providing the EM-SCAN unit used in this study and to Jason Weckstein for his tireless assistance in the field. Thanks to R. and T. Robinson, T. Dietsch, S. and J. Hinshaw, University of Michigan, and personnel of Ledges State Park, Indiana University, Fountain Grove Wildlife Area, Eufaula NWR, and the U. S. Army Corps of Engineers for providing access to field sites. T. Root, K. Hall, R. Burke, B. Fahey, and J. Parody made helpful comments on earlier drafts, and G. Fowler provided statistical advice. This research was performed under appointment to the U. S. Department of Energy, Graduate Fellowships for Global Change Program, administered by the Oak Ridge Institute for Science and Education. Additional funding was provided by the U. S. Fish and Wildlife Service.

## Literature Cited

ASCH, A., AND D. D. ROBY. 1995. Some factors affecting precision of the total body electrical conductivity technique for measuring body composition in live birds. Wilson Bulletin 107:306–316.

CASTRO, G., AND J. P. MYERS. 1990. Validity of predictive equations for total body fat in Sanderlings from different nonbreeding areas. Condor 92:205–209.

CASTRO, G., B. A. WUNDER, AND F. L. KNOPF. 1990. Total body electrical conductivity (TOBEC) to estimate total body fat of free-living birds. Condor 92: 496–499.

CONWAY, C. J., W. R. EDDLEMAN, AND K. L. SIMPSON. 1994. Evaluation of lipid indices of the Wood Thrush. Condor 96:783–790.

EM-SCAN INC. 1993. EM-SCAN/TOBEC model SA-3000 multi-detector small animal body composition analysis system operator's manual. EM-SCAN Inc., Springfield, Illinois.

JOHNSON, D. H., G. L. KRAPU, D. J. REINICKE, AND D. G. JORDE. 1985. An evaluation of condition indices for birds. Journal of Wildlife Management 49:69–575.

KRUTCHKOFF, R. G. 1967. Classical and inverse regression methods of calibration. Technometrics 9:425–439.

KUBOKAWA, T., AND C. P. ROBERT. 1994. New perspectives on linear calibration. Journal of Multivariate Analysis 51:178–200.

LYONS, J. E., AND S. M. HAIG. 1995. Estimation of lean and lipid mass in shorebirds using total-body electrical conductivity. Auk 112:590–602.

MORTON, J. M., R. L. KIRKPATRICK, AND E. P. SMITH. 1991. Comments on estimating total body lipids from measures of lean mass. Condor 93:463–465.

NETER, J., W. WASSERMAN, AND M. H. KUTNER. 1990. Applied linear statistical models, 3rd ed. Richard D. Irwin, Inc., Bur Ridge, Illinois.

OSBORNE, C. 1991. Statistical calibration: A review. International Statistical Review 59:309–336.

ROBY, D. D. 1991. A comparison of two noninvasive techniques to measure total body lipid in live birds. Auk 108:509–518.

SCOTT, I., M. GRANT, AND P. R. EVENS. 1991. Estimation of fat-free mass of live birds: Use of total body electrical conductivity (TOBEC) measurements in studies of single species in the field. Functional Ecology 5:314–320.

SKAGEN, S. K., F. L. KNOPF, AND B. S. CADE. 1993. Estimation of lipids and lean mass of migrating sandpipers. Condor 95:944–956.

WALSBERG, G. E. 1988. Evaluation of a nondestructive method for determining fat stores in small birds and mammals. Physiological Zoology 61:153–159.

*Received 28 June 1996, accepted 14 March 1997.*
*Associate Editor: M. E. Murphy*

---

*The Auk* 114(4):769–773, 1997

# Nest Predation in Black-capped Chickadees: How Safe are Cavity Nests?

BETH J. CHRISTMAN[1,3] AND ANDRÉ A. DHONDT[2]

[1] *Section of Ecology and Systematics, Corson Hall, Cornell University, Ithaca, New York 14853, USA; and*
[2] *Cornell Laboratory of Ornithology, 159 Sapsucker Woods Road, Ithaca, New York 14850, USA*

Cavity nests traditionally have been thought to offer birds a greater degree of protection against nest predation than open-cup nests (Lack 1954, Nice 1957, Ricklefs 1969, Martin and Li 1992; but see Nilsson 1986). However, early work on the relative safety of cavity nests primarily was conducted on nests built in boxes, which often exhibit lower predation rates than nests in natural cavities (Nilsson 1984). Recent attention has focused on nest predation in natural situations. Because nest predation is important in shaping life-history evolution (Martin and Clobert 1996), it is important to con-

[3] E-mail: bjc14@cornell.edu

sider biases introduced into studies of birds that use nest boxes (Møller 1989).

Information on nest predation in natural cavities is important to understanding the influence of predation on the nesting behavior of birds. Many studies have described the characteristics of cavity nests without reporting the success or failure of these nests (e.g. Stauffer and Best 1982, Raphael and White 1984, Peterson and Gauthier 1985, Swallow et al. 1986, Gutzwiller and Anderson 1987, Runde and Capen 1987, Belthoff and Ritchison 1990, Kerpez and Smith 1990, Sedgwick and Knopf 1990). Although such descriptions lead to an understanding of nest-site selection, they do not identify the quality or suitability of a site in regards to nesting success.

Nest structure can influence nesting success in cavity nesters. For example, in a study of Carolina Chickadees (*Parus carolinensis*), depredated nests were excavated in significantly softer wood than successful nests (Albano 1992). No differences were found in nest height, diameter of limb, entrance diameter, depth of nest hole, thickness of cavity wall, or vegetation concealment. Toward quantifying the influence of nest structure on predation risk in Black-capped Chickadees (*P. atricapillus*) using natural cavities, we examined structural characteristics of successful versus depredated nests.

Chickadees are small (10 to 12 g) primary cavity nesters. Because they have small bills, they are unable to excavate cavities in wood that is very hard. When searching for excavation sites, Black-capped Chickadees are attracted to dead trees in which some sort of small hole is present (e.g. a woodpecker drilling, knothole, or broken-top snag) in order to access the softer heartwood that usually is rotten (Smith 1991, pers. obs.). Both males and females excavate, typically starting several holes on their territory before choosing the final nest hole.

*Study area and methods.*—Research was conducted in recent second growth woods near Ithaca, New York, from April to August 1996. All nests were located in forested areas of 100 ha or smaller. Agricultural and residential land surrounded the study sites. Nests were located in deciduous forests composed primarily of sycamore (*Platanus occidentalis*), white oak (*Quercus alba*), sugar maple (*Acer saccharum*), and aspen (*Populus* spp.).

Potential nest predators observed near nests included raccoons (*Procyon lotor*), eastern chipmunks (*Tamias striatus*), red squirrels (*Tamiasciurus hudsonicus*), eastern gray squirrels (*Sciurus carolinensis*), mink (*Mustela vison*), Pileated Woodpeckers (*Dryocopus pileatus*), and Red-bellied Woodpeckers (*Melanerpes carolinus*). Striped skunks (*Mephitis mephitis*) and black rat snakes (*Elaphe obsoleta*) also occurred in the area.

Beginning in late April, we surveyed study areas for Black-capped Chickadee nests. Frequent surveys continued through early summer for late nests and renesting attempts. When a nest was found, it was visited every other day until it was determined that it was abandoned, depredated, or successful (i.e. fledged at least one young). As a precaution against attracting predators, nests were approached directly only in order to band nestlings and were not marked in any way. Nesting phenology was determined by observations (through binoculars) of parental behavior at distances of 10 to 20 m from the nest. Nests that were abandoned during building were excluded from analyses. Adults were individually colorbanded on the breeding territory using taped calls to lure them into mist nets. In many cases, it was only possible to capture one member of the pair.

We tentatively identified nest predators by the appearance of the nest after predation. Cavities that were extensively ripped apart most likely were depredated by raccoons or skunks. Woodpecker nest predation was fairly easy to distinguish because the only damage to the depredated cavity was a cylindrical hole in the side of the tree trunk at the level of the nest chamber. Failed nests that showed little or no modification of the cavity most likely were depredated by snakes or small mammals.

After nesting attempts were terminated, we measured the following structural parameters: (1) height ($\pm$ 0.1 m) from ground to nest entrance, (2) circumference of tree ($\pm$ 0.01 m) at height of nest chamber, (3) thickness of cavity wall ($\pm$ 0.1 mm) at thinnest part, (4) hardness of the wood enclosing the cavity on a scale of 1 to 3 (1 = rotten wood that crumbles when sawed with a hand-held saw; 2 = wood that saws easily; 3 = wood that saws with effort). Circumference was a more accurate measure of the size of the nest substrate than diameter because many nests were located in elliptical limbs or trunks.

In order to determine which of the nest-cavity measurements best described successful versus depredated nests, we performed stepwise discriminant function analysis following the selection procedure outlined in Rencher (1995). Stepwise MANOVA was used to identify the variables that separate the two groups and were not redundant, and then a discriminant function was computed for the selected subset of variables. The discriminant function was tested for significance by calculating a $T^2$ statistic. Systat 5.2.1 was used for all analyses.

*Results.*—We found 21 nests built by 19 pairs of chickadees. Of these, five (24%) were successful, two (9%) were abandoned after eggs had been laid, one (5%) was taken over by House Wrens (*Troglodytes aedon*), and 13 (62%) were depredated. One pair of chickadees lost two nests to predators and abandoned a third clutch. All other nesting attempts represent the efforts of separate pairs. Nesting success calculated by the Mayfield method (Mayfield 1975, Hensler and Nichols 1981) was 27% with a daily mortality rate of 0.036 $\pm$ SE of 0.009, based on 449 exposure days for all 21 nests.

TABLE 1. Cavity characteristics ($\bar{x} \pm$ SE) of Black-capped Chickadee nests, Ithaca, New York.

| Variable | All nests | Successful nests | Depredated nests |
|---|---|---|---|
| Number of nests | 21 | 5 | 13 |
| Nest height (m) | 3.14 ± 2.40 | 3.66 ± 3.76 | 3.50 ± 1.77 |
| Circumference (m)[a] | 0.38 ± 0.13 | 0.43 ± 0.15 | 0.32 ± 0.07 |
| Thickness of wall (mm)[b] | 15.30 ± 12.80 | 26.16 ± 7.90 | 9.18 ± 6.64 |
| Wood hardness[c] | 11, 6, 4 | 1, 1, 3 | 7, 5, 1 |

[a] At height of nest chamber.
[b] Thickness of cavity wall at thinnest part.
[c] Number of nests scoring 1, 2 and 3. See text for explanation of scores.

Four nests clearly were depredated by medium-sized mammals, most likely raccoons, and three other nests probably were taken by medium-sized mammals. Two nests were depredated by woodpeckers, and it was likely that one other was taken by a woodpecker. Pileated and Red-bellied woodpeckers often were seen near chickadee nests, but it was not clear which species was responsible for predation in the three cases noted above. One nest almost certainly was destroyed by a small mammal, most likely a chipmunk or red squirrel. Another may have been depredated by a black rat snake, because the nest itself was undisturbed. At one nest we were unable to guess the identity of the predator.

The structural characteristics for all 21 nests are shown in Table 1. The two abandoned nests and the nest taken over by House Wrens are not included in further analyses of successful versus depredated nests. Stepwise MANOVA indicated that circumference, wood hardness, and thickness of cavity wall were important in distinguishing successful from depredated nests. Based on standardized coefficients determined from the discriminant analysis, thickness of cavity wall (0.664) was the most important variable influencing nesting success, followed by wood hardness (0.543) and circumference (0.496). The mean values of these variables differed significantly for successful versus depredated nests based on the discriminant analysis ($T^2 = 29.1$, df $= 16$, $P = 0.002$).

*Discussion.*—Traditionally, studies of cavity nesters have been concerned with birds in nest boxes. In this respect, our results are important in adding to the pool of knowledge of nest safety in natural situations and exploring aspects of nest-site choice. In our study of Black-capped Chickadees, nest predation in natural cavities was very high, and the structural attributes of successful and depredated nests differed significantly.

Nilsson (1984) addressed the question "do predation rates differ between nests in nest-boxes and nests in natural cavities?" He found that predation rates were higher in natural cavities versus nest boxes for some species (i.e. Great Tit [*Parus major*] and Pied Flycatcher [*Ficedula hypoleuca*]) and roughly equal in other species (i.e. Marsh Tit [*P. palustris*] and Blue Tit [*P. caeruleus*]). All of Nilsson's study species were secondary cavity nesters, which are subjected to different selective pressures than excavator species. Secondary cavity nesters may suffer higher nestling mortality for several reasons, e.g. from increased parasite loads (Møller 1989), because predators may remember nest locations and revisit cavities (Sonerud 1989, 1993), and because of increased competition for preexisting cavities (Johnsson et al. 1993, Dobkin et al. 1995). Li and Martin (1991) determined that non-excavators suffered higher nest predation than excavators because they were forced to use lower, more concealed holes.

Nest predation in other studies of parids in natural cavities varied from 14 to 71% (Table 2). Nest predation in our study (62%) was among the highest reported but was not outside the range of variation. These studies show that both excavating and non-excavating cavity nesters may suffer high rates of nest predation.

The influence of cavity characteristics on nesting success has been examined by only a few researchers. Nest height usually is cited as the most important factor influencing predation, although this relationship may be stronger for secondary cavity nesters (Nilsson 1984, Li and Martin 1991). In our study, nest height was not different between successful and depredated nests. Cavity-wall thickness, wood hardness, and circumference of the trunk at cavity height were the important factors influencing nesting success. Successful nests had thicker walls, greater circumference, and were in harder wood than depredated nests. Because most of the predation we observed involved partial destruction of the nest cavity, the general solidity of the nest substrate appeared to be an important factor in the outcome of a nesting attempt. Wall thickness and hardness relate directly to the sturdiness of the nest cavity. Albano's (1992) work with Carolina Chickadees lends additional support to our conclusion that overall soundness of the nest cavity is important for nesting success in chickadees.

The observed high level of nest predation in our study area raises certain questions regarding the habit of cavity nesting. It is interesting to consider reasons other than increased protection from pre-

TABLE 2. Nest predation for populations of parids nesting in natural cavities.

| Species | % Nest predation | Type | Location | Reference |
|---|---|---|---|---|
| Black-capped Chickadee (*Parus atricapillus*) | 62 | Excavator | New York | This study |
| Black-capped Chickadee | 18 | Excavator | New York | Odum 1941 |
| Carolina Chickadee (*P. carolinensis*) | 21 | Excavator | Illinois | Albano 1992 |
| Crested Tit (*P. cristatus*) | 14 | Excavator | Finland | Ojanen and Orell 1985 |
| Crested Tit | 71[a] | Excavator | Belgium | Lens and Wauters 1996 |
| Crested Tit | 16 | Excavator | Scotland | Denny and Summers 1996 |
| Willow Tit (*P. montanus*) | 61 | Excavator | Germany | Ludescher 1973 |
| Marsh Tit (*P. palustris*) | 55[b] | Non-excavator | Germany | Ludescher 1973 |

[a] For first broods.
[b] Probably higher than natural levels; many nests in repaired cavities of previously depredated Willow Tit nests.

dation that may have led to some parids becoming excavators. Benefits such as decreased parasite loads, or competition with larger secondary cavity nesters may have been more important in the evolution of excavation behavior.

*Acknowledgments.*—Chris Caudill and Tim Carr assisted in finding nests, and Dave Able provided invaluable support throughout the study. Tom Martin, Mikko Mönkkönen, and an anonymous reviewer provided helpful comments on the manuscript. This research was supported by the Section of Ecology and Systematics and the Cornell Laboratory of Ornithology.

## LITERATURE CITED

ALBANO, D. J. 1992. Nesting mortality of Carolina Chickadees breeding in natural cavities. Condor 94:371–382.

BELTHOFF, J. R., AND G. RITCHISON. 1990. Nest-site selection by Eastern Screech-Owls in central Kentucky, USA. Condor 92:982–990.

DENNY, R. E., AND R. W. SUMMERS. 1996. Nest site selection, management and breeding success of Crested Tits *Parus cristatus* at Abernethy Forest, Strathspey. Bird Study 43:371–379.

DOBKIN, D. S., A. C. RICH, J. A. PRETARE, AND W. H. PYLE. 1995. Nest-site relationships among cavity nesting birds of riparian and snow pocket aspen woodlands in the northwestern Great Basin. Condor 97:694–707.

GUTZWILLER, K. J., AND S. H. ANDERSON. 1987. Multiscale associates between cavity-nesting birds and features of Wyoming streamside woodlands. Condor 89:537–548.

HENSLER, G. L., AND J. D. NICHOLS. 1981. The Mayfield method of estimating nesting success: A model, estimators and simulation results. Wilson Bulletin 93:42–53.

JOHNSSON, K., S. G. NILSSON, AND M. TJERNBERG. 1993. Characteristics and utilization of old Black Woodpecker *Dryocopus martius* holes by hole-nesting species. Ibis 135:410–416.

KERPEZ, T. A., AND N. S. SMITH. 1990. Nest-site selection and nest-cavity characteristics of Gila Woodpeckers and Northern Flickers. Condor 92: 193–198.

LACK, D. 1954. The natural regulation of animal numbers. Oxford University Press, Oxford.

LENS, L., AND L. A. WAUTERS. 1996. Effects of population growth on Crested Tit *Parus cristatus* post-fledging settlement. Ibis 138:545–551.

LI, P., AND T. E. MARTIN. 1991. Nest-site selection and nesting success of cavity-nesting birds in high elevation forest drainages. Auk 108:405–418.

LUDESCHER, F.-B. 1973. Sumpfmeise (*Parus p. palustris* L.) und Weidenmeise (*P. montanus salicarius* Br.) als sympatrische Zwillingsarten. Journal für Ornithologie 114:3–56.

MARTIN, T. E., AND J. CLOBERT. 1996. Nest predation and avian life-history evolution in Europe versus North America: A possible role of humans? American Naturalist 147:1028–1046.

MARTIN, T. E., AND P. LI. 1992. Life history traits of open- vs. cavity-nesting birds. Ecology 73:579–592.

MAYFIELD, H. F. 1975. Suggestions for calculating nest success. Wilson Bulletin 87:456–466.

MØLLER, A. P. 1989. Parasites, predators and nest boxes: Facts and artefacts in nest box studies of birds? Oikos 56:421–423.

NICE, M. M. 1957. Nesting success in altricial birds. Auk 74:305–321.

NILSSON, S. G. 1984. The evolution of nest-site selection among hole-nesting birds: The importance of nest predation and competition. Ornis Scandinavica 15:165–175.

NILSSON, S. G. 1986. Evolution of hole-nesting in birds: On balancing selection pressures. Auk 103:432–435.

ODUM, E. P. 1941. Annual cycle of the Black-capped Chickadee. 2. Auk 58:518–535.
OJANEN, M., AND M. ORELL. 1985. Changes in the breeding parameters of the Crested Tit *Parus cristatus*. Ornis Fennica 62:161–167.
PETERSON, B., AND G. GAUTHIER. 1985. Nest site use by cavity-nesting birds of the Caribou Parkland, British Columbia. Wilson Bulletin 97:319–331.
RAPHAEL, M. G., AND M. WHITE. 1984. Use of snags by cavity-nesting birds in the Sierra Nevada. Wildlife Monographs No. 86.
RENCHER, A. C. 1995. Methods of multivariate analysis. John Wiley and Sons, New York.
RICKLEFS, R. E. 1969. An analysis of nesting mortality in birds. Smithsonian Contributions to Zoology 9:1–48.
RUNDE, D. E., AND D. E. CAPEN. 1987. Characteristics of northern hardwood trees used by cavity-nesting birds. Journal of Wildlife Management 51:217–223.
SEDGWICK, J. A., AND F. L. KNOPF. 1990. Habitat relationships and nest site characteristics of cavity-nesting birds in cottonwood floodplains. Journal of Wildlife Management 54:112–124.
SMITH, S. M. 1991. The Black-capped Chickadee. Cornell University Press, Ithaca, New York.
SONERUD, G. A. 1989. Reduced predation by pine martens on nests of Tengmalm's Owl in relocated boxes. Animal Behaviour 37:332–334.
SONERUD, G. A. 1993. Reduced predation by nest box relocation: Differential effect on Tengmalm's Owl nests and artificial nests. Ornis Scandinavica 24:249–253.
STAUFFER, D. F., AND L. B. BEST. 1982. Nest site selection by cavity-nesting birds of riparian habitats in Iowa. Wilson Bulletin 94:329–337.
SWALLOW, S. K., R. J. GUTIÉRREZ, AND R. A. HOWARD, JR. 1986. Primary cavity-site selection by birds. Journal of Wildlife Management 50:576–583.

*Received 9 December 1996, accepted 18 March 1997.*
*Associate Editor: T. E. Martin*

---

*The Auk* 114(4):773–778, 1997

# Geographical Trends in Clutch Size: A Range-wide Relationship with Laying Date in American Pipits

PAUL HENDRICKS[1]
*Department of Zoology, Washington State University, Pullman, Washington 99164, USA*

Many species of terrestrial birds produce larger clutches at higher latitudes within their breeding ranges. This pattern has been explained as a response to increased day length (Lack 1954, Hussell 1985), increased seasonality of food resources (Ricklefs 1980), or decreased climatic stability (Cody 1966) as one moves from equatorial to polar regions. In each case the outcome is an increased availability of food that can be delivered to dependent offspring, thus allowing for larger clutches and broods. Several modifications and refinements of these hypotheses have been advanced (e.g. Skutch 1967, Murray 1979, Slagsvold 1981), and the topic remains an active area of investigation.

The relationship between laying date and clutch size is another pattern that has been widely documented in birds. Earlier laying within a season typically results in larger clutches (Lack 1954, Perrins 1970), and mean clutch size increases during years of early nesting (Järvinen 1989a, Perrins and McCleery 1989). Few studies of single species, however, have examined a number of populations over a large range of latitudes to see if latitudinal patterns in mean clutch size relate in some predictable way to annual variation in mean laying date within populations.

Here, I present evidence that annual mean clutch size of American Pipits (*Anthus rubescens*) is strongly correlated with the annual mean date of clutch initiation for each population, and that latitudinal differences in day length, seasonality of food, and climatic instability need not be invoked to explain the larger average clutch size at higher latitudes shown by this species. A corollary resulting from this observation is that egg laying begins earlier (on average) at higher latitudes for American Pipits, a pattern counter to the normal expectation for most species.

*Study areas and methods.*—American Pipits breed in treeless tundra habitats in North America and eastern Siberia. They occupy high-elevation alpine areas

[1] Present address: Montana Natural Heritage Program, 909 Locust Street, Missoula, Montana 59802, USA. E-mail: phendricks@nris.mt.gov