



Management and Conservation Note

Thermal Properties of Tree Cavities During Winter in a Northern Hardwood Forest

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ABSTRACT Tree cavities likely vary in their thermal quality for cavity-nesting animals, which could be especially important during winter. We conducted a winter field experiment to test whether cavities vary either in their buffering capacity or in their mean temperature according to predictable characteristics. We found that cavities buffered temperature and that there was a lag effect in temperature that appeared to be related to heating and cooling. Diameter at breast height was the most important variable influencing cavity temperature during the day, with smaller trees warming up more. During the night, diameter at breast height and tree decay class were important, such that larger, live trees cooled down less. Maintaining live trees with cavities in managed forests should be considered in addition to snag retention, because live trees appear to provide warmer structures during winter.

KEY WORDS cavity nest, deciduous, energetics, *Glaucomys*, microclimate, Ontario, *Poecile*, temperature, winter, woodpecker.

In seasonal environments, winter creates a thermoregulatory challenge for animals. One strategy employed by many species to avoid temperature extremes is to use tree cavities for nests. For example, during winter, Carolina chickadees (*Poecile carolinensis*) use cavities to reduce radiant heat loss (Mayer et al. 1982), and flying squirrels (*Glaucomys* spp.) use cavities for both nests and food caches (Weigl 1968, Carey et al. 1997, Smith 2007). In late winter, fishers (*Martes pennanti*) use cavities for natal dens (Paragi et al. 1996). The types of cavities used range from naturally occurring tree defects such as knots, splits, or trunk rot to animal-excavated cavities in both live and dead trees.

Tree cavity microclimates tend to be less variable than either open nest microclimates or ambient temperature (Martin and Ghalambor 1999, Sedgely 2001). The buffering capacity of cavities has been shown to vary, however, with both tree and cavity characteristics (Hooge et al. 1999, Wiebe 2001). Large, live trees tend to heat and cool slowly, creating more stable cavity temperatures relative to dead and small trees, which tend to have more variable temperatures (Hooge et al. 1999, Wiebe 2001). More exposed trees tend to cool faster than those within the forest canopy, and cavity volume does not seem to have an effect on either temperature extremes or spatial variability in microclimate (Wiebe 2001, Willis and Brigham 2007). To date, however, cavity microclimate studies have been limited to summer and so nothing is known about cavity microclimates and buffering capacity during winter, when cavity temperature may be important to survival of both active and hibernating species. We considered it important to assess cavity temperatures in winter for 2 reasons. First, fluid transport dynamics of trees differ between seasons and may affect cavity microclimates differently (Tyree and Zimmerman 2002). Second, cold ambient temperatures in

winter mean that cavities should be warmer than ambient temperatures, whereas in summer cavities often provide a cooling shelter (Inouye et al. 1981). Thus, in winter, the highest quality nest sites are likely those that are warmest and permit the greatest reduction in energy spent by occupants on thermoregulation. If these high-quality cavities are sought after by animals for their thermal properties, these cavities may be limiting, particularly in harvested and regenerating forests.

We measured tree and cavity characteristics for a sample of trees in a mature, shade-tolerant deciduous forest in Ontario, Canada. We then compared models relating these characteristics to internal cavity and ambient temperatures during winter. Our objectives were to identify characteristics of tree cavities that 1) buffered ambient temperatures (i.e., reduced temp variation in cavities compared to ambient temperatures) and 2) increased mean cavity temperatures relative to ambient temperatures. We hypothesized that tree cavities buffer temperatures and predicted that temperatures in cavities would be less variable than ambient temperatures. We further hypothesized that south-facing cavities would result in warmer temperatures during the day than would north-facing cavities. Finally, we expected various other attributes of tree cavities to affect their temperature, mostly by affecting the buffering capacity of the cavities and also in some cases by increasing mean cavity temperatures. We sought to use these tree and cavity characteristics to develop a model relating tree and cavity features to cavity temperature.

STUDY AREA

We conducted our study in central Ontario, at the Trent University James McLean Oliver Research Centre (44°34'N, 78°30'W) during the winter of 2008. The site consisted of 38 ha of mature hardwood woodlot, dominated by sugar maple (*Acer saccharum*), white birch (*Betula*

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papyrifera), trembling aspen (*Populus tremuloides*), red oak (*Quercus rubra*), American beech (*Fagus grandifolia*), eastern white cedar (*Thuja occidentalis*), and white pine (*Pinus strobus*). Canopy height of overstory trees varied from 20 m to 30 m. Our study area was the site of a related long-term southern flying squirrel (*Glaucomys volans*) research project (Bowman et al. 2005, Garroway et al. 2010).

METHODS

We selected cavities at a density of 4/ha and used a 32-square (100 m × 100 m each) grid superimposed on a map of the property to stratify our selection. We walked through each grid after leaf fall to search for a representative sample of cavities, which we selected to reflect variation in opening size, internal volume, and height from ground. We used a TreeTop Peeper video camera (Sand Piper Technologies, Inc., Manteca, CA) to aid selection of cavities.

We deployed 3 temperature data loggers (ibutton, model DS1922L; measurement error $\pm 0.5^\circ$ C; Maxim Integrated Products, Inc., Sunnyvale, CA) at each of 2 shaded sites for the duration of the study to measure ambient temperature ($n = 6$ overall). We placed these data loggers at 3 heights (1 m, 2.5 m, 4 m) to encompass variability in temperature due to height. We monitored 2 cavities to examine potential differences between north- and south-facing cavities. Though the cavities were in separate trees, both trees were the same species, cavities were of the same height and similar size, and the trees were within several meters of each other. We covered cavities we used in this test of aspect with mesh to prevent animals from entering cavities and affecting their microclimates. Finally, we monitored temperatures in 3 cavities per day for ≥ 24 hours each between 10 January and 20 March 2008. We moved ibuttons each day to 3 new cavities such that we monitored 104 cavities during winter. We inserted temperature data loggers 10 cm into cavities and suspended them from the cavity wall. We programmed all temperature data loggers to record temperature simultaneously, every 15 minutes. We pooled all 6 ambient temperature data loggers into respective 15-minute intervals and averaged them for subsequent analyses. If we monitored a cavity for >1 day, we averaged estimates for each 15-minute interval across days. Thus, we obtained one estimate of ambient temperature every 15 minutes (averaged from 6 temp loggers) for the duration of winter and estimates of cavity temperature (each 15 min) for 104 cavities, each measured for 24 hours.

We did not apply mesh covers to the 104 cavities that we sampled for model selection because we wished to avoid influencing air flow through cavity openings. Instead, to ensure that temperature was not affected by squirrels using the cavities, we equipped each of the cavities with an antenna that recorded passive integrated transponder (PIT) tags (Eidap Inc., Sherwood Park, AB, Canada). Intensive livetrapping and marking of southern flying squirrels at the site resulted in the population of squirrels being marked with PIT tags (C. J. Garroway and J. Bowman, Trent University, unpublished data); therefore, the antenna would identify whether flying squirrels were using cavities while we

were monitoring temperature, which was important to ensure that our cavity temperature estimates were not compromised by squirrel body temperature. We also spot-checked cavities using a TreeTop Peeper to ensure that other unmarked species were not using the cavities during temperature monitoring. We detected no animals using cavities while we were monitoring them for temperature, though we visually identified one cavity as being used by a southern flying squirrel while it was not being monitored.

For each cavity, we recorded internal height and depth, cross-sectional length and width, opening height and width, left and right cavity wall thickness (measured with a caliper), cavity height from ground, cavity type (hollow trunk, knot, broken branch, split, excavated), azimuth of the cavity entrance, diameter at cavity height (DCH), and diameter at breast height of the tree. We made internal cavity measurements with a length of wire. We also determined species and decay class for each tree (Thomas et al. 1979). We converted the azimuth to northness using $\text{northness} = \cos(\text{aspect [in radians]})$ (Roberts 1986, Psyllakis and Brigham 2006). In addition, we calculated opening area assuming a square using both the opening height and width in the formula $A = h \times w$ and we calculated cavity volume assuming a cylinder, $V = \pi \times (\text{cavity height} + \text{cavity depth}) \times \{[(\text{cross-sectional length} + \text{cross-sectional width})/2]^2\}$ (Willis et al. 2006). We estimated cavity wall thickness as a mean of left and right cavity wall thickness measurements.

We estimated cavity temperature values and ambient values (\bar{x} , min., max., and SD) to assess differences between internal cavity temperature and ambient temperature. We used an F -test to compare standard deviations and Kruskal–Wallis tests to compare mean, minimum, and maximum temperatures. We averaged temperatures of the north- and south-facing cavities hourly for each month (excluding Mar, because the mesh was compromised during that month) and then we compared them to assess the effect of aspect. We estimated mean, maximum, and minimum temperatures as well as standard deviations for north- and south-facing cavities. We made only qualitative comparisons of these values, because we had $N = 1$ cavity for both north and south aspect.

As both cavity and ambient temperature showed fluctuations in a daily cycle (cavities were cooler than ambient temperature during the day but warmer than ambient during the night), we developed separate day and night temperature models. We tested subsets of 7 uncorrelated ($r < 0.50$) variables that we expected might influence cavity temperature: cavity volume, opening area of cavity, average cavity wall thickness, northness, cavity height from ground, diameter at breast height of tree, and the decay class of the tree. Cavity volume incorporated several measures, and we suspected it could affect heat conduction (a larger vol should respond to ambient temp more slowly). Opening area of cavity incorporated opening height and width, and could affect air flow into cavities and thus heat conduction (larger openings should conduct heat more quickly). Average cavity wall thickness could affect insulation and heat conduction (thicker walls should be more insulated).

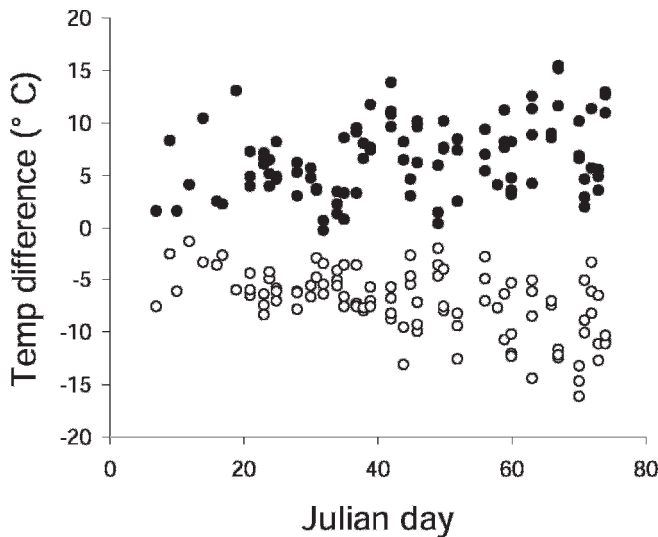


Figure 1. The difference between tree cavity and ambient temperature ($T_{\text{cavity}} - T_{\text{ambient}}$; °C) compared to Julian day during winter 2008 in a deciduous forest in Ontario, Canada. Closed circles represent temperatures at the coldest point during the night, whereas open circles represent the warmest point during day. Cavities were colder than ambient temperatures during day and warmer than ambient during night.

Northness was the direction in which the cavity was facing and could be related to sun exposure (a southern exposure should gain more heat during the day). Height of the cavity from the ground could affect canopy microclimate exposure (higher cavities should retain less heat). Diameter at breast height was closely correlated with diameter at cavity height, so we used it instead of DCH because it was more widely used in ecology and forestry. Diameter at breast height is related to thickness of the tree and so could affect insulation (trees with larger dbh should respond to ambient temp more slowly). Decay class is related to wood quality and buffering capacity (live trees should buffer ambient temp better than dead trees; Wiebe 2001).

Daily differences between cavity temperature and ambient temperature varied with Julian date, suggesting a seasonal trend in temperature during the study period (Fig. 1), which meant that we could not compare raw temperature data among cavities monitored on different days during winter because we risked detecting effects due to temporal changes in weather rather than microclimate. Instead, for each cavity, we selected the warmest ambient temperature to represent the day temperature for that cavity, and we selected the coldest ambient temperature to represent its night temperature. Then we regressed those cavity temperatures (pooled across cavities) against corresponding ambient temperatures. We used the residuals of these relationships between ambient and cavity temperature as new response variables, which removed the Julian date relationship as well as the local weather pattern. Residuals represented deviations in cavity temperature from the mean ambient temperature, such that a positive residual represented a warm cavity and a negative residual represented a cold cavity (Fig. 2).

We selected model parameters from uncorrelated internal cavity and external tree variables. Our model set included

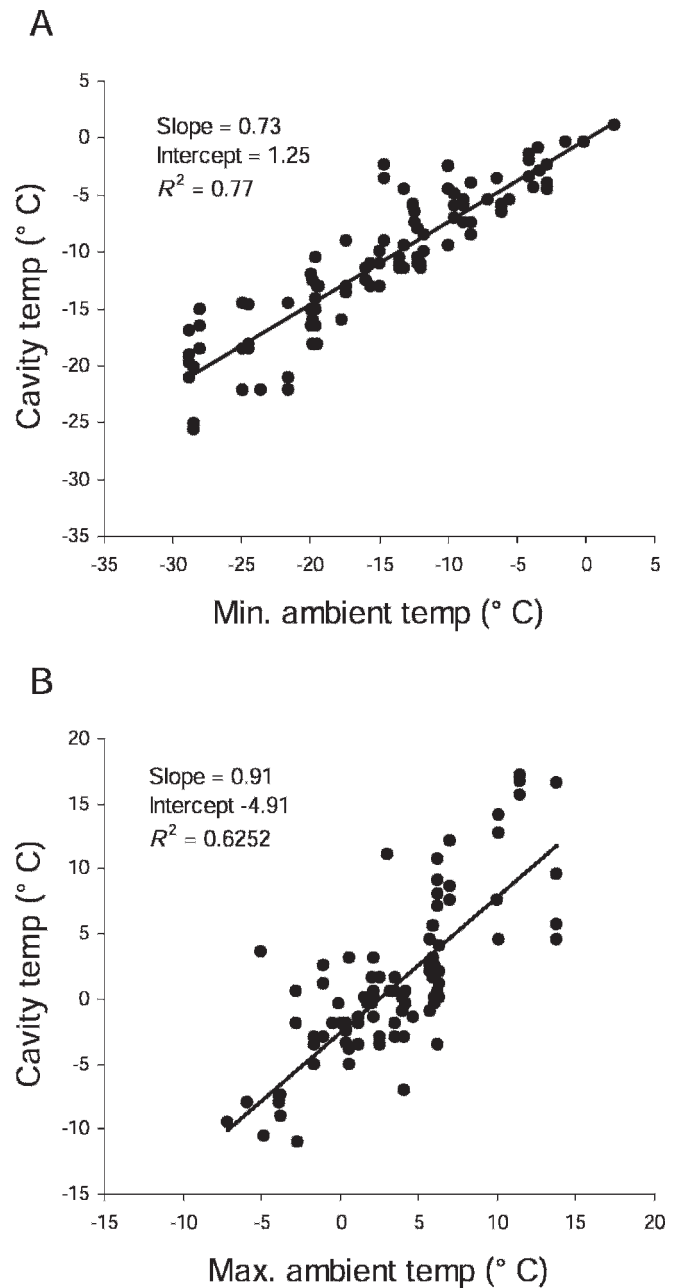


Figure 2. Regression plots of the relationship between tree cavity and ambient temperature (°C) during winter 2008 in a deciduous forest in Ontario, Canada. We compared (A) minimum (during night) and (B) maximum (during day) ambient temperatures to a simultaneous measurement of cavity temperature.

each parameter singly: cavity volume, opening area of cavity, average cavity wall thickness, northness, cavity height from ground, diameter at breast height, and decay class; a tree-level model (dbh + decay class); a cavity-level model (cavity vol + opening area of cavity + average cavity wall thickness + northness + cavity ht from ground); and a global model with all variables. After we used Akaike's Information Criterion (AIC) to rank models, we summed Akaike weights (probability that a model is the best in the model set) until the sum of weights was ≥ 0.95 . We used this model set to calculate model-averaged coefficients and 95% confidence

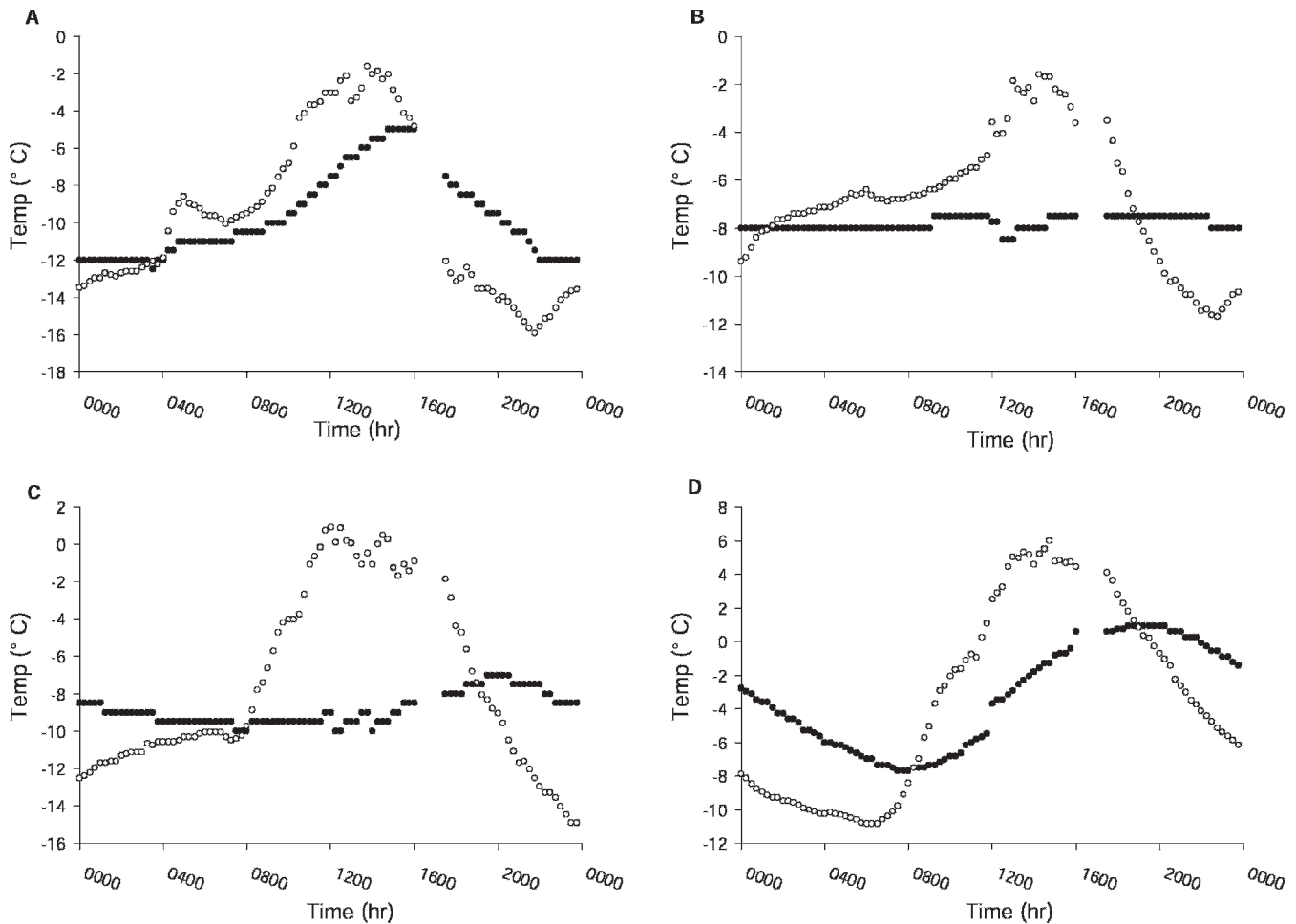


Figure 3. Examples of temperature buffering in several cavities sampled during winter 2008 in a deciduous forest in Ontario, Canada: (A) cavity 01-2 (24 Jan 2008), (B) cavity 07-4 (31 Jan 2008), (C) cavity 10-3 (13 Feb 2008), and (D) cavity 22-6 (3 Mar 2008). Open circles are ambient temperature and closed circles are cavity temperature.

intervals (Burnham and Anderson 2002). We calculated parameter importance by summing AIC weights over the entire set of models (Anderson 2008).

RESULTS

Cavities buffered ambient temperature such that cavities were warmer than ambient temperature at night and cooler than ambient temperature during the day. In general, ambient temperatures were warmest during the day and coldest at night. Cavity temperatures had the same pattern with less extreme highs and lows (Fig. 3). There was also an apparent lag effect, with cavities heating up after ambient temperature had risen and cooling down after ambient temperature had fallen (Fig. 3).

Standard deviation of cavity temperature (2.8) was smaller than the standard deviation for ambient temperature (7.1; $F_{1,206} = 2.5$, $P < 0.05$). Mean (\pm SE) minimum temperature in cavities ($-10.9^\circ\text{C} \pm 0.3$; $n = 104$) was higher than mean minimum ambient temperature ($-29.0^\circ\text{C} \pm 2.9$; $n = 6$; $\chi^2 = 16.88$, $P < 0.001$), and mean maximum temperature in cavities ($0.4^\circ\text{C} \pm 0.3$; $n = 104$) was lower than mean maximum ambient temperature (13.7°C

± 2.9 ; $n = 6$; $\chi^2 = 13.89$, $P < 0.001$). Overall mean temperature in cavities ($-5.9^\circ\text{C} \pm 0.3$; $n = 104$) was not different, however, than mean ambient temperature ($-4.7^\circ\text{C} \pm 2.9$; $n = 6$; $\chi^2 = 0.26$, $P = 0.61$).

North- and south-facing cavities differed in that the south-facing cavity had more variable temperatures, which appeared to be largely due to greater afternoon temperatures, leading also to warmer overall temperatures (North SD = 4.9, mean temp = -6.2°C , min. temp = -24.1°C , max. temp = 1.6°C , $n = 4,834$ measurements; South SD = 5.3, mean temp = -5.7°C , min. temp = -25.7°C , max. temp = 4.1°C , $n = 4,834$ measurements).

For the temperature in cavities during the day, when cavities were colder than ambient temperature, the top candidate model of cavity temperature contained only the parameter diameter at breast height (Table 1). Day models, however, were generally only weakly supported (global model $R^2 = 0.05$). The most important parameter among averaged models was a negative relationship with diameter at breast height, which was 1.5 times more important than the next most important parameter, although its confidence limits overlapped zero (Table 2). All other variables showed

Table 1. Models tested for their effect on cavity temperature for a sample of trees in winter in a deciduous forest in Ontario, Canada, during 2008. Models were for effects on temperature either during the day (day model) or night (night model). For each model, number of parameters (K), distance to lowest Akaike's Information Criterion value (ΔAIC), and Akaike weight (w_i) are shown.

Models tested	K	ΔAIC	w_i
Day model			
Dbh	2	0.0000	0.2082
Average wall thickness	2	0.2742	0.1815
Cavity vol	2	0.2866	0.1804
Northness	2	1.5474	0.0960
Decay class	2	1.7706	0.0859
Ht from ground	2	1.8035	0.0845
Opening area	2	1.8298	0.0834
Dbh + decay class	3	2.0728	0.0739
Average wall thickness + ht from ground + northness + opening area + cavity vol	6	7.4271	0.0051
Decay class + average wall thickness + ht from ground + dbh + northness + opening area + cavity vol	8	10.6515	0.0010
Night model			
Dbh + decay class	3	0.0000	0.6477
Dbh	2	2.7797	0.1614
Decay class	2	3.4441	0.1157
Cavity vol	2	6.7018	0.0227
Opening area	2	7.4021	0.0160
Average wall thickness	2	7.9190	0.0124
Ht from ground	2	8.4272	0.0096
Northness	2	8.4307	0.0096
Decay class + average wall thickness + ht from ground + dbh + northness + opening area + cavity vol	8	9.8948	0.0046
Average wall thickness + ht from ground + northness + opening area + cavity vol	6	14.7792	0.0004

low importance values as well as confidence limits that spanned zero.

For the temperature in cavities during the night, when cavities were warmer than ambient temperature, the top candidate model of cavity temperature contained the parameters diameter at breast height and decay class (Table 1; global model $R^2 = 0.11$). No other models had $\Delta AIC < 2$. The most important parameters among averaged models were a positive relationship with diameter at breast height and a negative relationship with decay class (Table 2). Diameter at breast height and decay class were both about 38 times more important than the next most important parameter. Confidence limits of diameter at breast height spanned zero, but those of decay class did not.

DISCUSSION

Our findings confirmed that during winter, tree cavity temperature is buffered from ambient temperature. Furthermore, temperature in the cavity with a south-facing aspect was both warmer and more variable than in the cavity with a northern aspect. Cavity characteristics we assessed in our models, however, did not appear to have important effects on cavity temperature. Instead, the 2 most important parameters were tree characteristics: decay class and diameter at breast height. The direction of the diameter at breast height relationship changed between day and night in an intuitive way. During the day, cavities in large trees stayed colder than ambient temperatures, whereas at night cavities in large trees stayed warmer than ambient

Table 2. Confidence sets of variables with coefficients (with 95% upper and lower CLs) and importance. We tested variables for their effect on cavity temperature for a sample of trees in winter in a deciduous forest in Ontario, Canada, during 2008. Models were for effects on temperature either during the day (day model) or night (night model).

Variable	Estimate	Lower limit	Upper limit	Importance
Day model				
Dbh	-0.0296	-0.1782	0.1188	0.2830
Average wall thickness	-0.1036	-0.2632	0.0559	0.1876
Cavity vol	-6.195E-06	-1.576E-05	3.377E-06	0.1865
Decay class	0.0578	-0.2025	0.3182	0.1608
Northness	-0.2790	-1.232	0.6744	0.1021
Ht from ground	0.0418	-0.3143	0.3980	0.0905
Opening area	-0.0002	-0.0032	0.0027	0.0894
Night model				
Dbh	0.0447	-0.2676	0.3572	0.8136
Decay class ^a	-0.4266	-0.5178	-0.3353	0.7680
Cavity vol	5.929E-06	-2.876E-06	1.473E-05	0.0277

^a Confidence limits that did not span zero.

temperatures. These relationships were weak, however, because the confidence intervals of the diameter at breast height coefficient in both models overlapped zero. Thus, overall we did not find strong predictors of daytime cavity temperature. The decay class relationship at night was stronger, because confidence intervals did not cross zero, and suggested that dead trees did not buffer temperatures as well as live trees and therefore became colder at night. Thus, a prominent finding was the importance of tree decay class to cavity temperature on winter nights. We assume that this effect was present because there is additional latent heat associated with fluids in live tree stems; therefore, it takes longer to conduct heat across live than dead wood (McComb and Noble 1981), which would have important implications to animals seeking thermal benefits from tree cavities during winter. We expect that live trees would also stay cooler on summer days.

Irrespective of decay class, however, we found that cavities buffered ambient temperature (cavity temp SD < ambient temp SD). The buffering capacity of cavities during summer has been well established. Sedgeley (2001) showed that ambient temperatures fluctuate more widely than cavity temperatures during this season. Temperature has also been shown to vary between less insulated and more insulated bat roosts, and roost minimum and maximum temperatures were found to be neither as cool nor as warm as ambient temperatures (Sedgeley and O'Donnell 2004, Ruczynski 2006). Given our winter findings, we conclude that in general, cavities buffer ambient temperatures similarly during different seasons. Buffering capacity is a function of heat conduction and retention across cavity walls plus the rate that the internal air is circulated. Wiebe (2001) showed a lag effect of heating in northern flicker (*Colaptes auratus*) nests in the summer, with cavity temperature peaking later than ambient temperature, which is comparable to our winter data (Fig. 3). The lag effect we observed was also likely a result of this process, reflecting the time heat takes to conduct across cavity walls or through openings.

In the northern hemisphere, south-facing cavities are likely to have more sun exposure, so it is not surprising that the cavity temperature in the south-facing cavity was warmer than in the north-facing cavity in the afternoon, especially during winter in the northern hemisphere, when the sun is low in the sky. Similarly, Wiebe (2001) found that orientation of a cavity affected high temperature, mean temperature, and temperature range, and that south-facing cavities had the highest daily temperatures. Hooge et al. (1999) found that east-facing cavities in California, USA, warmed up faster and maintained warmer temperatures until the afternoon, similar to how south-facing cavities heat up farther north. Woodpeckers have been shown to select north-facing cavities to gain thermoregulatory benefits in hot climates (Inouye et al. 1981), and farther north, various species could potentially select south-facing cavities to gain thermoregulatory benefits in cold climates.

During the night, we expected that cavities in larger trees would stay warmer because the wood might take longer to cool to the core. Similarly, we expected large diameter at

breast height trees to warm slower during the day. We did not find, however, that there was a strong effect of diameter at breast height on cavity temperature. Despite a high importance weight, parameter effect size was small and 95% confidence intervals were broad and overlapped zero. Many cavity-selection studies have shown selection for trees with a large diameter at breast height and inferred that selection was based on microclimate (Sedgeley 2001, Wiebe 2001, Psyllakis and Brigham 2006, Willis et al. 2006, Holloway and Malcolm 2007). It is possible, however, that animals may select large trees for other reasons, such as cavity volume, which can facilitate social thermoregulation (e.g., Willis and Brigham 2007). The apparent selection for large diameter at breast height may also simply be a result of older trees being more likely to contain defects than younger, smaller trees.

Much like artificial nest boxes are less well insulated than available natural cavities, we found that cavities in live trees seem to be better insulated than cavities in dead trees (e.g., Freezer 2005). We suggest that animals selecting tree cavities for thermal benefits over the winter would select live tree cavities over dead ones, whereas most other cavity variables have no effect on temperature.

Management Implications

Our results suggest that maintaining live trees with cavities in managed forests should be considered in addition to snag retention, because live trees may provide warmer nesting structures, which could be especially important at northern latitudes or during winter. Trees with cavities are undoubtedly important to many forest species, and maintaining live trees with cavities should be considered in cold environments.

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LITERATURE CITED

- Anderson, D. R. 2008. Model based inference in the life sciences: a primer on evidence. Springer Science and Business Media, New York, New York, USA.
- Bowman, J., G. L. Holloway, J. R. Malcolm, K. R. Middel, and P. J. Wilson. 2005. Northern range boundary dynamics of southern flying squirrels: evidence of an energetic bottleneck. *Canadian Journal of Zoology* 83:1486-1494.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information-theoretic approach. Second edition. Springer, New York, New York, USA.
- Carey, A. B., T. M. Wilson, C. C. Maguire, and B. L. Biswell. 1997. Dens of northern flying squirrels in the Pacific Northwest. *Journal of Wildlife Management* 61:684-699.
- Freezer, J. W. 2005. Efficacy of thermochron I-buttons in assessment of nest box occupancy by squirrels. Thesis, Southeast Missouri State University, Cape Girardeau, USA.

- Garroway, C. J., J. Bowman, G. L. Holloway, C. G. Mahan, J. R. Malcolm, T. J. Cascaden, M. A. Steele, G. Turner, and P. J. Wilson. 2010. Climate change induced hybridization in flying squirrels. *Global Change Biology* 16:113–121.
- Holloway, G. L., and J. R. Malcolm. 2007. Nest-tree use by northern and southern flying squirrels in central Ontario. *Journal of Mammalogy* 88:226–233.
- Hooge, P. N., M. T. Stanback, and W. D. Koenig. 1999. Nest-site selection in the acorn woodpecker. *Auk* 116:45–54.
- Inouye, R. S., N. J. Huntly, and D. W. Inouye. 1981. Non-random orientation of gila woodpecker nest entrances in saguaro cacti. *Condor* 83:88–89.
- Martin, T. E., and C. K. Ghalambor. 1999. Males feeding females during incubation. I. Required by microclimate or constrained by nest predation. *American Naturalist* 153:131–139.
- Mayer, L., S. Lustick, and B. Battersby. 1982. The importance of cavity roosting and hypothermia to the energy-balance of the winter acclimatized Carolina chickadee. *International Journal of Biometeorology* 26:231–238.
- McComb, W. C., and R. E. Noble. 1981. Microclimates of nest boxes and natural cavities in bottomland hardwoods. *Journal of Wildlife Management* 45:284–289.
- Paragi, T. F., S. M. Arthur, and W. B. Krohn. 1996. Importance of tree cavities as natal dens for fishers. *Northern Journal of Applied Forestry* 13:79–83.
- Psyllakis, J. M., and R. M. Brigham. 2006. Characteristics of diurnal roosts used by female *Myotis* bats in sub-boreal forests. *Forest Ecology and Management* 223:93–102.
- Roberts, D. W. 1986. Ordination on the basis of fuzzy set-theory. *Vegetatio* 66:123–131.
- Ruczynski, I. 2006. Influence of temperature on maternity roost selection by noctule bats (*Nyctalus noctula*) and Leisler's bats (*N. leisleri*) in Białowieża Primeval Forest, Poland. *Canadian Journal of Zoology* 84:900–907.
- Sedgeley, J. A. 2001. Quality of cavity microclimate as a factor influencing selection of maternity roosts by a tree-dwelling bat, *Chalinolobus tuberculatus*, in New Zealand. *Journal of Applied Ecology* 38:425–438.
- Sedgeley, J. A., and C. F. J. O'Donnell. 2004. Roost use by long-tailed bats in South Canterbury: examining predictions of roost-site selection in a highly fragmented landscape. *New Zealand Journal of Ecology* 28:1–18.
- Smith, W. P. 2007. Ecology of *Glaucomys sabrinus*: habitat, demography, and community relations. *Journal of Mammalogy* 88:862–881.
- Thomas, J. W., R. G. Anderson, C. Maser, and E. L. Bull. 1979. Snags. Pages 60–77 in J. W. Thomas, editor. *Wildlife habitats in managed forests—the Blue Mountains of Oregon and Washington*. United States Department of Agriculture Forest Service, Washington, D.C., USA.
- Tyree, M. T., and M. H. Zimmerman. 2002. *Xylem structure and the ascent of sap*. Second edition. Springer, New York, New York, USA.
- Weigl, P. D. 1968. The distribution of the flying squirrels, *Glaucomys volans* and *G. sabrinus*: an evaluation of the competitive exclusion idea. Thesis, Duke University, Durham, North Carolina, USA.
- Wiebe, K. L. 2001. Microclimate of tree cavity nests: Is it important for reproductive success in northern flickers? *Auk* 118:412–421.
- Willis, C. K. R., and R. M. Brigham. 2007. Social thermoregulation exerts more influence than microclimate on forest roost preferences by a cavity-dwelling bat. *Behavioral Ecology and Sociobiology* 62:97–108.
- Willis, C. K. R., C. M. Voss, and R. M. Brigham. 2006. Roost selection by forest-living female big brown bats (*Eptesicus fuscus*). *Journal of Mammalogy* 87:345–350.

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