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MICROCLIMATE OF TREE CAVITY NESTS: IS IT IMPORTANT FOR REPRODUCTIVE SUCCESS IN NORTHERN FLICKERS?

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ABSTRACT.—I measured structural characteristics of 160 Northern Flicker (*Colaptes auratus*) nests at Riske Creek, British Columbia, and placed electronic data-loggers in a subsample of 86 nests to record internal temperatures after the flickers completed nesting. Using multiple regression, I found that the best predictors of a variety of nest-cavity temperature variables were tree health, diameter of the tree at cavity height, and orientation of the cavity. Small and dead trees showed the most extreme (maximum and minimum) temperatures during the day, but, on average, were the coldest nests from the perspective of incubation. South-facing cavities reached the highest temperatures during the day, and the orientation of natural cavities was also biased towards the south. I predicted that cold nests would be energetically expensive for adults and nestlings, and found that clutch size was positively correlated with mean cavity temperature. However, there did not appear to be any relationship among nest temperature and hatching or fledging success. *Received 18 January 2000, accepted 27 November 2000.*

DEAD OR DYING trees provide essential nest sites for a wide variety of cavity-nesting birds and mammals in forest ecosystems (Raphael and White 1984, Harestad and Keisker 1989). Use of such nests forms a nest web analogous to a food web whereby primary cavity excavators (such as woodpeckers) build nests that are used subsequently by a guild of secondary cavity nesters (Martin and Eadie 1999). Therefore, the stability of forest ecosystems may depend on presence of suitable trees, and stable populations of primary cavity nesters to excavate them. Much of what we know about the reproductive success of cavity-nesting species is based on nest-box studies, yet nest boxes may not be representative of natural nests (Møller 1989, Purcell et al. 1997; *but see* Robertson and Rendell 1990).

Researchers have accumulated much descriptive information on characteristics of cavity nests, and several studies have shown that features of a nest tree differ from random trees in the surrounding habitat (e.g. Gutzwiller and Anderson 1987, Harestad and Keisker 1989, Hooper et al. 1991, Schepps et al. 1999). Assuming that cavities must be excavated in trees of a minimum size and with a minimum softness of wood, nonrandom characteristics of nest trees on a coarse scale are probably not surprising. However, without knowing how reproductive success varies with features of cavity nests, it is impossible to determine whether birds are choosing optimal nest sites or are constrained in their placement of nests. A few studies have found that secondary cavity nesters do not always use types of cavities that are correlated with highest reproductive success (Nilsson 1984, Brawn 1988, Li and Martin 1991); the implication is usually that interspecific competition limits cavity availability. Presumably, primary cavity excavators have fewer constraints than secondary cavity nesters because they can construct their own nests. Red-cockaded Woodpeckers (*Picoides borealis*) chose trees with high resin production to protect them from predators (Conner et al. 1998) whereas Acorn Woodpeckers (*Melanerpes racemosa*) preferred some, but not all, features of nests associated with the highest reproductive success (Hooge et al. 1999).

Characteristics of nests that could influence fitness include susceptibility of the site to predation or parasites, proximity to food, and microclimate. Ambient temperatures may affect viability of birds' eggs (Webb 1987), and energy budgets of the incubating adult (White and Kinney 1974) and nestlings (Webb and King 1978). Several studies have measured the microclimate of open nests and the effects on parental behavior (e.g. Naylor et al. 1988, Gloutney and Clark 1997), and others have compared the microclimate of open nests to cavities (Mar-

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tin and Ghalambor 1999). None has measured the microclimate of cavity nests and related those temperature profiles to reproductive success in the cavities. My purpose in this study was not to test whether nest sites used by Northern Flickers (*Colaptes auratus*) differed from random, but rather to see how reproductive success might vary with the microclimate of trees actually used. I first obtained temperature profiles of cavities and then related the nest microclimate to structural characteristics of the nest. Finally, I examined whether nest microclimate was correlated with reproductive performance of flickers, a primary cavity nester.

METHODS

Study area and species.—The study area near Riske Creek, British Columbia (51°52′N, 122°21′W) encompassed approximately 75 km^2 of grassland with patches of trembling aspen (*Populus tremuloides*), lodgepole pine (*Pinus contorta*), and numerous small lakes and ponds. Particularly at higher elevations, forest cover was more continuous and contained Douglas fir (*Pseudotsuga menziesii*) and hybrid spruce (*Picea engelmannii* × *glauca*). Northern Flickers are medium-sized woodpeckers weighing ~150 g. Most individuals on the study area appear to be hybrids but tend towards the red-shafted subspecies, *C. a. cafer* (Wiebe 2000). Individuals arrive on territories after migration in mid to late April, after which both sexes participate in nest excavation, incubation, and brood rearing (Moore 1995). Clutch size varies from 4–13 eggs on the site.

In 1998 and 1999, I searched for flicker territories in spring using tape-recorded territorial calls. Potential nest cavities in the area were checked every 2–3 days with a flashlight and mirror until eggs were found. Once the clutch was complete and there was little chance of the pair abandoning, a small door was cut, using a keyhole saw, into the tree cavity below the natural nest hole and ~4 cm above the nest bottom (depth determined by plumb-bobbing the cavity). That afforded easy access to the eggs and nestlings. Adult flickers were trapped at the nest either by stuffing the nest hole during incubation, or by pulling a net over the hole during brood-rearing. In both situations, the cut door often had to be removed to flush the adults into a net held over the natural cavity entrance (to reduce the chance of breaking eggs, adults were not grabbed off the nest). Trapped adults were weighed, measured, and aged according to molt criteria in Pyle (1997). Nests were visited at hatching and about every 4–5 days thereafter to record mortality and to weigh and measure nestlings. I only included nests in analyses of success if they were visited frequently enough to determine exactly how many eggs were laid, how many hatched, and how many chicks fledged.

Cavity and microclimate.—After nestlings fledged, characteristics of the nest site were recorded. Cavity measurements included diameter and orientation of the entrance hole, vertical depth (from bottom of entrance to cavity bottom), horizontal depth (from inside lip of entrance hole to where a ruler touched the back wall), floor area (calculated as the area of an ellipse based on length and width of the floor), and wall thickness (where the door was cut). Cavity volume was estimated by multiplying the floor area by the vertical depth. In addition to the species of nest tree, several other measurements were recorded including height of cavity above ground, diameter at breast height (DBH) and diameter at cavity entrance height (DCH). Tree health was ranked in five categories: 1 = live tree no dead branches, 2 = live tree with 1–49% of the crown dead, 3 = partly live tree with 50–99% of crown dead, 4 = tree dead but retaining limbs, 5 = a single, dead stub. The shortest distance of the tree to a dry edge such as a field or meadow was recorded, as was the distance to the nearest stream or pond.

After fledglings left the nest, I placed electronic HOBO data loggers (Onset Computer Corporation, Pocasset, Massachusetts) on the floor of the cavity in the center. Those loggers recorded temperatures between −30 and +45°C with internal temperature sensors. Doors cut into the cavity were sealed with caulking to reduce the effect on internal cavity temperatures. Data loggers were programmed to take temperature readings every 3–4 min and provided a temperature profile for at least three consecutive days. Because there were fewer loggers than cavity trees, I sampled trees during three periods in 1998, and two periods in 1999 by transferring loggers to a new set of trees each time. During each sampling period, a control logger was placed at chest-height in an open area to record ambient temperatures in the sun. Those ambient temperatures were used to interpret data collected on different sampling days, and also approximate an open (noncavity) nest. Sampling dates were 7–18 July in 1998 and 10–18 July in 1999. Temperatures recorded in an empty nest obviously are not those actually experienced by eggs or nestlings being warmed by parents. However, such data should relate to the energy exchange between nest contents or parent birds and the ambient nest environment. In turn, that should correlate with potential energy expenditure by parents as they try to regulate the temperature of nest contents.

Statistical analysis.—From each 3–4 day sampling period, a single day (24 h period) was chosen with an ambient maximum temperature that most closely matched days in the other sampling periods. Still, ambient temperatures differed among the five sampling periods by 1–3°C, so a categorical variable,

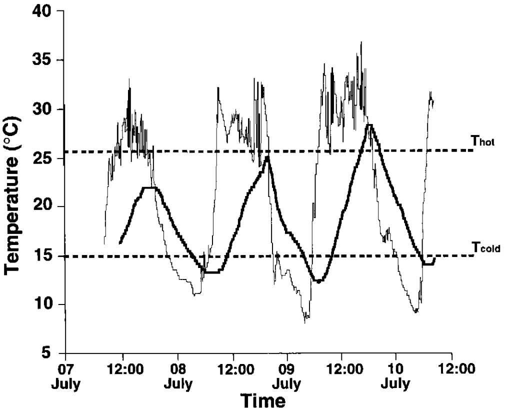

FIG. 1. An example of temperatures measured by electronic data loggers concurrently in the open sun (thin line) and in a cavity nest of a Northern Flicker (thick line). Noon is indicated at 12:00 h (PST). *Tcold* is the threshold temperature chosen for this study below which energetic costs of incubation are presumed to increase (*Tdeficit* is the sum of temperatures below this threshold). *Thot,* at 26°C, is the threshold temperature above which abnormal embryonic development may occur in unattended, unincubated eggs. Presumably, the optimum nest temperature lies between those two thresholds.

sampling period, was included in all regression analyses. I entered the 13 independent tree variables into a forward, stepwise multiple regression that included a variable in the model at a significance of $P < 0.05$, and removed it when $P > 0.10$. The dependent microclimate variables that were assessed in separate regressions were: (1) maximum temperature in the 24 h period (*Tmax*), (2) minimum daily temperature (*Tmin*), (3) range in daily temperature (*Tdiff*), (4) mean daily temperature (*Tmean*) and (5) rate of heating (measured from *Tmin* in the morning to *Tmax*).

I also tried to derive two temperature variables that had biological relevance to incubation. Unincubated eggs left exposed to ambient temperatures >26°C but <38°C (approximately normal incubation temperature) may show abnormal embryonic development (Webb 1987). Therefore, I did a logistic regression to test whether a cavity heated above 26°C or not. Other studies have shown that below a threshold ambient temperature, an incubating adult bird expends more energy to keep eggs warm; the increase in energy expenditure shows a positive linear relationship with decreasing temperature (Kendeigh 1963, Vleck 1981). The exact threshold temperature has not been measured for flickers, so I chose a value of 15°C which is the threshold for cavity-nesting Blue Tits, *Parus caeruleus* (Haftorn and Reinertsen 1985). Next, I summed (using 1 min intervals in the 24 h period) the degrees below the 15°C threshold for a total temperature deficit (*Tdeficit,* see Fig. 1). The threshold value chosen will certainly affect the absolute values of *Tdeficit,* but I assumed the relative ranking of the coldness of cavities would be meaningful when comparing reproductive success among them. The statistical significance of analyses using *Tdeficit* based on 18°C were not different from those using 15°C, so the conclusions seem robust within that range of values.

For circular statistics on cavity orientation, I used the Rayleigh test (Brown and Downhower 1988). For regression and ANOVA analyses, orientation was divided into four categories centered around the ordinal directions (e.g. 46–115° = east). Analyses were performed using SPSS (1992) software, and all tests of significance were two-tailed.

RESULTS

Characteristics of cavities.—I monitored 180 nesting attempts of flickers in the two years, but some nest trees were reused, leaving a sample of 160 different cavities (Table 1). Of those trees, one was a Douglas fir, five were lodgepole pines, and the rest (96.3%) were trembling aspens. Flickers used trees in all five health

TABLE 1. Nest cavity measurements of Northern Flickers at Riske Creek, British Columbia. Sample sizes differ because not all cavities were accessible or had doors cut.

Variable	*n*	Mean	Minimum	Maximum	SD
Height (cavity above ground) (m)	159	3.32	0.41	22.10	2.82
Diameter breast height (cm)	160	33.87	8.28	84.35	10.34
Diameter cavity height (cm)	133	31.35	15.6	61.43	6.71
Vertical depth (cm)	144	38.42	13.0	156.0	13.31
Horizontal depth (cm)	143	14.48	7.2	28.6	3.30
Floor area (cm^2)	139	166.59	77.41	791.0	76.81
Cavity volume (cm^3)	139	6,859	1,006	59,376	6,248
Cavity wall thickness (cm)	139	4.92	1.20	10.80	1.93
Orientation	157	210°	—	—	—
Diameter of entrance hole (cm)	143	6.42	4.2	9.6	0.91

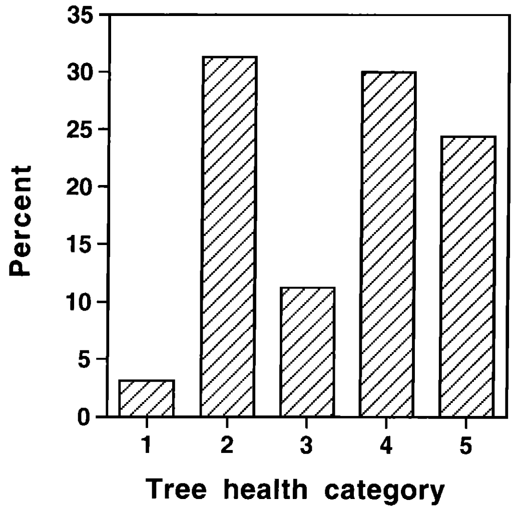

FIG. 2. Percentage of 160 Northern Flicker nests in the five categories of tree health (see methods for definitions of the categories).

TABLE 2. Descriptive statistics on the thermal characteristics of 86 Northern Flicker cavities in British Columbia sampled with data loggers during 7–18 July, 1998 and 1999. See methods for definitions of the thermal variables.

Variable	Minimum	Maximum	Mean ± SD
Tmax (°C)	18	31.4	23.1 ± 2.87
Tmin (°C)	5.4	22.5	12.5 ± 2.97
Tdiff (°C)	2.2	22.1	10.6 ± 3.76
Tmean (°C)	12.9	23.5	17.6 ± 2.24
Heating rate (°C/h)	0.24	2.92	1.14 ± 0.53
Tdeficit (°C min)	0	5204	1249 ± 1454
Time minimum (h)	5.05	9.50	6.77 ± 1.03
Time maximum (h)	12.25	22.8	17.86 ± 2.27

classes; 47% of trees were alive or partly alive (classes 1–3), and the rest (53%) were dead (Fig. 2). Nest holes were oriented in all directions, but were not random (Rayleigh test: $W = 6.31$, $P < 0.05$). The mean orientation was nearly south at 210°. Temperature loggers were placed in a subsample of 86 cavities over the two years. Ambient temperatures in an exposed area during the five sample days ranged from a lows of 5–7°C at night to highs around 27–32°C. Temperatures within cavities did not generally reach the extremes of ambient temperatures in the sun (see Fig. 1). The highest cavity temperature recorded was 31.4°C, the lowest was 5.4°C, with a mean temperature of 17.6°C (Table 2). As expected, the heating of cavities in the day lagged behind ambient temperatures with mean peak temperatures occurring around 1751 h but as late as 2248 h (PST). Most minimum temperatures occurred between 0600–0700 h (Table 2, Fig. 1).

Tree structure and cavity temperatures.—Regression analyses showed that *Tmax* was positively associated with the tree health category, that is, "deader" trees had higher temperatures (model $r^2 = 0.55$, $F = 15.6$, $P < 0.001$; Table 3). In addition, nests with a smaller tree diameter (DCH) became hotter than larger trees as did those with a more southerly orientation (Fig. 3). The sample period and DCH were the only significant predictors of minimum daily temperatures, although distance to dry edge ($P = 0.058$) was almost included in the model ($r^2 = 0.28$, $F = 7.94$, $P < 0.001$; Table 3). Thus, smaller diameter cavities cooled to lower temperatures at night and there was a trend that more exposed trees cooled more than trees within a forest canopy. Using the variable *Tdiff* which encompassed the range between maximum and minimum temperatures, DCH, health, sample period, and orientation were all important in the model ($r^2 = 0.68$, $F = 19.7$, $P < 0.001$; Table 3). Aside from sampling period, the only variable that significantly predicted *Tmean* was orientation ($r^2 = 0.13$, $F = 5.8$, $P = 0.004$; Table 3). Thus, orientation affected the high temperature, the mean temperature, and temperature range of a cavity, but was not important for minimum temperatures; presumably all trees had enough time during the night to cool to low levels regardless of orientation.

Tree health and size were the two predictors of cavity heating rate ($r^2 = 0.34$, $F = 10.6$, $P < 0.001$; Table 2), and together with the sample period, also explained the overall coldness (*Tdeficit*) of cavities ($r^2 = 0.48$, $F = 25.3$, $P < 0.001$; Table 3). A logistic regression on whether a cavity heated above the critical temperature of 26°C showed that DCH ($r^2 = 0.22$, $P = 0.009$), orientation ($r^2 = 0.20$, $P = 0.0024$), and sample period ($r^2 = 0.31$, $P < 0.001$) were the important predictors. Of the 86 sampled cavities, 21 (24%) reached the critical hot temperature during the days I sampled. In general, live and large trees heated and cooled more slowly, leading to more stable temperatures during the day (Figs. 4 and 5). Small and dead trees, which showed more extreme temperatures, tended to be cold-

TABLE 3. Characteristics of Northern Flicker nests in British Columbia that were significant predictors of five dependent cavity temperature variables (see methods for definitions). Regression statistics are from stepwise multiple regressions on 86 nests with temperatures measured during 7–18 July, 1998 and 1999.

Dependent variable	Predictors	Slope (b)	Significance (P)	Model r^2
Tmax	tree health	1.44	<0.001	0.55
	DCH	−0.12	0.004	
	orientation	−0.78	0.007	
Tmin	DCH	0.19	0.001	0.28
	sample period	−0.69	0.038	
Tdiff	DCH	−0.32	<0.001	0.68
	tree health	1.80	<0.001	
	sample period	0.88	0.008	
	orientation	−0.80	0.039	
Tmean	sample period	−0.38	0.020	0.12
	orientation	−0.44	0.021	
Heating rate	tree health	0.214	0.001	0.34
	DCH	−0.032	0.002	
Tdeficit	sample period	577.1	<0.001	0.48
	DCH	−55.1	0.001	
	tree health	245.1	0.012	

est overall with the greatest *Tdeficit* for incubation.

Temperature and reproductive performance.—Because a tree's health, its DCH, and its orientation appeared in most of the regression models for microclimate, I tested whether reproductive performance of flickers was related to those nest measurements. For that analysis, I used the larger sample of nests that included those not sampled with temperature data loggers. Clutch size with laying date as a covariate was not related to tree health (ANCOVA: health effect, $F = 0.48$, df = 4 and 151, $P = 0.75$), orientation category (ANCOVA: orientation effect, $F = 0.16$, df = 3 and 151, $P = 0.92$), or to DCH in a partial correlation controlling for laying date ($r = 0.05$, $n = 136$, $P = 0.50$). Independent of clutch size, hotter cavities may have reduced hatching success if high temperatures during laying caused reduced viability of embryos. Some nests failed completely because of predation, but the risk probably is not related to microclimate, so I excluded depredated nests from analyses of hatching and fledging success. Of 140 clutches that survived to hatching, 53 (38%) had at least one egg fail to hatch. Hatching success (number of eggs hatched divided by number of eggs laid) could not be transformed to a normal distribution, so I analyzed two categories: clutches with no egg failures versus those where at least one egg did not hatch. Tree health was not associated with distributions in the two hatching-success categories ($\chi^2 = 4.77$, $n = 138$, $P = 0.31$), nor was orientation ($\chi^2 = 2.77$, $n = 138$, $P = 0.31$) or DCH (logistic regression: Wald statistic = 0.87, $P = 0.35$). The subset of hot cavities that reached 26°C during the sample periods ($n = 18$) did not have lower hatching success than all

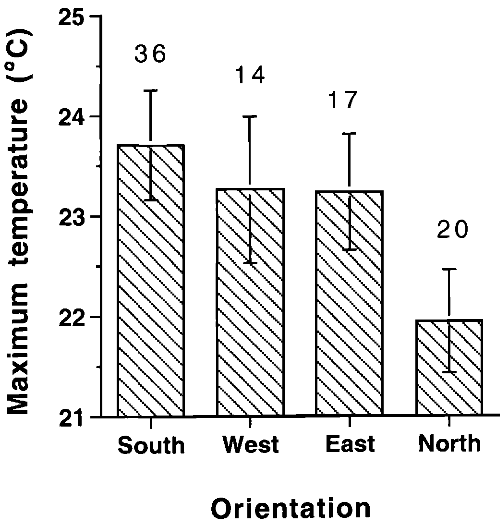

FIG. 3. Maximum daily temperatures achieved in Northern Flicker cavities oriented in the four directions. Means and SE are given with sample sizes above the bars.

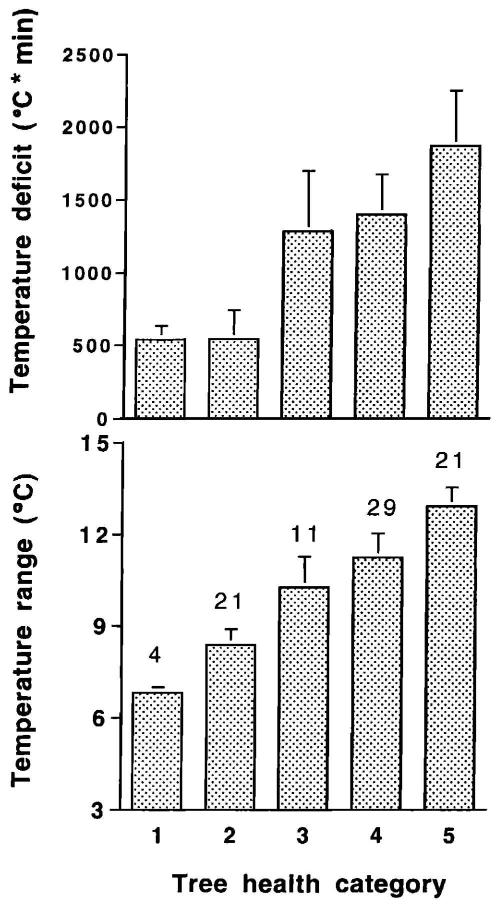

FIG. 4. Daily temperature range (bottom) and temperature deficit (top) of Northern Flicker nests in the five tree health categories. Means and SE are given with sample sizes above the bars.

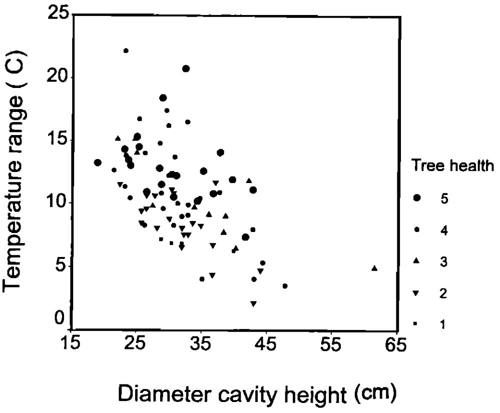

FIG. 5. Daily temperature range within Northern Flicker cavities in relation to tree diameter at cavity height. Points are classified according to tree health in the legend (see text for definition of tree health categories).

other nests measured during the sample periods ($\chi^2 = 2.65$, $n = 59$, df = 1, $P = 0.10$).

Fledging success (number of nestlings fledged divided by number hatched) for those nests that survived to hatch was also analyzed as a variable with two categories as to whether or not at least one nestling died. Nestling mortality was not associated with health of the tree ($\chi^2 = 4.92$, $n = 108$, $P = 0.29$) or orientation ($\chi^2 = 2.17$, $n = 108$, $P = 0.530$). Trees with a DCH >37 cm seemed to have better success than smaller trees, and all complete nest failures occurred in trees with a DCH <37 cm (Fig. 6). However, fledging success was not related to DCH in a logistic regression (Wald-statistic = 0.13, $n = 111$, $P = 0.72$). In another analysis, with DCH categorized as smaller or larger than 37 cm, there was still no significant relationship ($\chi^2 = 0.26$, $n = 111$, df = 1, $P = 0.61$).

For another set of analyses, I used only those trees with specific temperatures recorded by data loggers. A reproductive attempt in the same tree in the second year was considered an independent observation if the nesting pair was different. Clutch size was positively correlated with *Tmean* when laying date and floor area of the cavity was controlled (partial correlation: $r = 0.22$, $n = 87$, $P = 0.04$; Fig. 7), and negatively correlated with *Tdeficit* ($r = -0.21$, $n = 87$, $P = 0.04$). The analysis for the two temperature variables produced similar results when control-

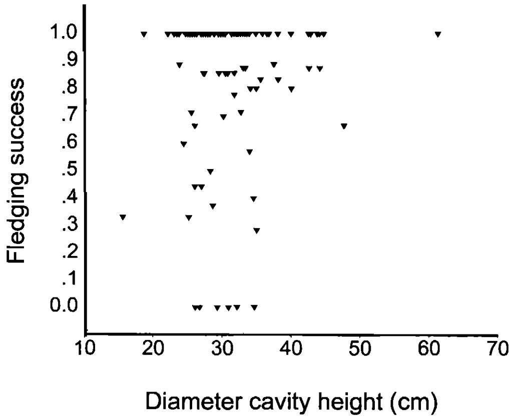

FIG. 6. Fledging success (proportion of hatched nestlings that fledged) in Northern Flicker nests in relation to diameter of the nest tree at cavity height.

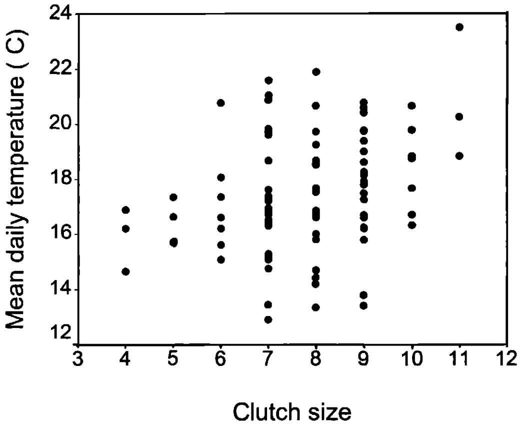

FIG. 7. Clutch size of Northern Flickers in relation to mean temperature of their cavity. Sample size is 87 nests that had temperature profiles recorded with electronic data loggers.

ling for cavity volume rather than floor area ($r = 0.21$, $n = 85$, $P = 0.05$ and $r = -0.19$, $P = 0.05$, respectively). That relationship between cavity temperature and clutch size was not driven by age or experience because neither male age ($F = 1.3$, $P = 0.28$) nor female age ($F = 0.67$, $P = 0.57$) was associated with clutch size in an ANCOVA with laying date as the covariate. Further, neither male age ($F = 0.83$, $P = 0.48$) nor female age ($F = 2.4$, $P = 0.08$) was related to mean temperature in their cavity. When considering later stages of reproduction, there was no association among *Tmean* or *Tdeficit* and hatching success category (depredated nests excluded, logistic regression: $n = 78$, $P > 0.17$) or fledging success category (logistic regression: $n = 77$, $P > 0.18$). At the end of the nestling period, there was no overall relationship between total number of fledglings produced and *Tmean* or *Tdeficit* (correlations, $n = 77$, $P > 0.75$).

DISCUSSION

Physical and thermal properties of flicker cavities.—The characteristics of flicker nests in this study were similar to those reported for other populations. The internal dimensions and entrance-hole size of cavities at Riske Creek were within the range reported in at least six other studies (review in Moore 1995). Although I did not analyze tree preference in relation to availability in this study, flickers appear to prefer trembling aspen over conifers because use of aspen was 96%, yet the relative proportion of aspen on the landscape is less than that, ~24% (see Martin and Eadie 1999). Preference for aspen is typical for many primary cavity nesters elsewhere (e.g. Li and Martin 1991), perhaps because aspen rots from the inside out and is easier to excavate (Harestad and Kiesker 1989). About 47% of nest trees used by flickers at Riske Creek were at least partially alive (Fig. 2). That is a higher percentage than reported for other populations, for example, 8% (Burkett 1989), 24% (Lawrence 1966), 26% (Gutzwiller and Anderson 1987), 36% (Ingold 1994), and 38% (Dennis 1969). The orientation of flicker cavities appears random in some studies (Stauffer and Best 1982, Ingold 1994) but, similar to our population, may show south, southeast, or east bias in others (Lawrence 1966, Dennis 1989, Burkett 1989).

I focussed on cavity temperatures in this study rather than other measurements of microclimate such as wind speed. Wind speeds in nest boxes are barely registered by instruments (Wachob 1996), and convection effects seem to be negligible in natural cavities (Mayer et al. 1982). Of the 13 independent tree variables, tree health, cavity orientation, and DCH consistently described most of the variation in cavity temperatures. That live wood has more stable temperatures and warmer temperatures during the night is consistent with Hooge et al. (1999), who compared mean temperatures of Acorn Woodpecker cavities between five live trees and five dead trees. Cavity orientation enhances microclimate effects in many avian species (Connor 1975) by limiting wind exposure (Williams 1993, Haggerty 1995), limiting sun exposure (Inouye et al. 1981, Korol and Hutto 1984) or, conversely, by increasing sun exposure (Inouye 1976, Balgooyen 1990, Kalcounis and Brigham 1998). Hooge et al. (1999) looked at the effect of orientation by measuring temperatures in nest boxes placed in four directions. They reported that east-facing boxes had the highest maximum and warmest average temperatures, and that natural cavities of Acorn Woodpeckers in California were also biased towards the east. In contrast, I found that south-facing flicker nests had the warmest temperatures (Fig. 3), and that flicker nests were biased towards the south. Perhaps latitude affects the relationship between orientation and heating. At the higher latitude of my study area, the sun stays at a lower angle in the southern sky, accentuating the difference between a northern and southern orientation.

Trees with a larger diameter had more stable and overall warmer temperatures. DCH was positively correlated with cavity volume, that is, flickers excavated larger cavities in larger trees, but none of the interior dimensions of the cavity entered the models. The larger volume of air in a large cavity may heat more slowly, but a greater DCH may also indicate a greater thickness of the walls surrounding the cavity. The variable "wall thickness" itself (Table 1) may not have been very accurate because it was measured only at one location where I cut the door to the cavity. Nest height above ground was not important in predicting cavity microclimate, although it may influence risk of predation and choice of nest site (Li and Martin 1991, Hooge et al. 1999). With respect to position of the tree at a landscape scale, trees more distant from the forest edge cooled less at night, but distance to edge was not important in predicting the daytime cavity temperature.

Temperature and reproductive success.—Northern Flickers probably select nest trees nonrandomly from those available (Li and Martin 1991), and cavity nests in general have more stable temperatures than open nests (Martin and Ghalambor 1999), but there still was substantial variation in the thermal properties of the cavities they used (Table 2). A nonrandom orientation of entrance holes towards the south, and the relatively high use of live trees in that population suggests that individuals may prefer warmer cavities. However, I did not detect any relationship between univariate structural measurements of cavity trees associated with temperature and reproductive success in the larger data set. Using the smaller data set and actual temperatures measured by the data loggers, larger clutches were laid in warmer cavities. In some cavity nesters, clutch size is positively correlated with cavity (or nest box) size (e.g. Karlsson and Nilsson 1977, Rendell and Robertson 1989), but that was not the case for flickers (Wiebe and Swift 2001). Still, after controlling for cavity size, the clutch-size effect in this study remained. Therefore, it seems that larger clutches are directly linked to warm temperatures and the effect is not confounded by a correlation between cavity (tree) size and warmer temperatures. The mechanism responsible for larger clutches is unknown, but it was not related to older birds choosing warmer cavities. Perhaps females have energy savings during laying and incubation and choose to invest more into eggs.

Although there was a clutch size effect for flickers detected at the beginning of reproduction (Fig. 7), hatching success and fledging success did not seem to be affected by temperatures, and no more fledglings overall were produced from warm cavities than cold cavities. Because the clutch-size effect was weak to begin with, sample sizes may have been too small to detect an effect at the fledging stage. Nestling mortality is easy to quantify and would represent a severe fitness cost to parents, but it is possible that there were more subtle consequences of nest microclimate, such as those to chick growth or to the body condition of adults (i.e. lifetime reproduction), which I did not measure. Nevertheless, microclimate did not have a large effect on the productivity of flickers in the two years it was measured.

What is the general importance of cavity temperatures?—The thermal environment of a nest should be important to cavity-nesting birds in systems where thermal stress influences reproductive success. The fact that some, but not all, populations of woodpeckers show nonrandom orientation of nest holes (see Ingold 1994)′may indicate that constraints imposed by microclimate are more important in habitats or years with more extreme weather. There is little empirical data on reproductive success in relation to nest temperature for any cavity-nesting species. Blue Tits in warm nestboxes had fewer interruptions in laying (Yom-Tov and Wright 1993) and lower incubation costs (Haftorn and Reinertsen 1985), but patterns in natural cavities are unknown. Life history traits and morphology may cause a certain cavity-nesting species to be more or less susceptible to temperature changes. For example, flickers with their relatively larger body size and thus lower surface-area-to-volume ratio than many other species of cavity nesters may be more tolerant of temperature extremes. Biparental care may also be a trait affecting tolerance of nest temperatures. Mountain Chickadees (*Poicile gambeli*) had higher fledging success in warm than in cold nest boxes; apparently, energy savings during incubation was small (3%), but most benefits accrued because warmer nests prevented chilling of the eggs or nestlings when the female left to forage (Wachob 1996). In contrast, both sexes of flickers alternate in incubation bouts (Moore 1995), so there is little danger of the eggs chilling.

A goal of modern forest management practices is to provide suitable trees for nesting, and information about tree preference has been used in the conservation of endangered species such as the Red-cockaded Woodpecker (Hooper et al. 1991). Measuring which trees are used for nesting is a first step, but more information is needed on how reproductive success is actually influenced by cavity parameters. The correlations between tree and temperature parameters in this study are probably applicable to the tree nests of many species. In general, large and living trees with stable and moderate temperatures may be optimal from the perspective of microclimate. However, weak excavators may be constrained to use very decayed trees. It is also unwise to manage for nest trees on the basis of a single criteria because the benefits of a cavity nest site are a complex result of multiple factors including predation risk (Nilsson 1984, Li and Martin 1991) and energetic costs of excavation (Schepps et al. 1999).

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