

Individual and sex-based differences in behaviour and ecology of rat snakes in winter

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Abstract

Most research on the winter ecology of temperate-zone snakes is restricted to aspects of hibernation, because that is largely how snakes spend the winter. At lower latitudes, however, the same snake species may be active during winter, although why they are active and how much individuals vary in activity is unknown. We used radio-telemetry data from three winters to document winter movements of 30 rat snakes (*Elaphe obsoleta*) in Texas. Snakes moved in all months, although there was substantial individual and gender-based variation. Consistent with active snakes foraging, monthly variation in movement was associated with availability of 'thermal windows' that would allow digestion of a meal. Females were more active than males, suggesting increased foraging demands. Individual activity in winter was positively correlated with activity the previous summer, particular among females. This may reflect enduring effects of variation in reproductive costs, or intrinsic variation in activity of individual snakes. Variation in activity was associated with differences in habitat use but not thermoregulation, although the data available to assess thermoregulation allowed limited resolution. Climate warming will increase the thermal opportunities for winter foraging, which will have implications both for snakes and their prey.

Introduction

Behaviour and ecology vary seasonally for animals in the temperate zone, particularly for ectotherms. Not surprisingly, therefore, ecological interest in temperate-zone ectotherms has focused principally on what happens in spring and summer. Although winter dormancy can span many months at higher latitudes (e.g. 6–7 months; Hirth, 1966; Weatherhead, 1989), at lower latitudes in the temperate zone, dormancy is not only shorter, but warmer temperatures allow some winter activity. Because field research on temperate-zone ectotherms has been largely restricted to summer, however, we know little about winter activity. Here we document winter movement patterns, thermoregulation and habitat characteristics of rat snakes (*Elaphe obsoleta*) in Texas and examine individual and gender-based variation in those behaviours.

At higher latitudes, snakes spend the winter in hibernacula (e.g. Macartney, Larsen & Gregory, 1989; Prior & Weatherhead, 1996). At lower latitudes, however, snakes either do not use hibernacula or use shallow hibernacula for only brief periods (Shine, 1979; May *et al.*, 1996), with some species encountered throughout the year (Shine, 1979; Bernardino & Dalrymple, 1992; May *et al.*, 1996). We assume the most likely reason for a snake to move during the winter is to find food. Basking near hibernation sites could serve purposes such as

improving immune function (Zimmerman, Vogel & Bowden, 2010), but movements during winter seem likely to involve foraging, particularly given probable costs such as vulnerability to predation and to sudden cold spells. The trade-off between these costs and any benefits is likely to vary among individuals, which should result in some individuals being more active during winter than others. For example, given that snakes have been hypothesized to be capital breeders (Bonnet, Bradshaw & Shine, 1998), building energy stores for future breeding could favour winter foraging more for females than for males.

Previously, we documented that although rat snakes are less active in winter, some movement occurs in every month (Sperry *et al.*, 2010). Annual survival is lower for females than males and is associated with greater activity, which may be a consequence of females foraging more to rebuild energy reserves following egg laying (Sperry & Weatherhead, 2009a). Our goal here is to determine whether sex and individual differences in activity continue through the winter and how winter activity relates to habitat use. An additional goal is to determine the extent to which snakes exploit opportunities for thermoregulation sufficient to allow activity. Assuming that active snakes are foraging, they must not only get warm enough to hunt for prey, but also maintain body temperatures high enough for long enough to digest any prey they capture.

Snakes that cannot maintain body temperatures sufficient for digestion regurgitate their prey (Lillywhite, 1987), rendering a foraging bout unsuccessful. We used weather records to determine the frequency of warm spells that were long enough for rat snakes to digest a meal. We predicted that rat snake activity should be correlated with these thermoregulatory opportunities. Finally, we consider the implications of our results for how rat snakes and other snakes are likely to be affected by climate warming.

Methods

We conducted this study in 2005–2007 at Fort Hood, Texas (30°10' N, 97°45' W). The topography of Fort Hood consists of tabletop mesas with woodlands along the slopes, clumped shrubby vegetation on the mesa tops, and open savannahs in the bottomland areas. We considered winter to include October through April. Details of active season (May–Sept) thermoregulation, activity and habitat use are presented elsewhere (Sperry & Weatherhead, 2009b; Sperry *et al.*, 2010; Weatherhead *et al.*, 2012).

Rat snakes were caught opportunistically and implanted with temperature-sensitive radio-transmitters (Model SI-2T, Holohil Systems Ltd, Carp, ON, Canada) and released at their capture locations (Blouin-Demers & Weatherhead, 2001b). Evidence from our study population indicates little adverse effects to snakes from implanted transmitters (Sperry *et al.*, 2009). We relocated snakes every 48 h in March, April, October and November and once a week December–February and recorded the snake's location (Universal Transverse Mercator coordinates) and body temperature (using transmitter pulse rates). We limited habitat analysis to locations where snakes were stationary when found (88% of all locations) to limit instances where snakes may have been traversing non-preferred habitat or moving in response to us. All methods were approved by the University of Illinois Animal Care and Use Committee (protocol # 07003).

Thermoregulation

We determined operative environmental temperatures (T_e) available to snakes using biophysical models (e.g. Bakken & Gates, 1975; Brown & Weatherhead, 2000). Models were water-filled copper pipes (40 cm × 4 cm) containing a thermocouple attached to a data logger (HOBO Temp, ONSET Computer Corporation, Cape Cod, MA, USA) that recorded temperatures every 10 min, which we averaged for each hour. These models accurately reflect the thermal properties of rat snakes (Blouin-Demers & Weatherhead, 2001a). We placed models in a variety of microhabitats (e.g. under logs/rocks, in brush piles, in grass) for 1–2 weeks per microhabitat in each major habitat type (forested mesa slopes, savannah oak clumps and open savannah). To determine T_e s, we first derived equations that best predicted model temperatures in each habitat based on solar radiation, air temperature, precipitation and wind speed from nearby weather stations. We then used these equations and weather records to predict hourly T_e

values for each habitat throughout the period of the study. Weatherhead *et al.* (2012) provide details of these methods.

The preferred temperature range (T_{set}) of rat snakes, determined from snakes in a thermal gradient, is 28.4–29.7°C (Weatherhead *et al.*, 2012). We quantified how often preferred temperatures were realized by snakes when conditions allowed (E_s ; Christian & Weavers, 1996) by calculating the proportion of T_b values within T_{set} when preferred temperatures were available in at least one habitat. We quantified the thermal quality of the environment (d_e) as the absolute value of the difference between T_e and T_{set} and the accuracy of body temperature (d_b) was calculated as the absolute value of the difference between T_b and T_{set} (Hertz, Huey & Stevenson, 1993). The difference between d_e and d_b is a measure of thermoregulatory effectiveness (Blouin-Demers & Weatherhead, 2001b), with high values of $d_e - d_b$ indicating disproportionate use of thermally favourable habitat, low values of $d_e - d_b$ indicating thermoconformity, and negative values indicating avoidance of thermally favourable sites. Analyses of thermoregulation here are less expansive than those we performed for the active season (Weatherhead *et al.*, 2012) because here T_b data were limited to measurements taken each time we located a snake rather than from automated loggers.

We relied on previous studies to estimate the environmental temperatures necessary for snakes to digest prey. Greenwald & Kanter (1979) found that captive corn snakes (*Elaphe guttata*) could digest meals at T_b s of 18°C. Passage time was 7.5 days at 18°C and 5.5 days at 20°C in winter. Naulleau (1983) found that at 15°C, captive asp viper (*Vipera aspis*) regurgitated approximately 50% of prey and digestion (i.e. passage time) took 10 days. At 20°C, approximately 10% of prey was regurgitated and digestion took 5 days. In both studies, snakes were fed mice, so results are applicable to rat snakes whose diet consists primarily of small mammals (Sperry & Weatherhead, 2009b). Michel & Bonnet (2010) reported that variance in temperature does not affect digestion rate in snakes, so what is important for our purposes is the time mean environmental temperatures remain high enough for digestion. Therefore, we assumed that rat snakes would need 10 days with mean temperatures of 15°C, 7 days with mean temps of 18°C, and 5 days with mean temps of 20°C to digest a meal.

We used our estimates of T_e to determine how often and for how long thermal conditions necessary for digestion were met each month. We illustrate our approach using the 15°C threshold and a 10-day digestion period. Assuming a snake would initiate a foraging bout only on a day it could achieve a body temperature equal to or above the threshold for digestion, we first determined the number of days each month that the mean T_e in the warmest habitat that day reached or exceeded 15°C. For each of those days, we then determined the mean highest available T_e for the 9-day period that followed (producing a period of 10 days counting the initial day) to determine how many of these 10-day periods had mean T_e values above 15°C. Each of those days represented a potential opportunity for a snake to have initiated a successful foraging attempt, with the percentage of those days in a month an estimate of the profitability for snakes to attempt to forage

that month. Note that this is a liberal estimate, however, because no time is allocated for prey capture. We used the same approach for the 18°C and 20°C thresholds, with 7 and 5 days digestion periods, respectively.

Habitat use

Rat snakes shift habitats between the active season and winter, with active season sites generally in areas with less structure (Sperry & Weatherhead, 2009b). Here we focused exclusively on winter habitats and examined how behaviour relates to habitat use. We defined winter dormancy sites as the site of the longest period of inactivity (no movement between successive relocations) for each snake. We considered all other locations used throughout the winter to be active sites. To compare dormancy and active sites, we quantified habitat at every other active site and at the dormancy site for each snake. For this study, we used a subset of habitat variables from the larger dataset collected previously (Sperry & Weatherhead, 2009b). Our index of habitat complexity included canopy cover, litter depth, distance to nearest cover (rock or log) and number of trees. Canopy cover, estimated using a sighting tube with a crosswire at one end (Winkworth & Goodall, 1962), was the percentage of canopy 'hits' out of 20 random sightings at an angle >45° from horizontal. Litter depth was the average of four measurements, in each cardinal direction, at 1 m radius. Distance to nearest cover was estimated as the distance to any rock (≥ 20 cm length) or log (≥ 7.5 cm dbh) within a 30-m radius. Number of trees included trees (≥ 7.5 cm dbh) within a 10-m radius.

We determined whether dormancy sites were within active season home ranges using ArcMap 9.3 (ESRI, Redlands, CA, USA) to construct minimum convex polygons around active season relocations and plotting dormancy sites on those maps.

Statistical methods

We compared duration of dormancy and body temperatures, averaged by individual, between sexes using a two-sample *t*-test. For snakes that were tracked over multiple years, we used only the first year each snake was tracked. We examined the relationship between summer and winter daily distances travelled using linear regression. Daily distance travelled was calculated as the straight line distance between successive relocations, divided by the number of days between relocations. We used mixed models (Proc MIXED) to compare habitat use between males and females and between active and dormancy sites. We included individual as a random effect in our models. Analyses were performed using Program SAS version 4.3 (SAS Institute Inc., Cary, NC, USA). Means are presented \pm 1 SE.

Results

We tracked 63 snakes between 2004 and 2007. Of these, 30 snakes (10 females and 20 males) were tracked over at least one complete winter and so were included in analyses. We

relocated these snakes 2566 times and recorded T_b 2380 times and assessed habitat at 344 unique locations.

Activity patterns

Snakes were often in retreat sites when relocated and were visible during only 9% of relocations from October through April (<1% of relocations December through February). Snake movement between tracking events varied substantially among months. Early and late in winter movement was moderate (mean distance moved per day = 13–16 m in October, November and March, and 35 m in April), but very limited December through February (mean = 1–3 m month⁻¹). This pattern is reflected in the mean time between movements over the winter, with periods of inactivity lasting much longer in the middle of winter (Fig. 1). For most snakes, dormancy (the longest period of inactivity) was distinct from the rest of that individual's inactive periods. Dormancy lasted on average 12.9 ± 1.4 (range 4.3–27.9) times longer than the average period of inactivity for each snake. Mean dormancy duration was 84.4 ± 5.4 days, but varied extensively among individuals (29–148 days). Males were dormant longer than females (means = 96.8 ± 7.7 and 65.7 ± 7.5 days, respectively; $t = -2.5$, $P = 0.02$). Female dormancy ranged from 29 to 113 days and male dormancy from 43 to 148 days. Illustrating these extremes, one male did not move from 5 November 2005 to 2 April 2006, whereas a female tracked at the same time moved throughout the winter and was only inactive from 17 January 2006 to 22 February 2006. While the male was dormant (5 November–2 April), we located both snakes 34 times and the female moved 22 times.

The mean daily distance travelled in winter was 16.6 ± 1.4 m, much less than the 43.6 ± 2.6 m recorded for these snakes during summer. Although males moved less often than females, when they moved, both sexes moved similar distances (mean distances for males and females were 16.4 ± 1.4 and 17.0 ± 3.2 m, respectively). Mean daily distances travelled were correlated between summer and winter ($R^2 = 0.29$, $P < 0.01$; Fig. 2). This pattern was more pronounced for females ($R^2 = 0.75$, $P < 0.01$; Fig. 2) than for males ($R^2 = 0.12$, $P = 0.13$; Fig. 2).

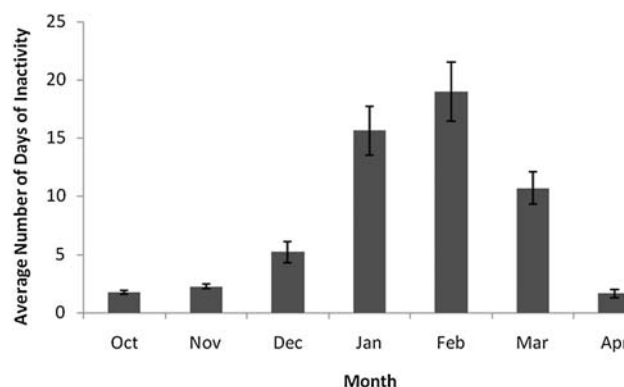


Figure 1 Mean number of days of inactivity by month for Texas rat snakes at Fort Hood, Texas in 2005–2007.

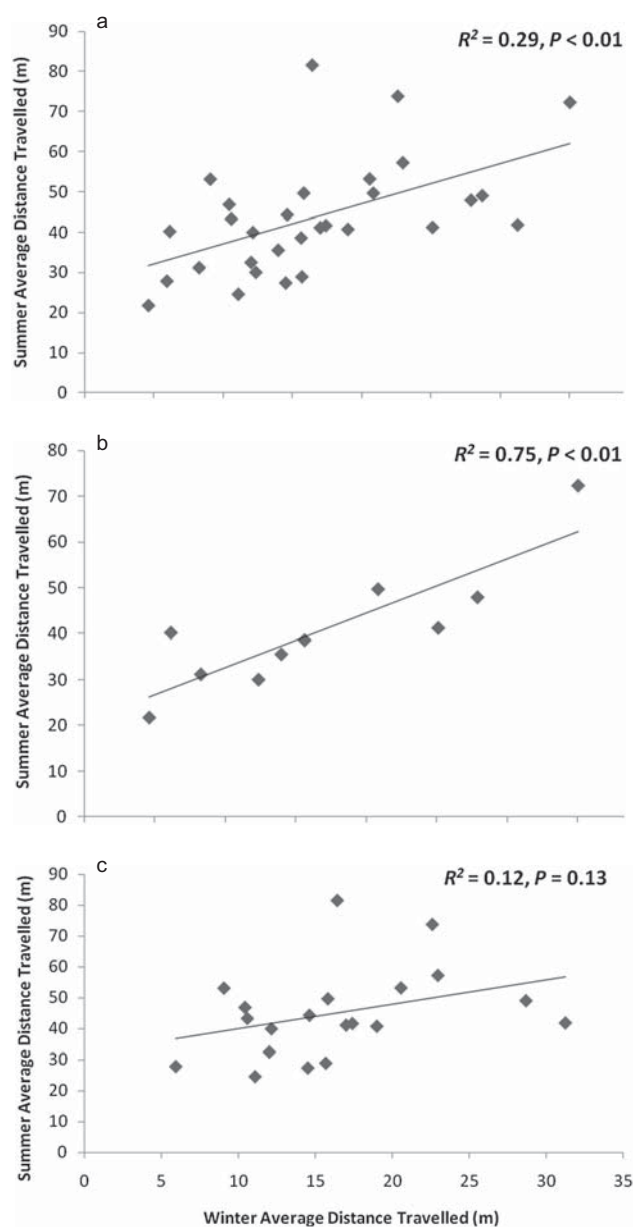


Figure 2 Relationship between summer and winter distances travelled (m/day), averaged by individual for (a) all, (b) female and (c) male black rat snake. Data collected using radio-telemetry at Fort Hood, Texas in 2005–2007.

Analysis of T_e s available to snakes over the study indicated that although successful foraging was potentially possible throughout the winter, those opportunities varied substantially between months (Fig. 3). Early and late in winter, most days were warm enough for snakes to initiate foraging and temperatures remained warm enough for successful digestion. Those opportunities declined in mid-winter such that in December and January there were some short, warm spells (i.e. 20°C for 5 days) that would have allowed digestion but

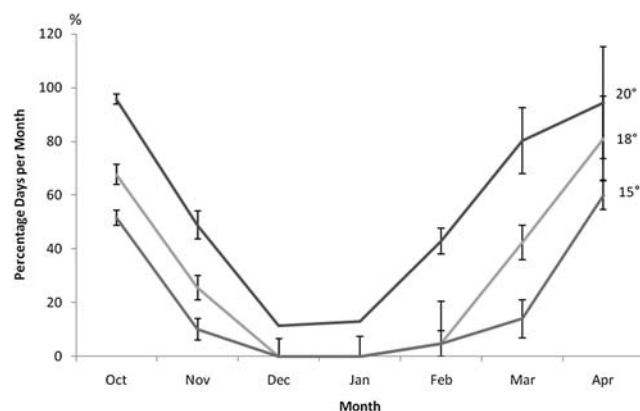


Figure 3 Percentage of days each month that mean environmental temperatures (maximum available T_e) equal or exceed 15°, 18° or 20°C long enough (10, 7 or 5 days, respectively) to allow digestion.

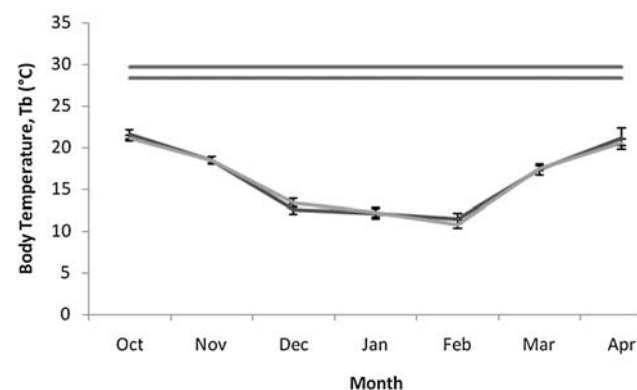


Figure 4 Average black rat snake body temperatures (T_b) for male (grey line) and female (black line) each month at Fort Hood, Texas in 2005–2007. Upper lines indicate range of preferred temperatures (T_{set} ; Weatherhead *et al.*, 2012).

none of the cooler warm spells (15°C and 18°C) lasted long enough for digestion to be completed.

Thermoregulation

Overall, mean snake body temperatures (T_b) were below preferred (T_{set} ; 28.4–29.7°C) for all winter months (Fig. 4). Averaged by individual, mean T_b s did not differ between the sexes ($t = -0.10$, $P = 0.92$) and variation was similar ($F_{76,201} = 1.11$, $P = 0.55$). Periodic temperature warm-ups led to T_e reaching T_{set} in at least one habitat at the time of 12.6% of snake relocations. Averaged by snake and by month, when T_{set} was possible in at least one habitat, rat snake body temps reached T_{set} only 8.8% of the time (Ex). This is substantially less than the 23.9% exhibited in summer (Weatherhead *et al.*, 2012), indicating that snakes took less advantage of warmer temperatures in winter. Although T_e occasionally reached T_{set} in November–February in at least one habitat at the time of

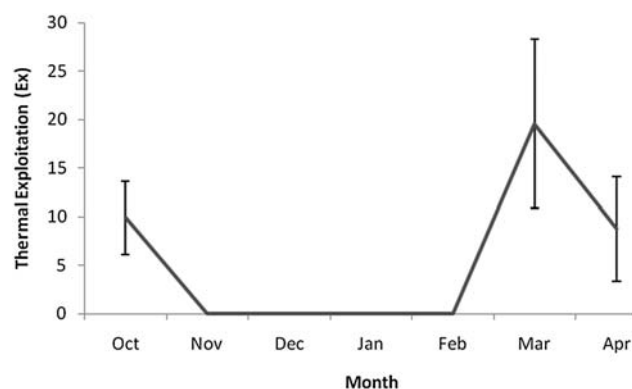


Figure 5 Average black rat snake thermal exploitation (E_x) index, by month, at Fort Hood, Texas in 2005–2007. Thermal exploitation was calculated as the percentage of time, on average, that black rat snake body temperature (T_b) was within preferred range, when it was possible ($T_e = T_{set}$ in at least one habitat), for each month at Fort Hood, Texas.

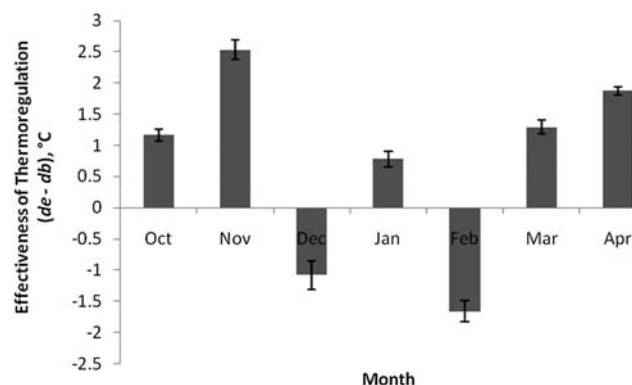


Figure 6 Average (± 1 SE) effectiveness of thermoregulation ($d_e - d_b$) by month for Texas rat snakes at Fort Hood, Texas in 2005–2007.

relocation (7, 8, 3, and 9% of time respectively), none of the snakes' T_b reached T_{set} during those months (Fig. 5). Similarly, effectiveness of thermoregulation ($d_e - d_b$) was higher in October, November, March and April compared to low or negative numbers in December–February (Fig. 6). Negative values of $d_e - d_b$ indicate that snakes actually avoided thermally favourable habitats in December and February.

Habitat use

We compared habitat used by active and dormant snakes, and because females were more active than males, we compared habitat use (both active and dormancy sites) between females and males. Dormancy sites differed from active winter sites and were located in areas with higher canopy closure ($F_{1,318} = 5.93$, $P = 0.02$), closer to cover objects ($F_{1,324} = 4.04$, $P = 0.05$), and with more trees ($F_{1,315} = 10.20$, $P < 0.01$). Only litter depth did not differ between the sites ($F_{1,274} = 0.23$, $P = 0.63$). For active snakes, relative to males,

females were found more in areas with less leaf litter ($F_{1,23} = 10.65$, $P < 0.01$), lower canopy closure ($F_{1,23} = 9.49$, $P < 0.01$) and fewer trees ($F_{1,22} = 5.29$, $P = 0.03$). Distance to nearest cover was similar between the sexes ($F_{1,33} = 1.35$, $P = 0.25$). In contrast to active sites, dormancy sites did not differ between the sexes (all $F < 1.89$, all $P > 0.18$). We found dormant snakes under rocks (19/40 sites; 48%), under soil/litter (17/40; 45%), under logs (3/40; 8%) or under brush piles (1/40; 3%). We found no evidence of communal behaviour when snakes were dormant and all dormancy sites were within the active season home range of the individual. In fact, 13 (32.5%) of the dormancy sites had been used as retreat sites by the individual during the previous active season.

Discussion

Collectively, rat snakes exhibited some movement throughout the winter, although individuals varied greatly. Some snakes were inactive for months and others moved often and exhibited only short periods of inactivity. Unlike more northern populations (Fitch, 1963; Weatherhead, 1989; Blouin-Demers & Weatherhead, 2002; Carfagno & Weatherhead, 2008), Texas rat snakes did not exhibit population-wide hibernation, did not hibernate communally and did not travel outside their active season home ranges to hibernation sites. When snakes were inactive for extended periods (i.e. dormancy) they did not use specialized sites, often using retreat sites they had used the previous summer. Habitat of dormancy sites differed from habitat used by the snakes when active during the winter, however, occurring in more wooded habitat with greater canopy closure.

We assumed that the most plausible reason for snakes to move in winter is to forage. Raising body temperature to improve immune function (Zimmerman *et al.*, 2010) might cause snakes to bask (e.g. Jacob & Painter, 1980; Burger *et al.*, 1988), but not to move away from retreat sites, particularly given that movement is correlated with increased mortality (Sperry & Weatherhead, 2009a). Monthly patterns of movement and temperature are consistent with this assumption. For snakes to digest a meal, they need to maintain mean body temperatures above certain thresholds or be forced to regurgitate the prey (Lillywhite, 1987). Based on previous studies (Greenwald & Kanter, 1979; Naulleau, 1983), we assumed that rat snakes would need at least 10 days in which they could maintain a mean body temperature of 15°C, 7 days at 18°C, or 5 days at 20°C. Those minimum conditions were regularly met early and late in the winter, but in mid-winter (December–February), warm spells were infrequent and brief, and would have allowed digestion to be successful only a few times each month and only under the 5-day–20°C conditions. Therefore, considering only the probability of digestion being successful, foraging in mid-winter would be a risky undertaking. The likelihood of higher predation risks for snakes active at sub-optimal temperatures would make mid-winter foraging even more perilous. Consistent with this seasonal variation in risk, snake activity varied over the winter, with mid-winter characterized by extended periods of inactivity.

Despite poor prospects for a rat snake to forage successfully (including digesting the meal) in mid-winter, we nonetheless documented some snake movement in every month. Some of the individual variation in activity was associated with sex. Females moved more often than males, consistent with them having a greater need to forage. Although little is known about rat snake reproductive energy storage, it is plausible that a successful winter foraging bout would allow a female to rebuild energy reserves depleted by reproducing the previous season and thus to begin accumulating energy stores for the next reproductive bout (Bonnet *et al.*, 1998). Given greater activity by females, we would have expected females to maintain higher body temperatures than males, but failed to find such a difference. This result may reflect shortcomings in how the data were collected. By recording a single body temperature for each snake, only every second day in early and late winter and once a week in mid-winter, we had inadequate data to compare body temperatures of active and inactive snakes. This was particularly so in mid-winter when most snakes were inactive most of the time and exploited few of the limited opportunities to raise their body temperatures. We expect that more comprehensive sampling would show that active snakes are warmer than inactive snakes, and thus on average, females would be warmer than males.

In addition to sex-related differences, there was substantial within-sex variation in activity. Furthermore, the extent to which an individual moved during winter was correlated with their movement the previous summer, particularly among females. This variation may be entirely ecologically based, such that an individual's activity in a given year is based on its energetic needs, so the same individual could be relatively active one year and inactive another year. The correlation between winter and summer activity patterns could result from variation in reproductive effort, whereby higher effort in a given year requires increased foraging effort that carries over from summer to winter. The stronger association between summer and winter activity for females could reflect that not all adult females reproduce every year, contrary to what we have assumed previously, albeit on limited evidence (Sperry & Weatherhead, 2009a).

Alternatively, the correlation between summer and winter activity may be evidence of intrinsic differences in behaviour, whereby some individuals are consistently more active than others. Recent studies on a variety of taxa have shown that variation in behaviour can be consistent within individuals over time, even when behaviours that are beneficial in one context may be detrimental in another (e.g. behavioural syndromes; Sih, Bell & Chadwick Johnson, 2004). Given the prevalence of behavioural syndromes in other species, it is likely that they occur in snakes. Anecdotal evidence suggests that there is wide variation in individual snake behaviour but this concept has received only scant attention (Burger & Zappalorti, 1989; Shine, Shine & Shine, 2003), with the majority of work focused on individual anti-predator behaviours (e.g. Brodie, 1993; Roth & Johnson, 2004). More work is needed to determine if the behavioural consistencies we observed in rat snakes are a

result of behavioural syndromes or individual physiological requirements.

We assumed that being active in winter would increase a rat snake's risk of predation. However, we did not document any mortality during the coldest months when activity would presumably be most dangerous. The snakes were also predominantly inactive during the coldest months, so even if the risk of predation is higher, if a snake is active at that time, low levels of activity would make predation relatively rare and thus harder to document. We previously reported that female snakes had higher mortality in April and November compared to males (Sperry & Weatherhead, 2009a), indicating that spring/fall movement may have survival consequences.

Our results suggest that even a modest increase in temperatures would allow rat snakes in Texas more foraging opportunities in winter. Under current conditions, warm spells occurred in the coldest months but seldom lasted long enough to allow digestion of prey, and correspondingly, rat snake activity was greatly reduced. Given that some snakes are still active under these circumstances, more frequent and longer warm spells are likely to be readily exploited by rat snakes. Similarly, warmer temperatures at higher latitudes would likely extend the active season for those populations (Sperry *et al.*, 2010) and allow foraging later into the fall and beginning earlier in spring. Extended foraging at all latitudes is likely to have consequences both for the snakes and their prey. For prey of conservation concern, such as Golden-cheeked Warblers (*Dendroica chrysoparia*; Stake, Faaborg & Thompson, 2004) in Texas, the consequences could be serious. This species begins nesting early in the spring, prior to the current peak of rat snake activity (Sperry *et al.*, 2008). If warming climates allow rat snakes to become active earlier in the spring, the warblers are likely to suffer higher nest predation unless their breeding chronology undergoes a concomitant shift. More generally, climate warming will make the 'winter' ecology of temperate-zone snakes both more interesting and a more important research focus.

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