Scaling the heights: thermally driven arboreality in garter snakes

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Abstract

Occasional use of arboreal habitats is common in many otherwise-terrestrial species, but the functions of facultative arboreality remain unclear. Red-sided garter snakes (*Thamnophis sirtalis parietalis*) are small nonvenomous terrestrial snakes, recorded to climb only rarely. During springtime fieldwork near a large communal overwintering den in Manitoba, we observed occasional episodes when hundreds of snakes climbed into low trees and remained in the branches for periods ranging from minutes to hours. Our data suggest a thermoregulatory basis for this behaviour. During daylight hours when the snakes were active, ambient temperatures generally were higher on the ground than in trees; but this thermal cline reversed occasionally, especially after the ground was cooled by light rain. Arboreality was most common during those thermal reversals. Experimentally simulating rain in the field (sprinkling with water) induced climbing behaviour; and in laboratory enclosures, snakes climbed to avoid a cold substrate. Thus, red-sided garter snakes ascend trees to access higher temperatures than are available on the ground.
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1. Introduction

Although some species are highly specialised to exploit a narrow range of habitats, most taxa utilise a broader range—at least occasionally (Heatwole, 1977). Understanding why animals shift facultatively among habitat types is important for many reasons, ranging from monitoring population numbers (especially, if observability differs among habitats) through to conservation planning (especially, if important resources are unavailable in the primary habitat). More generally, an understanding of both the proximate and ultimate causes for shifts in habitat use can clarify important aspects of an organism's ecology (Southwood, 1977; Bell et al., 1991; Huey, 1991).

Analysis of habitat shifts is facilitated if the two habitat types are clearly and unambiguously distinguishable, and differ in ways that are likely to influence the costs and benefits of habitat occupancy. The occasional use of arboreal habitats by terrestrial species (and vice versa) offers a good opportunity in this respect. Terrestrial and arboreal habitats differ profoundly in many ways, including the types and amounts of food available, vulnerability to predators, and physical factors such as temperature and humidity. Those differences have resulted in many taxa becoming highly specialised for either terrestrial or arboreal life, and rarely venturing to the alternative habitat (e.g. Plummer,

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1981; Vitt and Decarvalho, 1992; Luiselli et al., 2000).
Nonetheless, many species do use both habitats (often
for different functions) and thus, must move between the
two types of habitat either regularly or intermittently
(Weatherhead and Charland, 1985; Li, 1995; Mullin and
Gutzke, 1999; Vitt et al., 2000). Although such
facultative shifts between terrestrial and arboreal habits
are widespread, the cues that elicit such movements
remain unstudied for most kinds of animals.

The present paper describes a serendipitous extension
of our long-term ecological research on garter snakes at
dens on the Canadian prairies. We noticed that although
these snakes are usually terrestrial, occasionally many of
them would climb into stunted aspen and willow trees.
This resulted in a sudden shift in habitat use, with many
hundreds of snakes ascending within a few minutes. The
animals sometimes remained in the trees for an hour or
so, but more frequently returned to the ground several
minutes later. We wondered why this occurred. The
most likely answer appeared to be thermoregulation,
with snakes climbing trees to attain higher body
temperatures. To test this hypothesis, we quantified the
incidence of arboreality and its thermal correlates, and
conducted simple experiments on proximate cues for this
habitat shift.

2. Materials and methods

2.1. Study species and area

Red-sided garter snakes (*Thamnophis sirtalis parietalis*) are small (adult males average 45 cm snout-vent
length [SVL], females 55 cm) nonvenomous natricine
colubrid snakes that are widely distributed through
North America (Rossman et al., 1996) (Fig. 1). Near the
northern edge of their geographic range, these snakes
overwinter in large communal dens (usually in limestone
caverns) among aspen woodland, emerging in spring
(May) to court and mate for a few weeks prior to
dispersing to their summer ranges (Gregory, 1974;
Gregory and Stewart, 1975). The consequent massive
aggregations of courting snakes provide an exceptional
research opportunity, so that this system has been the
focus of detailed studies for many years (Mason, 1993).

In May 2003 and 2004, we worked at a den containing
>50,000 snakes 1.5 km N of the town of Inwood, 250 m
E of Highway 17 in central southern Manitoba
(50°31.58′N 97°29.71′W). The snakes emerge from
between limestone boulders at the edge of a quarry,
courting on this open rocky area by day and returning to
shelter between and beneath the rocks at night. The only
vegetation in this area consists of low (to 1.5 m) aspen
(*Populus tremuloides*) and willow (*Salix amygdaloides*).
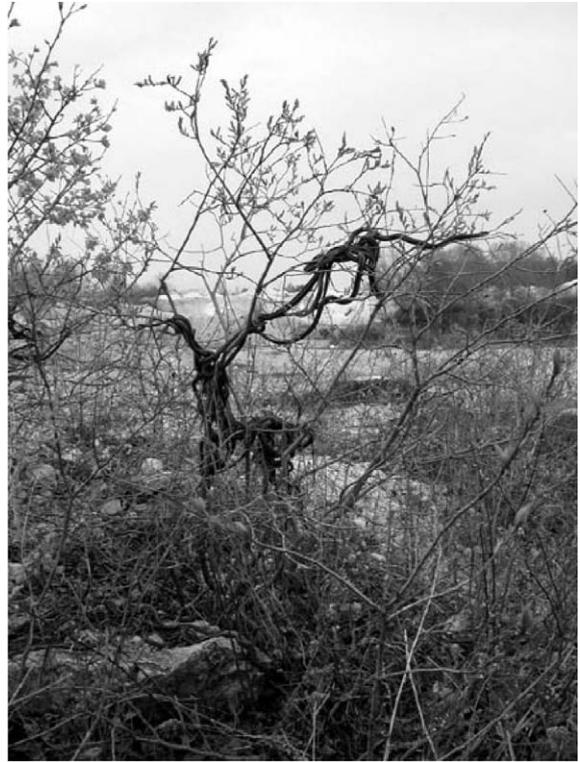The trees are generally leafless during the initial phase of

Fig. 1. Garter snakes (*Thamnophis sirtalis parietalis*) in a small
tree at the Inwood den in Manitoba.

snake emergence in spring, but sometimes leaf out fully,
prior to the snake's dispersal from the den (R. Shine,
pers. obs.).

2.2. Habitat use

Within the main Inwood den, we selected 10 trees in
which we sometimes saw snakes, and counted the
numbers of snakes in each tree vs. on the ground
beneath it (i.e. in the area under the branches). We
conducted one such count per day, on 5 days in May
2003 and 9 days in May 2004. We restricted the counts
to noncourting male snakes, because these were by far
the most numerous (generally >90% of animals active
at the den) and these males rarely interacted with each
other in any overt way (whereas females were courted by
large groups of males, and thus the locations of
individuals in such groups were not independent of each
other). Because snakes were in trees only rarely,
randomly timed surveys would have included few or
no such periods; thus, we targeted sampling to times
when arboreality occurred, as well as sampling an
equivalent number of times when there were no snakes
in trees. We may have inadvertently recorded individual

snakes more than once (on different days) but this is unlikely given the huge numbers of animals at the den.

2.3. Ambient temperatures

On 5 days, we recorded shaded ambient (air) temperatures at heights above ground of 0, 20, 40, 50, 60, 80 and 100 cm (using an electronic thermometer) at the same times as we counted snakes. We took four readings at each height on each occasion, at points at least 50 cm apart. Most snakes in trees were 20–80 cm above ground level, so heights for ambient measurements bracketed that range. On a further 10 occasions we counted snakes as above, and recorded temperatures at ground level and at 50 cm above ground. These data enable us to look for any consistent association between thermal regimes and snake locations.

To obtain continuous records of thermal profiles at ground and tree levels, we deployed six thermal data-loggers (thermochron ibuttons, Dallas Semiconductor, Dallas, Texas, USA; diameter 15 mm, height 6 mm, mass 3.3 g; three on the ground, three 50 cm above the ground) to record temperatures at 15-min intervals over a 5-day period.

2.4. Field experiments

During fieldwork at the den, we noticed that snakes often began climbing into trees as soon as light rain began to fall. To quantify this trend, we scored numbers of snakes climbing up vs. down trees over a 30-s period immediately after the rain commenced at 0920 h on 18 May 2003. To test possible explanations for this effect, we conducted simple experiments whereby we sprinkled snakes on the ground with water, and recorded their responses over the following 10 s. To mimic the physical stimulus of raindrops hitting the ground but without the cooling due to evaporation, we repeated these trials using fine sand instead of water. Our control treatments consisted of either no stimulus, or closely approaching snakes to startle them and induce retreat. In each case we scored whether snakes remained still, and (if they moved) whether they stayed on the ground or climbed into trees. The procedure was to select a solitary stationary male snake on the ground and record its response to the experimental stimulus over the next 10 s, then to repeat the process with another snake. The order of presentation of stimuli was randomised.

2.5. Laboratory experiment

To clarify whether cooling of the substrate (perhaps due to rain: see above) induced arboreality in the snakes, we set up nylon arenas ("Space Pop", Smash Enterprises, Melbourne; circular with 48 cm diameter, 56 cm deep). Each arena contained a "tepee" of four 50-cm-long sticks lashed together at their tops, enabling the snakes to climb if they so desired. We placed a cooler brick ($18 \times 12 \times 2$ cm) beneath each arena; half the bricks were cooled prior to use (so substrate temperature ranged from 5.2 to 7.0 °C), and the other half were at ambient temperature (approx. 21.8 °C). Air temperatures near the top of the "tepee" structure ranged from 16.8 to 19.8 °C, and did not differ between the cooled vs. control arenas. We placed 20 male garter snakes into each arena, and scored the numbers on the ground vs. up on the sticks after 5 min.

3. Results

3.1. Incidence of arboreal behaviour

Contingency-table analysis confirms that the proportions of surveyed snakes that were in trees differed significantly among sampling episodes (range 0–79%; $\chi^2 = 644.23$, 14 df, $P < 0.001$). Although we did not quantify the effects of rain, observations immediately after light rain commenced falling on 18 May 2003 at 0920 h showed that of 20 snakes actively moving during the next 30 s, 17 were ascending trees and only three were descending (against a null of 50%, $\chi^2 = 9.80$, 1 df, $P < 0.001$). These data are consistent with the idea that rain stimulates arboreality.

3.2. Ambient temperatures

On two sampling occasions when all snakes were on the ground (12 and 13 May 2003), ambient temperatures were generally high, and averaged about 2 °C higher on the ground than in the trees (Fig. 2). In contrast, samples taken while some snakes were in trees showed lower ambient temperatures, and less difference between trees and ground (Fig. 2; 8, 15 and 18 May 2003). Temperatures at 1 m above the ground were slightly higher than ground temperatures on two of these three days (Fig. 2). To evaluate the statistical validity of this apparent pattern, we conducted repeated-measures ANOVA on the thermal data in Fig. 2, using whether or not snakes were in trees as the factor, days as replicates, and height above ground as the repeated measure. To avoid pseudoreplication, mean temperature values were calculated for each height for each day. The analysis confirmed that days when snakes were in trees were cooler overall than days when snakes were not in trees (but not significantly so; $F_{1,15} = 9.76$, $P = 0.052$), and that temperature changed with height above ground ($F_{5,15} = 7.42$, $P < 0.002$). More importantly, the way in which temperature changed with height above ground differed between sampling occasions when snakes were
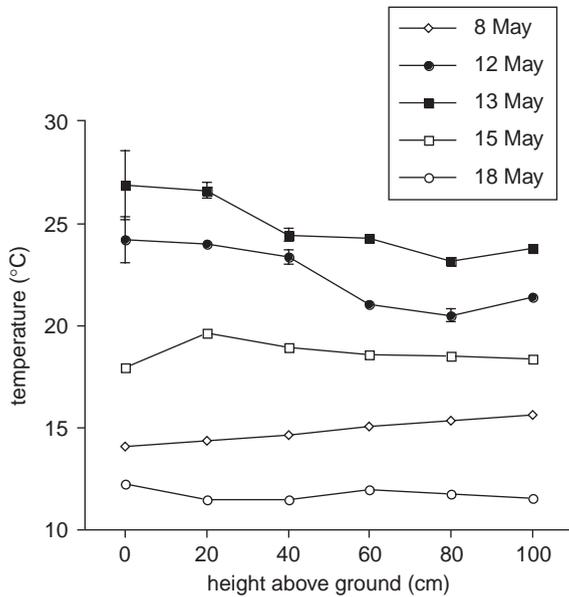
Fig. 2. Ambient (air) temperatures as a function of height above the ground on five sampling occasions at the Inwood snake den. The filled symbols represent data for two occasions (on 12 and 13 May 2003) when all snakes were on the ground rather than in trees. The open circles (for 8, 15 and 18 May 2003) represent times when some snakes were in trees. Graphs show mean values and standard errors; the latter are so small that they are generally not visible.

in trees and when they were not (interaction term, $F_{5,15} = 10.30$, $P < 0.0003$). Inspection of the data shows that this significant result reflects a trend for height above ground to have less effect on ambient temperature on days when snakes were arboreal than on days when they were not (Fig. 2).

Continuous records confirm that ambient temperatures at ground level, were higher than those 50 cm above the ground for most of the snakes' activity period each day (approx. 1000–1900 h: Fig. 3). However, tree temperatures were consistently higher early in the morning (0700–1000 h) because branches were exposed to direct sun at that time whereas the ground was not (because of shading by trees, hillocks, etc.). A shorter period of thermal reversal also occurred during most evenings, as ambient temperatures at ground level typically fell slightly faster than those at tree level at this time of day (Fig. 3). Thermal differentials between tree and ground were relatively slight throughout most of the day, so that even a minor depression in ground temperature due to light rain was enough to push substrate temperature below ambient temperatures available higher in the trees.

Data on snake locations and simultaneously measured air temperatures at ground level and 50 cm above the ground showed a consistent pattern, whereby snakes were in trees only when they were thereby exposed to warmer
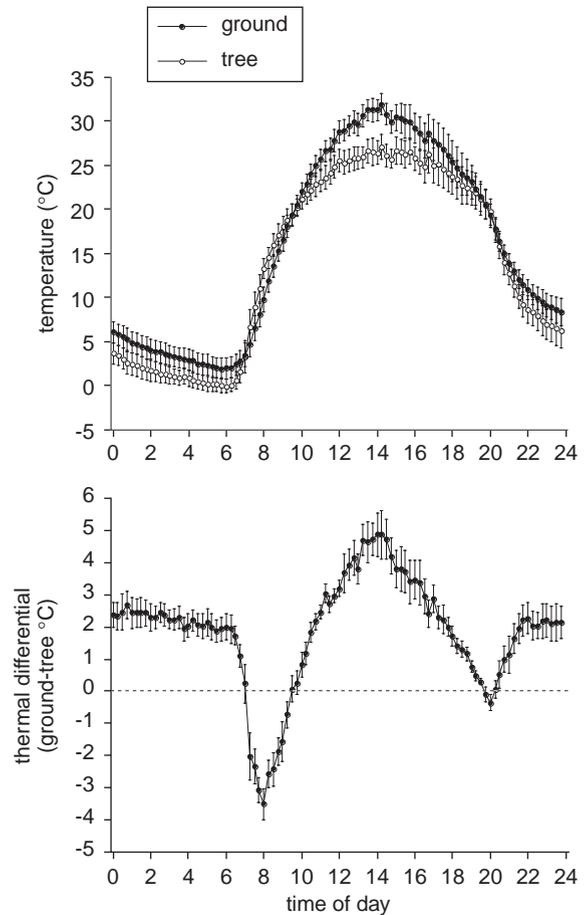

Fig. 3. Thermal differentials between ground level, and 50 cm above the ground, at the Inwood snake den. The graphs show mean values and standard errors based on six thermochrons (three in trees, three on the ground) over a typical 5-day period (12–16 May 2003). The upper graph shows mean values for thermochrons in the trees vs. on the ground, whereas the lower graph plots the difference between temperatures in these two locations as a function of the time of day. The dotted horizontal line in the lower graph shows equal temperatures in the trees vs. on the ground.

temperatures than were available at ground level (Fig. 4; $n = 14$ sampling occasions, spearman rank correlation $\rho = -0.86$, $P = 0.002$). Interestingly, the proportions of snakes in trees were highest when thermal differentials were small (Fig. 4). This pattern reflected the fact that arboreality was fairly short-lived; if the ground continued to cool, most snakes (including those that have moved to trees) retreated to underground shelters.

3.3. Field experiments

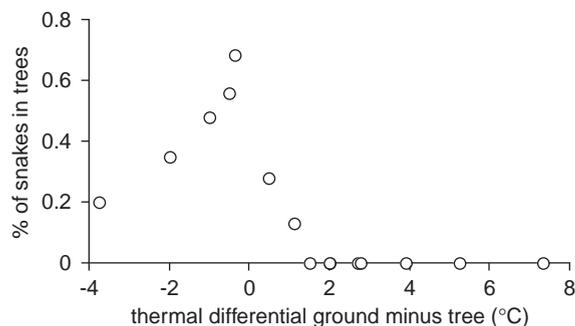Twenty of 20 "control" snakes (observed, not disturbed) remained stationary throughout the 10-s

Fig. 4. Air temperatures at ground level and at 50 cm above ground at the Inwood den, relative to the numbers of garter snakes in the trees vs. on the ground. Each data point is a mean based on 10 temperature measurements in the trees and 10 on the ground, and counts of snakes in 10 trees and on the ground under those trees.

observation period. Of the 20 snakes that were directly approached very closely that they fled, only one climbed into a nearby tree; the rest crawled away across the ground. Of 20 snakes sprinkled with water, 13 began to climb within 10 s. Of 20 snakes sprinkled with fine sand, three began to climb within 10 s. Contingency-table analysis confirms that the incidence of climbing was significantly higher for snakes sprinkled with water than for any of the other treatments ($\chi^2 > 8.00$, 1 df, $P < 0.004$ for all comparisons against simulated rain; after Bonferroni correction for multiple tests, all $P < 0.015$).

3.4. Laboratory experiment

In 30 trials, 0–8 snakes per arena had climbed into the tepee of sticks when checked after 5 min. On average, more snakes had climbed when the substrate was cool (mean $\pm$ SE = 2.33 ± 0.54 snakes, range 0–8) than when the substrate was warmer (0.87 ± 0.36 snakes, range 0–4; ANOVA, $F_{1,28} = 5.07$, $P < 0.04$).

4. Discussion

In combination, our descriptive and experimental data suggest that red-sided garter snakes utilise arboreal habitats primarily for thermoregulation. Doubtless, garter snakes ascend trees for other reasons as well; for example, one animal fled into a tree to escape our close approach (above). Also, female garter snakes sometimes climb into trees to escape vigorous courtship (Shine et al., 2003), and are courted and sometimes mated in the trees by males that manage to follow or find them (R. Shine, pers. obs.; see Aleksiuk and Gregory, 1974; Gregory, 1975; Galbraith, 2001). However, it is unusual to see more than a few snakes in trees

at the Inwood den, compared to the many thousands moving on the ground. This situation makes it particularly striking on the rare occasions when many animals move into the trees almost simultaneously. Gregory (1975) reported one case of a similar mass movement of garter snakes into trees at a den near Inwood, but was unable to explain the reason for this unusual behaviour. Our study suggests that this synchrony reflects a rapid response to changes in weather conditions (especially, the onset of light rain) that chills the ground and hence, reverses the usual thermal gradient from the ground to the trees.

Correlations between thermal conditions and arboreality (e.g. Fig. 4) offer only weak evidence as to causation; any thermal effects of climbing might be secondary consequences of tree use rather than primary cause. Thus, the most convincing evidence of a causal link between temperature and arboreality comes from our experimental trials. In the field, garter snakes were reluctant to climb trees under any conditions other than sprinkling with water; thus, the climbing response to water cannot be attributed to antipredator tactics or simple disturbance. Similarly, climbing was induced by low substrate temperatures in laboratory trials, suggesting that temperature per se (rather than moisture, for example), acts as a proximate cue to elicit arboreality.

A previous study on Manitoba garter snakes emphasised the low priority accorded to thermoregulation by courting males (Shine et al., 2000). The likely reason for that result was the low thermal inertia of these small elongate animals, such that close bodily contact during courtship inevitably results in rapid heat transfer among individuals (Shine et al., 2001) and thus eliminates any advantage to prior warming (Shine et al., 2000). However, the present study shows that in cool cloudy conditions when courtship is sporadic or nonexistent, thermoregulatory issues influence habitat selection.

Climbing above ground level to facilitate thermoregulation is undoubtedly widespread in snakes as it is in other ectotherms. Biophysical models suggest that a reptile on a tree branch experiences very different routes and rates of thermal exchange than does the same animal on the ground (Bakken and Gates, 1975). Field studies provide many examples of thermally driven arboreality, either to avoid or obtain higher body temperatures. For example, small arid-zone lizards select increasingly higher perches in hotter weather, to avoid lethally high ambient temperatures close to ground level (Heatwole, 1970). Carpenter (1952) suggested that *Thamnophis sirtalis* sometimes may be arboreal in midsummer for the same reason. In many forested habitats, solar penetration (and thus, the opportunity to bask) is limited at ground level, and reptiles must climb to achieve access to radiant energy (e.g. Fitzgerald et al., 2003). Both of these situations are probably more common than that seen in the Manitoba

garter snakes, where arboreality occurs in cool cloudy conditions and is driven by a relatively slight (< 2 °C: Fig. 3) differential in available temperature. Nonetheless, we have also seen garter snakes at a nearby den, climb onto a wooden fence to bask in the early morning sunlight (R. Shine, pers. obs.); and thus, arboreal habitats are used for basking as well as to avoid transiently low soil temperatures due to rain. A similar use of arboreal habitats for basking has been reported in other usually terrestrial garter snake taxa (e.g. *T. atratus*: Stitt, 2003). To more fully understand the thermal consequences of arboreality, future studies could incorporate direct measures of operative (rather than ambient) temperatures, as well as snake body temperatures.

Our study indicates that the garter snakes of Manitoba are capable climbers and are willing to use arboreal habitats whenever there is a thermal advantage to doing so. Perhaps the most interesting aspect of our results was that the thermal gradients to which the snakes responded were relatively subtle and short-lived, suggesting a high level of precision in temperature perception and responses. Captive reptiles show similarly precise selection of parts of their enclosures that offer even very minor thermal advantages (pers. obs.), suggesting that many reptile species are capable of equally subtle responses to spatial and temporal heterogeneity of environmental temperatures.

Acknowledgements

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