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Jinelle H. Sperry

Gabriel Blouin-Demers

Gerardo L.F. Carfagno
Gettysburg College

See next page for additional authors

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Abstract
The ecology of ectotherms should be particularly affected by latitude because so much of their biology is temperature dependent. Current latitudinal patterns should also be informative about how ectotherms will have to modify their behavior in response to climate change. We used data from a total of 175 adult black ratsnakes (Elaphe obsoleta) radio tracked in Ontario, Illinois, and Texas, a latitudinal distance of > 1500 km, to test predictions about how seasonal patterns of activity and mortality should vary with latitude. Despite pronounced differences in temperatures among study locations, and despite ratsnakes in Texas not hibernating and switching from diurnal to nocturnal activity in the summer, seasonal patterns of snake activity were remarkably similar during the months that snakes in all populations were active. Rather than being a function of temperature, activity may be driven by the timing of reproduction, which appears similar among populations. Contrary to the prediction that mortality should be highest in the most active population, overall mortality did not follow a clinal pattern. Winter mortality did increase with latitude, however, consistent with temperature limiting the northern distribution of ratsnakes. This result was opposite that found in the only previous study of latitudinal variation in winter mortality in reptiles, which may be a consequence of whether or not the animals exhibit true hibernation. Collectively, these results suggest that, at least in the northern part of their range, ratsnakes should be able to adjust easily to, and may benefit from, a warmer climate, although climate-based changes to the snakes' prey or habitat, for example, could alter that prediction.

Keywords
activity, climate change, ectotherm, Elaphe obsoleta, latitude, mortality, season, snakes

Disciplines
Animal Sciences | Biology | Other Animal Sciences

Authors
Jinelle H. Sperry, Gabriel Blouin-Demers, Gerardo L.F. Carfagno, and Patrick J. Weatherhead

Notes

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Latitudinal variation in seasonal activity and mortality in ratsnakes (*Elaphe obsoleta*)

JINELLE H. SPERRY,[1,3] GABRIEL BLOUIN-DEMERS,[2] GERARDO L. F. CARFAGNO,[1,4] AND PATRICK J. WEATHERHEAD[1]

[1]*Program in Ecology, Evolution, and Conservation Biology, University of Illinois–Urbana-Champaign, 606 East Healey, Champaign, Illinois 61820 USA*
[2]*Department of Biology, University of Ottawa, 30 Marie Curie, Ottawa, Ontario K1N6N5 Canada*

Abstract. The ecology of ectotherms should be particularly affected by latitude because so much of their biology is temperature dependent. Current latitudinal patterns should also be informative about how ectotherms will have to modify their behavior in response to climate change. We used data from a total of 175 adult black ratsnakes (*Elaphe obsoleta*) radio-tracked in Ontario, Illinois, and Texas, a latitudinal distance of >1500 km, to test predictions about how seasonal patterns of activity and mortality should vary with latitude. Despite pronounced differences in temperatures among study locations, and despite ratsnakes in Texas not hibernating and switching from diurnal to nocturnal activity in the summer, seasonal patterns of snake activity were remarkably similar during the months that snakes in all populations were active. Rather than being a function of temperature, activity may be driven by the timing of reproduction, which appears similar among populations. Contrary to the prediction that mortality should be highest in the most active population, overall mortality did not follow a clinal pattern. Winter mortality did increase with latitude, however, consistent with temperature limiting the northern distribution of ratsnakes. This result was opposite that found in the only previous study of latitudinal variation in winter mortality in reptiles, which may be a consequence of whether or not the animals exhibit true hibernation. Collectively, these results suggest that, at least in the northern part of their range, ratsnakes should be able to adjust easily to, and may benefit from, a warmer climate, although climate-based changes to the snakes' prey or habitat, for example, could alter that prediction.

Key words: *activity; climate change; ectotherm;* Elaphe obsoleta; *latitude; mortality; season; snakes.*

INTRODUCTION

Variation in climate associated with latitude affects many aspects of animal physiology, ecology, and life history (e.g., metabolism, Kendeigh 1976; home range size, Gompper and Gittleman 1991; predator–prey interactions, Sanford et al. 2003). Because so many aspects of ectotherm physiology are temperature dependent (Huey 1982), the ecology of ectotherms should be particularly affected by latitude. For example, more frequent suboptimal temperatures, shorter active seasons, and extended hibernation result in slower growth with increasing latitude (e.g., Blouin-Demers et al. 2002, Laugen et al. 2003, Blanckenhorn and Demont 2004). Although latitudinal variation in ectotherm demography and physiology have received some attention (e.g., Davies and Bennett 1981, Wilson 1991, Blouin-Demers et al. 2002), little attention has been paid to behavioral variation. Changes in behavior can have important demographic consequences. For example, more active animals are more exposed to predators (e.g., Sih and Moore 1989, Werner and Anholt 1993, Sperry and Weatherhead 2009*a*). If animals are more active at lower latitudes, predation risks that are already expected to be higher at lower latitudes (e.g., Cody 1966, Palmer 1979, Fawcett 1984, Rypstra 1984) could be exacerbated. Here we document latitudinal variation in seasonal activity and mortality of black ratsnakes (*Elaphe obsoleta*; see Plate 1) in three populations that span the species' distribution from Ontario to Texas.

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[3] Present address: Environmental Studies Program, Southwestern University, 1001 East University Avenue, Georgetown, Texas 78626 USA. E-mail: sperryj@southwestern.edu

[4] Present address: Department of Biology, Gettysburg College, 300 North Washington Street, Gettysburg, Pennsylvania 17325 USA.

PLATE 1. A black ratsnake (*Elaphe obsoleta*) in Ontario, Canada. Photo credit: G. Blouin-Demers.

Ectotherm activity is tightly linked to temperature (e.g., Gibbons and Semlitsch 1987, Dalrymple et al. 1991), so the length of their active season should vary with latitude. Although snakes can exercise considerable control over their body temperature by exploiting thermal heterogeneity in their environment (e.g., Bogert 1949, Peterson et al. 1993), the amount of time each year that behavioral thermoregulation is feasible will decline with increasing latitude. Thus, at higher latitudes active seasons will become shorter as hibernation lasts longer. A less obvious effect of latitude on activity involves the extent to which snakes are actually active during the active season. Seasonal variation in activity should vary substantially with latitude, reflecting variation in opportunities for behavioral thermoregulation. Our first objective was to determine how seasonal activity patterns, and by inference the constraints on activity, varied with latitude.

Latitudinal variation in both the extent of activity and the duration of hibernation should affect mortality. Even without predators being more abundant at lower latitudes (e.g., Cody 1966, Palmer 1979, Fawcett 1984, Rypstra 1984), longer active seasons should increase predation rates simply by increasing exposure of snakes to predators (Adolph and Porter 1993). To our knowledge no one has documented how snake mortality during the active season varies with latitude, but it is apparent that such data would be most valuable if collected in conjunction with data on activity. Our second objective was to determine whether active-season mortality decreases with increasing latitude, and whether mortality is higher in the most active populations. We have already demonstrated that within one of the populations, mortality increases with activity (Sperry and Weatherhead 2009*a*).

Our final objective was to determine how winter mortality in ratsnakes varied across our study populations. Because latitudinal range limits of reptiles are thought to be determined by thermal constraints (e.g., Kiester 1971, Spellerberg 1972, Gregory 1982, Porter and Tracy 1983), it follows that winter mortality should increase with latitude. This could result from the risk of freezing and the duration of hibernation increasing with latitude (Gregory 1982). Total metabolic costs of hibernating longer could increase mortality despite reduced metabolic rates during hibernation. In the only study to examine latitudinal variation in winter mortality in reptiles, however, Wilson and Cooke (2004) found that at higher latitudes, daily mortality in side-blotched lizards decreased and overall winter mortality appeared to decline, which is inconsistent with thermal limitation of distributions and increased winter mortality at higher latitudes. Knowing how winter mortality varies with latitude is important for understanding what determines reptile range limits and for predicting how reptile populations are likely to be affected by climate change.

STUDY AREA AND METHODS

Data were collected from 1996 to 2004 at Queen's University Biological Station in eastern Ontario, Canada (44°34′ N, 76°19′ W), from 2002 to 2004 at Cache River State Natural Area in southern Illinois, USA (37°23′ N, 88°54′ W), and from 2004 to 2007 at Fort Hood in central Texas, USA (30°10′ N, 97°45′ W). The

Ontario and Texas sites are near the northern and southern limits of ratsnake distribution, respectively, and the Illinois site is in the middle of the latitudinal range. The coldest month in Texas is warmer than all but five months in Ontario and seven months in Illinois based on daily maximum temperatures, and four and five months, respectively, based on minimum temperatures (see Supplement). Snakes in Ontario emerge from hibernation between mid-April and late May and return in late September (Weatherhead and Hoysak 1989, Blouin-Demers et al. 2000). In Illinois snakes emerge from hibernation from early April to early May and return in October (Carfagno and Weatherhead 2008). Ratsnakes in Texas are active on warm days throughout the year (see *Results*).

Although we refer to ratsnakes at our three study sites as populations, the taxonomy of ratsnakes is unclear (see Burbrink et al. 2000, Burbrink 2001, Gibbs et al. 2006). What is important for our purposes, however, is that our study "populations" are closely related and ecologically similar. Two potentially important differences among the populations are that during winter ratsnakes in Texas do not hibernate, although they alter habitat use (Sperry and Weatherhead 2009*b*), whereas ratsnakes in both Illinois and Ontario hibernate, and that ratsnakes in Ontario and Illinois are exclusively diurnally active, but in Texas switch from being diurnally to nocturnally active during summer (J. Sperry, *unpublished data*).

Data on activity and mortality were collected using radiotelemetry. For Ontario, we used activity data from snakes tracked from 1996 to 1999, using the same methods used at the other two sites. We expanded our survival data by including snakes tracked in 2001–2004 that provided mortality but not activity data. In Ontario and Illinois, snakes were caught as they emerged from communal hibernacula in spring and opportunistically throughout the season. In Texas, ratsnakes were caught only opportunistically. At all sites, transmitters weighed <3% of snake body mass, transmitters were surgically implanted (Reinert and Cundall 1982, Blouin-Demers and Weatherhead 2001), and snakes were released at their capture locations. Transmitters weighed 9 or 13 g with batteries lasting 12 and 24 months, respectively (Model SI-2T, Holohil Systems, Carp, Ontario, Canada). Snakes were relocated approximately every 48 h and date and location (UTM coordinates) were recorded.

Temperature data were obtained from weather stations at Queen's University Biological Station, Ontario; Carbondale, Illinois; and Fort Hood, Texas. All weather stations were <40 km from snake study areas.

Statistical analysis

We used the straight-line distance between snake locations as our index of activity. Distance moved and frequency-of-movement are positively correlated in ratsnakes (Sperry and Weatherhead 2009*a*). Distance moved was calculated using Hawth's Analysis Tools (Beyer 2004) in ESRI ArcGIS version 9 (Environmental Systems Research Institute, Redlands, California, USA). We excluded commuting movements to and from hibernacula, which can be atypically long when hibernacula are not part of an individual's home range (Blouin-Demers and Weatherhead 2002). We also excluded snakes tracked <50% of the active season. All analyses were performed on data averaged for individual snakes over the appropriate time period (i.e., hour, day, month). Relationships between monthly snake activity and mean daily maximum temperatures were analyzed using linear regression. Snake activity was compared among populations using ANOVA. All means are presented ± SE.

All snakes, including those removed from activity analyses due to small sample sizes, were included in survival analyses. Snakes were considered dead if we found a carcass or transmitter alone, although we cannot rule out transmitter expulsion (Pearson and Shine 2002) for those with no associated carcass. Snakes were considered alive (survived) if they were alive at completion of the study or if we removed the transmitter. For some snakes the transmitter signal was lost permanently. This could result from transmitter failure, or could indicate mortality (e.g., the snake was carried out of the study area by a predator). Results were qualitatively the same if these snakes were assumed to be alive or assumed to have died, so we present only the former. Daily mortality was calculated as the number of mortalities/total observation days. Annual mortality was calculated as number of mortalities/total observation years, where observation years is total observation days/365. For snakes that died in hibernation, we assumed that death occurred midway between when the snake entered the hibernaculum and mean date that other snakes emerged from that hibernaculum. Survival is considered 1 − mortality. Based on hibernation periods for Ontario and Illinois and activity patterns for Texas (see *Results*), we considered the active season to be May through September for Ontario, April through October for Illinois, and April through November for Texas. These boundaries are somewhat arbitrary in that ingress and egress from hibernacula is not highly synchronous.

Results

Activity analyses were based on 50 ratsnakes (37 females and 13 males) with a mean of 56.1 ± 5.20 locations per snake in Ontario, 19 ratsnakes (9 females and 10 males) with a mean of 44.8 ± 5.11 locations per snake in Illinois, and 57 ratsnakes (25 females and 38 males) with a mean of 129.8 ± 11.71 locations per snake in Texas. Only adult ratsnakes were included in

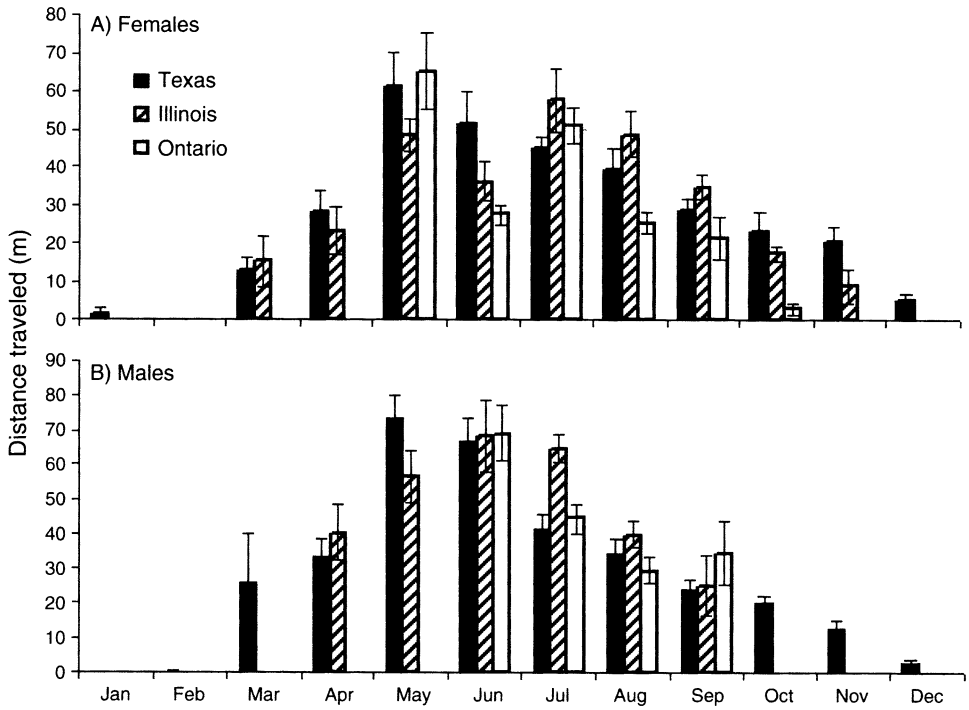

FIG. 1. Monthly activity of ratsnakes, *Elaphe obsoleta* (distance traveled, mean ± SE) for (A) females and (B) males at Fort Hood, Texas (2004–2007), Cache River State Natural Area, Illinois (2001–2004), and Queen's University Biological Station, Ontario (1996–2000).

analyses. Although Illinois snakes were slightly larger than Texas and Ontario snakes (snout–vent length = 126.74 ± 3.53 cm, 120.11 ± 1.99 cm, and 117.19 ± 2.12 cm, respectively; $F_{2,122} = 2.69$, $P = 0.07$), size of snake and distances traveled were not correlated ($R^2 = 0.13$) and so should not affect activity comparison among populations. For activity analyses, we included only months in which we had activity data at all three sites (May–September). Averaged by individual snake, overall distances (meters) traveled by females were shorter in Canada compared to Illinois and Texas (31.29 ± 3.17 m, 44.17 ± 6.44 m, and 47.22 ± 4.12 m, respectively; $F_{2,65} = 5.20$, $P < 0.01$), whereas distances traveled by males were similar among populations (40.40 ± 4.91 m, 54.12 ± 5.59 m, and 46.87 ± 2.99 m, respectively; $F_{2,56} = 1.70$, $P = 0.19$). Contrary to the expectation that seasonal activity would vary substantially with latitude, activity profiles across the three populations were remarkably similar (Fig. 1). For females in both Ontario and Illinois, activity peaked in May and July and then declined thereafter, whereas activity of females in Texas peaked only in May. For males, we did not have sufficient data for May in Ontario, but all three populations peaked in early summer and declined thereafter. The early summer peak in activity did not coincide with the peak in ambient temperature, which occurred in July for both Illinois and Ontario and in August in Texas. Monthly activity was negatively related to temperatures during the active season in Texas ($R^2 = 0.30$, $P = 0.02$) but not related to temperature for the other sites (Ontario $R^2 < 0.01$, $P = 0.91$ and Illinois $R^2 < 0.01$, $P = 0.99$).

Eighty-nine snakes (28 males and 61 females) were included in survival analyses for Ontario, 23 snakes (12 males and 11 females) for Illinois, and 63 snakes (38 males and 25 females) for Texas. Overall yearly survival rates were highest in Illinois (0.73, 95% CI = 0.52–0.89) followed by Ontario (0.62, 95% CI = 0.50–0.73) and Texas (0.57, 95% CI = 0.39–0.73). This pattern was the same when we examined males and females separately (Illinois, 0.83 and 0.68, respectively; Ontario, 0.71 and 0.56, respectively; Texas, 0.66 and 0.34, respectively). That trend was also apparent during the active season, which is not consistent with the prediction that active season survival should increase with latitude.

Winter mortality patterns were consistent with the expectation that winter mortality should increase with latitude. Winter mortality was highest in Ontario (16 deaths; survival = 0.75, 95% CI = 0.61–0.86) and intermediate in Illinois (1 death; survival = 0.92, 95% CI = 0.77–0.99), with no winter mortality recorded in Texas. Four deaths in Ontario during winter were aboveground predation immediately prior to or following hibernation. The rest occurred while snakes were hibernating. Winter accounted for 37% of Ontario deaths, 12.5% of Illinois deaths, and none of the deaths in Texas (Fig. 2).

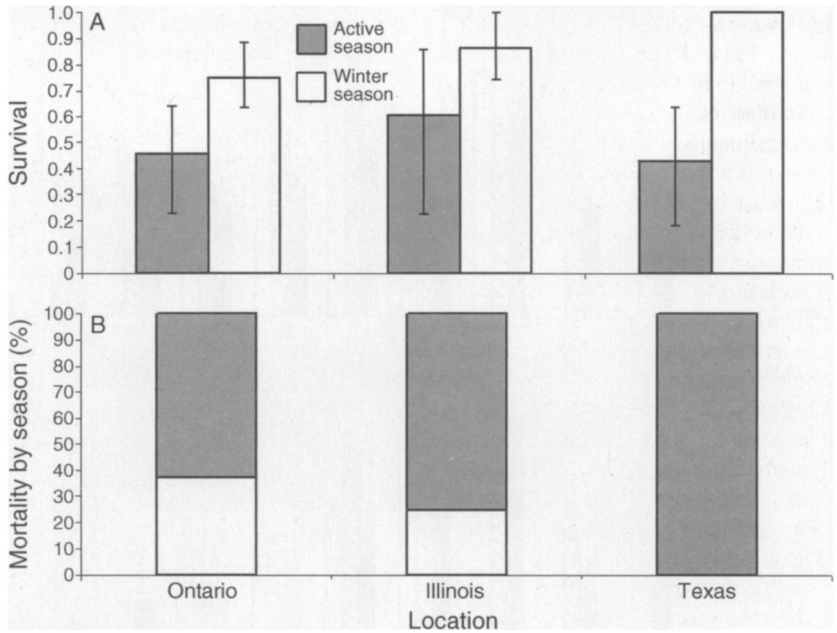

FIG. 2. (A) Annual survival rates during the winter and active seasons at Fort Hood, Texas (2004–2007), Cache River State Natural Area, Illinois (2001–2004), and Queen's University Biological Station, Ontario (1996–2004). Error bars are 95% CI. Active season was considered to be May through September for Ontario, April through October for Illinois, and April through November for Texas. Survival rates are based on 22 712 winter and 18 041 summer observation days in Ontario; 5280 winter and 5517 summer observation days in Illinois; and 4815 winter and 15 420 summer observation days in Texas. (B) Percentage of mortalities that occurred in winter vs. active seasons at Fort Hood, Texas (2004–2007), Cache River State Natural Area, Illinois (2001–2004), and Queen's University Biological Station, Ontario (1996–2004).

DISCUSSION

As North American ratsnakes expanded their range northward following the last glaciation, their seasonal activity pattern appears to have remained highly conserved. The pattern in Illinois looks like that in Texas but with November to March removed. Further removal of October and April produces the pattern in Canada. The similarity among populations is all the more remarkable given climate differences among sites and the fact that ratsnakes in Texas do not hibernate and switch from diurnal to nocturnal activity during summer. We did find pronounced differences in mortality patterns among ratsnake populations, however. We did not find the predicted latitudinal cline in overall predation rate, but winter mortality increased substantially from Texas to Ontario. We first consider why seasonal activity is so conserved in ratsnakes and then address the links between activity and mortality and the broader implications of our results.

Our expectation that patterns of activity would vary latitudinally was based on temperature being of general importance to ectotherms. However, monthly activity was related to temperature only for the Texas population, where activity peaked in May when temperatures were mild and then declined as temperatures increased. Activity also peaked in May for ratsnakes in Illinois and Ontario, even though temperatures peaked later in the summer but remained well below the hotter conditions associated with reduced activity in Texas. If seasonal activity is not simply a function of temperature, at least in Illinois and Ontario, some other factor that varies seasonally must underlie activity. Snakes in each population presumably use behavioral thermoregulation to maintain activity levels necessary to meet those other seasonal needs. Reproduction is a likely candidate for what that seasonal need might be. In Ontario, ratsnakes mate between 15 May and 30 June, which coincides with the peak in activity (Blouin-Demers and Weatherhead 2002). The timing of reproduction is less well documented for the other two populations, but the available evidence indicates that mating also occurs in spring (April–June) in both Illinois (Carfagno and Weatherhead 2008) and Texas (Sperry and Weatherhead 2009*a*).

An implication of the snakes being most active during the mating season is that, following mating, the snakes become less active than thermal conditions would allow. Given that activity increases mortality risks in ratsnakes (Sperry and Weatherhead 2009*a*), the decline in activity following mating may reflect the snakes balancing foraging with survival (Lima and Dill 1990). We had predicted that active season mortality should increase from Ontario to Texas because longer active seasons should increase overall exposure to predators (Adolph and Porter 1993). Also, predators are expected to be

more abundant at lower latitudes (e.g., Cody 1966, Palmer 1979, Fawcett 1984, Rypstra 1984). In fact, mortality rates were similar in Ontario and Texas and lower in Illinois. Studies of lizards over latitudinal (Wilson 1991) and altitudinal (Sears 2005) gradients also failed to find that mortality increased as active seasons became longer. Failure of the prediction suggests that factors relevant to the activity–mortality trade-off (e.g., prey availability, predator abundance) affect mortality much more than does latitude.

We did find that winter mortality increased from Texas to Ontario, as expected if climate limits northern distributions of reptiles (e.g., Kiester 1971, Spellerberg 1972, Gregory 1982, Porter and Tracy 1983). This result also suggests that any advantage from reduced metabolic rates during winter at higher latitudes (Gregory 1982, Zani 2008) was minor compared to having to hibernate longer. Our result for ratsnakes is opposite that found by Wilson and Cooke (2004) for side-blotched lizards. This may be explained by differences in winter ecology of the two species. Wilson and Cooke (2004) interpreted winter mortality as most likely resulting from predation on active lizards. The decline in mortality at higher latitudes resulted from those populations being less active in winter and, therefore, less exposed to predators. Ratsnakes in Texas are similar to side-blotched lizards in that they did not hibernate but just became inactive during cold weather. In Illinois and Ontario, however, the snakes stayed below ground throughout the winter and few winter mortalities were attributable to predation. Therefore, to the extent that one can generalize from these two studies, the nature of the latitudinal gradient in winter mortality in ectotherms may depend on whether the animals actually hibernate or just limit activity to warmer days. In the former case mortality will be driven by abiotic factors (i.e., climate) and increase with latitude whereas in the latter case biotic factors (i.e., predation) will determine mortality.

Reptiles are thought to be at considerable risk from climate change (Gibbons et al. 2000). However, given the highly conserved active season we documented in ratsnakes, a likely response to climate warming would be lengthening of the active season for northern populations, but no change in the general pattern of activity. Southern populations may shift their active seasons to earlier in the year to take advantage of milder temperatures. Additionally, assuming the switch from diurnal to nocturnal activity is entirely facultative, southern populations could respond to a warmer climate by increasing the proportion of the active season that they are active at night. Warmer temperatures should reduce winter mortality in northern populations, which should allow ratsnakes to expand their range northward. Of course, these simple projections do not consider how climate change might affect ratsnakes' predators, their prey, or their habitat, changes in any of which could potentially complement or cancel any direct effect of temperature on ratsnakes.

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SUPPLEMENT

A data file of daily minimum and maximum air temperatures at Fort Hood, Texas, USA (2004–2007), Carbondale, Illinois, USA (2001–2004), and Queen's University Biological Station, Ontario, Canada (1996–2000) (*Ecological Archives* E091-123-S1).