugia. However, laboratory-based thermal selection studies on *C. horridus* emphasizing responses to thermal extremes are required to elucidate such thresholds.

Including latitude afforded us to examine the effects of temperature-related variables between sites and across latitudes. Acknowledging the model included only additive effects, not interactive, between latitude, maximum daily temperature, and degree days is critical for correct interpretation. At both sites, *C. horridus* responded equally to temperature, but the probability of surface presence was higher in Jo Daviess County than in Jersey County. Such a difference likely reflects the distinct habitat configurations at each site, which influenced the post-emergent behavior of *C. horridus* and the cameras' subsequent ability to detect surface activity. Specifically, all refugia in Jo Daviess County were on sun-exposed outcrops with abundant crevices and rock shelves, providing a thermally superior basking habitat and protective cover.

Post-emergent *C. horridus* would frequently use such basking habitat, remaining within the camera's view and thus increasing the probability of surface presence.

Conversely, refugia in Jersey County were on closed-canopy, loess-covered talus slopes with a notable lack of undergrowth or rocks near the entrances. Post-emergent *C. horridus* did not linger at the entrances but dispersed from the camera's view to nearby "transient" open habitats such as the bluff front or adjacent hill prairies. Such behavior resulted in fewer daily observations and a lower probability of surface presence. Thus, our model's observed effect of latitude implies the probability of observing snake presence via cameras can differ depending on proximate site characteristics rather than intra-population differences in response to temperature.

With a notable exception in the southeastern U.S., our top model accurately predicted the average egress day for other *C. horridus* populations as reported by studies across the species' geographic range. We should expect some discrepancy between reported versus predicted values due to potential sources of error, including the precision of weather station data used for model predictions and the study's sample size and sampling methods providing egress estimates. Despite these potential sources of error, our model provides accurate predictions for most of the sites examined and indicates temperature is largely responsible for the phenological plasticity of spring egress exhibited by *C. horridus*. Consequently, there is a strong correlation between spring egress and latitude, with spring warming occurring progressively later in northern sites (Fig. 5), resulting in delayed *C. horridus* egress. We also see delayed egress at higher, colder altitudes (Martin, 2002). The reported average mean egress day 135 at a high-elevation site at 1,075 m on the Allegheny Plateau, WV, resembles the northern extreme of the species range, approximately 5° latitude north.

Prolonged cold temperatures and subsequent delays in spring emergence at higher latitudes and altitudes (Martin, 1992; Brown, 1992) result in increasingly shorter active seasons with later egress and earlier ingress, directly impacting life histories. Shorter active seasons reduce the time dedicated to foraging, thus limiting yearly energy acquisition and subsequent adjustment of energy budgets between growth, maintenance, and reproduction (Brown, 2016). Consequently, alongside potentially milder temperatures during the active season, *C. horridus* in colder climates tend to exhibit slower growth rates, delayed sexual maturity, longer intervals between reproductive events, smaller offspring sizes, and lower reproductive success (Aldridge and Brown, 1995; Brown, 2016; Martin, 2002). Ultimately, prolonged cold temperatures are likely responsible for a reduction in overall fitness, as seen in the apparent vulnerability of northern populations, including extirpations from Canada and the northwestern U.S. (Environment Canada, 2010)

Our model failed to predict the average egress day at the southernmost two sites in Hampton and Beaufort County, SC (Andrews and Waldron, 2017). We are uncertain about the reasons for the difference but suspect the region's distinct climate might permit an alternate dormancy strategy our model does not account for. The study falls between 32–33° latitude and represents the only populations we examined to fall within the humid subtropical climate of the lower East Coast states. Relative to the other study locations, winter temperatures throughout the Lower East Coast are milder, with average maximum daily temperatures of 15–17 °C in the region's coldest months of January and February (Andrews and Waldron, 2017). Because of the warmer climate, degree days in Hampton and Beaufort Counties accumulate faster and reach our model's peak predictions much earlier in the season than the observed egress. According to Andrews and Waldron (2017), a maximum daily temperature of ~15 °C represents the 50% probability threshold of daily surface presence, suggesting surface activity of *C. horridus* could occur on most days throughout the winter months, but they did not comment on any midwinter surface activity.

While relatively rare, we observed occasional midwinter surface activity in Jersey county throughout all months except January. We also witnessed the winter emergences of non-target species, including *Agkistrodon contortrix*, *Coluber constrictor*, and *Thamnophis sirtalis*. Other studies note winter emergences in several other snake species, including *A. contortrix* (Sanders and Jacob, 1981), *C. adamanteus* (Stevenson, 2003), *C. horridus* (Nordberg and Cobb, 2016), *C. viridis* (Jacob and Painter, 1980), *Heterodon platirhinos* (Plummer, 2002), and *Sistrurus miliarius barabouri* (May et al., 1996). Notably, Nordberg & Cobb (2016) identified 60 winter emergence events from 13 *C. horridus* in Tennessee via indicative spikes in body temperature. However, despite the number of observations, relatively little is known regarding the frequency and ecological significance of winter surface activity in snakes. Presumably, such activity becomes progressively less frequent in higher latitudes where persistently low temperatures restrict surface activity (Brown, 1982; Viitanen, 1967), partially supported by the lack of early winter emergences in Jo Daviess compared to Jersey County and the lack of observed winter activity at other high-latitude sites (Brown, 1992). Furthermore, our predictions of surface activity reveal a progressively higher probability of early surface presence at lower latitudes in Illinois.

While we can only speculate on the significance of such winter surface activity without further study, we suspect such activity is the exception and not the rule. Most early emergences in Jersey County were "one-off" events, typically characterized by a single snake emerging and basking at a refugium entrance on warmer days which permitted surface activity. The snakes perhaps attempted to elevate body temperature to fight disease or infection (Nordberg and Cobb, 2016; Clarke et al., 2011; Kluger, 1979). Nordberg and Cobb (2016) observed over 60 emergence events from 12 *C. horridus* surgically implanted with radio transmitters only a few days before their ingress into refugia. Thus, it is possible the surgical incision sites did not fully heal before the onset of cold-induced dormancy and necessitated above-ground basking. Additionally, Clarke et al. (2011) and Nordberg and Cobb (2016) noted snakes emerging with skin lesions early in the spring were not uncommon and may indicate Snake Fungal Disease. We also observed *C. horridus* in Jersey County with severe skin lesions and contusions, and although we do not know their causes, they may motivate snakes to emerge and bask. Although the causes behind early emergences are unknown, the surprising frequency of such events warrants further investigation.

Conservation implications. — Spring emergence is a vulnerable period for *C. horridus*, particularly in northerly latitudes where post-emergent and lethargic individuals congregate at communal refugia and are consequently susceptible to local threats, including management activities (Beaupre and Douglas, 2012). Reducing the risk of such threats is vital for effective conservation; for example, scheduling prescribed burn regimes to occur when snakes are less likely to be surface active to reduce potential fire-induced mortality. Yet, the enigmatic nature of *C. horridus*, paired with the apparent phenological variation across both latitudinal and altitudinal clines, makes determining site-specific spring phenologies difficult and consequently limits conservation. Our model's ability to generate the probability of surface presence for any given day during spring egress is, therefore, a valuable tool for defining conservation and management schedules. However, predictions to new sites should be treated as hypotheses requiring verification through site-specific phenological studies.

One strategy to direct such schedules is to define specific probability thresholds, which can be translated into dates useful for management and conservation. For example, management activities could be conducted around refugia until the probability of surface presence exceeds a selected threshold. From a management perspective, the probability of surface presence is synonymous with risk; a higher probability indicates a greater potential for snake surface presence and subsequent exposure to management activities. Consequently, the selection of appropriate thresholds depends on the amount of risk willing to be taken given a specific application. We provide a variety of date thresholds for each latitude of Illinois (Table 7), as determined from general probability trends (i.e., 14 day averages across all years; Fig. 6) to aid in conservation and management scheduling.

Ideally, harmful activities would occur only when there is minimal risk of snake presence (e.g., probabilities < 5%; Table 7), corresponding to sustained temperatures below the species' suspected thermal limits of 11 °C. However, such thresholds would likely limit management schedules, particularly in milder southern regions (below 39° latitude) where warmer temperatures increase the probability of surface presence earlier in the season. In such cases, effective cutoffs must balance the risk of snake exposure with time allocated to management activities. We also encourage flexible scheduling whenever possible to account for intra-year and latitudinal climatic differences, although we recognize such scheduling would require the frequent calculation of model predictions based on current temperatures, which are not as readily accessible or practical as a single fixed date threshold. Providing managers access to our model to generate up-to-date predictions, for example, via a web portal, could allow for more flexible scheduling.

This seems a little bit too much. I think more validation is needed before wildlife managers start making management decisions based solely on predictions.

An obvious disadvantage of our study methodology is our inability to determine the abundance of surface-active snakes at refugia using only wildlife cameras. Insight into the number of surface-active snakes would afford a more detailed assessment of the spring emergence phenology of *C. horridus* and the implementation of more effective conservation strategies by incorporating population-level risk assessments. Knowledge of snake abundance would also help differentiate between early "one-off" emergence events by a single snake, particularly in more southern regions, and general spring egress when most snakes emerge and resume active season pursuits. Both differ in associated risk, which we cannot currently distinguish between. Anecdotal observations of the amount of surface activity seen on the cameras (not reported here) suggest the probability surface presence is positively correlated with surface abundance, although such evidence could be misleading as identifying individuals via photographs was not possible. Future research should focus on determining snake abundance to examine population-level risk further, but we are under no illusion obtaining such information for such an enigmatic snake would undoubtedly be time- and energy-intensive, as shown by Brown (1993) and Martin (1993) who spent upward of a decade obtaining such data.

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References

Aldridge, R. D. 1979. Seasonal spermatogenesis in sympatric *Crotalus viridis* and *Arizona elegans* in New Mexico. Journal of Herpetology. 13(2):187–192.

Aldridge, R. D., and W. S Brown. 1995. Male reproductive cycle, age at maturity, and cost of reproduction in the Timber Rattlesnake *(Crotalus horridus)*. Journal of Herpetology. 29(3):399–407.

Andrews, K. M., and J. L. Waldron. 2017. Comparative overwintering ecology of a coastal and inland population of Canebrake Rattlesnake (*Crotalus horridus*) in the southern United States. In: M. J. Dreslik, W. K. Hayes, S. J. Beaupre, S. P. Mackessy, editors. The Biology of The Rattlesnakes II. 196–212.

Angilletta Jr, M. J., and M. J. Angilletta. 2009. Thermal adaptation: a theoretical and empirical synthesis. Oxford University Press, Oxford UK.

Angilletta Jr, M. J., P. H. Niewiarowski, and C. A. Navas. 2002. The evolution of thermal physiology in ectotherms. Journal of Thermal Biology. 27(4):249–268.

Aslam, M. A., M. Ahmed, C. O. Stöckle, S. S. Higgins, F. U. Hassan, and R. Hayat. 2017. Can growing degree days and photoperiod predict spring wheat phenology? Frontiers in Environmental Science. 5(2017):57.

Bartholomew G. A. 1982. Physiological control of body temperature. Pages 273–320 in C. Gans and F. H. Pough, editors. Biology of the Reptilia. Volume 12. Academic Press, London, UK.

Bartón, K. 2014. Package 'MuMIn'. Model selection and model averaging based on 775 information criteria. R package version 3.0.2.

Beaupre, S. J., and L. E. Douglas. 2012. Responses of Timber Rattlesnakes to fire: lessons from two prescribed burns. Proceedings of the 4th fire in eastern oak forests conference 192–204.

Bielema, B. J. 2022. Reproduction in a Relict Population of Timber Rattlesnakes (*Crotalus horridus*) in Northwestern Illinois, USA. Herpetological Review. 53(2):201–207.

Bishop, D. C., and A. C. Echternacht. 2004. Emergence behavior and movements of winter-aggregated Green Anoles *(Anolis carolinensis)* and the thermal characteristics of their crevices in Tennessee. Herpetologica, 60(2):168–177.

Blouin-Demers, G., K.A. Prior, and P. J. Weatherhead. 2000. Patterns of variation in spring emergence by black rat snakes (*Elaphe obsoleta obsoleta*). Herpetologica. 56(2):175–188.

Boutin, S., and J.E. Lane. 2014. Climate change and mammals: evolutionary versus plastic responses. Evolutionary Applications. 7(1):29–41.

Brown, W. S. 2016. Lifetime reproduction in a northern metapopulation of timber rattlesnakes (*Crotalus horridus*). Herpetologica. 72(4):331–342.

Brown, W. S. 1991. Female reproductive ecology in a northern population of the Timber Rattlesnake, *Crotalus horridus*. Herpetologica. 47(1):101–115.

Brown, W. S. 1993. Biology, status, and management of the Timber Rattlesnake *(Crotalus horridus)*: a guide for conservation. Herpetological Circulars. 22:1–78.

Brown, W. S., D. W. Pyle, K. R. Greene, and J. B. Friedlaender. 1982. Movements and temperature relationships of Timber Rattlesnakes (*Crotalus horridus*) in northeastern New York. Journal of Herpetology. 16(2):151–161.

Brown, W. S., M. Kéry, and J. E. Hines. 2007. Survival of Timber Rattlesnakes *(Crotalus horridus)* estimated by capture-recapture models in relation to age, sex, color morph, time, and birthplace. Copeia. 2007(3):656–671.

Browning, D.M., S. J. Beaupre, and L. Duncan. 2005. Using partitioned Mahalanobis D2 (k) to formulate a GIS-based model of Timber Rattlesnake hibernacula. Journal of Wildlife Management. 69(1):33–44.

Burger, J. 2019. Vulnerability of Northern Pine Snakes (*Pituophis melanoleucus Daudin*, 1803) during fall den ingress in New Jersey, USA. Amphibian & Reptile Conservation. 13(2):102-114.

Burger, J., R. T. Zappalorti, and M. Gochfeld. 2000. The defensive behaviors of Pine Snakes (*Pituophis melanoleucus*) and Black Racers (*Coluber constrictor*) to disturbance during hibernation. Herpetological Natural History. 7(1):59–66.

Burger. J. 2019. Vulnerability of Northern Pine Snakes (*Pituophis melanoleucus Daudin*, 1803) during fall den ingress in New Jersey, USA. Amphibian and Reptile Conservation. 13(2):102–114.

Cayton, H. L., N. M. Haddad, K. Gross, S. E. Diamond and L. Ries. 2015.. Do growing degree days predict phenology across butterfly species? Ecology. 96(6):1473–1479.

Clark, R. W., W. S. Brown, R. Stechert and K. R. Zamudio. 2008. Integrating individual behavior and landscape genetics: the population structure of Timber Rattlesnake hibernacula. Molecular Ecology. 17(3):719–730.

Claussen, D. L., P. M. Daniel, S. Jiang, and N. A. Adams. 1991. Hibernation in the Eastern Box Turtle, *Terrapene c. carolina*. Journal of Herpetology. 34–341.

Costanzo, J. P., and D. L. Claussen. 1990. Natural freeze tolerance in the terrestrial turtle, *Terrapene carolina*. Journal of Experimental Zoology 254(2):228–232.

Costanzo, J. P., J. B. Iverson, M. F. Wright, and R. E. Lee. 1995. Cold hardiness and overwintering strategies of hatchlings in an assemblage of northern turtles. Ecology. 76(6):1772–1785.

Cox, C. L., M. L. Logan, O. Bryan, D. Kaur, E. Leung, J. McCormack, J. McGinn, L. Miller, C. Robinson, J. Salem, and J. Scheid. 2018. Do ring-necked snakes choose retreat sites based upon thermal preferences? Journal of thermal biology 71(2018):232–236.

DeGregorio, B. A., T. D Tuberville, R. A. Kennamer, B.B. Harris, and I. L. Brisbin Jr. 2017. Spring emergence of Eastern Box Turtles (*Terrapene carolina*): influences of individual variation and scale of temperature correlates. Canadian Journal of Zoology. 95(1):23–30.

Dunham, A. E., B.W. Grant, and K.L. Overall. 1989. Interfaces between biophysical and physiological ecology and the population ecology of terrestrial vertebrate ectotherms. Physiological Zoology. 62:335–355.

Durso, A. M., J. D. Willson, and C. T. Winne. 2011. Needles in haystacks: estimating detection probability and occupancy of rare and cryptic snakes. Biological Conservation. 144(5):1508–1515.

Environment Canada. 2010. Recovery Strategy for the Timber Rattlesnake (*Crotalus horridus*) in Canada. Species at Risk Act Recovery Strategy Series. Environment Canada, Ottawa.

Firth, B. T., and I. Belan. 1998. Daily and seasonal rhythms in selected body temperatures in the Australian lizard *Tiliqua rugosa* (*Scincidae*): field and laboratory observations. Physiological Zoology. 71(3):303–311.

Foster, C. D., S. Klueh, and S. J. Mullin. 2006. Extirpation of a relict Timber Rattlesnake (*Crotalus horridus*) population in Clark County, Illinois. Bulletin of the Chicago Herpetological Society 41:147–148.

Gardner-Santana, L. C., and S. J. Beaupre. 2009. Timber Rattlesnakes (*Crotalus horridus*) exhibit elevated and less variable body temperatures during pregnancy. Copeia. 2009(2):363–368.

Graves, B. M., D. Duvall. 1990. Spring emergence patterns of wandering garter snakes and prairie rattlesnakes in Wyoming. Journal of Herpetology. 24(4):351–356.

Graves, B. M., and D. Duvall. 1993. Reproduction, rookery use, and thermoregulation in free-ranging, pregnant *Crotalus v. viridis*. Journal of Herpetology. 27(1):33–41.

Gregory, P. T. 1974. Patterns of spring emergence of the Red-sided Garter Snake (*Thamnophis sirtalis parietalis*) in the Interlake region of Manitoba. Canadian Journal of Zoology. 52(8):1063–1069.

Gregory, P.T. 1982. Reptilian Hibernation. In pages 53-154 in C. Gans and F. H. Pough, eds. Biology

Harvey, D.S., and P. J. Weatherhead. 2006. Hibernation site selection by Eastern Massasauga Rattlesnakes (*Sistrurus catenatus catenatus*) near their Northern range limit. Journal of Herpetology. 40(1):66–73.

Herms, D. A. 2004. Using degree-days and plant phenology to predict pest activity. In IPM (integrated pest management), editors. Midwest Landscapes. Volume 58. St. Paul, MN: Minnesota Agricultural Experiment Station Publication. 49–59.

Hoffman, A. S. 2021. Managing Forests and Understanding Social Intolerance for Ohio's Declining Timber Rattlesnakes. Dissertation submitted to The Ohio State University.

Huey R. B. 1982. Temperature, physiology, and the ecology of reptiles. In C. Gans and F. H. Pough, editors. Biology of the Reptilia. Volume 13. Academic Press, London, UK. 25–91.

Huey, R. B., and R. D. Stevenson. 1979. Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. American Zoologist. 19(1):357–366.

Hyslop, N. L., R. J. Cooper, and J. M. Meyers. 2009. Seasonal shifts in shelter and microhabitat use of *Drymarchon couperi* (Eastern Indigo Snake) in Georgia. Copeia. 2009(3):458–464.

Jacob, J.S., and C. W Painter. 1980. Overwinter thermal ecology of *Crotalus viridis* in the north-central plains of New Mexico. Copeia. 1980(4):799–805.

Keller, W. L., and E. J. Heske. 2000. Habitat use by three species of snakes at the Middle Fork Fish and Wildlife Area, Illinois. Journal of Herpetology. 34(4):558–564.

Kleiber, C. and A. Zeileis. 2008.Applied Econometrics with R. Springer Science & Business Media, Berlin/Heidelberg, Germany.

Laidig, K. J., and D. M. Golden. 2004. Assessing Timber Rattlesnake movements near a residential development and locating new hibernacula in the New Jersey Pinelands. Unpublished Report, Pinelands Commission, New Lisbon, NJ.

Lowe, C. H., and V. J. Vance. 1955. Acclimation of the critical thermal maximum of the reptile *Urosaurus ornatus*. Science. 122(3158):73–74.

Lutterschmidt, D. I., M. P. LeMaster, and R. T. Mason. 2006. Minimal overwintering temperatures of Red-sided Garter Snakes (*Thamnophis sirtalis parietalis*): a possible cue for emergence? Canadian Journal of Zoology. 84(5):771–777.

Macartney, J. M., K.W. Larsen, and P.T. Gregory. 1989. Body temperatures and movements of hibernating snakes (*Crotalus* and *Thamnophis*) and thermal gradients of natural hibernacula. Canadian Journal of Zoology. 67(1):108–114.

Martin W. H. 1993. Reproduction of the Timber Rattlesnake (*Crotalus horridus*) in the Appalachian Mountains. Journal of Herpetology. 27(2):133–143.

Martin, W. H. 1992. Phenology of the Timber Rattlesnake (*Crotalus horridus*) in an Unglaciated Section of the Appalachian Mountains. In J. A. Campbell and E. D. Brodie, Jr. Biology of the Pitvipers. 259–277.

Martin, W. H. 2002. Life history constraints on the timber rattlesnake (*Crotalus horridus*) at its climatic limits. In: G. W. Schuett, M. Hoggren, M. E. Douglas, and H. W. Greene, Editors. Biology of the Vipers, Eagle Mountain Publishers. 285–306.

Mittelbach, G.G., D.W Schemske,H. V. Cornell, A. P. Allen, J. M. Brown, M. B Bush, S. P. Harrison, A. H. Hurlbert, N. Knowlton, and H. A. Lessios. 2007. Evolution and the latitudinal diversity gradient: speciation, extinction, and biogeography. Ecology Letters. 10(4):315–331.

Nordberg, E. J., and V. A. Cobb. 2016. Midwinter emergence in hibernating Timber Rattlesnakes (*Crotalus horridus*). Journal of Herpetology. 50(2):203–208.

Prior, K. A., and P. J. Weatherhead. 1996. Habitat features of Black Rat Snake hibernacula in Ontario. Journal of Herpetology 211–218.

Reinert, H. K. 1984. Habitat variation within sympatric snake populations. Ecology. 65:1673–1682.

Reinert, H. K., and R. T. Zappalorti. 1988. Timber Rattlesnakes (*Crotalus horridus*) of the Pine Barrens: their movement patterns and habitat preference. Copeia. 1988(4)964–978.

Rismiller, P. D., ad G. Heldmaier. 1982. The effect of photoperiod on temperature selection in the European Green Lizard, *Lacerta viridis*. Oecologia. 53(2):222–226.

Samson, F., and F. Knopf. 1994. Prairie conservation in North America. BioScience. 44(6):418–421.

Schulte, P. M., J. E. Podrabsky, J. H. Stillman, and L. Tomanek, L. 2015. The effects of temperature on aerobic metabolism: towards a mechanistic understanding of the responses of ectotherms to a changing environment. Journal of Experimental Biology. 218(12):1856–1866.

Sexton, O.J., and K. R. Marion. 1981. Experimental analysis of movements by Prairie Rattlesnakes, *Crotalus viridis*, during hibernation. Oecologia. 51(1):37–41.

Smith, P. W. 1961. *Crotalus horridus horridus Linnaeus*, Timber Rattlesnake. The Amphibians and Reptiles of Illinois, Bulletin of Illinois Natural History. 28:270–273

Smits, A. W., and C. D. Yorke, C. D. 1980. Winter activity and mortality in juvenile Chuckwallas (*Sauromalus obesus*). Journal of Herpetology. 14(1):100–101.

Smits, G., K. A. Prior, and P. J. Weatherhead 2000. Patterns of variation in spring emergence by Black Rat Snakes (*Elaphe obsoleta obsoleta).* Herpetologica. 56(2):175–188.

Stevenson, R. D. 1985. The relative importance of behavioral and physiological adjustments controlling body temperature in terrestrial ectotherms. The American Naturalist. 126(3):362–386.

Storey, K. B. 1990. Life in a frozen state: Adaptive strategies for natural freeze tolerance in amphibians and reptiles. American Journal of Physiology. 258(27):559–568.

Storey, K.B., and J. M. Storey. 1992. Natural freeze tolerance in ectothermic vertebrates. Annual Review of Physiology. 54(1):619–637.

Sunday, J. M., A. E. Bates, and N. K. Dulvy. 2011. Global analysis of thermal tolerance and latitude in ectotherms. Proceedings of the Royal Society B: Biological Sciences. 278(1713):1823–1830.

Sunday, J. M., A. E. Bates, M. R. Kearney, R. K. Colwell, N. K. Dulvy, J. T. Longino, and R. B. Huey. 2014. Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. Proceedings of the National Academy of Sciences 111(15):5610–5615.

Taylor, G. M., and E Nol. 1989. Movements and hibernation sites of overwintering Painted Turtles in southern Ontario. Canadian Journal of Zoology. 67(8):1877–1881.

Turner, R. K., and I. M. Maclean. 2022. Microclimate-driven trends in spring-emergence phenology in a temperate reptile (Vipera berus): Evidence for a potential "climate trap"? Ecology and Evolution. 12(2):8623.

Uelmen Jr, J. A., R. L. Lindroth, P. C. Tobin, P. B. Reich, E. G. Schwartzberg, and K. F. Raffa. 2016. Effects of winter temperatures, spring degree-day accumulation, and insect population source on phenological synchrony between forest tent caterpillar and host trees. Forest Ecology and Management. 362(2016):241–250.

Ultsch G. R. 1989. Ecology and physiology of hibernation and overwintering among freshwater fishes, turtles, and snakes. Biological Reviews. 64(4):435–515.

Viitanen, P. 1967. Hibernation and seasonal movements of the viper, *Vipera berus berus* in southern Finland. Annales Zoologici Fennici 4(4):472–546.

Voituron, Y., B. Heulin, and Y. Surget-Groba. 2004. Comparison of the cold hardiness capacities of the oviparous and viviparous forms of *Lacerta vivipara*. Journal of Experimental Zoology. 301(4): 367–373.

Warwick, C, Steedman, and T. Holford. 1991. Rattlesnake collection drives—their implications for species and environmental conservation. Oryx. 25(1):39–44.

Weatherhead, P. J. 1989. Temporal and thermal aspects of hibernation of Black Rat Snakes (*Elaphe obsoleta*) in Ontario. Canadian Journal of Zoology. 67(9): 2332–2335.

Weir, J. 1992. The sweetwater rattlesnake round-up: a case study in environmental ethics. Conservation biology. 6(1):116–127.

Wickham, H. 2009. ggplot2: elegant graphics for data analysis. Springer, New York, NY.

Wieser, W. 1973. Temperature relations of ectotherms: a speculative review. Effects of temperature on ectothermic organisms. Pages 1–24 in W. Wieser, ed. Effects of temperature on ectothermic organisms. Springer-Verlag, New York.

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*(3):325–334.

Wittenberg, R. D. 2012. Foraging ecology of the Timber Rattlesnake (*Crotalus horridus*) in a fragmented agricultural landscape. Herpetological Conservation and Biology. 7(3): 449–461.

Wittenberg, R. D., S. J. Beaupre, 2014. Growth of Timber Rattlesnakes (*Crotalus horridus*) in an agriculturally fragmented and a contiguously forested habitat. Herpetologica. *70*(2):171–183.

Yadav, V., and G. Malanson G. 2008. Spatially explicit historical land use land cover and soil organic carbon transformations in Southern Illinois. Agriculture, Ecosystems & Environment. 123(4):280–292.

Yagi, A.R., R. J. Planck, K. T. Yagi, G. J. Tattersall. 2020. A Long-Term Study on Massasaugas (*Sistrurus catenatus*) Inhabiting a Partially Mined Peatland: A Standardized Method to Characterize Snake Overwintering Habitat. Journal of Herpetology. 54(2):235–244.

Zappalorti, R, J. Burger J, and F. Peterson. 2015. Home range size and distance traveled from hibernacula in Northern Pinesnakes in the New Jersey Pine Barrens. Herpetologica. 71(1):26–36.

Figure 1

Location of Timber Rattlesnake (*Crotalus horridus*) overwinter sites in West Jo Daviess County (n = 3 refugia) and Principia College, Jersey County (n = 3 refugia), Illinois.

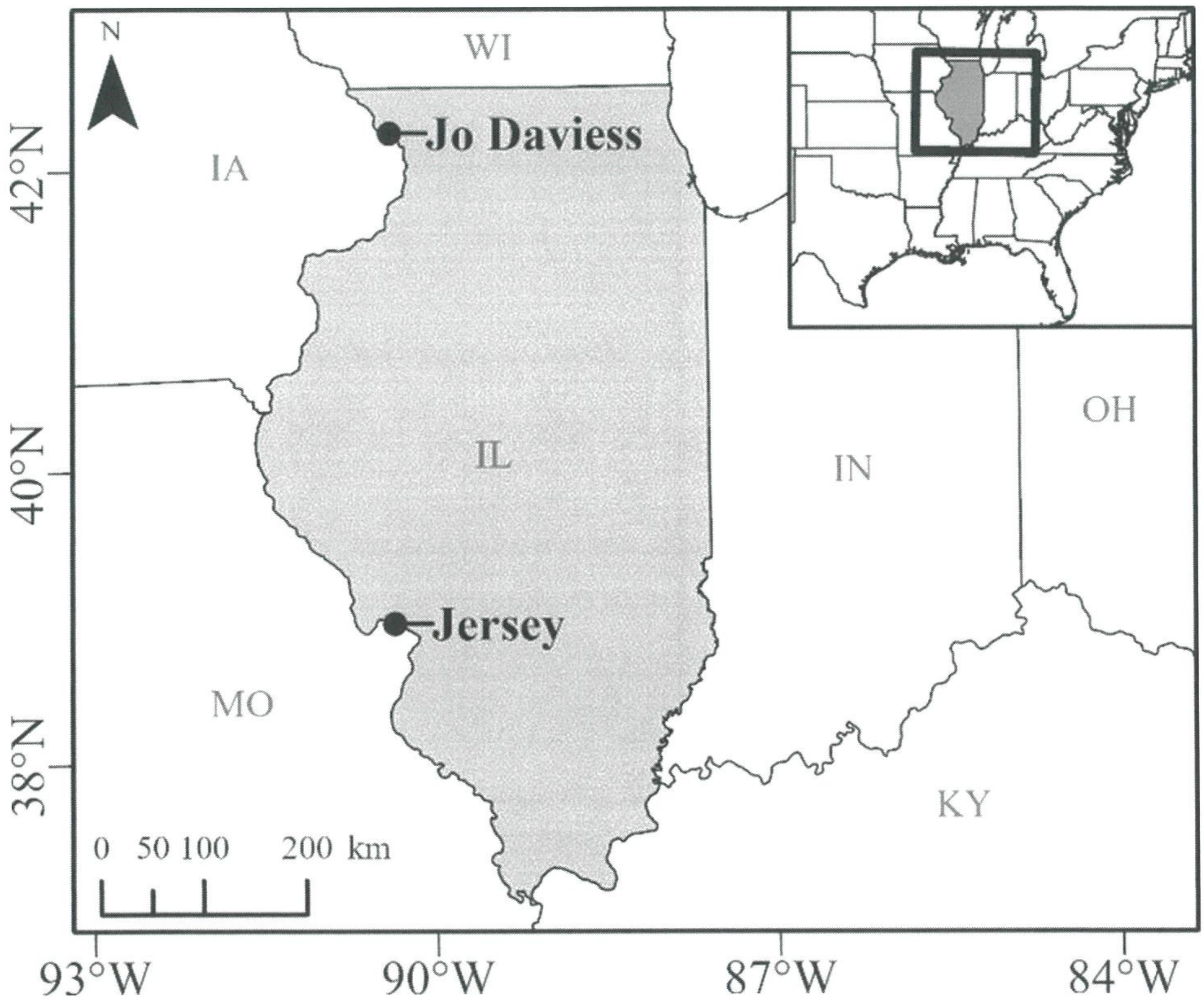

Figure 2

Days of surface presence (grey dots) for Timber Rattlesnakes (*Crotalus horridus*) at six communal overwinter refugia in Jo Daviess County (n = 3 dens), and Jersey County (n = 3 dens), Illinois.

We removed days of suspected gravid females (red dots) from further analysis. The mean day of emergence and bootstrapped 95% confidence intervals (solid black dot and error bars) are displayed for each refugia-year combination. *C. horridus* activity observed via Cameras deployed at the entrances of each refugium.

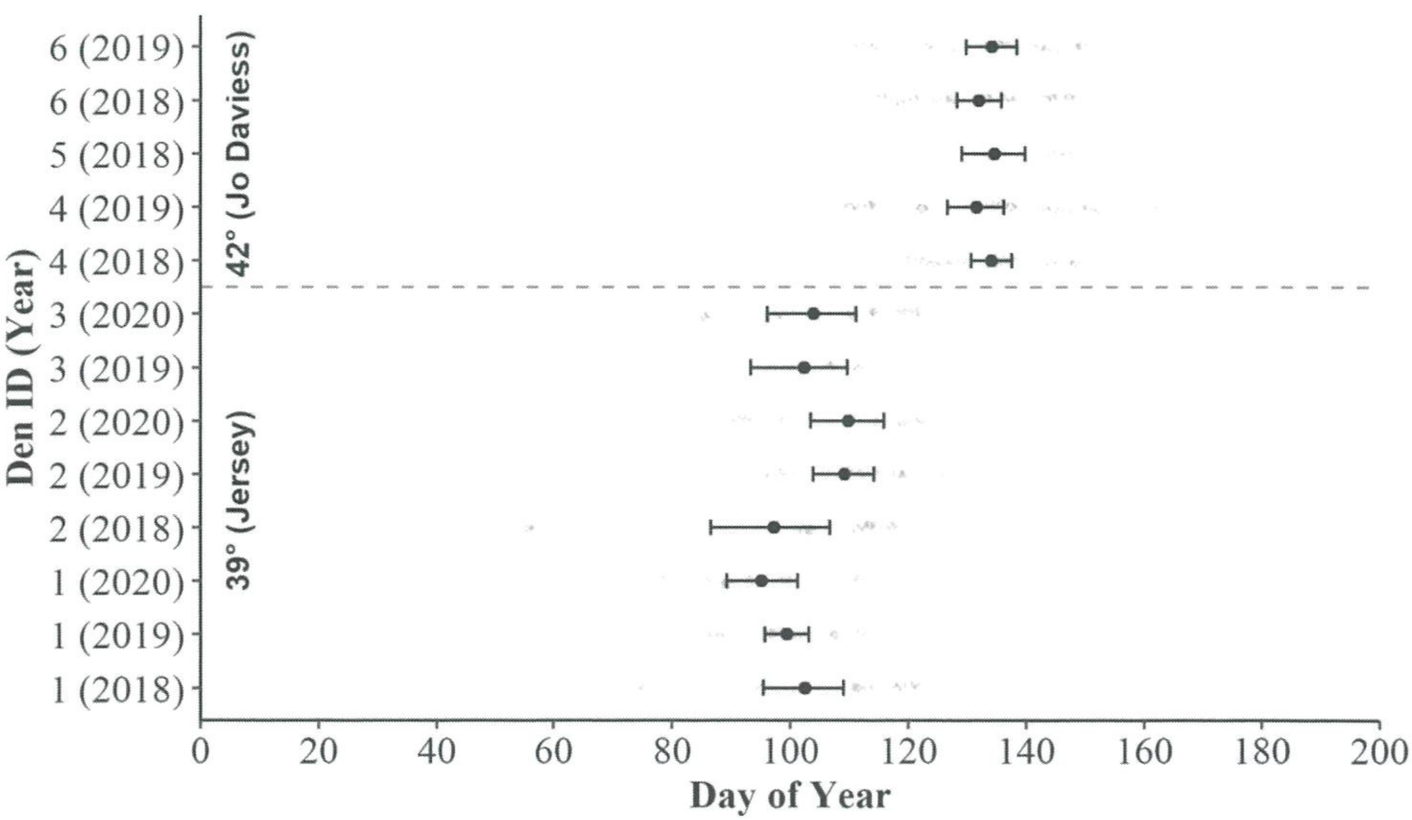

Figure 3

Site-level probabilities and 95% confidence intervals of surface presence by the Timber Rattlesnake (*Crotalus horridus*) at communal refugia in Jersey (n = 3) and Jo Daviess (n = 3) Counties, Illinois.

Plots represent: (A) the individual effects of accumulated degree days (ADD) (holding maximum daily temperature constant at its mean of 15.95 °C); (B) maximum daily temperature (holding ADD constant at its mean of 248.88 °C); and (C and D) the additive effects of both variables (in maximum daily temperature increments of 10 °C) for each county. Probabilities determined by the top-ranked AICc candidate model.

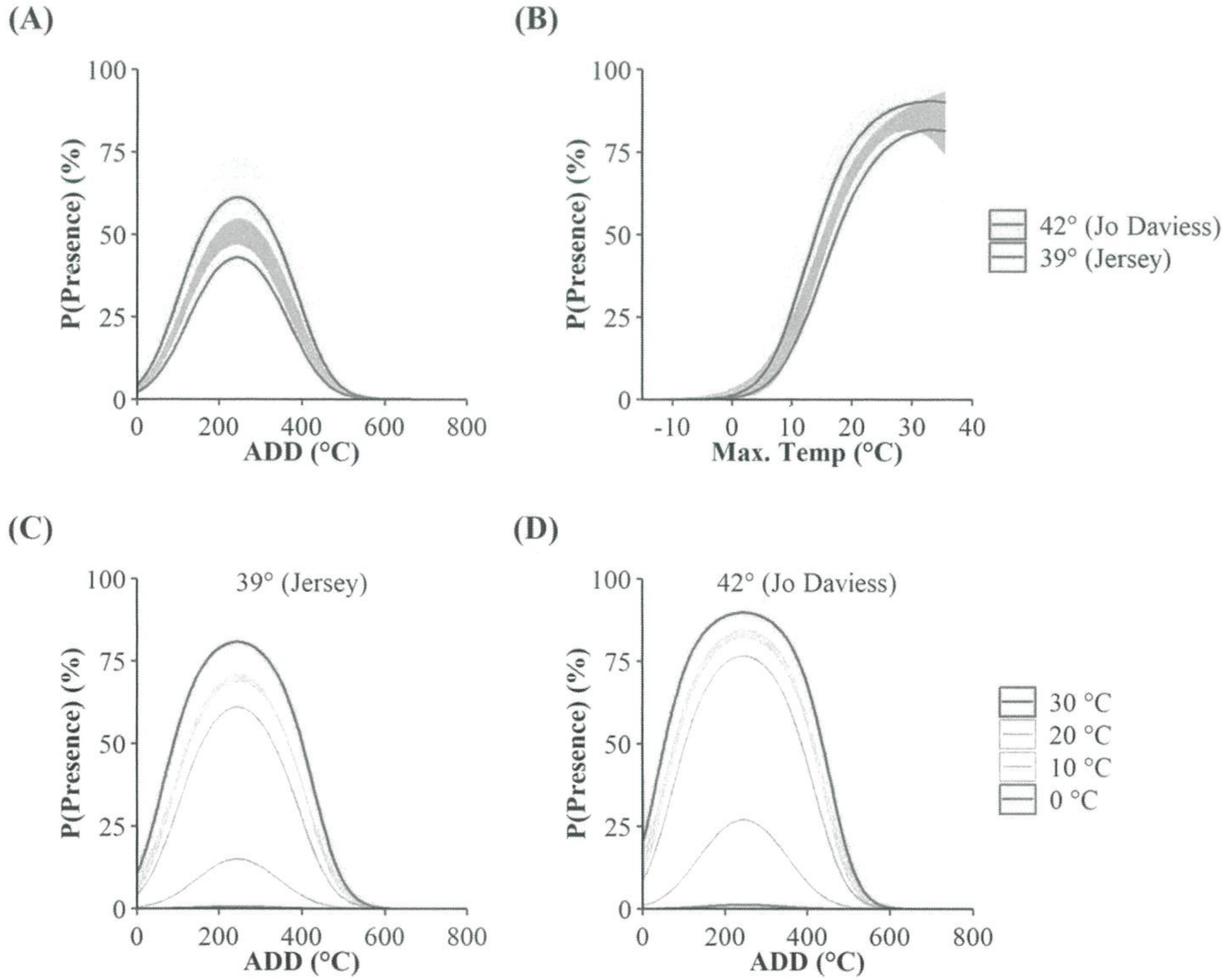
(A)
100
75
50
25
0
P(Presence) (%)
0 200 400 600 800
ADD (°C)
(B)
100
75
50
25
0
P(Presence) (%)
-10 0 10 20 30 40
Max. Temp (°C)
42° (Jo Daviess)
39° (Jersey)
(C)
39° (Jersey)
100
75
50
25
0
P(Presence) (%)
0 200 400 600 800
ADD (°C)
(D)
42° (Jo Daviess)
100
75
50
25
0
P(Presence) (%)
0 200 400 600 800
ADD (°C)
30 °C
20 °C
10 °C
0 °C

Figure 4

Population-level probabilities (holding latitude constant) of surface presence by the Timber Rattlesnake (*Crotalus horridus*) at communal refugia in Illinois.

Plots represent the individual effects of: (A) accumulated degree days (ADD) (holding maximum daily temperature constant at its mean of 15.95 °C); (B) maximum daily temperature (°C) (holding ADD constant at its mean of 248.88 °C); and (C) the additive effects of both variables (Plots C). Latitude was held constant in all plots (i.e., at the "population"-level). Probabilities were determined by the top ranked AICc candidate model.

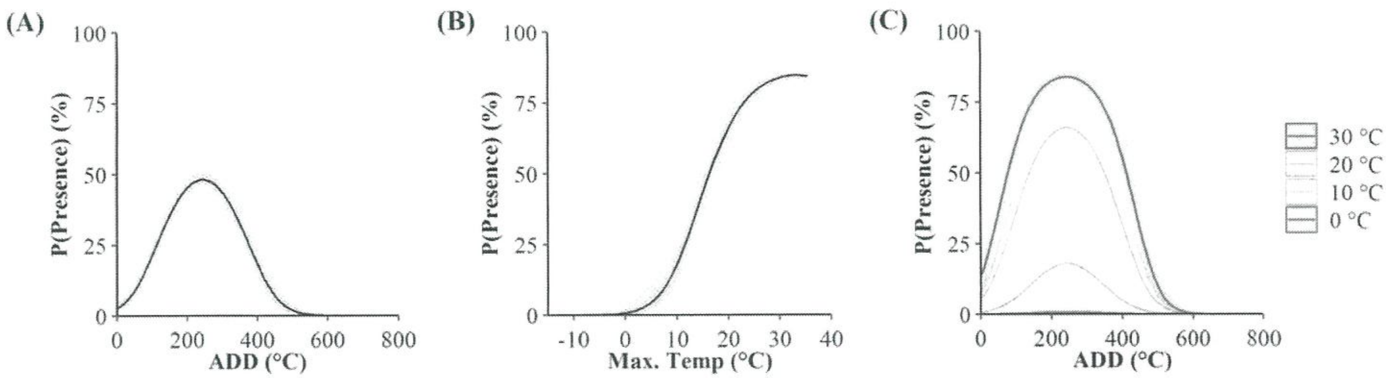

Figure 5

Simple linear regression between latitude and the average day of spring egress, as reported by other studies, overlain with the peak probability of surface presence as predicted by the top AICc model.

Black line and grey ribbon represents estimated values and 95% confidence intervals. Dashed lines connect each study site's reported egress day (black dots) and predicted probabilities (white dots). Letters correspond to the citation ID of each study detailed in Table 5. Model predictions were calculated using 15 year "normals" (averages) of the model covariates maximum daily temperature and accumulated degree days (ADD; base 5 °C), obtained from the closest weather stations to the site(s) of each respective study.

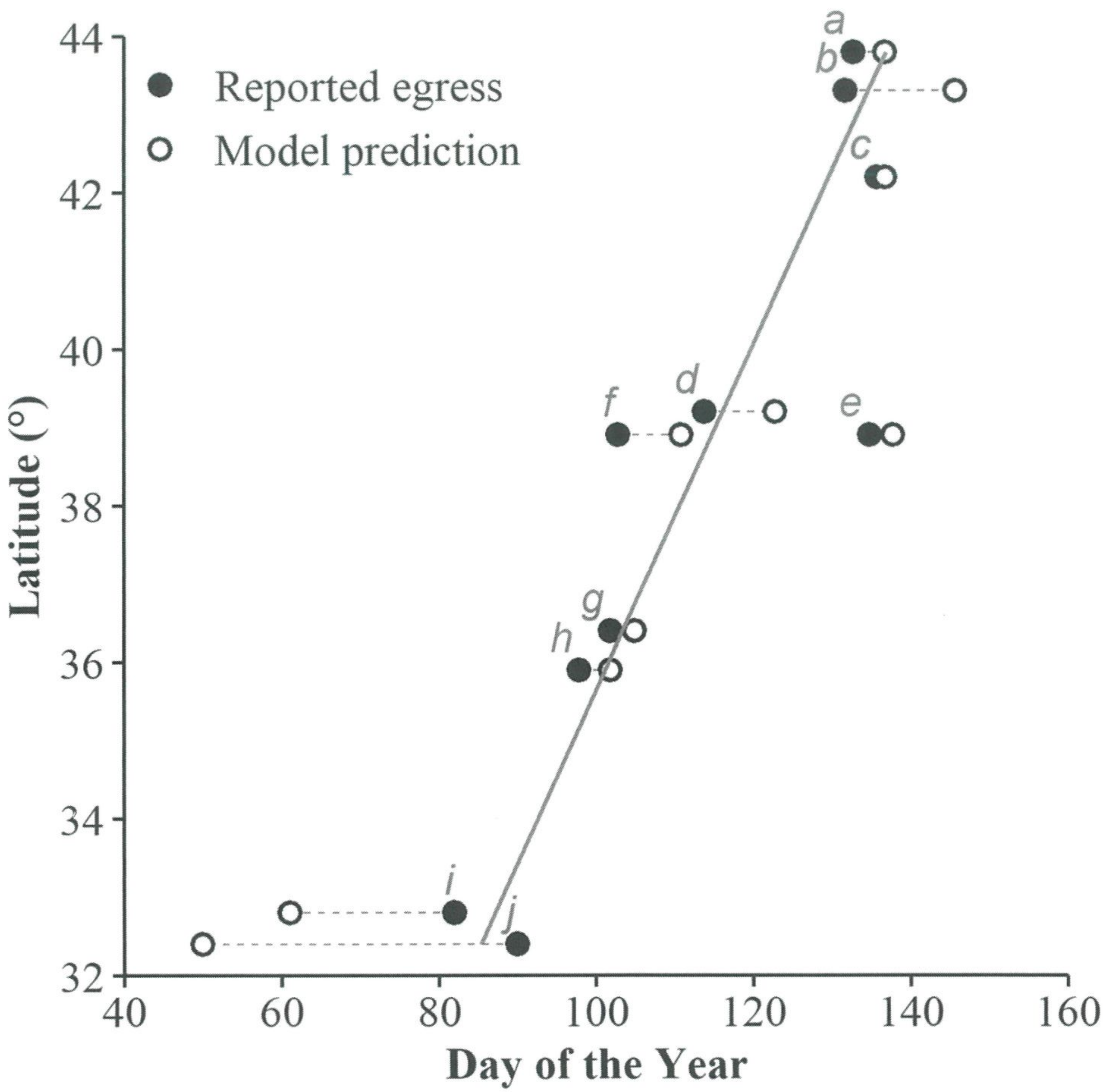
Reported egress
Model prediction
a
b
c
d
e
f
g
h
i
j
44
42
40
38
36
34
32
40
60
80
100
120
140
160
Latitude (°)
Day of the Year

Figure 6

Predicted probabilities of surface presence for the Timber Rattlesnake (*Crotalus horridus*) during the late winter and spring across the latitudinal gradient of Illinois (in increments of 1°).

Plots are displayed for each year of the study period (2018–2020) and averaged across years. Probabilities are displayed for each day (grey lines) and averaged across a 14 day moving window (black lines) alongside bootstrapped 95% confidence intervals (Grey ribbons). Vertical black lines and parenthesized numbers within each subplot represent the day of peak probability of presence. Predictions derived using the top AICc model examining surface presence as a function of the additive effects of accumulated degree days (ADD; base 5 °C) and maximum daily temperature (°C). Predictions were made on data derived from weather station data located within each degree of latitude.

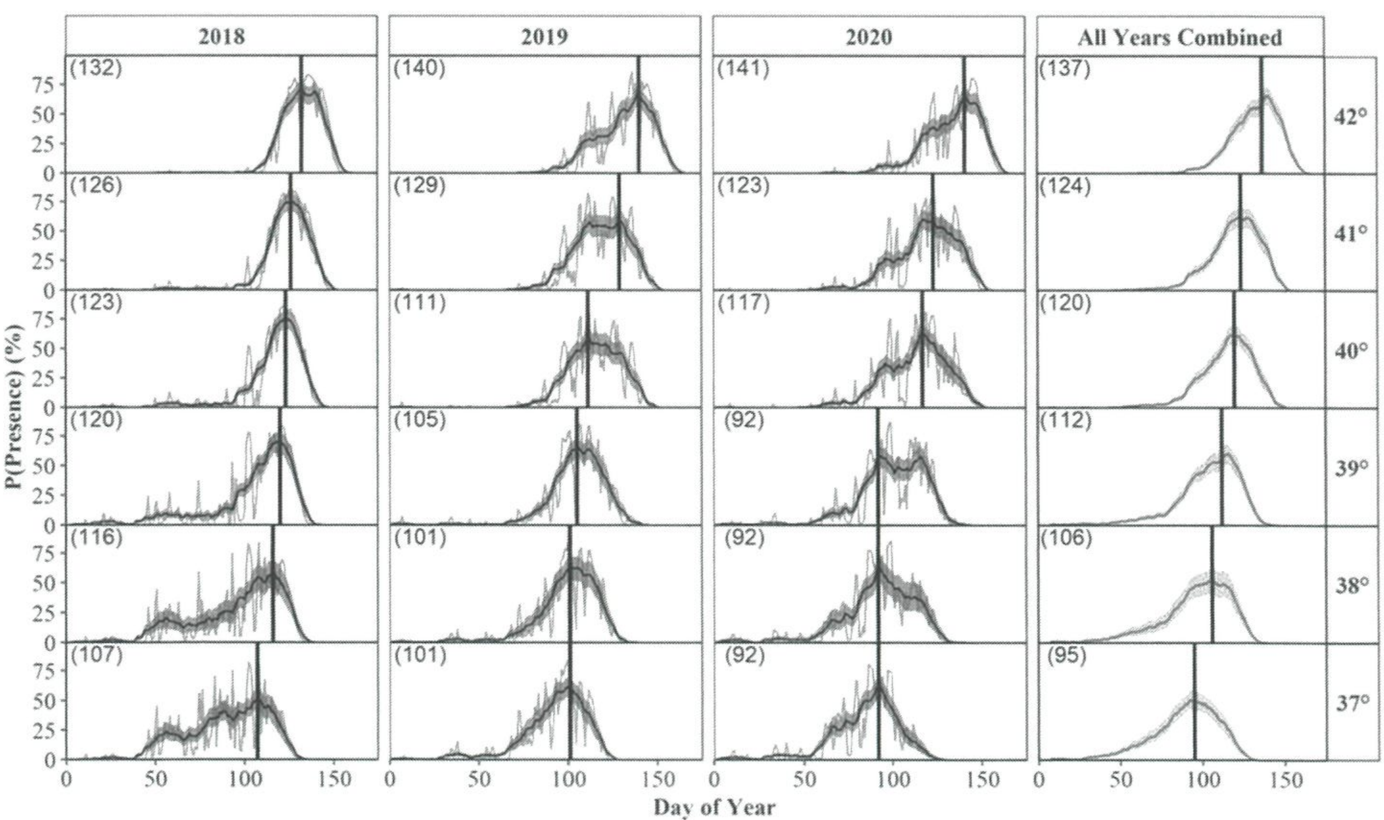

Table 1(on next page)

Environmental variables used to construct candidate models predicting the daily surface presence of *C. horridus*.

Data obtained from weather stations located < 30 km from each field site.

Predictor	Description (unit)
Min. Temp	Minimum daily temperature (°C)
Max. Temp	Maximum daily temperature (°C)
Mean. Temp	Mean daily temperature (°C)
Min_5. Temp	Five-day rolling minimum daily temperature (°C)
Max_5. Temp	Five-day rolling maximum daily temperature (°C)
Accumulated Degree Days (ADD)	Cumulative mean daily temperature above 5 °C (°C)
Day of Year	Ordinal date (1 = January 1st) (day)
Latitude	Numerical proxy for study site (degrees)

Table 2(on next page)

AIC_c candidate model set of mixed effects logistic regression models examining the effect of environmental variables on the surface presence of Timber Rattlesnakes (*Crotalus horridus*).

Data collected from refugia in Jo Daviess County (n = 3) and Jersey County (n = 3) during late winter and spring of 2018–2020.

Model	Parameters
1	Intercept only
2	Global
3	Latitude + ADD^2+ Min. $Temp^2$
4	Latitude * Min. $Temp^2$ + ADD^2
5	Latitude * ADD^2 + Min. $Temp^2$
6	Latitude * Min. $Temp^2$
7	Latitude + Min. $Temp^2$
8	Latitude + ADD^2 + Max. $Temp^2$
9	Latitude * Max. $Temp^2$ + ADD^2
10	Latitude * ADD^2 + Max. $Temp^2$
11	Latitude * Max. $Temp^2$
12	Latitude + Max. $Temp^2$
13	Latitude + ADD^2 + Mean $Temp^2$
14	Latitude * Mean. $Temp^2$ + ADD^2
15	Latitude * ADD^2 + Mean $Temp^2$
16	Latitude * Mean $Temp^2$
17	Latitude + Mean $Temp^2$
18	Latitude + ADD^2 + Min_5. $Temp^2$
19	Latitude * Min_5. $Temp^2$ + ADD^2
20	Latitude * ADD^2 + Min_5. $Temp^2$
21	Latitude * Min_5. $Temp^2$
22	Latitude + Min_5. $Temp^2$
23	Latitude + ADD^2 + Max_5. $Temp^2$
24	Latitude * Max_5. $Temp^2$ + ADD^2
25	Latitude * ADD^2 + Max_5. $Temp^2$
26	Latitude * Max_5. $Temp^2$
27	Latitude + Max_5. $Temp^2$
28	Latitude * Day of $Year^2$
29	Latitude * Day of $Year^2$ + Max. $Temp^2$
30	Latitude * Day of $Year^2$ + Min. $Temp^2$
31	Latitude * Day of $Year^2$ + Min_5. $Temp^2$
32	Latitude * ADD^2

Table 3(on next page)

Refugia by year deployment summaries of 6 Bushnell HD Trophy Cameras (Model 119736) installed at communal Timber Rattlesnake (*Crotalus horridus)* refugia in Jo Daviess County and Jersey County.

Columns represent camera deployment locations (County, Refugia); Year of camera deployment (Year); dates of camera deployment period (First, Last, Duration); total number of photos taken during the deployment period (Photos); and the number of days *C. horridus* were (Presence Days) or were not (Absence Days) photographed.

County	Refugia	Year	Deployment Dates			Photos	Presence Days	Absence Days
			First	Last	Duration			
Jersey	1	2018	2/24	6/1	98	27,376	27	71
		2019	1/1	6/6	157	69,260	19	138
		2020	1/1	5/31	152	72,002	19	133
Jersey	2	2018	2/24	5/31	97	17,914	19	78
		2019	1/1	6/7	158	46,243	22	136
		2020	1/1	5/31	152	50,230	20	130
Jersey	3	2019	1/1	6/7	158	36,283	13	115
		2020	1/1	5/29	150	67,045	24	126
Jo Daviess	4	2018	4/8	6/23	77	7,041	35*	32*
		2019	3/17	7/13	119	34,165	35*	64*
Jo Daviess	5	2018	4/8	6/13	67	4,567	20	47
Jo Daviess	6	2018	4/8	6/13	67	6,431	38	29
		2019	3/17	7/10	116	33,719	41*	47*

*Values represent the number of observed presence days after the removal of days of presumed gravid females (see text).

Change dates format to internationally recognized format

Table 4 (on next page)

AIC_c results for the top ten mixed effects logistic regression candidate models examining the effect of environmental variables on the surface presence of Timber Rattlesnakes (*Crotalus horridus*).

Results are sorted by ΔAIC_c, where: k = the number of parameters, AIC_c = Akaike score, w_i = Akaike Weights, LL = log-likelihood, R^2_m = marginal coefficient of determination, R^2_c = Conditional coefficient of determination

Model	*k*	AIC_c	ΔAIC_c	w_i	LL	R^2_m	R^2_c
Latitude + ADD^2 + Max. $Temp^2$	8	788.03	0.00	0.72	-385.97	0.83	0.84
Latitude * Max. $Temp^2$ + ADD^2	10	791.21	3.18	0.15	-385.53	0.84	0.84
Latitude * ADD^2 + Max. $Temp^2$	10	791.47	3.44	0.13	-385.66	0.84	0.84
Latitude + ADD^2 + Mean. $Temp^2$	8	801.19	13.16	0.00	-392.55	0.83	0.83
Latitude * Mean. $Temp^2$ + ADD^2	10	804.12	16.10	0.00	-391.99	0.83	0.84
Latitude * ADD^2 + Mean. $Temp^2$	10	804.73	16.70	0.00	-392.29	0.83	0.83
Global	16	842.46	54.43	0.00	-412.17	0.81	0.82
Latitude + ADD^2 + Min. $Temp^2$	8	850.43	62.40	0.00	-417.17	0.82	0.83
Latitude * Min. $Temp^2$ + ADD^2	10	852.12	64.09	0.00	-415.99	0.83	0.84
Latitude * ADD^2 + Min. $Temp^2$	10	853.22	65.19	0.00	-416.54	0.82	0.83

Table 5 (on next page)

Parameter estimates, standard error (SE), and 95% confidence intervals (CI) for top AIC_c model.

The top AICc model examined the additive effects of accumulated degree days (ADD), maximum daily temperature, and latitude on the surface presence of Timber Rattlesnakes (*Crotalus horridus*).

Parameter	Estimate	SE	Upper CI	Lower CI
Intercept	–4.61	0.36	–5.27	–3.90
ADD	–167.80	17.47	199.26	–133.40
ADD^2	–151.52	13.99	–177.20	–124.71
Latitude	0.36	0.28	0.03	0.63
Max. Temp	80.69	10.20	60.56	99.89
Max. $Temp^2$	–23.02	8.24	–38.37	–6.53

Table 6 (on next page)

Summary of studies used to examine the latitudinal variation in spring egress for the Timber Rattlesnake (*Crotalus horridus*), alongside testing our model predictions.

Columns represent the citation ID corresponding to the citation indexes in figure 5 (ID), study citation (Citation); Location of study (Study Location), the year(s) in which research was conducted (Year(s)); The approximate latitude (Lat.) and longitude (Lon.) of the study site (in decimal degrees; the reported average day of egress (Day of Egress); the day of peak probability of surface activity as predicted by the top AIC_c model; and the difference between the reported average day of egress and the day of peak probability of surface presence in days (Diff).

ID	Citation	Year(s)	Lat.	Lon.	Day of Egress	Peak Prob.	Diff
a	Brown (1992)	1981–1988	43.8	–73.6	133	137	4
b	Bauder et al. (2011)	2011	43.3	–73.6	132	145	13
c	Current study	2018–2020	42.2	–90.3	136	135	-1
d	Hoffman (2021)	2017–2020	39.2	–82.4	114	122	8
e	Martin (2002)	1989–2001	38.9	–79.3	135	137	2
f	Current study	2018–2020	38.9	–90.4	103	109	6
g	Sealy (2002)	1990–1997	36.4	–80.3	102	103	1
h	Nordberg & Cobb (2017)	2011–2013	35.9	–86.4	98	100	2
i	Andrews & Waldron (2017)	2002–2004	32.8	–81.1	82	59	–23
j	Andrews & Waldron (2017)	2006–2008	32.4	–80.7	90	48	–42

Table 7 (on next page)

The day of the year and corresponding date when the predicted probability of surface presence for *C. horridus* typically exceeded a given threshold in Illinois during our study (2018–2020).

We determined threshold dates for each latitude using 14-day moving averages of predicted probabilities averaged across all years, allowing examination of general phenological trends (Figure 6). We do not report probability threshold values > 60% as 14 day moving averages did not typically exceed this value. Additionally, we do not report probability threshold values of 0% as such occurrences were rare (i.e., there is always some probability of surface presence). Selection of probability thresholds should be determined by the appropriate authorities depending on the specific application (see "Conservation Implications" in the discussion).

	Latitude					
Threshold	**37°**	**38°**	**39°**	**40°**	**41°**	**42°**
5%	54 (2/23)	59 (2/28)	69 (3/10)	87 (3/28)	90 (3/31)	95 (4/5)
10%	56 (2/25)	62 (3/3)	84 (3/25)	93 (4/3)	94 (4/4)	110 (4/20)
15%	65 (3/6)	83 (3/24)	85 (3/26)	94 (4/4)	95 (4/5)	112 (4/22)
20%	80 (3/21)	84 (3/25)	87 (3/28)	95 (4/5)	96 (4/6)	114 (4/24)
25%	82 (3/23)	85 (3/26)	90 (3/31)	96 (4/6)	96 (4/6)	119 (4/29)
30%	85 (3/26)	86 (3/27)	94 (4/4)	97 (4/7)	99 (4/9)	120 (4/30)
35%	86 (3/27)	88 (3/29)	95 (4/5)	98 (4/8)	111 (4/21)	121 (5/1)
40%	90 (3/31)	90 (3/31)	95 (4/5)	99 (4/9)	112 (4/22)	122 (5/2)
45%	91 (4/1)	95 (4/5)	96 (4/6)	100 (4/10)	113 (4/23)	122 (5/2)
50%	92 (4/2)	95 (4/5)	98 (4/8)	111 (4/21)	116 (4/26)	124 (5/4)
55%	95 (4/5)	96 (4/6)	98 (4/8)	112 (4/22)	119 (4/29)	134 (5/14)
60%	96 (4/6)	99 (4/9)	99 (4/9)	114 (4/24)	121 (5/1)	135 (5/15)