

NESTING MORTALITY OF CAROLINA CHICKADEES BREEDING IN NATURAL CAVITIES¹

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Abstract. Nest-holes are conventionally thought to enhance avian breeding success by the protection they offer against inclement weather and predation. Studies of birds nesting in natural cavities are rare, however, and much remains to be discerned about the reproductive costs and benefits of the hole-nesting habit. This study documents nesting mortality within a southern Illinois population of Carolina Chickadees (*Parus carolinensis*) breeding in natural cavities, and relates variation in mortality with variation in nest-hole structure and microclimate. Ambient-air vs. nest-hole temperature differentials were used as indices of nest-hole insulative capacity. Little variation in air-nest temperature differentials was found among nests and variation in nest-hole structure was not strongly correlated with variation in any of the indices of insulative variation. No total nest failures were attributable to ambient extremes. Predation was the greatest influence on nesting success, accounting for every case of total nest-loss (11/51 nests) and 78.7% of all egg and chick mortality. Nests excavated nearer the ground and in softer wood were preyed upon significantly more than higher or more solidly-housed nests. The availability of nest-holes appeared to decline at greater, thus safer, heights as the breeding season progressed. This apparent temporal decline in the availability of optimal nest-sites may reflect the subordinate status of chickadees among larger, more aggressive hole-nesting species. I suggest that chickadees may compensate for this low ranking status with their great nest-site selection plasticity as well as their ability to rapidly renest following nest destruction.

Key words: Nesting success; natural cavities; predation; nest microclimate; Carolina Chickadee; *Parus carolinensis*.

INTRODUCTION

Early avian studies helped to establish the idea that breeding success is generally higher among hole-nesting species than among those birds that nest in the open (Lack 1954, Nice 1957). This idea persisted, largely without qualification, for many years in the literature as large bodies of data continued to lend it support (e.g., Ricklefs 1969). More recently, the relative breeding success of open vs. hole-nesting species has received greater scrutiny, as finer distinctions have been made concerning the methods used to both study and describe hole-nesting birds.

Of particular concern have been conclusions drawn from studies using artificial nest-boxes, as nest-box supplementation may have several unnatural effects on avian communities. Among these effects are elevated local population densities (von Haartman 1971, Nilsson 1984), altered local species composition (van Balen et al.

1982), and altered breeding parameters of birds occupying the boxes, including clutch size and nesting success (Mertens 1977). Hole-nesting birds using nest-boxes may also suffer artificially reduced rates of predation (Nilsson 1984, 1986; Møller 1989), as compared to the same species nesting in natural cavities. Based on these findings, Nilsson (1986) went so far as to suggest that, under certain conditions, breeding success of open and cavity nesting birds may be approximately equal.

Our understanding of breeding success among hole-nesting species has also been inhibited by the frequent failure to distinguish between those birds that excavate their own holes and those that must use previously excavated holes. Most discussions about breeding success among hole-nesters have arisen from studies of the latter class, secondary cavity nesters; again, these were studies conducted almost exclusively with nest-boxes (Lack 1954, Nice 1957, Ricklefs 1969). It now seems clear, however, that selection pressures, and thus sources and degrees of nesting mortality, may differ greatly between primary and secondary hole-nesting species (Li and Martin 1991). Any conclusions drawn from the study of either

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class alone will necessarily be an incomplete statement about hole-nesters in general. To best understand the costs and benefits of hole-nesting relative to open-nesting among birds, it is desirable to study hole-nesting under approximately the same conditions by which those costs and benefits have evolved and been maintained.

I document reproductive success within a population of Carolina Chickadees (*Parus carolinensis*) breeding in natural cavities, and examine relationships between nest-hole structural parameters and nesting mortality. Specifically, I attempt to characterize those nest-hole parameters effecting greater and lesser degrees of protection from predation and inclement weather, the two elements against which nest-holes are traditionally thought to offer greater protection than open-nests.

Carolina Chickadees are primary cavity nesters, yet will occasionally use previously excavated cavities. When occupying an old cavity, chickadees almost invariably modify its interior dimensions, often extensively (Brewer 1961, pers. observ.). They are non-migratory and among the earliest of birds nesting each spring in southern Illinois (Brewer 1963), the northern most part of their range (Tanner 1952). Chickadees are quite small (9–11 g), with a concomitant high surface area to volume ratio, and raise altricial young. All of these factors suggest that thermoregulation, and thus optimization of the nest microclimate, has a potentially significant influence on chickadee reproductive success.

STUDY AREA AND METHODS

Carolina Chickadee nests were found during the 1989 and 1990 breeding seasons in Jackson and Murphysboro Counties, Illinois. The study areas may be broadly characterized as containing mature, secondary growth deciduous or mixed coniferous/deciduous woods. The local climate supports upland plant communities dominated by oaks (*Quercus* spp.) and hickories (*Carya* spp.), while lowland areas are dominated by sweetgum (*Liquidambar* sp.), maples (*Acer* sp.) and elm (*Ulmus* sp.). The growing season begins in early March; the peak of plant species' flowering is May and June, and the greatest period of vegetative growth is in June and July (Mohlenbrock 1953). As the breeding season progresses, mean monthly temperatures in the study area exhibit a gradual linear rise from approximately (low/high) 6°/14°C in March to 18°/28°C in June.

Nests were located by observation of adult breeding behavior. Following their discovery, nests were visited every 2–3 days until fledging or nest failure. At each visit the status of the eggs/chicks was determined using a dental mirror and penlight, and a series of microclimate temperature variables was measured.

Hatching success was defined as the percentage of eggs laid that hatched. Nestling survival was the percentage of eggs hatched that fledged. Fledging success was the product of hatching success and nestling survival. Nest success, calculated in the traditional manner, was the percentage of nests that fledged at least one young. Nest success was also calculated according to Mayfield (1961, 1975). Nests were classified as either Early or Late based on their temporal relation to the median date of clutch completion for all nests.

MEASUREMENT OF MICROCLIMATE INDICES

Nest visits were scheduled such that all periods of the day (06:00–10:30 hr, 10:30–15:00 hr, and 15:00–19:30 hr) and nesting cycle (incubation and brood rearing) were equally represented. In order to standardize microclimate measures, nest-hole temperatures during incubation were measured immediately after flushing the parent from the nest. Due to irregular nest attendance throughout the nestling phase, temperatures were measured immediately upon my arrival when the nest was found unattended. If a parent was on the nest when I arrived, temperatures were not recorded until 10 min after the parent was flushed.

Five temperature measurements were made during each nest visit, always in the following sequence: (1) ambient air, or "T_a" (5 m from nest at nest height and out of direct sunlight); (2) nest level, or "T_n" (3 cm above eggs/chicks); (3) center of cavity, or "T_c" (entrance level); (4) nest entrance, "T_e" (1 cm exterior to entrance); (5) interior rear wall, or "T_r" (entrance level). All air temperatures were taken with a Barnant Omnitron 100 free-air probe (Model no. 600-2820, Barnatron Co., Barrington, Illinois). A Barnant surface-temperature probe was used to record rear wall temperatures. Based on their overall nest vs. ambient-air temperature differentials (T_n-T_a), nests were divided into either "HI" or "LO" categories; nests with overall T_n-T_a differentials above the median temperature differential were

classified as HI and those in the range below the median as LO.

MEASUREMENT OF NEST-HOLE STRUCTURAL VARIABLES

Each year, within two weeks of the last nest's fledging, all nest sites were visited and the following structural parameters recorded: orientation of nest-hole entrance (with a compass to the nearest 5 degrees); height of entrance from ground level; distance from entrance to stub/limb top (stubs are here defined as the central trunk of a snag, limbs as offshoots of the central trunk); least/greatest nest-hole entrance diameters; vertical depth of nest-hole (from lower rim of entrance to nest floor); horizontal depth of nest-hole (from inside entrance to rear wall); thickness of front, rear, and side walls (5 cm below entrance); diameter of stub/limb at nest-hole height; slope of stub/limb lean at nest-site; relative hardness of wood at nest level (based on ease of penetration by a penknife, 1 = softest, 5 = hardest); tree species; and the relative degree to which the nest-hole entrance was obscured by vegetation (1 = vegetation absent, 5 = nest-hole entrance covered). Due to destruction by predators during the course of the breeding season some nests' structural parameters were unavailable for analysis (i.e., nest-hole entrance diameters). Interior volume was calculated by assuming each cavity to be cylindrical.

CHARACTERIZATION OF UNUSED NEST-SITES

Six months after the end of the 1989 breeding season and after the trees had lost their leaves, one hectare plots surrounding each nest-site were surveyed to characterize those stumps and limbs available yet not used by the 1989 breeders. Potential nest-sites were defined as all non-living stumps and limbs falling within the range of structural parameters displayed by the 1989 nests. The following parameters were measured: height of stub/limb; slope of stub/limb lean at 1989 mean nest height; diameter of stub/limb at 1989 mean nest height; relative hardness of wood at mean 1989 nest height; and whether the potential nest-site was located on the edge of a vegetation clearing.

STATISTICAL ANALYSES

All temperature, reproductive success, and nest-site structural data were described and analyzed using SAS (SAS 1988). Differences in inter- and

intra-seasonal variation in reproductive success and nest dimensions were tested by ANOVA and Student's *t*-tests. Linear regression was also used to test for relationships among microclimate, reproductive success and nest-site dimensions. A significance level of 0.05 was used for all statistical tests. Unless otherwise indicated, all results are reported as means \pm standard error.

Orientation data were analyzed according to Batschelet (1981) and Zar (1984). Mean orientations were determined for nest-hole entrances as well as a relative index of dispersion (*r*) around this mean vector.

RESULTS

ACTIVE AND UNUSED NEST-SITES

I found 56 active nests in natural cavities, 23 in 1989 and 33 in 1990. Approximately half of the trees used for nesting (26/56) were located on the edge of vegetation clearings; 13 of these nests (50%) faced toward the clearing.

Nineteen genera and 28 species of trees were selected for cavity excavation. The most frequently used genera were elm (*Ulmus* spp.), maple (*Acer* spp.), birch (*Betula* sp.), oak (*Quercus* spp.) and sassafras (*Sassafras* sp.), these accounting for 53% of all trees selected. Forty-four of the nests (78.6%) were excavated in dead snags, while 12 (21.4%) were built in dead portions of living trees. Stubs were selected for nesting 47 times (83.9%) and limbs 9 times (16.1%).

On the sample plots surveyed ($n = 20$), I found and classified as potential nest-sites a total of 535 dead limbs and stumps ($\bar{x} = 26.8 \pm 2.5/\text{plot}$). Each sample plot contained from 0–17 limbs ($\bar{x} = 8.3 \pm 1.0$) and from 4–38 stumps ($\bar{x} = 18.5 \pm 2.2$). Potential nest-sites bordering clearings accounted for 21.1% of all those found.

While chickadees tended to choose nest-trees that were, on average, slightly shorter, of a slightly wider diameter, and of softer wood than those trees that were available, none of these differences were significant (Table 1). The birds nested significantly fewer times in limbs than stumps ($\chi^2 = 4.83$, $df = 1$, $P < 0.05$), and selected twice as many nest-sites bordering vegetation clearings as availability would predict ($\chi^2 = 12.31$, $df = 1$, $P < 0.001$).

NEST-HOLES

Nest-hole structural dimensions did not differ between years, or between Early and Late nests, and thus data for all periods were combined (Ta-

TABLE 1. Structural dimensions of active Carolina Chickadee nest-sites vs. unused potential nest-sites. Mean \pm SE (*n*). No differences were significant.

	Active nest-sites	Unused nest-sites	<i>t</i>
Tree height (cm)	341 \pm 27 (49)	384 \pm 11 (20)	-1.015
Diameter at nest height (cm)	13.2 \pm 0.7 (56)	11.9 \pm 0.2 (20)	1.114
Limb lean (degrees from vertical) ¹	140 \pm 7 (9)	146 \pm 3 (19)	-0.907
Stub lean (degrees from vertical) ¹	170 \pm 2 (47)	170 \pm 2 (20)	-0.044
Index of wood hardness	2.6 \pm 0.2 (32)	2.9 \pm 0.1 (20)	0.774

¹ Straight-up = 180°.

ble 2). Temporal trends were evident, though not significant, in the height of nest-trees and the height at which holes were excavated. Birds nesting in the early half of the breeding season selected trees with a mean height of 378 \pm 37 cm, while those nesting in the later half chose trees with a mean height of 287 \pm 36 cm ($t = 1.770$, $df = 39$, $P = 0.085$). Early nesters tended to excavate at greater heights, making their entrances at a mean height of 294 \pm 31 cm, while Late nesters excavated at 226 \pm 26 cm, ($t = 1.671$, $df = 45$, $P = 0.102$). Early nesters used one nest-hole excavated below 1.5 m (median nest-hole height = 267 cm), while Late nesters used six nest-holes excavated below 1.5 m (median nest-hole height = 220 cm).

The mean compass orientations of nest-hole entrances were calculated for various inter- and

intra-seasonal combinations (six nest-holes had vertically oriented entrances and were therefore not included). In none of the combinations was a mean orientation found that differed significantly from random (Table 3). The consistently low *r*-values reflect the high degree of dispersion among nest-entrance orientations (Fig. 1).

Nest entrance orientation was significantly associated with the direction of nest-stub/limb lean (Fig. 2). Of 26 nests for which comparison was applicable, 22 had entrances oriented within 45 degrees of the direct underside of the stub/limb's lean ($\chi^2 = 30.91$, $df = 25$, $P < 0.001$).

Mean ambient-air vs. nest-microclimate temperature differentials for 1990 nests (for which data were most complete) were compiled and separated into incubation and nestling periods (Table 4). Temperature differentials differed little

TABLE 2. Structural dimensions of Carolina Chickadee nest-holes.

Nest-hole parameter	<i>n</i>	Mean \pm SE	Range
Hole-height (cm)	55	275.0 \pm 23.0	65.0-762.0
Distance from entrance to stub/limb top (cm)	50	76.5 \pm 18.8	2.0-600.0
Entrance diameter (cm)	50		
Least		3.6 \pm 0.1	1.3-6.0
Greatest		5.5 \pm 0.4	2.7-18.5
Overall		4.6 \pm 0.2	2.7-11.0
Vertical hole depth (cm)	52	17.0 \pm 0.7	9.0-31.0
Horizontal hole depth (cm)	45	7.0 \pm 0.3	4.4-12.5
Wall thickness (cm)	50		
Front		1.9 \pm 0.2	0.4-7.5
Back		3.4 \pm 0.4	0.3-10.5
Left		3.4 \pm 0.5	0.4-26.0
Right		3.5 \pm 0.4	0.5-10.0
Overall		3.1 \pm 0.3	0.4-9.3
Vegetation index (1-5)	56	2.1 \pm 0.2	1-5

TABLE 3. Mean nest-hole entrance orientations, by year and period of breeding season. Mean \pm SD. No differences were significant.

Period (n)	Mean compass orientation ¹	r ²	Z
1989 (22)	197 \pm 76°	0.1249	0.3432
1990 (28)	148 \pm 80°	0.0245	0.0168
1989/1990 combined (50)	188 \pm 78°	0.0648	0.2100
1989/1990 Early combined (19)	37 \pm 77°	0.1087	0.2245
1989/1990 Late combined (22)	133 \pm 80°	0.0346	0.0263

¹ 0° = due north, 180° = due south, etc.

² "r²" represents the relative degree of dispersion among the samples (0 = maximum dispersion, 1 = maximum concentration).

between the two periods, despite the difference in mean ambient-air temperature between the two periods and the lack of parental heat contribution to measurements taken during the latter period. There was no significant relationship between mean ambient-air temperature during each period and mean $T_n - T_a$ ($F = 0.023$, $P = 0.882$).

NEST MICROCLIMATE AND NEST-HOLE STRUCTURAL CHARACTERISTICS

Nest-hole structural characteristics were, overall, poor predictors of air vs. nest microclimate temperature differentials. I found no significant associations between any structural parameter, or combination of parameters, and any of the microclimate indices. To test further for variation in insulative capacity, nest-stub/limbs were divided into large and small diameter classes and compared for mean differences in microclimate measurements. Large-diameter nests ($n = 15$) had a mean diameter at nest height of 18.6 ± 1.7 cm

and a mean total interior volume of 868.0 ± 118.1 cm³. Small-diameter nests ($n = 15$) had a mean diameter of 9.6 ± 0.4 cm and a mean total interior volume of 681.6 ± 106.2 cm³. No differences were found in overall $T_n - T_a$ between large- and small diameter classes.

Among both years' nests I classified 13 as HI $T_n - T_a$ nests and 14 as LO $T_n - T_a$ nests during the brood-rearing period (mean brood size did not differ between classes). The mean $T_n - T_a$ for HI nests was $1.8 \pm 0.2^\circ\text{C}$, and that for LO nests $0.8 \pm 0.1^\circ\text{C}$ ($t = 4.57$, $df = 25$, $P < 0.001$). There were no significant differences between the two classes with the exception of nest-hole height. LO nests were excavated almost a meter higher on average than HI nests (301 ± 34 cm vs. 213 ± 23 cm respectively, $t = -2.089$, $df = 25$, $P = 0.047$).

REPRODUCTIVE SUCCESS

The earliest evidence of Carolina Chickadee breeding activity that I witnessed was excavation

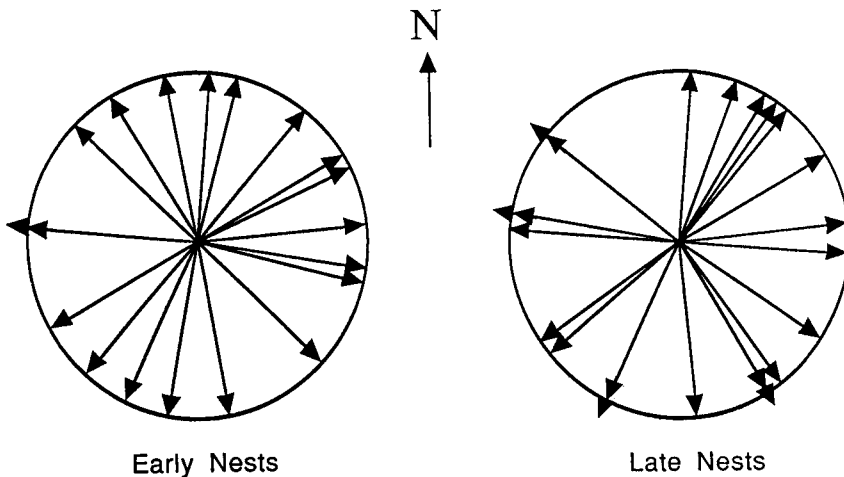


FIGURE 1. Nest-hole entrance orientations of Early ($n = 19$) and Late ($n = 22$) Carolina Chickadee nests found in southern Illinois.

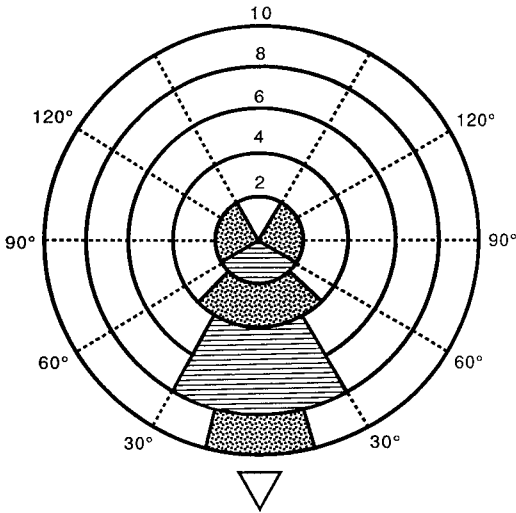


FIGURE 2. Tendency for nest-hole entrances to be oriented on the underside of leaning limbs and stubs. Each segment represents the number of nests with entrances oriented within the indicated number of degrees from the direction of stub/limb lean ($n = 26$, arrow indicates hypothetical direction of all stub/limb leans, i.e., the direct underside).

during the first week of March. The peak period of incubation was during the second and third weeks of April and the median fledge date was 16 May in 1989 and 14 May in 1990 (Fig. 3).

Eggs were incubated an average of 12.9 ± 0.4 days ($n = 12$), and the average time young remained in the nest was 16.8 ± 0.2 days ($n = 25$). Mean clutch size was 5.7 ± 0.1 eggs ($n = 42$).

Mean clutch size was not different between years ($t = -0.816$, $df = 40$, ns), or between Early and Late nesters ($t = 0.398$, $df = 38$, ns).

Of the 56 nests I found over the two breeding seasons, I was able to determine the ultimate fates of 51. In 1989, 80% of all nests fledged at least one young (16/20). All four cases of total nest loss were attributed to predation; three destroyed nests contained eggs, one contained chicks. In 1990 77.4% of all nests (24/31) fledged at least one young. Again, all total nest failures were attributed to predation, two nests contained eggs when destroyed, five contained chicks. The traditional measure of nest success was 78.4% for the two years (Table 5). There were eleven cases of partial clutch or brood loss: six nests failed to hatch a single egg, one nest failed to hatch two eggs, one nest failed to hatch three eggs, and three nests failed to fledge a single nestling.

Nest success varied according to the stage at which the nests were discovered. Of those nests found when the birds were excavating or nest-building, 66.7% (12/18) were successful, of those found during egg-laying or incubation, 78.0% (15/19) were successful, and of those found with nestlings, 92.9% (13/14) were successful. To correct for biases attributable to these unequal periods of observation, nest success was recalculated according to Mayfield (1961, 1975). These calculations yield nest success values of 63.5% for 1989 and 65.7% in 1990. Nest success was 65.7% for the two seasons combined (Table 6).

TABLE 4. Nest microclimate vs. ambient-air temperature. Numbers are means \pm SE ($^{\circ}$ C) of 1990 nest microclimate temperatures and nest/ambient-air temperature differentials (range). T_a = ambient-air temp., T_r = rear wall temp., T_n = nest level temp., T_c = center of cavity temp. and T_e = nest entrance temp.

	Incubation ($n = 15$)	Brood-rearing ($n = 18$)	Overall ($n = 19$)
T_a	14.8 ± 1.2 (6.0–23.1)	20.1 ± 0.6 (14.1–26.9)	18.8 ± 0.5 (14.1–22.3)
T_r	15.9 ± 1.4 (5.2–21.1)	20.8 ± 0.7 (13.5–27.4)	19.6 ± 0.6 (15.4–23.1)
$T_r - T_a$	0.9 ± 0.3 (–0.8–2.4)	0.7 ± 0.2 (–0.6–1.8)	0.8 ± 0.2 (–0.5–1.8)
$T_n - T_a$	0.6 ± 0.1 (–0.3–1.7)	0.8 ± 0.1 (–0.2–2.1)	0.8 ± 0.1 (–0.3–1.7)
$T_c - T_a$	0.6 ± 0.2 (–0.7–1.7)	0.6 ± 0.2 (–0.7–1.9)	0.6 ± 0.1 (–0.5–1.7)
$T_e - T_a$	0.4 ± 0.1 (–0.1–0.8)	0.3 ± 0.1 (–0.3–0.9)	0.3 ± 0.1 (–0.5–0.9)

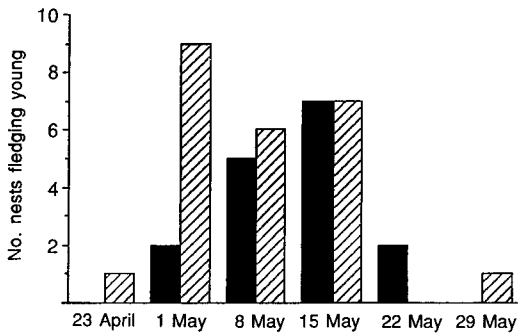


FIGURE 3. Fledging dates of Carolina Chickadees breeding in 1989 (solid bars) and 1990 (hatched bars). Bars represent the number of nests fledging young during week beginning on indicated date.

NEST-HOLE STRUCTURE AND REPRODUCTIVE SUCCESS

Predation accounted for 78.7% of all egg and chick losses and was responsible for all 11 cases of total nest failure. Discounting losses to predation, 94.4% of all eggs laid hatched successfully and 93.0% of all eggs laid survived to fledging. Structural parameters did not differ significantly between nest-holes that were depredated and those that were not. The single exception was the density of the stub/limb substrate; those nests that were depredated were excavated in significantly softer wood than those nests not depredated (Table 7).

While depredated nest-holes were not on average excavated higher than non-depredated holes, separating nest-holes into height classes reveals the great susceptibility to predation of nests at low heights (Fig. 4). Predation rates were highest on those nests closest to the ground; those nests excavated under 1.25 m suffered significantly more losses, proportionately, than those excavated at greater heights ($\chi^2 = 5.86$, $df = 1$, $P < 0.025$). Five of the six depredated nests that had nest material pulled out, and all three nest-holes with entrance walls torn out, were built under 2 m. These nests were considered depredated by large mammals. Likely predators in this area include raccoon (*Procyon lotor*), opossum (*Didelphis virginiana*) and striped skunk (*Mephitis mephitis*). Two destroyed nests were found with flying squirrels (*Glaucomys volans*) in them (both nests were > 2.5 m, see Stabb et al. 1989), and three nests were completely undisturbed when eggs/chicks were found missing. These three

TABLE 5. Reproductive success measures of Carolina Chickadees nesting in southern Illinois during 1989 and 1990.

Parameter	Mean \pm SE (n)
Eggs laid (no.)	5.7 \pm 0.1 (42)
Eggs hatched (no.)	4.8 \pm 0.3 (42)
Chicks fledged (no.)	3.9 \pm 0.4 (44)
Hatch success (%)	85.3 \pm 5.7 (42)
Nestling survival (%)	74.2 \pm 6.6 (44)
Fledge success (%)	69.6 \pm 6.4 (44)
Nest success (%)	78.4%

nests were considered lost to birds, snakes or small mammals.

DISCUSSION

NEST-MICROCLIMATE

I found little evidence to suggest that variation in nest-hole microclimate plays a significant role in the reproductive success of Carolina Chickadees breeding in southern Illinois. Of 51 nesting attempts of known outcome, no total nest failures were attributable to climatic influence. As I did not weigh nestlings or adults, however, it is possible that variation in nest-hole insulative quality was responsible for sublethal effects that I could not account for. Poorly insulated nests, for example, may stress nestlings, who must use extra energy to maintain body temperature, and may stress adults, who must sacrifice foraging time for increased nest attendance (Drent 1973). In this way, poor nest insulation might affect long term fitness, well after a nest has successfully fledged (Walsberg 1985).

Direct nestling mortality, nevertheless, was largely independent of climatic influence, and this independence may be associated with the poor correlations between nest-microclimate and nest-hole structure. In terms of thermoregulatory stress, and losses directly attributable to ambient extremes, there appears to be little for selection to act on in this population of chickadees. While HI and LO $T_n - T_a$ classes of nests had significantly different ambient-air vs. nest temperature differentials, there were no nest-hole structural characteristics that differed between the classes. Apparently there was little biological significance to the range of extremes in daytime air vs. nest temperature differentials. These findings may be a consequence of the relatively hospitable cli-

TABLE 6. Daily mortality and nest success of Carolina Chickadees calculated by the Mayfield (1975) method.

Year	Incubation		Brood-rearing		Hatch rate	Nest success
	Nest days	Daily mortality	Nest days	Daily mortality		
1989	112	0.0268 (0.9732) ¹	211	0.0047 (0.9953)	0.976	63.5% ²
1990	236	0.0085 (0.9915)	365	0.0137 (0.9863)	0.925	65.7%
1989/1990 combined	348	0.0144 (0.9856)	576	0.0104 (0.9896)	0.944	65.7%

¹ Numbers in parentheses indicate daily probability of survival.

² Nest success is the product of hatch rate and the cumulative daily probabilities of survival through incubation and brood-rearing.

mate of southern Illinois during the breeding season; mean weekly temperatures and precipitation levels during the two years of this study were consistent with those compiled from local airport weather data for the previous 50 years. It is likely that readily discernable nest-structure adaptations are restricted to areas with greater ambient extremes and a concomitantly greater degree of differential mortality on which selection might act (e.g., Austin 1974, Inouye et al. 1981).

Among species with large broods that nest in enclosed cavities, hyperthermia may be a sub-

stantial threat (van Balen and Cave 1970). This might be true for chickadees as well, who are inefficient at dissipating heat by evaporative cooling at high temperatures (Munzinger 1974). It is possible that chickadees attempt to avoid this threat temporally, rather than through some aspect of nest-site selection/construction, as they are amongst the earliest birds breeding in southern Illinois each spring and raise only a single brood. The highest daily temperature recorded in this study was 35°C on 1 June 1990. This was also the date of the latest known fledging.

TABLE 7. Placement and structural characteristics of depredated (D) vs. non-depredated (N-D) nests (all means are reported in cm with the exception of indices and mean wall thickness). Unequal sample sizes are the result of varying nest-hole accessibilities and/or predator destruction.

Parameter	Depredated/ non-depredated (n)	Mean ± SE	t	P
Tree height	D (10)	359 ± 65	0.3660	0.716
	N-D (38)	336 ± 30		
Distance from entrance to tree top	D (10)	113 ± 50	1.0267	0.310
	N-D (39)	66 ± 20		
Diameter of stub/limb at nest height	D (10)	13.4 ± 1.4	0.1422	0.887
	N-D (45)	13.2 ± 0.8		
Nest-hole height	D (10)	247 ± 60	-0.6292	0.532
	N-D (44)	282 ± 24		
Mean entrance diameter	D (8)	5.2 ± 0.8	0.9059	0.389
	N-D (41)	4.4 ± 0.2		
Vertical nest-hole depth	D (10)	15.5 ± 1.9	-1.1047	0.275
	N-D (42)	17.3 ± 0.7		
Mean wall thickness (mm)	D (9)	31.7 ± 5.3	0.1091	0.9136
	N-D (41)	30.9 ± 3.1		
Vegetation index (1-5)	D (11)	1.8 ± 0.3	-0.5743 ¹	0.5658
	N-D (45)	2.2 ± 0.2		
Hardness of wood index (1-5)	D (7)	2.2 ± 0.1	-2.1044 ¹	0.0353
	N-D (25)	2.8 ± 0.2		

¹ Z-statistic from non-parametric, Median 2-sample test.

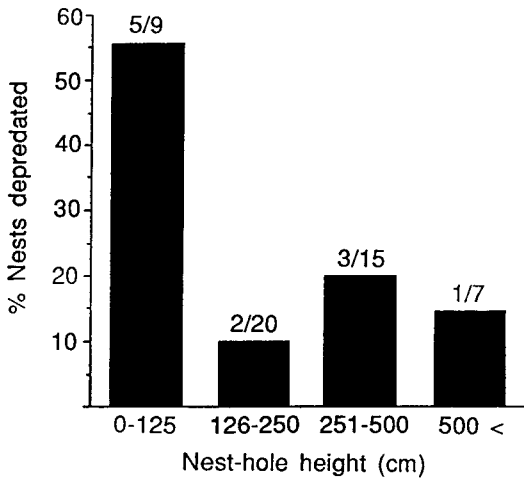


FIGURE 4. Nest predation and nest height. Bars represent the proportion of nests in each height class that were depredated ($n = 11$ nests depredated overall).

PREDATION AND INTERSPECIFIC COMPETITION

Predation is commonly the greatest cause of nesting mortality among birds, for both open and hole-nesting species alike (Skutch 1949, Nolan 1963, Ricklefs 1969, Nilsson 1984, Wilcove 1985, Martin 1988). I found this to be true for chickadees in this study, along with the oft-cited association between predation and nest-height (Best and Stauffer 1980, Nilsson 1984, Rendell and Robertson 1989). It is clear that nesting nearer the ground greatly increases the likelihood of nest loss through predation. Chickadees, who lack morphological adaptations for heavy excavation, also appear to be at a disadvantage by the necessity of their excavating in very soft, heavily decayed wood. Like nest-holes very close to the ground, those in softer wood were depredated significantly more, both factors apparently enhancing the accessibility of the nest contents to predators such as terrestrial mammals.

An element of nest-site selection/construction that might serve to lessen the accessibility of predators or would-be nest-hole usurpers is the placement of the nest-hole entrance. Nest-entrances in this study were almost invariably situated on the underside of leaning stubs and limbs, this placement being most often cited as an adaptation to prevent precipitation from entering the nest-hole (e.g., Conner 1975). I suggest that an equally plausible explanation for such a nest-entrance placement is that it may deter predator

access. For excavating species in particular, a destroyed or usurped nest-hole represents a great loss of time and energy investment. Placing the entrance at a downward angle may decrease the likelihood of the nest-hole being lost to either a predator or would-be usurper. Not only may the approach to a downward oriented nest-entrance be much more cumbersome than that to a horizontally oriented entrance, especially with a bird defending from within, the downward angle also effectively cuts off approach from above and concentrates the necessary field of vision of the hole-occupier (yet see Alatalo et al. 1990).

While such reasoning is largely speculative, the results of my study clearly show that loss of fitness through nest destruction is, potentially, a far greater selective force in this population than the ill effects of precipitation entering the nest-hole. That the six functionally open-nests (with vertically oriented nest-entrances) all fledged young (of 27 eggs laid in five observable nests, 25 chicks successfully fledged), argues further against the precipitation hypothesis.

The tendency for the lowest, and thus most vulnerable, holes to be used more often later in the season suggests a decline in the availability of optimal nest-sites as the breeding season progresses (e.g., Nilsson 1984, Rendell and Robertson 1989). As chickadees are intraspecifically territorial, and I found no evidence of a limitation in available nest-sites, the apparent decline in the availability of optimal holes is likely a result of competition from other hole-nesting species. Incidental observations made during this study support the idea that Carolina Chickadees are especially susceptible to nest-hole competition.

By late March 1990, I had located seven pairs of excavating chickadees. Over the course of a week, the nest-holes of two of these pairs were usurped by larger species that subsequently enlarged the cavity dimensions and laid eggs. Both usurped holes were well above the mean height of nest-holes in this study (a Northern Flicker, *Colaptes auratus*, took over a cavity at approximately 4 m and a Hairy Woodpecker, *Picoides villosus* at 6 m). Aside from intraspecific territorial disputes, the only aggression I witnessed among chickadees was that directed towards flickers, Red-bellied Woodpeckers (*Melanerpes carolinus*), and European Starlings (*Sturnus vulgaris*); all instances of aggression occurred in close proximity to nest-holes. Brewer (1963) reported a similar list of potential nest-hole competitors,

but included White-breasted Nuthatches (*Sitta carolinensis*), House Sparrows (*Passer domesticus*), and especially House Wrens (*Troglodytes aedon*).

The susceptibility of chickadees to predation and nest-hole usurpation may be allied with another behavior. I often witnessed chickadees inspecting nest-holes, and even carrying out cursory excavation, well into the breeding season. While some of these observations were possibly of birds attempting to renest, I frequently witnessed this behavior on territories with active nests. On two separate occasions in which I was certain of the birds' identities, I watched males inspecting cavities and/or carrying out wood chips while their mates were incubating full clutches of eggs elsewhere. I suggest that this habit reflects the relative insecurity of each nesting attempt, particularly at the beginning of the breeding season, and may be adaptive by its facilitating rapid renesting in the event of nest loss from predation or interspecific competition. Chickadees are well known for their apparent capriciousness when searching for nest-sites early in the spring, and often excavate at several sites before finally selecting a cavity in which to lay eggs (Brewer 1961, pers. observ.). This habit too may be associated with the advantages of increased nesting area familiarity should the necessity of renesting arise (Hinde 1952). While second broods are considered rare in this species (Dixon 1963), renesting commonly occurs following interference of the initial attempt (Brewer 1961).

That a high degree of competition exists for nest-holes, and that this competition may be ordered in an interspecific hierarchy along a gradient of body size has been reported elsewhere (Nilsson 1986, Li and Martin 1991). My observations, while admittedly anecdotal, suggest that chickadees may indeed be relegated to subordinate status in such a hierarchy. The great variability I found in nest-site parameters might support this scenario as well. Nest-hole heights, for example, varied by a factor of ten, while nest-hole diameters varied almost sevenfold. As mentioned, there were six functionally open nests (10.7% of all nests) with vertically oriented entrances. No species of tree was used more than seven times, while 28 species in all were represented. The timing of breeding also varied greatly, young fledging from late April to early June, a period comprising almost half the total time of breeding.

I suggest that the great variability in nest-site selection parameters I found, as well as the little difference between nest-site availability and use, may directly reflect the susceptibility of chickadees to nest-loss through predation and interspecific competition. If renesting requires the use of less preferable nest-sites (i.e., nest-holes nearer the ground), those characteristics of less preferable sites, when combined with those of more preferable sites, will create great variability in an overall nest-site characterization. The extent of this variation might represent the extent of chickadee subordinate status among other hole-nesting species, as well as the adaptiveness of immediate deference to dominants in lieu of the ability to rapidly renest.

While I did not take account of which nest-holes were newly excavated versus those that were modified existing nest-holes, primarily because of the aforementioned chickadee habit of extensively reexcavating old cavities, it would be of interest to note the relative use of new versus old nest-holes as the breeding season progresses. Within a facultative excavating species, one might expect to find increased use of older holes later in the breeding season as the necessity of renesting quickly becomes greater (see Nilsson et al. 1991). Assuming occupation of a newly excavated hole is preferable to modifying an existing hole, simply for having greater choice of placement and construction, as well as a new hole being not yet familiar to predators (Sonerud 1985) and more likely to be free of parasites (Brown and Brown 1986, Møller 1989), increased pressure to renest in an existing nest-hole would represent another temporal decline in optimal nest-site selection options.

Such a temporal decline may be likened to the situation chickadees appear to face with nesting height as the breeding season progresses—that of being “pushed down” by larger, more aggressive hole-nesting species and “pushed up” by the threat of predation (Nilsson 1984). Interestingly, such temporal differences in nest-site selection options are not unlike the differences in selection pressures between primary and secondary hole-nesting species. Secondary hole-nesters may be forced to use nest-holes that are both older and closer to the ground, and consequently may suffer greater rates of predation (Li and Martin 1991). Subordinate primary hole-nesting species may, in this sense, be temporally relegated to the status of functional secondary cavity nesters, as they

are forced to nest under similar selection pressures.

The ability of chickadees to respond to such a great range of selection pressures, apparently by being very plastic in their nest-site selection and very elastic in their ability to renest quickly following a nest loss, may help to account for their ubiquitous distribution.

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