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Thermal environments within aspen (*Populus tremuloides*) tree cavities during summer: Implications for breeding and roosting cavity users

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A R T I C L E I N F O

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A B S T R A C T

Summer temperature patterns within tree cavities might influence occupancy of cavities by different animals such as birds and bats, and furthermore, cavity temperatures can influence processes such as embryonic development or the development of young. Our study aimed to identify the environmental variables influencing cavity temperatures during summer (June–July) in quaking aspen (*Populus tremuloides*) in southeastern Idaho. We collected temperature data between June 22 and July 27, 2015 using iButtons distributed across 30 tree cavities in 30 aspen stands in the Craters of the Moon National Monument, Idaho. We used every third day of data to ensure temporal independence amongst readings from the same cavity. We used a multi-model selection framework to examine how environmental characteristics might influence cavity thermal environments, and we modeled how environmental variables, tree, and cavity characteristics might influence daily maximum cavity temperatures. Cavity temperatures ranged as low as 1 °C to as high as 46 °C. Approximately 13% of the cavities experienced temperatures above 40 °C for at least an hour, and these temperatures are noted to be lethal to developing avian embryos. The two top competing models explaining the daily maximum cavity temperatures included tree diameter at cavity height, canopy cover, cavity orientation, and daily maximum ambient temperature. Daily maximum cavity temperatures were significantly associated with daily maximum ambient temperatures and canopy cover; warmer cavities were positively associated with warmer ambient temperatures and negatively associated with canopy cover. Because cavities in aspen are an important resource for multiple species, understanding the factors that influence the microclimate of tree cavities can have broad implications for cavity using species in the context of changing climates.

1. Introduction

Tree cavities are an important resource used by a wide variety of vertebrates globally (e.g. Aitken and Martin, 2007; Goldingay, 2009; Cockle et al., 2010, 2011; Bunnell, 2013; van der Hoek et al., 2017). Almost 1900 bird species use tree cavities worldwide (van der Hoek et al., 2017), and Kunz and Lumsden (2003) report that hundreds of species of bats likewise are dependent upon trees (both cavities and foliage) for some aspect of their life cycle. Cavity use may be associated with multiple factors, including protection from predators (e.g. Martin and Li, 1992; Wesołowski, 2002; Parsons et al., 2003; Maziarz et al., 2016) and/or the provisioning of a dry and/or thermally suitable location in which to roost or breed (e.g. Wiebe, 2001; Wesołowski et al., 2002; Radford and Du Plessis, 2003; Covert-Bratland et al., 2007; Coombs et al., 2010; Clement and Castleberry, 2013; Maziarz and Wesołowski, 2013).

Thermal environments of tree cavities can have direct effects on avian embryonic development and nestlings. For instance, egg temperatures are a combination of ambient temperature as well as the ability of the incubating adult to transfer heat to the egg, and the thermal environment created by both incubating adults and ambient temperatures can influence the length of incubation and embryonic development differently for different species (Deeming, 2008). Changes in ambient temperature can also influence responses in cavity-user energy consumption (e.g. Webb and King, 1983; Du Plessis et al., 1994), nestling growth rates (e.g. Dawson et al., 2005), and nestling survival (e.g. Ardia, 2013). In general, temperatures that are lethal to developing embryos are typically above 40 °C, and temperatures between 34 and 40 °C generally provide conditions that are optimal for embryonic development for many species (Webb, 1987; Conway and Martin, 2000; DuRant et al., 2013; Mainwaring, 2015). The process at which initiation or resumption of embryonic development occurs is defined as physiological zero, which occurs between 24 °C and 26 °C for many bird species (Webb, 1987; DuRant et al., 2013; Reyna and Burggren, 2012;

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Mainwaring, 2015).

Furthermore, nest cavity temperatures might influence the activity and energetics of incubating birds. Haftorn and Reinertsen (1985) recorded the energetic costs of incubation for a free-living, cavity using species (the Blue tit, *Parus caeruleus*) and found that temperatures below 15 °C caused incubating females to start to produce additional heat. Ambient temperatures are likely to have species-specific effects during incubation (Deeming, 2008). The effect of ambient temperatures on adult energetics during incubation likely depends on interactions amongst factors such as the stage of the nest, temperature variability, the magnitude of the extreme temperatures, the duration of extreme temperatures, the condition of the incubating individual, and behavioral adaptations of incubating adults to warming temperatures (Conway and Martin, 2000; Mainwaring, 2015). Because these factors are likely to vary amongst individuals and across species, the effects of thermal environments on adult birds during incubation is likely to be highly variable (Conway and Martin, 2000; Mainwaring, 2015).

Cavity temperatures can also influence other groups of cavity users such as bats (e.g. Boyles, 2009), and different bat species are likely to respond differently to thermal environments within cavities. For big brown bats (*Eptesicus fuscus*), roost switching is relatively common (Willis and Brigham, 2004) and may be the result of bats seeking thermally appropriate environments that would reduce their energy expenditures (e.g. Hamilton and Barclay, 1994) and strengthen social bonds (Willis and Brigham, 2004). Big brown bats have an upper critical temperature of 36 °C and a lower critical temperature of ~27 °C (Willis et al., 2005). In comparison, the lower critical temperature of long-legged myotis (*Myotis volans*) in Idaho and Oregon is ~30 °C (Lacki et al., 2013). These data suggest that different species of bats will respond differently to the thermal environments within tree cavities. Furthermore, cavity thermal environments might have different effects on the energetics of different species of bats at different stages of breeding (i.e. pregnant bats and lactating bats; Ruczyński, 2006; Otto et al., 2016).

Cavity temperatures are influenced by a variety of factors. Clement and Castleberry (2013) found that ambient conditions were responsible for approximately 80% of the variability in cavity microclimate, and other studies have similarly noted the strong effect of ambient temperatures on thermal conditions within a cavity (e.g. Paclík and Weidinger, 2007; Coombs et al., 2010; Grüebler et al., 2014; Maziarz et al., 2017; Vierling et al., 2018). However, additional tree and cavity characteristics in temperate regions have also been hypothesized to influence cavity thermal environments. Tree characteristics that might influence thermal environments include diameter at breast (or cavity) height and the decay class of the nest tree. Larger trees (either measured at breast height or at the height of the cavity) have been associated with greater thermal stability within cavities (Wiebe, 2001; Rhodes et al., 2009; Clement and Castleberry, 2013; Maziarz et al., 2017). Multiple studies have indicated that cavities associated with "softer", more decayed wood have less insulative capacity (Wiebe, 2001; Paclík and Weidinger, 2007; Coombs et al., 2010; Vierling et al., 2018). The decay status of the tree may not be closely associated with the decay status near the cavity (e.g. Lorenz et al., 2015), and soft wood immediately around the cavity has also been found to influence cavity temperature variability as well as warmer cavity temperatures (Vierling et al., 2018). Cavity orientation has also been suggested to provide thermoregulatory advantages (Inouye, 1976; Inouye et al., 1981; Butcher et al., 2002) that could influence reproduction (Hooge et al., 1999; Wiebe, 2001; Sadoti and Vierling, 2010), and south-facing cavities can be warmer than cavities facing other directions (e.g. McComb and Noble, 1981; Wiebe, 2001).

Additional characteristics that could influence thermal environments in the summer might also include cavity entrance size, cavity volume in the summer, the width of the sill (the portion of the cavity below the cavity entrance between the cavity and the external environment; Lorenz et al., 2015) and canopy cover. Cavities with smaller entrance holes and larger volumes are likely to have temperatures that are different than the external environment due to reduced heat loss between inside the cavity and the external environment (Sedgeley, 2001; Paclík and Weidinger, 2007; Rhodes et al., 2009). Thinner sill widths are associated with more variable cavity temperatures as they likely lack the insulative characteristics associated with thicker sills (e.g. Wiebe, 2001; Vierling et al., 2018). Additionally, factors like canopy cover have also been suggested to be important in influencing cavity microclimates, where lower canopy cover is suggested to be positively associated with warmer cavities due to the lack of shading of the cavity (McComb and Noble, 1981; Dobkin et al., 1995; Kalcounis and Brigham, 1998; Clement and Castleberry, 2013; Vierling et al., 2018).

There have been a limited number of cavity temperature studies within the aspen (*Populus tremuloides*) forests in western North America (e.g. Kalcounis and Brigham, 1998; Wiebe, 2001; Parsons et al., 2003), and studies of tree cavity microclimates in aspen are of particular interest because these forests are considered to be extremely important to the maintenance of biodiversity in western North American landscapes (Bartos, 2001; DeByle, 1985; Stohlgren et al., 1997; Chong et al., 2001; Swift et al., 2017) and cavity user densities are generally high in aspen (Dobkin et al., 1995; Martin et al., 2004; Bunnell, 2013; Swift et al., 2017). The objectives of this study were twofold. First, we sought to describe cavity thermal environments within tree cavities in aspen during the summer when temperatures are generally highest in this region and reproductive and roosting activities are occurring. Second, we wanted to examine the relative importance of daily maximum ambient temperature, tree characteristics, cavity characteristics, and wood hardness on the daily maximum cavity temperatures during this period. We hypothesized that daily maximum temperatures (hereafter T_{max}) in cavities in the summer would be strongly influenced by the ambient T_{max}, and that warmer cavities would be associated with smaller trees, cavities that faced southward and low amounts of canopy cover. We furthermore expected that warmer cavities in the summer would have thin sills and large entrance holes.

2. Material and methods

2.1. Study area

We conducted our study in 2015 in quaking aspen stands found in the Pioneer Mountains of Blaine and Butte County, Idaho (approximately 43° 27 N, 113° 37 W) in the Middle Rockies ecoregion. Land ownership included private lands managed by Lava Lake Land and Livestock ranch and federal lands which included Craters of the Moon National Monument (Fig. 1). The region is considered a high desert ecosystem comprised of large basaltic lava fields, sagebrush steppe (*Artemesia* spp.) arid lands, and mountain riparian areas. Aspen was dominant, but other important plant species included Douglas-fir (*Pseudotsuga menziesii*), mountain snowberry *(Symphoricarpos oreophilus)*, and western chokecherry *(Prunus virginia)*. The majority of precipitation is deposited as snow in the winter, and the amount of precipitation ranges from 380 to 510 mm annually. Temperatures range from an average low of −7.2 °C in January to an average of 29.4 °C in July (Bell et al., 2009).

2.2. Field methods

Within 47 aspen stands (0.32–6.6 ha; mean 1.2 ha), we searched for cavities from June through the end of July 2015, which corresponds to the timing of nesting activities for multiple bird species (Jackson et al., 2002; Vierling et al., 2013; Johnson, 2014) and bat roosting activities (Kalcounis and Brigham, 1998, Lacki et al., 2013). We conducted cavity surveys by walking in parallel and perpendicular transects 30 m apart every 7–10 days to identify excavated aspen tree cavities. Potential cavities were marked with a GPS and to reach the cavities, an

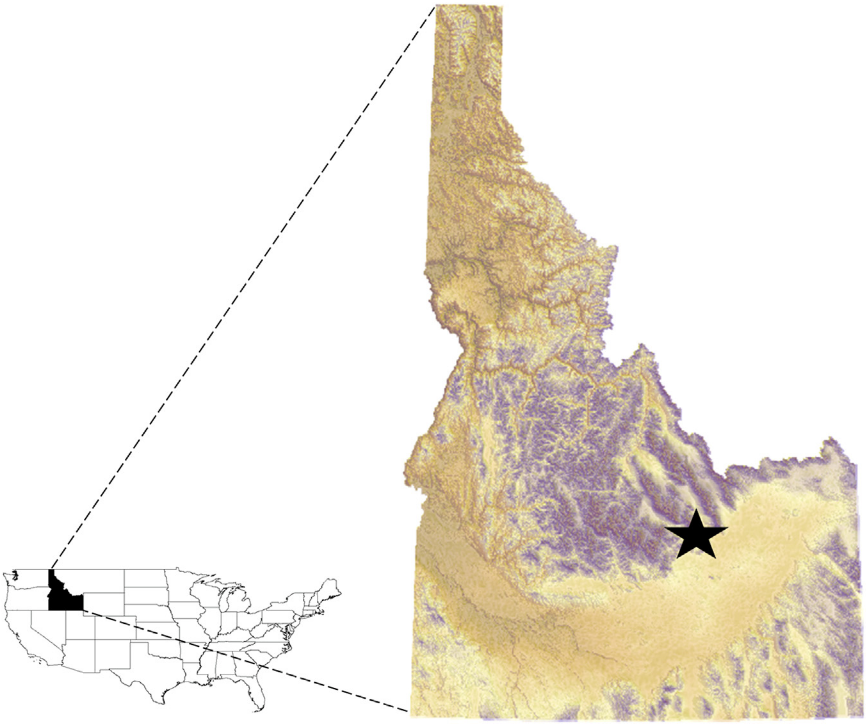

Fig. 1. Location of study sites used to examine thermal characteristics of tree cavities in aspen stands in the Pioneer Mountains, Idaho, U.S.A.

extendable ladder was used. If cavities were unsafe to access, these cavities were excluded from the study. We then chose one cavity randomly within each stand from the subset that were accessible and used DS1921G Thermochron iButtons (accuracy ± 1.0 °C, resolution 0.5 °C; Embedded Data Systems, Inc.) to record temperatures. These data loggers were calibrated to record temperature at 1-h intervals, and they remained within cavities for approximately 2–3 weeks before being rotated to different cavities. The onset of data collection for session 1 began between June 22–June 29, and the onset of session 2 began ~July 14.

A total of 47 pairs of iButtons were used; these were attached to one another with a fishing line that was draped over the sill such that one iButton was in the cavity and the other was located immediately outside of the cavity. The iButton inside the cavity was suspended as deep as possible within the cavity without it touching the floor of the cavity. We attached the fishing line associated with the external iButton to the tree exterior with a nail below the deepest part of the cavity. The use of fishing line eased the extraction process of the iButton within the cavity, and because the external iButton was secured to the exterior of the tree, equipment loss was minimized. We also constructed a thermal shield to cover the external iButton; Hubbart et. al (2005) noted that this is important to reduce excessive ambient influence from direct sunlight on the metal device. For the shield, we used light colored cardboard and in some cases pieces of bark. The shield was secured with a nail to create a bottomless tent to allow airflow (Hubbart et al., 2005). If the data download was incomplete, the tree fell down during the study due to severe wind storms, or the iButton was ejected within the period of deployment, the cavity was excluded from the study. For iButtons that remained in the cavities, we detected no abnormal spikes in temperature readings or signs of use (i.e. feathers, feces, etc.) that would suggest that cavities were used during data collection.

We measured predictor variables that could influence the mean cavity T_{max} (Table 1), and these variables were selected based on their use in previous studies. We included variables that represented tree, cavity and wood hardness characteristics. Tree parameters included canopy cover, orientation, and diameter at cavity height (DCH). An open reel measuring tape was used to measure the DCH (cm) at the cavity entrance, and canopy cover was measured with a spherical densitometer at the cavity entrance. The spherical densiometer has a convex mirrored surface upon which a grid of squares appear, and the recorder stands under the tree and holds the densiometer level at approximately elbow height (Lemmon, 1956). The mirror reflects the amount of canopy above the recorder's location, and we followed Lemmon (1956) to estimate the amount of canopy coverage reflected on the mirror surface. We took this measurement on the side of the tree in which the cavity occurred. The cavity orientation was measured with a compass to identify the cardinal direction on the tree where the cavity occurred.

Cavity variables included cavity entrance area (cm^2), cavity volume (cm^3), and sill width (mm). For our determination of cavity entrance area, we used digital calipers to measure the entrance height and width at its narrowest points. We assumed the cavity entrance was elliptical ($\pi * h/2 * w/2$) where h is cavity entrance height and w is cavity entrance width, and we calculated the area based on this equation (Vierling et al., 2018). To calculate cavity volume, we measured horizontal and vertical depth of the cavity using a flexible ruler. For horizontal depth, the distance from back of the cavity to the front of the cavity was measured. Vertical depth was calculated by summing three measurements: 1) the distance from the cavity floor to the bottom of the cavity entrance, 2) the height of the cavity entrance, and 3) the distance from the upper edge of the cavity entrance to the roof of the cavity. Assuming the cavity was cylindrical, the measurements were used to calculate cavity volume ($\pi r^2 h$). Sill width was measured with a ruler.

We used methodology developed by Matsuoka (2000) to characterize wood hardness in newton Meters (NM). After the termination of the temperature data collection, a 9 mm diameter hole was drilled approximately 15 cm into the tree and 5 cm above the cavity; the small distance above the cavity for this pre-drilled hole has been used in other studies to represent the pattern of wood hardness associated with tree cavity excavations (Matsuoka, 2008; Lorenz et al., 2015). The drill bit of an increment borer with an attached torque meter was then placed at the surface of the tree over the pre-drilled hole. The drill bit of the increment borer was ~2 mm larger than the pre-drilled hole. We turned the increment borer crank, and the torque needed to advance the borer

Table 1
Description of parameters used to model mean cavity T_{max} (daily maximum temperatures) in aspen stands in the Pioneer Mountains, Idaho, U.S.A. 2015.

Parameter	Definition
Mean ambient T_{max} (°C)	The mean of daily maximum temperatures obtained from an iButton every third day directly outside the tree cavity
Entrance area (cm^2)	The area of the cavity entrance estimated from width and height ($A = \pi * h/2 * w/2$) assuming entrances were ellipses, where h = height and w = width; measurements were taken with a ruler.
Cavity volume (cm^3)	The volume of the cavity estimated from vertical and horizontal depth ($V = \pi r^2 h$) assuming cavities were cylindrical (r = the radius). Depth measurements were taken with a flexible ruler as described in the text.
Sill width (mm)	The sill is the cavity wall immediately below the cavity entrance; measurements were taken with a ruler.
Diameter at cavity height (cm)	The diameter of tree at cavity height (referred to as DCH); this was measured with a measuring tape
Canopy cover (%)	Percent canopy cover directly above cavity; this was estimated using densiometer as described in the text.
Cavity orientation	Cardinal direction of cavity placement on the tree; this was measured with a compass
Hardness body (N m)	Torque required to turn increment borer into a pre-drilled hole, 3–10 cm within a tree's bole; this was measured following Lorenz et al. (2015)
Hardness sill (N m)	Torque required to turn increment borer into a pre-drilled hole, from tree surface to 3 cm; this was measured following Lorenz et al. (2015)

by 1 cm was measured (Lorenz et al., 2015). Higher values of torque represented wood that was harder while softer wood required less torque for the increment borer to “bore” through. Torque values were taken every 1 cm, and the wood hardness of the sill (from the tree surface to 3 cm) and the body (3–10 cm within a tree's bole) of the cavity (e.g. Lorenz et al., 2015) were used in the modeling process.

2.3. Data approaches and statistical analysis

To provide context for the thermal environments within aspen stands and the tree cavities contained within, we summarized patterns of daily mean temperatures (T_{mean}) in these aspen stands over the course of the study as well as the distribution of different temperatures that occurred within tree cavities. We provide these data because different species (both birds and bats) are likely to utilize cavities that are at different temperatures, and a general histogram describing the distribution of nest cavity temperatures can provide a current perspective on nest cavity temperatures during this study and will provide a baseline for future studies. Webb (1987) noted that some avian species had negative responses to a single hour of exposure to temperatures above 40 °C, and so we used that as a minimum temporal threshold with which to describe the distribution of temperatures within these cavities.

Following Wiebe (2001), temperature data from every third day was used in our modeling approaches. Only data from every third day was used in our modeling approaches to ensure that temperature readings were not temporally autocorrelated (e.g. Wiebe, 2001). For instance, the temperature on day 1 could have a lag effect on the temperature on day 2 due to the ability of wood to retain heat. The maximum temperature for a 24-h period every 3rd day was recorded for all iButtons, and the mean Tmax was then calculated for each cavity and external iButton. The mean ambient T_{max} did not differ significantly between the two sampling periods ($p = 0.08$) so all data were pooled.

We used R Studio Version 0.98.1103 statistical software and the lme4 package (Linear Mixed-Effects Models using 'Eigen' and S4) for statistical analysis (Bates et al., 2015) and considered results significant at a $\alpha = 0.05$. We modeled mean cavity T_{max} as the response variable and predictor variables included multiple tree, cavity, and hardness characteristics as well as the mean ambient T_{max}. Since ambient temperature has been shown to influence internal cavity thermal environments (e.g. Clement and Castleberry, 2013; Maziarz et al., 2017; Vierling et al., 2018), we included the mean ambient T_{max} as a covariate in all models for mean cavity T_{max} except for the null model, and the null model contained no predictor variables and only the intercept (Table 2). A total of 9 models were evaluated (Table 2), and using a linear mixed effect model, we ranked models based on Akaike's Information Criterion (AIC; Burnham and Anderson, 2002). Models that were within a ΔAIC of 2 were considered competitive; Akaike weights and parameter estimates were also calculated following Burnham and Anderson (2002). The cavity was identified as a random effect to account for the multiple temperature measurements from the same cavity. Variables used in the model were checked for correlations, and variables were excluded from the model if a significant ($p = 0.05$) correlation existed.

3. Results

Of the initial 47 iButtons deployed in our study, our final data set included 30 cavities due to falling trees (n = 14) and ejected iButtons (n = 3). A mean of 339 h (± 27.8 h) of data were collected for each cavity and its paired external iButton. T_{mean} in the aspen stands was widely variable during the data collection period (Fig. 2). Within tree cavities, air temperatures ranged from 1 °C to 46 °C, and T_{mean} was similar between ambient environments and within cavities (Table 3). There was also a high correlation between T_{max} outside and inside the cavities ($R^2 = 0.99$; Table 3). All cavities exceeded the threshold for physiological zero (> 24 °C) for at least an hour, and that ~13% of cavities exceed temperatures above 40 °C for at least an hour (Fig. 3).

The two top ranked models that explained the mean cavity T_{max} included: 1) tree characteristics (DCH, canopy cover, and orientation) and the mean ambient T_{max}, and 2) the mean ambient T_{max} alone (Table 4). Parameter estimates in the top model that were statistically significant included canopy cover and the mean ambient T_{max} because those were the only two parameter estimates whose 95% confidence intervals did not cross zero (Table 5). Canopy cover was negatively associated with the mean cavity T_{max}, suggesting that as local canopy cover decreased, the mean cavity T_{max} increased. The mean ambient T_{max} was significantly and positively associated with mean cavity T_{max} (Table 5). The mean ambient T_{max} parameter estimate was approximately 15 times higher than canopy cover, indicating that its effect on mean cavity T_{max} was stronger than that of canopy cover. Means and ranges of predictor variables are provided in Appendix A.

4. Discussion

We found that mean ambient T_{max} and canopy cover influenced mean cavity T_{max}, and our findings are consistent with other studies. Ambient temperature has been previously suggested to strongly affect the internal temperatures of tree cavities (Paclík and Weidinger, 2007; Coombs et al., 2010; Grüebler et al., 2014; Maziarz et al., 2017; Vierling et al., 2018). Additionally, the relationship we found between low canopy cover and higher cavity temperatures has been reported elsewhere (Clement and Castleberry, 2013; Vierling et al., 2018), although some studies have found no effects of canopy cover on nest temperatures (e.g. Otto et al., 2016). Other variables that appeared in our top model (diameter at cavity height and cavity orientation) did not have significant effects on maximum cavity temperatures, but the direction of the effect was similar to other studies. Warmer cavities were associated with a southerly cavity orientation (e.g. McComb and Noble, 1981; Wiebe, 2001) and smaller diameters (Wiebe, 2001; Clement and Castleberry, 2013; Maziarz et al., 2017), although Coombs et al. (2010) found that the effect of diameter at cavity height on temperatures shifted between day and night time.

Table 2
Models used to examine the effects of site characteristics on mean cavity T_{max} for 30 cavities in the Pioneer Mountains, Idaho, 2015. Diameter at cavity height is referred to as DCH.

Model	Explanation	Parameters
1	Global	Mean ambient T_{max}, DCH, entrance area, cavity volume, sill width, canopy cover, cavity orientation, hardness body, hardness sill
2	External	Mean ambient T_{max}
3	Cavity characteristics only	Mean ambient T_{max}, entrance area, cavity volume, sill width
4	Tree only	Mean ambient T_{max}, DCH, canopy cover, cavity orientation
5	Hardness only	Mean ambient T_{max}, hardness body, hardness sill
6	Cavity characteristics and hardness	Mean ambient T_{max}, entrance area, cavity volume, sill width, hardness body, hardness sill
7	Tree and cavity characteristics	Mean ambient T_{max}, DCH, entrance area, cavity volume, cavity orientation, sill width
8	Tree and hardness	Mean ambient T_{max}, DCH, canopy cover, cavity orientation, hardness body, hardness sill
9	Null	Contained only the intercept term

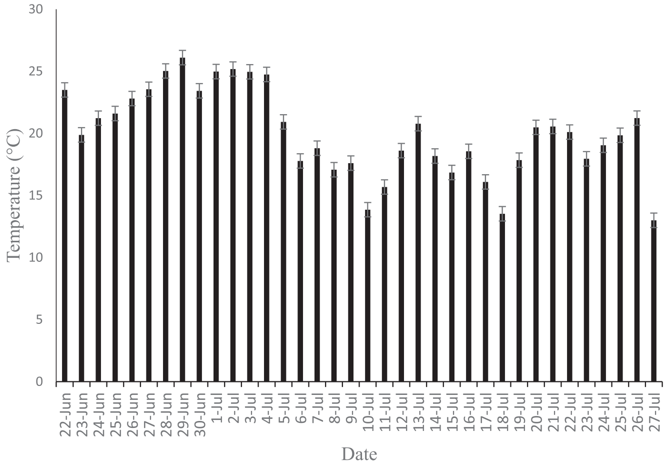

Fig. 2. Mean daily temperatures (°C) ± s.e. in aspen stands in southeastern Idaho during June and July 2015. These temperatures represent the ambient temperature data collected from 30 iButtons hanging directly outside the tree cavity.

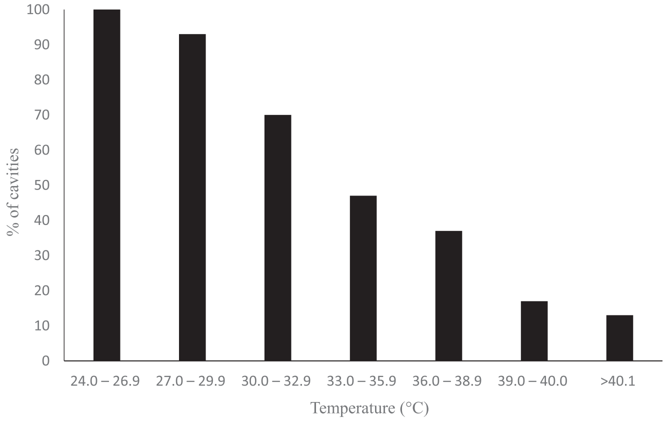

Fig. 3. Proportion of tree cavities in aspen that experienced temperature ranges between 24 °C and 40.1 °C for at least an hour in June and July 2015. Physiological zero for embryonic development of avian species can occur between 24 and 26 °C. Nest temperatures above 40 °C for at least an hour can be lethal to developing avian embryos while temperatures for optimal development of avian embryos varies by species but typically occurs between 36 °C and 40 °C.

Table 3
Daily temperatures (°C) patterns recorded by iButtons placed inside and outside 30 cavities in the Pioneer Mountains, Idaho 2105. Sensors were in place for 15–21 days in each cavity from June 22 to July 27, 2015, and each cavity was monitored for an average of 339 h (± 27.8). The temperature range was the difference between the daily maximum and daily minimum temperatures.

	Mean	SD	Min	Max
Daily ambient temperature	19.1	2.0	0.5	44.5
Daily internal cavity temperature	19.8	3.2	1	46.0
Mean daily maximum temperature (ambient)	28.9	4.3	21.0	37.0
Mean daily maximum temperature (cavity)	28.8	4.1	21.2	36.2
Daily temperature range within cavities	15.4	3.3	4	21
Daily temperature range outside of cavities	16.9	3.1	8	36.5

There are few studies of thermal environments within aspen cavities, and our data are most comparable to Wiebe (2001), who studied aspen tree cavity microclimates during the same time in the summer (mid-late July) in British Columbia. In general, we recorded higher temperatures than Wiebe (2001), and this may be due to latitudinal differences between our study locations. We recorded a maximum cavity temperature of 46 °C and that is higher than the 31.4 °C maximum that Wiebe (2001) reported. Additionally, our mean cavity T_{max} of 28.8 °C (± 4.1) was higher than the mean cavity T_{max} of 23.1 °C (± 2.87) that Wiebe (2001) reported. Other studies in aspen have focused on different time scales than our study (i.e. daily variability in temperatures; Kalcounis and Brigham, 1998) and we would suggest that there is a greater need for studies that address aspen cavity microclimates that extend our knowledge geographically as well as temporally.

This study only addressed thermal characteristics of cavities unoccupied during the duration of our study. Although the thermal characteristics reported here are obviously not those that nesting adults, eggs, nestlings, or roosting bats might be exposed to e.g. (Wiebe, 2001; Ruczyński, 2006), multiple studies have been conducted in the absence of cavity users and the information contained within this study can still provide important information regarding the factors that are potentially the most important in influencing thermal environments within nest cavities (Wiebe, 2001; Rhodes et al., 2009; Maziarz et al., 2017; Vierling et al., 2018). Wiebe (2001) noted that thermal data from unoccupied nest cavities should provide insight on the potential energy exchanges that could happen between nest contents or parent birds. Similarly, Boyles (2009) summarized the need for better describing microclimates for bats and suggested that understanding the thermal characteristics of both occupied and unoccupied cavities is important in order to better understand the factors that affect roost site selection. Kalcounis and Brigham (1998) described a scenario whereby unoccupied tree cavities at temperatures close to the upper critical temperature of little brown bats (*Myotis lucifugus*) are unlikely to be occupied because the addition of heat via roosting bats was likely to make the cavity thermally unsuitable as a roost site. The fact that the cavities that we included in this study were not used during the course of the study suggests that cavities are not a limiting factor in these specific aspen stands; however, the lack of occupancy during the period of our study might also be related to mismatches in timing between our study and the peak of cavity usage, cavity user densities, the thermal suitability of the cavities for different species, or interactions amongst all of these variables (e.g. Sedgeley, 2001). It was outside the scope of this

Table 4
Support for competitive models addressing mean cavity T_{max} in the Pioneer Mountains, Idaho 2015. Parameters are explained in Table 1 and models are listed in Table 2. Only competitive models with a ΔAIC < 2 are shown in this table; all other models examined had a ΔAIC of at least 3.4.

	AIC_c	Δ_i	Akaike weight	P-value
Mean ambient T_{max}, DCH, canopy cover, cavity orientation	627.39	0	0.47	< 0.001
Mean ambient T_{max}	628.46	1.07	0.27	< 0.001

Table 5
Parameter estimates with confidence intervals for the top ranked model explaining differences between thermal environments and tree characteristics for 30 cavities in Pioneer Mountains, Idaho 2015. Parameters with confidence intervals that do not cross zero were considered to be statistically significant and are in bold and italicized.

Parameter	Estimate (95% confidence interval)
DCH	−0.001 (−0.015 to 0.013)
Orient (North)	−0.105 (−3.773 to 3.562)
Orient (South)	1.966 (−2.609 to 6.542)
Orient (West)	1.284 (−2.324 to 4.893)
Canopy cover	***−0.064 (−0.116 to −0.123)***
Mean ambient T_{max}	***0.894 (0.791–0.998)***

study to assess broader patterns of cavity availability, cavity usage, and their associated microclimates, but we recognize that this is an important next step in determining how variations in microclimates across time and space might influence cavity using animals (e.g. Sedgeley, 2001; Boyles, 2009; Otto et al., 2016).

The thermal environments within tree cavities have important implications for breeding birds but also for other species that use these cavities during their life cycle. A wide assumption is that tree cavities used by bats and birds (Conway and Martin, 2000; Boyles, 2009) are selected for in part because they have characteristics that provide favorable conditions which ultimately influences reproduction and/or survival (Sedgeley, 2001; Wiebe, 2001; Newlon and Saab, 2011; Deng and Zhang, 2016). Temperatures in our study region are projected to rise 0.1–0.6 °C (0.2–1.0 °F) per decade (Mote and Salathé, 2010), and increases in the magnitude, frequency, and duration of heat waves are predicted to occur into the later part of the 21st century (Meehl and Tebaldi, 2004). For bats, selection for environments with higher temperatures may provide acceleration of fetal development (e.g. Racey, 1973) or energy savings for lactating females (Law and Chidel, 2007), assuming that ambient temperatures do not exceed upper lethal limits. Higher cavity temperatures might also benefit some bird species via providing climatic conditions that enhance fledgling growth rates (Dawson et al., 2005) and/or reduce the energetic costs to the young (Howe et al., 1987; Robertson, 2009). In general, though, knowledge about species-specific responses to thermal environments within cavities are limited, and the fitness consequences to these microclimate characteristics requires further study (Conway and Martin, 2000; Boyles, 2009; Mainwaring, 2015).

Tree cavities used by birds and bats in the Pacific Northwest region of North America occur in a variety of tree species, but few microclimate studies have been conducted on the thermal environments in other species of trees. Lacki et al. (2013) collected microclimate data within aspen stands but focused upon microclimate characteristics underneath bark. Vierling et al. (2018) recently reported upon thermal environments within tree cavities located within ponderosa pine (*Pinus ponderosa*) stands in the Pacific Northwest. The mean daily cavity temperatures were similar between the two studies; Vierling et al. (2018) recorded a mean of 20.9 °C ± 2.9 compared to this study (19.8 °C ± 32) but the maximum cavity temperature recorded in a cavity was 62 °C compared to the maximum reported in this study (46 °C). Different tree species are likely to have different abilities to buffer temperatures (e.g. Kalcounis and Brigham, 1998) and additional studies in tree cavities of multiple tree species should help to determine how wood characteristics as well as other environmental characteristics influence cavity temperatures.

Aspen are a particularly important for maintaining high levels of biodiversity in this region (Dobkin et al., 1995; Bartos, 2001; Aitken et al., 2002; Martin et al., 2004; Bunnell, 2013; Swift et al., 2017), and the predicted warming patterns in summer temperatures in this region (Abatzoglou et al., 2014; Mote et al., 2014) are likely to shift aspen distributions (Rehfeldt et al., 2009; Strand and Bunting, 2010; Whitebeck et al., 2016) as well as the thermal environments within tree cavities in these forests. Because of the strong association we found between ambient temperatures and tree cavity temperatures, it will become increasingly important to begin to synthesize information on species-specific cavity use patterns, demography, and physiology. Understanding relationships between cavity temperatures and environmental conditions is the first step in evaluating how changing climates might influence cavity use and population dynamics of cavity-using species.

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Appendix A. Means, standard deviation, and range of values associated with tree, cavity, and wood hardness characteristics

Variable	Mean (s.d.)	Range
Diameter at cavity height (cm)	265.8 (92.9)	22.6–531.6
Canopy cover (%)	43.6 (24.2)	7.0–88.0
Cavity entrance size (cm^2)	1292.4 (466.3)	467.2–2345.6
Cavity volume (cm^3)	1450.4 (1517.1)	118.1–6005.7
Sill width (mm)	20.8 (9.7)	7.8–45.7
Wood hardness (sill; N m)	2.7 (0.6)	1.5–4.0
Wood hardness (body; N m)	2.9 (1.2)	1.1–5.5

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