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Variation in winter microclimate and its potential influence on Virginia opossum (*Didelphis virginiana*) survival in Amherst, Massachusetts

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Abstract. If climate limits the geographical distribution of a species, local variation in microclimate may affect the species' local distribution at the edge of its range. We hypothesized that warm urban microclimates may explain the distribution of the Virginia opossum (*Didelphis virginiana*) in central Massachusetts. We recorded winter temperatures with data-logging sensors in urban, coniferous, deciduous, and open habitats in the human-dominated landscape of the Connecticut River Valley of Massachusetts. Overall, temperatures decreased with elevation. Daily maximum temperatures, a variable used in models of opossum biophysical constraints, were lowest at forested sites, intermediate at urban sites, and highest at open sites; however these were a poor indicator of evening temperatures, which are important to the nocturnal opossum. Open sites had the highest daily temperature fluctuations, and were the coldest at night. Urban and coniferous sites had the least pronounced daily fluctuations in temperature, and urban sites had the warmest nights. Habitat-specific winter temperatures in the Connecticut River Valley indicated that urban sites were most conducive to opossum persistence, but even they were unlikely to sustain populations. Other factors likely help mitigate the influence of harsh climatic conditions on persistence of opossum populations in western Massachusetts.

Keywords: microclimate, species distribution, temperature selection, urban, Virginia opossum

Introduction

Where temperature-induced energetic constraints are important, animals should select habitats with favorable thermal microclimates (Humphries *et al.*, 2002). On a landscape scale,

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this may be reflected in patchy local distributions. At climatically constrained distributional edges, local variations in habitat and microclimate will define the exact geographical boundaries of the species' range. Although human alteration of the landscape clearly alters local microclimate (notably the "urban heat island" effect; e.g., Brazel *et al.*, 2000), the biological significance of the climatic difference for local fauna is rarely noted. Perhaps this is because urbanization effects such as gross habitat loss, replacement by non-native species, and availability of urban food resources are far more dramatic (McKinney, 2002). For species at a climatic distributional limit, however, an altered urban climate may change the species' range, particularly where warming from human development ameliorates restrictively cold climatic regimes.

Virginia opossums (*Didelphis virginiana*) are generalist medium-sized mammals that are thought to be highly sensitive to local winter temperature regimes at their northern distributional limit in northern New England and southern Ontario (Brocke, 1970). However, their current distribution (Gardner and Sunquist, 2003) extends farther north than these putative climatic limits (Brocke, 1970; Kanda, in press). The opossum is also an adaptable mesopredator able to coexist with humans throughout the urbanized landscape (Crooks, 2002). We investigated whether the presence of human development may be extending the opossum range by providing tolerable winter microclimates.

Previous examinations of Virginia opossum energetics have relied on generalizations based on the number of days with daily maxima $\leq 0°C$, as recorded by local weather stations (Brocke, 1970; Kanda, in press). The energetic modeling relies on two inputs: opossum weight at the onset of winter and the winter temperature regime as represented by daily maxima, and the relationship between these based upon the temperature at which opossums cease foraging activity. The opossum, which is generally nocturnal, does not forage on days when the evening temperature is less than or equal to approximately $-4°C$ (Brocke, 1970, Kanda *et al.*, in press). Brocke (1970) hypothesized that in Lansing, Michigan (where he conducted his energetics research), $-4°C$ evening temperatures occurred on days when the daily maximum was $0°C$. Days at least this cold restrict opossum foraging, and thus opossum winter starvation hinges on how many cold, non-foraging days occur. Predictions of opossum winter survival in an area are therefore predicated upon (1) the relationship between evening temperatures and daily maximum temperatures, and (2) the ability of the daily maximum temperature set, usually from the local weather station, to predict landscape temperature regimes.

Opossums are not expected to exist in Amherst, Massachusetts, based on energetic modeling (Kanda, in press). Only a small proportion (e.g., 32% in 1999) of female juveniles, the most important breeding cohort yet the lightest weight class, would be expected to survive the winters, based upon daily maximum temperatures reported by the local weather station (Amherst, Massachusetts; National Oceanic and Atmospheric Administration, 2004). Such low over-winter survival would lead to population declines, and eventual local extinction (Kanda and Fuller, 2004). Nevertheless, opossums are known to occur patchily throughout the Amherst region, with a correlation of opossum occurrence and human development (Kanda, 2005).

We hypothesized that opossums use urban refugia with microclimates more favorable than those reported by the local weather station. We suspected that in Amherst the warming effect of human development in town would be sufficient to increase expectations of opossum survival, because as little as a 1°C overall difference in the daily temperature could dramatically increase expected opossum survival rates (Kanda, in press). We therefore attempted to identify the magnitude of temperature differences among natural and urban habitat patches in the Amherst region, and whether daily maxima of ≤ 0°C are accurate predictors of evening temperatures ≤ -4°C within these regimes. Also, because predictions of opossum survival in other areas will likely continue to rely on summary data from weather stations, we examine the relationship between weather station data and the evening temperatures measured across the landscape. By understanding microclimate variation due to time of day, habitat, and elevation, we hope to identify regions in central Massachusetts where opossum populations should be expected to persist.

Methods

Sites

Amherst, Massachusetts, lies in the Connecticut River Valley of central Massachusetts (42°23' N, 72°32' W). Anecdotal, road-transect survey, and camera-trap evidence suggest that opossums are less common in the Pelham Hills (elevation 335 m) that border the valley than in the valley itself (elevation 45 m) (Kanda, 2005). The hills also have less human development and more forested areas (coniferous, deciduous, and mixed), whereas the valley supports extensive urban, suburban, and agricultural development (cf. Danielson *et al.*, 1997). Though Amherst, Massachusetts is not a large town (17,000 people in Amherst Town Center; U.S. Census Bureau, 2003), it is contiguous with the University of Massachusetts campus with an additional 11,000 resident students (University of Massachusetts Amherst Housing Services, 2004).

We deployed [1]20 HoBo^{TM} data loggers that recorded air temperature every 30 minutes with an accuracy of ±0.5°C for 125 consecutive days during November 1999 to March 2000. 18 loggers were placed in a factorial design across three habitats (coniferous forest, deciduous forest, and open meadow) and three elevations (45, 165, and 335 m; each ±10 m), with two replicate sites for each habitat-elevation combination. These “natural” habitat sites were in habitat patches <1 ha to 100 ha in size imbedded in a matrix of human development at low elevation (urban, suburban, and agricultural) and a matrix of mixed natural habitats interspersed with suburban development at higher elevations (landuse types identified from Southern New England Gap Analysis Project; Slaymaker *et al.*, 1996). Most patches available in the landscape were <50 ha, although deciduous forest formed blocks as large as 373 ha at the highest elevation. Uncultivated open land was rare and found only in patches smaller than 3 ha throughout the study area; however, cultivated open land was common at low elevation. In addition, two loggers were placed at urban sites on the University of Massachusetts Amherst campus, which lies at the low elevation (54 m). There is no comparable concentration of human development (a block of 188 ha) at the higher elevations in the study area. The total study area was 216 km^2.

Data-loggers were placed on level ground at least 20 m from the habitat edge and greater than 50 m from open water or marsh. The temperature loggers were placed in waterproof clear plastic containers and hung in small three-sided covered shelters (20 × 20 × 30 cm) on stakes. The open face of the shelter was oriented north. Sensors were 60 cm above the ground and greater than 2 m from the nearest tree (>10 cm dbh).

We obtained daily mean, minimum, and maximum temperatures for the winter from the Amherst Weather Station located at a sewage treatment plant at the west end of the University of Massachusetts Amherst campus (National Oceanic and Atmospheric Administration, 2004). Using the criteria we applied to other sites, the station is a low-elevation (45 m), open habitat site.

Analysis

Our first objective was to document temperature regime variation across the central Massachusetts landscape. To do this, we compared the daily maximum, minimum, and mean temperatures (1) among three elevations and (2) among four habitat types representative of the landscape. Because night temperatures are important to the opossum, we compared different habitat/elevation combinations by time of day to identify regional variation in this ecologically important variable.

For our examination of temperature differences by elevation, we restricted our analysis to the 18 natural habitat sites. Daily mean, minimum, and maximum temperatures were calculated for each site. Of course, these daily parameters are, at all sites, most strongly influenced day to day by the seasonal weather pattern. Because we wished to look for how sites differ from one another, we concentrated on the difference among the sites for each parameter each day by standardizing daily parameters to the deviation from the average across sites. The resulting 125 samples of each deviation parameter were found to be normally distributed at each site. For each parameter we used SAS v.8 (SAS Institute, 1999) to perform a mixed-model ANOVA considering habitat and elevation as fixed effects, with individual site as a nested random effect. Least squares means with Bonferroni corrections were used in pairwise comparison among elevations.

In comparing temperature regimes across four habitat types (urban, coniferous, deciduous, and open), we used only low-elevation sites (the only elevation of urban sites). As described above, we calculated the difference from the mean for each parameter (in this case, the mean of 8 low-elevation sites) for each day. We again performed a mixed-model ANOVA on these deviation parameters, considering habitat as a fixed effect and individual site as a random nested effect.

To examine the temperature variation among sites by time of day, we focused on the contrast between natural habitat sites and urban sites. The difference between each natural site and the urban average was calculated for every time point. For each time of day, a natural site's deviations from the urban were averaged over all days. We selected four time points for statistical comparison: 19:00 (used to predict opossum foraging by Brocke, 1970) and three other times spaced at 6-hour intervals (01:00, 07:00, 13:00). Bonferroni corrections were used to adjust for family-wise Type I error rates when comparing the four time points.

Because our sensors were of different type and in different housing than the local weather station, direct comparison of temperature records between our sites and the local station was not appropriate. However, we wished to evaluate the temperature index currently used for evaluating regimes for opossum survival, the count of daily maxima $\leq 0°C$ as recorded by the weather station, for its ability to act as proxy for evening temperature regimes across the landscape. We counted the records from the local weather station of days with daily maximum $\leq 0°C$, the days with evening temperatures $\leq -4°C$ at each site and the days with daily maximum $\leq 0°C$ at each site. Counts from sites and station were compared to identify which (if any) evening temperature regimes across the landscape were warmer than predicted by maximum daily temperatures at the weather station.

Results

Temperature variation by elevation

Elevation was a significant effect on differences among natural sites in daily maxima, mean, and minima, but did not have high explanatory power. Maximum temperatures cooled as elevation increased ($p = 0.013, r^2 = 0.123$), though only the difference between the low and high elevations was significant ($p = 0.014$). Daily mean temperatures also cooled with higher elevation ($p = 0.013, r^2 = 0.193$). Pairwise comparisons could not distinguish between daily means at low-and mid-elevation sites, but found high-elevation sites to be cooler than both ($p = 0.016$ and $p = 0.026$, respectively).

Habitat played a larger role than elevation in site differences for daily maxima ($p < 0.001, r^2 = 0.424$) and daily minima ($p < 0.001, r^2 = 0.258$). The interaction between habitat and elevation was significant only for site differences in daily minima ($p = 0.034, r^2 = 0.078$). Low-elevation open sites reached significantly cooler daily minima than all other habitat-elevation combinations ($p \leq 0.04$) except low-elevation deciduous habitat ($p = 0.218$) and high-elevation open habitat ($p = 0.192$).

Differences between replicates were significant for daily maxima, mean, and minima among natural sites. However, these accounted for only a small fraction of the total variation among sites (all $p < 0.001$, maxima $r^2 = 0.076$, mean $r^2 = 0.107$, minima $r^2 = 0.042$).

Temperature variation among habitats at low elevation

At low elevation, habitat was a significant effect on differences in daily maxima ($p < 0.001$, $r^2 = 0.664$), mean ($p = 0.005$, $r^2 = 0.458$), and minima ($p = 0.003$, $r^2 = 0.677$) among sites. Differences among replicate sites were also significant, but represented only a small proportion of the total variation (all $p < 0.001$, maxima $r^2 = 0.010$, mean $r^2 = 0.026$, minima $r^2 = 0.027$).

Open sites had the highest daily maxima (3.16°C above the low-elevation average), and were distinct from all other sites ($p \leq 0.007$). Deciduous sites attained the next warmest maxima, warmer than coniferous sites ($p = 0.009$), though not distinguishable from urban sites ($p = 0.214$). Natural habitats did not differ among themselves in daily mean, but the urban sites had daily mean temperatures warmer than all natural sites (0.83°C warmer than the low-elevation average, $p \leq 0.02$). Open habitats had the coldest minima (2.4°C below the low elevation average) and attained minimum temperatures colder than coniferous

($p = 0.012$) and urban ($p = 0.005$) habitats, though not significantly different from deciduous sites ($p = 0.162$). Like the open sites, deciduous sites were colder in their daily minima than urban sites ($p = 0.027$).

Temperature variation among sites by time of day

For each of the 18 natural habitat sites, the mean deviation from the urban site was calculated for 48 time periods, averaging data from 125 days. Standard errors for the 864 means (48 periods $\times 18$ sites) ranged from 0.05 to 0.33°C.

The coniferous sites were most similar to the urban sites (Figure 1), though generally cooler than the urban sites throughout the 24-hour period (Table 1). If only nighttime hours were considered (18:00–06:00), the difference from urban sites remained similar to the 24-hour estimates. Examination of the four specific times of day (01:00, 07:00, 13:00, and 19:00) showed that all coniferous sites were significantly colder than urban at each time of day ($p < 0.001$).

Temperatures at the deciduous sites fluctuated more than at urban sites over the course of the day (Figure 1). Nighttime deciduous site temperatures ranged from 1.8 to 2.7°C colder than those at urban sites (Table 1). Near the middle of the night (01:00), at dawn (07:00), and at dusk (19:00), all deciduous sites were cooler than the urban average ($p < 0.001$). Near midday (13:00), the low-elevation deciduous sites were warmer than the urban average ($p < 0.001$). One mid-elevation deciduous site was warmer than the urban (0.6°C, $p < 0.001$) while the other site remained cooler (−0.9°C, $p < 0.001$) at 13:00. At midday the deciduous sites at high elevation did not differ from the urban average ($p = 0.524$ and $p = 0.826$).

The open sites showed the highest daily variation in temperature, as previously indicated by their having the highest daily maxima but lowest daily minima (Figure 1). Those low

Table 1. Temperature differences between natural sites and the urban average for the average 12-hr night (18:00–06:00) and the average 24-hrs in the winter of 1999–2000.

		Ave. difference from urban (°C)	
Elevation	Habitat	12-hr night	24-hr
Low	Conifer	−1.0	−1.1
Mid	Conifer	−1.1	−1.3
High	Conifer	−2.2	−2.2
Low	Deciduous	−2.2	−1.2
Mid	Deciduous	−1.9	−1.4
High	Deciduous	−2.4	−1.9
Low	Open	−3.3	−1.1
Mid	Open	−2.1	−0.9
High	Open	−2.8	−1.9

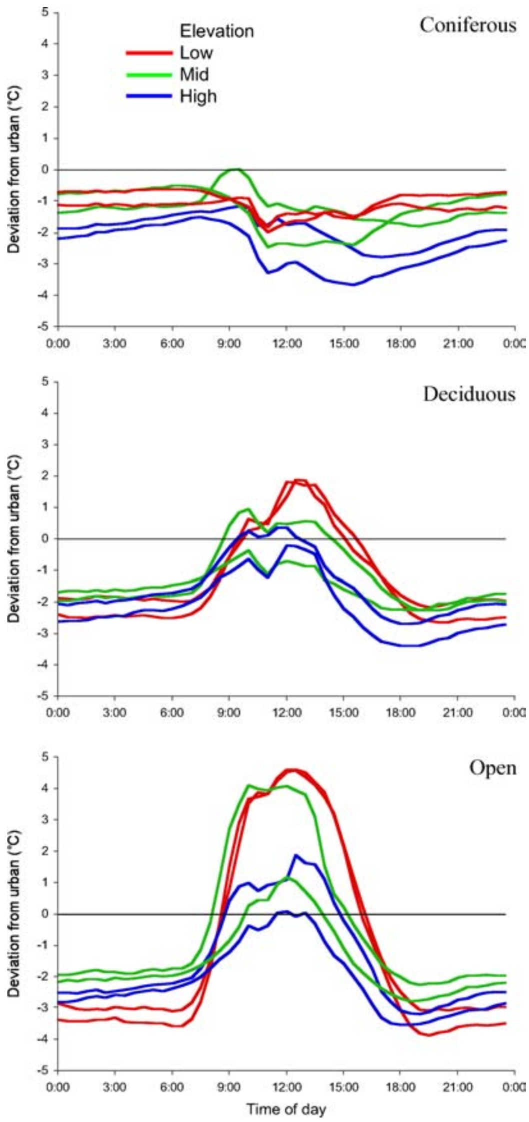

Figure 1. The temperature difference between natural sites and the urban average throughout the average 24-hour day in the winter of 1999–2000.

daily minima occured, not surprisingly, at night (Table 1). Averaging over the night, open site were 1.9–3.5°C colder than urban. At dusk, dawn, and the middle of the night, all open sites were significantly cooler than urban ($p < 0.001$). In contrast, during the day all but one open site were significantly warmer than urban sites ($p < 0.001$ except one high-elevation open site with $p = 0.826$). Both low-elevation open sites and one of the mid-elevation open sites warming to >4°C warmer than temperatures achieved by urban sites.

Table 2. Average number of days with daily maxima $\leq 0°C$ and evening temperatures of $\leq -4°C$ at each habitat/elevation combination and at the local weather station in the winter of 1999–2000.

Elevation/Habitat	Max $\leq 0°C$	19:00 $\leq -4°C$
Local Station	24	
Low Urban	24	24
Low Conifer	34	29
Mid Conifer	37	32
High Conifer	43	42
Low Deciduous	19	38
Mid Deciduous	29	38
High Deciduous	27	43
Low Open	13	49
Mid Open	17	40
High Open	22	44

Daily maximum and evening temperature counts

Comparison of the number of days with maxima $\leq 0°C$ to the number of evenings with temperatures $\leq -4°C$ within each habitat showed that the counts match only in urban areas (Table 2). The simple index of number of sub-zero days over winter varies by as much as 30 days across the landscape, and the count of days with evenings $\leq -4°C$ differs by 25 days. The number of days with below-freezing maxima in coniferous sites overestimated the number of cold evenings slightly, by an average of 4 days. Counts of daily maxima $\leq 0°C$ in open and deciduous sites greatly underestimated the number of cold evenings by averages of 27 and 15 days, respectively. Because of these differences among the habitats, the overall correlation between the days with maxima $\leq 0°C$ in a habitat and the evenings $\leq -4°C$ is very poor ($y = -0.27x + 44.9$, $r^2 = 0.12$). The local weather station count of 24 days with maxima $\leq 0°C$ during this study was an underestimate of the number of evenings $\leq -4°C$ in all natural habitats, but matched the urban number of evenings $\leq -4°C$.

Discussion

Winter microclimates around the Connecticut River Valley landscape follow typical patterns by elevation and habitat. The 300-m rise in elevation between the valley and surrounding hills produces a small cooling effect at higher elevations. Increased cover in the natural landscape reduces daily fluctuations in temperature, and urbanization even in a small town creates a heat island effect.

Variation among sites

Overall, the temperatures in each natural habitat decreased with increasing elevation. Daily maximum and mean temperatures tended to decrease with increasing elevation, whereas daily minimum temperatures were generally constant, with the exception that low open sites had colder minima than all other sites. With respect to opossum survival and distribution, we are interested in microclimates that are warmer than those reported by the weather station, thus low-elevation sites appear to be the most favorable.

The pattern of variation among habitats is best understood by examining circadian patterns. Exposed open areas are most susceptible to temperature fluctuation. Open areas have the warmest maxima each day, but also the coldest minima each night, thus giving the appearance of a stable environment if only mean temperatures are considered. Coniferous areas possess the most stable temperature regime, but are overall colder than the urban environment. The evergreen cover provides shade during the day, preventing warming, but also insulates from temperature loss at night. It follows that the deciduous sites, with intermediary cover between the coniferous and open areas, display intermediate temperature fluctuations.

Increasing cover from open, to deciduous, to coniferous, tends to increase the winter nighttime temperature, but all natural areas were cooler at night than urban areas. Analyses of the 19:00, 01:00, and 07:00 time periods show that this pattern persists throughout the night. As we originally predicted, the urban sites provide the greatest thermal refuge for opossums at night, including early in the evening (19:00) when opossums begin to forage.

Local weather station

The local weather station would be considered a low-elevation open site by our criteria, and was in fact less than 500 meters from one of the low-elevation open site sensors. However, it was located adjacent to a sewage treatment plant which may have acted as a thermal buffer. Housing and sensor type also differ between the weather station and our sensors; thus, we are not comparing how local microclimates differ from the microclimate at the sewage plant but rather evaluating how local microclimates differ among themselves and from the characterization made by the local weather station.

The climatic characterization made by the daily maxima temperatures recorded at the local weather station poorly represents the diversity of winter microclimates available in the region. The number of daily maxima $\leq 0^\circ$C cannot be easily translated to evening winter temperatures throughout the diverse landscape. However, in urban areas the count of subzero days is a good approximation for evenings $\leq -4^\circ$C. The local weather station daily maxima data badly underestimates the number of cold evenings in natural habitats, but does represent the regime in urban areas.

Translation to opossum survival

Based upon the daily maxima from our sites, we would expect highest survival of opossums in low-elevation open areas, as those have the most favorable daily maximum temperatures.

However, for open sites the daily maxima greatly underestimate the number of days having evening temperatures ≤ -4°C, the time and temperature of greatest importance to opossums. Because all the natural sites had colder evenings than the urban sites, opossums in natural sites should fare worse than at urban sites, as their winter foraging opportunities are more restricted. At least in the winter of 1999–2000, the Amherst weather station accurately represented the urban evening microclimate. The urban areas are indeed the most favorable microclimate for overwintering opossums, however urban areas are not warmer than indicated by the weather station as we had hypothesized. Under the climatic regime indicated by the weather station, Kanda's (in press) energetic modeling suggested that breeding female opossums would not survive winter in sufficient numbers to maintain a population. The urban microclimate described here was not warmer than the weather station represented, and therefore cannot alter that conclusion.

Implications

Our sensors only provide a coarse index to the true thermal environment that an opossum experiences. However, this index provides a more accurate measure than the local weather stations, and allows us to examine microclimate variation on spatial and temporal scales of relevance to opossums.

While we did find that winter temperature regimes varied among different habitats and elevations in the Amherst region, none of the habitats examined had warmer evening temperatures than indicated by the proxy of weather station maxima ≤ 0°C. Urban development in the valley appears to provide the best thermal refuge for opossums. However, we cannot explain the existence of the species in the Connecticut River Valley of Massachusetts solely on the basis of urban temperature regimes, despite the fact that temperature regime has been considered the determining factor for the northern edge of the species' range (Brocke, 1970; Tyndale-Biscoe, 1973; Gardner and Sunquist, 2003). It seems likely that urbanization is providing multiple resources, such as food and den sites, in addition to temperature amelioration, that together allow opossum survival in this area and north throughout New England.

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Note

1. Mention of trade names or commercial products does not constitute endorsement or recommendation by the U.S. Government.

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