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NESTING SUCCESS OF CAVITY-NESTING BIRDS USING NATURAL TREE CAVITIES

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Abstract.—This paper presents new data on the nesting success of House Wrens (*Troglodytes aedon*) using natural nest sites (tree cavities) in north-central Wyoming, and summarizes information on the nesting success of other North American cavity-nesting birds using natural nest sites. Of 99 House Wren nests in natural cavities observed over a 4-yr period, an estimated 63% of nests produced at least one fledgling. Nest failure occurred more frequently during the laying and incubation stages of breeding (62% of failures) than during the nestling stage. The success rate of nests in natural cavities did not differ significantly from the success rate of nests in tree-mounted boxes in the same population, probably because predators destroyed a relatively high proportion of nests in tree-mounted boxes. Nest failure in tree-mounted boxes also occurred more frequently during the laying and incubation stages of breeding (60% of failures) than during the nestling stage. The incidence of nest failure was greatly reduced by mounting nest boxes on greased metal poles. A literature survey revealed that rates of nesting success for North American cavity-nesting birds using tree cavities as nest sites range from 22 to 100% with a mean of 68%. Woodpeckers have the highest mean rate of success (77%), followed by other types of birds that excavate their own cavities (66%), and birds that use pre-existing cavities (54%). Excavators, as a group, have significantly greater success (74%) than non-excavators.

EXITO DE ANIDAMIENTO DE AVES QUE ANIDAN EN CAVIDADES NATURALES DE ÁRBOLES

Sinopsis.—En este trabajo se presentan nuevos datos en referencia al éxito de anidamiento del reyezuelo común (*Troglodytes aedon*) en cavidades naturales y se resume y analiza la información sobre el éxito de anidamiento de otras aves que también anidan en cavidades. El estudio se llevó a cabo en la parte norcentral de Wyoming. Durante un período de cuatro años, se estudiaron 99 nidos de reyezuelo de los cuales el 63% produjo al menos un volantón. El fracaso de anidamiento ocurrió más frecuentemente durante la etapa de puesta e incubación (62%) que durante la etapa de polluelos. El éxito de anidamiento en cavidades naturales no resultó diferente al de cavidades artificiales montadas en árboles debido, probablemente, a que los depredadores destruyeron una proporción mayor de los nidos artificiales colocados en los árboles. El fracaso de nidos en cavidades artificiales también resultó mayor (60%) durante el período de puesta e incubación. La incidencia de fracasos se redujo considerablemente montando las cajas artificiales en tubos de metal engrasados. El examen y análisis de la literatura reveló que el éxito de anidamiento de aves que utilizan cavidades naturales en Norte América promedia 68% (varía de 22 a 100%). Los pájaros carpinteros tienen el mayor éxito (77%) seguidos de otras aves que excavan sus cavidades (66%) y estos a su vez de aves que utilizan cavidades abandonadas (54%). Los que excavan sus cavidades, como grupo, tienen um éxito significativamente mayor (74%) que los no excavadores.

Ornithologists generally agree that cavity-nesting bird species have greater nesting success than open-nesting species, primarily because cavities provide better protection from nest predators (e.g., Gill 1990). This view stems largely from interspecific comparisons of nesting success made by Nice (1957), Lack (1954), and Ricklefs (1969). As Nilsson (1986) recently noted, in each of these reviews nesting success data for cavity-nesting species came almost exclusively from studies in which researchers provided birds with nest boxes. Nilsson and others have cautioned that nest box studies may be biased because of lower incidences of predation and ectoparasitism when birds use boxes compared to when they use natural cavities (see also Møller 1989, Wesołowski and Stawarczyk 1991).

At present, few data exist on the nesting success of North American cavity-nesting birds using natural cavities. We have three main objectives in this paper. First, we present data on the nesting success of House Wrens (*Troglodytes aedon*) using natural nest sites in north-central Wyoming, and compare the success of wrens using natural sites to the success of wrens using nest boxes in the same population. Second, we review findings of other studies that have compared the relative success of birds using natural cavities and birds using boxes. Finally, we present the first summary of information concerning the nesting success of other North American cavity-nesting birds using natural tree cavities. Much of this information was gleaned from unpublished sources.

METHODS

Nesting success of House Wrens.—We studied House Wrens on several neighboring cattle ranches near Big Horn, Sheridan County, Wyoming (44°40′N, 106°56′W; 1310 m elevation). Wrens on these ranches occupy wooded areas along creeks and rivers that flow through pastures and hayfields. Predominant tree species include Manitoba maple (*Acer negundo*), cottonwoods and aspens (*Populus* spp.), hawthorn (*Crataegus* spp.), river birch (*Betula occidentalis*), and common chokecherry (*Prunus virginiana*). Aside from allowing light grazing by livestock, humans have left these woodlands largely undisturbed for at least the last 100 yr. The study area contains few European Starlings (*Sturnus vulgaris*) or House Sparrows (*Passer domesticus*) and we observed no interactions between wrens and starlings or House Sparrows during 8 yr of study. Known nest predators in the study area include long-tailed weasels (*Mutela frenata*), raccoons (*Procyon lotor*) and bull snakes (*Pituophis melanoleucas*). Other suspected nest predators include feral cats, red squirrels (*Tamiasciuris hudonicus*) and chipmunks (*Tamias* spp.).

We observed the reproductive success of pairs using boxes in the 1986 and the 1988–1990 breeding seasons. In 1986, relatively few boxes (~15) were present, in most cases 50–125 m apart, in one corner of the study site. In 1987, we erected no boxes and observed wrens using natural nest cavities over a much wider area. During the 1988–1990 seasons, we erected one box on most of the territories that we observed in 1987, and additional boxes in areas that seemed suitable for wrens but appeared not to contain any natural nest sites. The study area contained between 45 and 60 boxes, usually 50–125 m apart, during each of the 1988–1990 seasons. Although we increased the density of breeding wrens in some local areas each season, at no time was the study area saturated with boxes: an estimated 20–30% of breeding wrens on the study site nested in natural cavities in each season. Territories with natural cavities were interspersed among the territories with boxes.

In 1986 and 1988, we mounted boxes 1.5–2.0 m above ground on the trunks of trees (or in some cases, on wooden fenceposts). In 1989 and 1990, we mounted boxes 1.5–2.0 m above ground on greased metal poles in an effort to deter potential nest predators (to facilitate other aspects of our studies). Each year, we visited all territories containing boxes every 1–4 d to determine the identity of males in control of boxes, male mating status, dates of first eggs, clutch sizes and dates when eggs began hatching. We considered a female to have attempted nesting if she laid at least one egg. We visited territories at irregular intervals during resident females' incubation and nestling stages to count eggs and young. All nests were checked at least through Nestling Day 16 (Nestling Day 1 = day that hatching first begins). Young usually fledge as a group on Day 16–18 and we considered a nesting attempt to be successful if it contained at least one nestling on or after Day 16. Occasionally a brood will fledge on Day 15, especially in hot weather. In cases where nests were found to be empty on Day 16, we assumed that nest was successful if: (1) the nest was known to contain at least one nestling on or after Day 12 and (2) there was no evidence that predation or brood death had occurred between the current and previous visit. Analyses included nesting attempts that failed because: (1) eggs did not hatch; (2) females disappeared, deserted the nest or died non-violently in the nest (presumably from starvation); (3) nestlings died apparently from starvation, hyperthermia or predation (the latter was inferred when the nest lining and/or the grease on the box pole were obviously disturbed); or (4) conspecific intruders removed offspring from nests (inferred when eggs or chicks were found uneaten on the ground and/or nest lining and grease on pole was undisturbed).

We observed the reproductive success of wrens using natural cavities in the 1987–1990 breeding seasons. We made most of our observations in 1987 when the study site contained no nest boxes. Each breeding season, we surveyed a pre-determined portion of our study site every 4–6 d in May and June in an attempt to locate *all* newly-settled males on territories that contained only natural cavities. We found all natural nest sites either before attending males mated, or very soon after mating occurred, as judged by male song output, male behavior towards females and female nest building activities (Johnson and Kermott 1991a,b).

We did not observe the contents of any nests in natural cavities and judged breeding progress using only the birds' behavior. We observed the activities of wrens in each active territory either daily, or at irregular intervals usually not exceeding 7 d. Observation sessions lasted 10–60 min. To determine the date that eggs began hatching in a nest, on most territories we observed nests daily as the estimated day of egg-hatching approached. We considered the date of hatching to be the first day that we saw parents delivering food to nests. If, on any day before fledging could have occurred (<Nestling Day 15), we detected no activity at the nest site after 30 min, or the attending male appeared to be unmated and advertising for a new mate, we scheduled a second 30-min observation session for the following day. If the expected breeding activity (i.e., incubation or feeding of nestlings) had not resumed the next day, we considered the nesting attempt to have failed. Unfortunately, we were not able to determine causes of nesting failure. All nests included in analyses were checked at least through Nestling Day 14 (>80% of nests still active on Day 14 were checked on 1–4 additional days). We considered a nesting attempt in a natural cavity to be successful if: (1) we observed parents feeding nestlings at least through Nestling Day 14 (after which broods potentially could fledge and move off the territory between our visits), and (2) there was no obvious evidence of nest predation (e.g., torn out nest-lining) on or before Day 16. A small proportion of broods credited as having fledged could instead have been taken by predators or died of hyperthermia. Although this would cause a slight overestimate of nesting success, it may be counterbalanced by the fact that six nests (about 6% of all nests observed) were excluded from analyses because they were observed only through Nestling Day 11, 12 or 13 due to time limitations. Most of these nests would probably have produced fledglings. Thus we expect that we estimated nesting success with reasonable accuracy.

We marked almost all males during all years of study with individual combinations of colored leg bands before or shortly after they first mated. Banding allowed us to identify bigamous males, which was important because "secondary" females of bigamous males breed less successfully than "primary" females or females paired with monogamous males (Johnson et al. 1993; the latter two groups of females have similar success at breeding: Johnson 1992). In this paper, we compare nesting success at nests attended only by primary and monogamous females.

Nesting success of other species using natural cavities.—We identified all North American cavity-nesting birds using Ehrlich et al. (1988). We limited our attention to species found primarily in the temperate zone and species that consistently nested in "deep" tree cavities. We did not include waterfowl and raptors. A list of species included in the survey appears in the Appendix. We used *Wildlife Abstracts* (1935–1970) and *Wildlife Review* (1971–1992) to identify studies that potentially contained data on nesting success for focal species. When it appeared that researchers collected nesting success data but did not report them, we attempted to contact authors of the study to obtain relevant data. We present the measure of nesting success reported in most studies: the proportion of nests from which at least one nestling was known or strongly suspected to have fledged (hereafter termed nesting success). We include data only from nests that researchers found before egg-laying began (and, when possible, the subset of these nests known to have contained at least one egg), or nests found during egg-laying. We include only those studies with data on five or more nests.

Results

House Wrens.—We observed 99 nesting attempts by House Wrens in natural cavities, including 91 attempts by monogamous pairs and eight attempts by bigamous males and their primary mates. Overall, pairs produced at least one fledgling in 62 (63%) of the 99 attempts (Table 1). Yearly success rates varied between 54 and 75%. Of the 37 nesting attempts that failed, 23 (62%) failed during the laying or incubation stages.

Wrens produced at least one fledgling in 63 (68%) of 93 nesting attempts made using boxes mounted on trees in 1986 and 1988 (Table 1). This should be considered a slight overestimate of nesting success because we switched most boxes from trees to greased poles midway through the 1988 season (the season in which most observations were made) in response to an increasing incidence of nest predation that season (note that data for 1988 include only boxes that we did not switch to poles). Thus, data pooled for all years suggest that birds using tree-mounted boxes and natural cavities have quite similar rates of nesting success (Table 1). One must interpret pooled data cautiously, however, because most natural nests were observed in 1987 when no boxes were available. The 1988 season was the only season in which we recorded nesting success for wrens using both tree-mounted boxes and natural cavities. In this year, wrens using cavities had a higher rate of success than wrens using boxes but the difference in success rate was not statistically significant. Twenty-one and 27% of box-nesters lost entire clutches or broods to nest predators in 1986 and 1988, respectively. Of the 30 nesting attempts that failed, 18 (60%) failed during the laying or incubation stages.

Mounting boxes on greased metal poles improved nesting success. Wrens produced at least one fledgling in 119 (89%) of 133 nesting attempts made using boxes mounted on greased poles in 1989 and 1990. Box-nesters had greater success than cavity-nesters in both breeding seasons (Table 1), but the difference in success rate was significant only in 1990. Six and one percent of box-nesters lost entire clutches or broods to predators in 1989 and 1990, respectively. In all cases, predators apparently gained access to boxes by using vegetation near boxes to bypass greased poles.

Other cavity-nesting species.—We obtained nesting success data from 20 separate studies on eight woodpecker species, seven studies on four non-woodpecker species that usually excavate their own nest cavities, and 10 studies on seven non-excavating species (including the current study on House Wrens). Overall, rates of nesting success ranged from 22 to 100%, with a mean of 68% (±20% SD; mean weighted by sample size = 69%). Rates of nesting success varied significantly among woodpeckers, excavating non-woodpeckers, and non-excavators (Table 4). We found

TABLE 1. Nesting success of House Wrens using different types of nest sites.

Year	# successful breeding attempts/ total attempts (percent)[1] Natural cavity	Box on tree	Box on greased metal pole	P^2
1986	—	10/14 (71%)	—	—
1987	31/53 (58%)	—	—	—
1988	10/13 (77%)	53/79 (67%)	—	NS
1989	14/20 (70%)	—	46/54 (85%)	NS
1990	7/13 (54%)	—	73/79 (92%)	<0.001
All	62/99 (63%)	63/93 (68%)	119/133 (89%)	—

[1] An attempt was considered successful if pairs produced at least one fledgling.
[2] Log-likelihood ratio (G) test to determine whether success rate varied with nest site type (NS = not significant).

that excavators, as a group, had significantly higher rates of nesting success than non-excavators. One concern with our comparison is the small number of nests observed in some studies. Nest success rates from these studies may be relatively inaccurate. Even when we include in analyses only studies with data from ≥20 nests, however, we still find that excavators have higher rates of nesting success than non-excavators (Table 4).

DISCUSSION

The overall rate of nesting success for House Wrens using natural cavities in our Wyoming study population (63%) is similar to that recorded recently in an Arizona population (70%; Li and Martin 1991). Rates of success for these two House Wren populations exceed those reported for populations of most other non-excavating species (see Table 2 and Li and Martin 1991). House Wrens may have high success because their unusually aggressive nature provides them greater access to the best available nest sites (see Finch 1990, Rendell and Robertson 1990, and references therein).

In the Wyoming population, wrens using boxes attached to trees and wrens using natural cavities had similar rates of nesting success. Predators destroyed 26% of nests in boxes, a relatively high rate of destruction compared with rates reported for other species using natural cavities (Table 2) or boxes (see below). We did not obtain the rate of predation on nests in natural cavities, but it probably does not exceed 26% and there is reason to suspect that it could be lower. In a number of cavity-nesting species, the probability of nest predation declines as nest height increases (e.g., Alatalo et al. 1990, Albano 1992, Nilsson 1984a, Rendell and Robertson 1989). We did not measure height of natural nest cavities but the mean height of these cavities would undoubtedly have exceeded that of boxes. All boxes were situated 1.5–2.0 m above ground whereas almost all natural cavities were situated 3–25 m above ground.

A review of the literature reveals no consistent pattern in the relative

TABLE 2. Nesting success of cavity-nesting birds using natural tree cavities.

Species[1]	Location of study	% success[2]	% predation[3]	Source
Northern Flicker	OH	75 (20)	—	Kendeigh (1942)
	BC	62 (21)[4]	—	Erskine and McLaren (1976) A. J. Erskine (pers. comm.)
	CO	50 (12)	—	Bergstrom (1977)
	WI	86 (14)	14	Burkett (1989)
Red-bellied Woodpecker	IL	47 (15)	—	Stickel (1965)
	MS	82 (38)	—	Ingold (1989) and D. J. Ingold (pers. comm.)
Red-headed Woodpecker	CO	75 (8)	—	Bergstrom (1977)
	MS	78 (18)	—	D. J. Ingold (pers. comm.)
Acorn Woodpecker	CA	74 (34)	—	Troetschler (1976)
	NM	79 (39)	—	Stacey (1979)
	CA	73 (183)	6–11	Koenig and Mumme (1987)
Williamson's Sapsucker	AZ	100 (6)	0	Li and Martin (1991)
Yellow-bellied Sapsucker	NH	100 (10)	0	Kilham (1971)
Red-naped Sapsucker	AZ	100 (5)	0	Li and Martin (1991)
	MT	100 (5)	0	Tobalske (1992) B. W. Tobalske (pers. comm.)
Red-cockaded Woodpecker	FL	50 (6)	—	Ligon (1970)
	FL	84 (31)	—	DeLotelle and Epting (1992)
	SC	70 (118)	—	E. E. Stevens (pers. comm.)
	GA	66 (324)	—	E. E. Stevens (pers. comm.)
Tree Swallow	BC	53 (15)	—	A. J. Erskine (pers. comm.)
	ON	42 (86)	24	Robertson and Rendell (1990)

TABLE 2. Continued.

Species[1]	Location of study	% success[2]	% predation[3]	Source
Black-capped Chickadee	NY	64 (11)	18	Odum (1942)
	WI	59 (39)	—	Meyer (1973)
Carolina Chickadee	OK	50 (12)	42	J. R. Curry (pers. comm.)
	IL	68 (22)	32	Albano (1992) and D. J. Albano (pers. comm.)
Mountain Chickadee	AZ	29 (7)	—	Li and Martin (1991)
Tufted Titmouse	OK	90 (5)	0	J. R. Curry (pers. comm.)
	AR	77 (22)	—	C. R. Preston (pers. comm.)
Red-breasted Nuthatch	AZ	40 (5)	—	Li and Martin (1991)
Pygmy Nuthatch	AZ	88 (147)	3	Sydeman et al. (1988)
	AZ	90 (5)	—	Li and Martin (1991)
House Wren	AZ	70 (50)	—	Li and Martin (1991)
	WY	63 (99)	—	This study
Eastern Bluebird	MI	56 (27)	—	Pinkowski (1977)
Mountain Bluebird	BC	22 (9)[4]	—	Erskine and McLaren (1976) and A. J. Erskine (pers. comm.)
Prothonotary Warbler	TN	33 (9)	22	L. J. Petit (pers. comm.)

[1] Scientific names appear in the Appendix.
[2] Percent of nesting attempts that produced at least one fledgling.
[3] Percent of *all* nests destroyed by predators (not just failed nests).
[4] European Starlings interfere with some nestings.

TABLE 3. Comparison of nesting success for secondary-cavity-nesting birds using boxes and natural cavities. N/A = data not available.

Species[1]	Location	Rate of nesting success (n)[2]		Relative rates of nest predation[3]	Reference
		Boxes	Cavities	Boxes vs. Cavities	
		Success significantly greater in cavities			
Bufflehead	BC, Canada	48% (75)	81% (77)	N/A	Gauthier (1989)
		Success in cavities and boxes similar			
Tree Swallow	ON, Canada	37% (137)	42% (86)	29% vs. 24%	Robertson and Rendell (1990)
Eastern Bluebird	MI, USA	56% (272)	56% (27)	N/A	Pinkowski (1977)
House Wren	WY, USA	68% (93)[4]	63% (99)	26% vs. N/A	This study
Marsh Tit	S. Sweden	N/A (31)	64% (28)	32% vs. 32%	Nilsson (1984a)
Blue Tit	S. Sweden	N/A (27)	75% (60)	19% vs. 22%	Nilsson (1984a)
Tengmalm's Owl	W. Finland	N/A (231)	N/A (30)[5]	23% vs. 27%	Korpimäki (1984)
		Success significantly greater in boxes			
European Nuthatch	Germany	93% (?)	83% (42)	N/A	Löhrl (1957, in Nilsson 1984a)
Pied Flycatcher	S. Sweden	84% (112)	68% (31)	5% vs. 23%	Nilsson (1984b)
	Cnt. Sweden	88% (194)	48% (84)	6% vs. 39%	Alatalo et al. (1990)
Great Tit	S. Sweden	N/A (112)	72% (76)	5% vs. 17%	Nilsson (1984a)
	England	87% (92)	44% (25)	N/A	East and Perrins (1988)
Blue Tit	England	78% (104)	55% (55)	N/A	East and Perrins (1988)
Common Treecreeper[6]	Finland/ Lithuania	85% (>300)	36% (42)	8% vs. 37%	Kuitunen and Aleknonis (1992)

[1] Scientific names appear in the Appendix.
[2] Percent of nests that produced at least one fledgling (number of nests observed in parentheses).
[3] Percent of all nests destroyed by predators.
[4] Data for boxes mounted only on trees or wooden fenceposts (other studies in table involve mainly boxes mounted on trees and wood posts).
[5] No data on nesting success as defined above were presented. However, there was no difference in the mean number of fledglings produced from nests in boxes and nests in natural cavities.
[6] Note that this species does not nest in deep cavities.

TABLE 4. Rates of nesting success (percent of nesting attempts that produced one fledgling) for woodpeckers, non-woodpeckers that usually excavate their own nest cavities, and non-excavating non-woodpeckers. Presented are unweighted means ± 1 SD with number of studies involved in parentheses and, in square brackets, means weighted by sample size. Means were calculated from data presented in Table 2.

	Bird type				Statistical comparisons	
	Woodpeckers	Excavating non-woodpeckers	All excavators[1]	Non-excavators	Success vs. bird type[2]	Success of excav. vs. non-excav.[3]
All studies	77 ± 16 (20) [72]	66 ± 18 (7) [78]	74 ± 17 (27) [73]	54 ± 22 (10) [56]	$F_{2,34} = 5.14$ $P < 0.02$	$F_{1,34} = 5.61$ $P < 0.03$[4]
Studies with ≥20 nests	75 ± 7 (10) [72]	72 ± 15 (3) [80]	74 ± 9 (13) [73]	62 ± 13 (5) [58]	(no test[5])	$Z = -1.73$ $P < 0.09$[6]

[1] Woodpeckers and excavating non-woodpeckers combined.
[2] ANOVA (using transformed percentages) asking whether success rates vary among woodpeckers, excavating non-woodpeckers, and non-excavators.
[3] Linear contrast test (above) or two-tailed Wilcoxon Rank Sum test (below) asking whether excavators and non-excavators have different rates of success.
[4] $P \sim 0.06$ if data from Li and Martin (1991) are excluded.
[5] Small sample sizes precluded a meaningful comparison.
[6] $P \sim 0.05$ if data from Li and Martin (1991) are excluded.

nesting success of birds using boxes and those using natural cavities (Table 3: survey includes studies that observed rates of nesting success directly or inferred relative rates of nesting success using rates of nest predation, reportedly the major cause of nest failure). In six studies, including the current study on House Wrens, birds using boxes and natural cavities had similar rates of nesting success. This similarity occurred primarily because predators destroyed nests in boxes and natural cavities with roughly equal and relatively high frequencies. In seven other studies, birds using boxes had higher rates of nesting success than birds using natural cavities (see also Wesołowski and Stawarczyk 1991). In most of these cases, nests in boxes experienced much lower rates of predation than did nests in cavities. Clearly then, the relative success of birds using boxes and natural cavities depends largely on whether nests in boxes experience normal or reduced levels of predation. Why rates of predation on nests in boxes vary so dramatically between studies remains unclear.

Before proceeding, we must note that in our study and apparently most others, it was assumed that birds using natural cavities and birds using boxes differed only in the type of nest site that they used. This may not be the case, however. For example, take situations in which both boxes and natural cavities are available in the same local area (as was the case in 3 of the 5 yr of our study). If birds prefer one type of nest site over the other, and if there is a limited supply of preferred sites for which birds compete (e.g., Brawn 1984, Brawn and Balda 1988), then birds controlling preferred sites may, as a group, be older, more experienced and/or in better condition than birds using less preferred sites. This could contribute to a difference in the success rates of birds using different types of nest sites.

Li and Martin (1991) studied a community of cavity-nesting birds occupying high-elevation drainages in central Arizona. They found that excavating species had, on average, significantly greater rates of nesting success than non-excavating species. Our summary of studies from a variety of locations confirms this finding. Non-excavators may have lower nesting success than excavators for several reasons. A substantial portion of non-excavators occupy cavities used as nest sites in previous years and some evidence suggests that predators remember locations of nest cavities from one year to the next (Nilsson et al. 1991; Sonerud 1985, 1989). By nesting in previously used cavities, non-excavators may also increase their exposure to ectoparasites and disease-carrying microbes (Møller 1989, Nilsson 1986). In their community, Li and Martin (1991) found that chance of nest failure increased with decreasing nest height and increasing foliage around the nest, and that non-excavators tended to use lower and more concealed nest sites than excavators. This pattern may hold true on a continent-wide basis as well. Li and Martin (1991) also noted that non-excavators, as a group, tend to be smaller in size than excavators and hence may have less success driving off nest predators.

As indicated above, early surveys by Lack (1954), Nice (1957) and Ricklefs (1969) suggested that cavity-nesters have greater rates of nesting success than open-nesters, primarily because cavity-nesters experience lower rates of nest predation. Researchers have used this finding to explain several differences in the biology of cavity- and open-nesting species, most notably the slower nestling growth rates and larger clutch sizes of cavity-nesters (see Martin and Li 1992 and references therein). Almost all studies of cavity-nesters, however, included in the surveys cited above involved populations using nest boxes. As nesting success of birds using boxes can often exceed that of birds using natural cavities (Table 3), success of non-excavating cavity-nesters relative to open-nesters was probably overestimated (Nilsson 1986). Martin and Li (1992) compared the success of open-nesting species and cavity-nesting species using natural cavities in one Arizona bird community and generally confirmed the assumption that nesting success of cavity-nesters exceeds that of open-nesters (their data challenge a number of other nest-site related dogmas, however; see Martin 1993a,b). A continent-wide comparison of nesting success between open-nesters and cavity-nesters in a variety of communities would also be of interest. Although too few data on the nesting success of cavity-nesters using natural cavities exist for such a comparison at present, we hope that this review will stimulate collection and reporting of additional data so that such a comparison is possible in the future.

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APPENDIX

Species included in survey of nesting success in natural cavities. Species are grouped according to whether individuals usually excavate their own cavity or use a pre-existing cavity ("non-excavators").

Exclusively or predominantly excavators of nest cavities

Red-bellied Woodpecker, *Melanerpes carolinus*
Gila Woodpecker, *Melanerpes uropygialus*
Golden-fronted Woodpecker, *Melanerpes aurifrons*
Red-headed Woodpecker, *Melanerpes erythrocephalus*
Acorn Woodpecker, *Melanerpes formicivorus*
Lewis' Woodpecker, *Melanerpes lewis*
White-headed Woodpecker, *Picoides albolarvatus*
Williamson's Sapsucker, *Sphyrapicus thyroideus*
Red-breasted Sapsucker, *Sphyrapicus ruber*
Yellow-bellied Sapsucker, *Sphyrapicus varius*
Red-naped Sapsucker, *Sphyrapicus nuchalis*
Downy Woodpecker, *Picoides pubescens*
Hairy Woodpecker, *Picoides villosus*
Three-toed Woodpecker, *Picoides tridactylus*
Black-backed Woodpecker, *Picoides arcticus*
Ladder-backed Woodpecker, *Picoides scalaris*
Red-cockaded Woodpecker, *Picoides borealis*
Nuttall's Woodpecker, *Picoides nutalli*
Strickland's Woodpecker, *Picoides stricklandi*
Ivory-billed Woodpecker, *Campephilus principalis*
Pileated Woodpecker, *Dryocopus pileatus*
Black-capped Chickadee, *Parus atricapillus*
Carolina Chickadee, *Parus carolinensis*
Pygmy Nuthatch, *Sitta pygmaea*
Red-breasted Nuthatch, *Sitta canadensis*
Brown-headed Nuthatch, *Sitta pusilla*

Exclusively or predominantly users of pre-formed cavities

Sulphur-bellied Flycatcher, *Myiodynastes luteventris*
Great-crested Flycatcher, *Myiarchus crinitus*
Brown-crested Flycatcher, *Myiarchus tyrannulus*
Ash-throated Flycatcher, *Myiarchus cinerascens*
Dusky-capped Flycatcher, *Myiarchus tuberculifer*
Tree Swallow, *Tachycineta bicolor*
Violet-green Swallow, *Tachycineta thalassina*
Purple Martin, *Progne subis*
Tufted Titmouse, *Parus bicolor*
Chestnut-backed Chickadee, *Parus rufescens*
Siberian Tit, *Parus cinctus*
Boreal Chickadee, *Parus hudsonicus*

Plain Titmouse, *Parus inornatus*
Bridled Titmouse, *Parus wollweberi*
Mexican Chickadee, *Parus sclateri*
Mountain Chickadee, *Parus gambeli*
White-breasted Nuthatch, *Sitta carolinensis*
House Wren, *Troglodytes aedon*
Carolina Wren, *Thryothorus ludovicianus*
Bewick's Wren, *Thryomanes bewickii*
Eastern Bluebird, *Sialia sialis*
Western Bluebird, *Sialia mexicana*
Mountain Bluebird, *Sialia curricoides*
Prothonotary Warbler, *Protonotaria citrea*
Lucy's Warbler, *Vermivora luciae*

Scientific names of other species discussed in the text

Bufflehead, *Bucephala albeola*
Tengmalm's Owl, *Aegolius funereus*
Marsh Tit, *Parus palustris*
Blue Tit, *Parus caeruleus*
Great Tit, *Parus major*
European Nuthatch, *Sitta europaea*
Common Treecreeper, *Certhia familiaris*
Pied Flycatcher, *Ficedula hypolueca*
European Starling, *Sturnus vulgaris*

GRADUATE AND POST-GRADUATE RESEARCH GRANTS

The Biological Research Station of the Edmund Niles Huyck Preserve offers grants of up to $2500 (US) to support biological research that utilizes the resources of the Preserve. Among the research areas supported are basic and applied ecology, animal behavior, systematics, evolution and conservation. The 800-ha Preserve is located on the Helderberg Plateau, 50 km southwest of Albany, New York. Habitats include northeast hardwood-hemlock forests, conifer plantations, old fields, permanent and intermittent streams, 4- and 40-ha lakes and several waterfalls. Facilities include a wet and dry lab, library and houses/cabins for researchers. Deadline is 1 Feb. 1994. Application material may be obtained from Dr. Richard L. Wyman, Executive Director, E. N. Huyck Preserve and Biological Research Station, P.O. Box 189, Rensselaerville, New York 12147 USA.