

A COMPARISON OF THE BREEDING ECOLOGY OF BIRDS NESTING IN BOXES AND TREE CAVITIES

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ABSTRACT.—We compared laying date, nesting success, clutch size, and productivity of four bird species that nest in boxes and tree cavities to examine whether data from nest boxes are comparable with data from tree cavities. Western Bluebirds (*Sialia mexicana*) gained the most advantage from nesting in boxes. They initiated egg laying earlier, had higher nesting success, lower predation rates, and fledged marginally more young in boxes than in cavities but did not have larger clutches or hatch more eggs. Plain Titmice (*Parus inornatus*) nesting in boxes had marginally lower predation rates, hatched more eggs, and fledged more young. They did not have higher overall nesting success, nor did they initiate clutches significantly earlier in boxes. House Wrens (*Troglodytes aedon*) nesting in boxes laid larger clutches, hatched more eggs, and fledged more young and had marginally higher nesting success and lower predation rates. Ash-throated Flycatchers (*Myiarchus cinerascens*) experienced no apparent benefits from nesting in boxes versus cavities. No significant relationships were found between clutch size and bottom area or volume of cavities for any of these species. These results suggest that researchers should use caution when extrapolating results from nest-box studies of reproductive success, predation rates, and productivity of cavity-nesting birds. Given the different responses of these four species to nesting in boxes, the effects of the addition of nest boxes on community structure also should be considered. Received 19 September 1996, accepted 21 April 1997.

NEST BOXES MAY BE USED AS A CONSERVATION TOOL to augment populations of secondary cavity-nesting birds. Much of what we know about cavity nesters is based on nest-box studies, but this information may not be representative of individuals breeding in natural cavities (van Balen et al. 1982; Nilsson 1986; Møller 1989, 1992; Robertson and Rendell 1990). Studies that compared birds nesting in tree cavities versus nest boxes have shown lower predation rates (Nilsson 1975, 1984a, b; Robertson and Rendell 1990), larger clutch sizes (Nilsson 1975, 1984b; Robertson and Rendell 1990), and more young fledged (Nilsson 1986, East and Perrins 1988, Alatalo et al. 1990, Kuitunen and Aleknonis 1992) from nest boxes than from tree cavities. Ectoparasite loads also may differ between cavities and nest boxes because of the greater amount of nesting material in boxes (Pinkowski 1977, Rendell and Verbeek 1996c) or be-

cause investigators generally remove old nests from boxes between breeding seasons (Nilsson 1986; Møller 1989, 1992; Rendell and Verbeek 1996a, b, c). In addition, high densities of nest boxes may result in artificially high densities of breeding birds (Nilsson 1984a), which may influence aggressive interactions and competition for nest sites (Gowaty and Wagner 1988, Robertson and Rendell 1990), predation rates (Dunn 1977), and mating behavior (Alatalo and Lundberg 1984, Gowaty and Bridges 1991). More information on individuals breeding in cavities is needed to understand factors that regulate populations of secondary cavity nesters and influence community structure.

If tree cavities are smaller than nest boxes, differences in clutch size could be influenced by the area of cavity bottoms (Ludescher 1973, Nilsson 1984a). A positive relationship between clutch size and nest-box size has been demonstrated for Great Tits (*Parus major*; Löhr 1973, 1980; Karlsson and Nilsson 1977; van Balen 1984), Pied Flycatchers (*Ficedula hypoleuca*; Karlsson and Nilsson 1977, Gustafsson and Nilsson 1985), Collared Flycatchers (*Ficedula albicollis*; Gustafsson and Nilsson 1985), and Tree

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Swallows (*Tachycineta bicolor*; Rendell and Robertson 1993). This relationship also was found for Willow Tits (*Parus montanus*) and Marsh Tits (*Parus palustris*) nesting in cavities (Ludescher 1973), for Tree Swallows nesting in cavities (Rendell and Robertson 1989), and for the open-nesting Barn Swallow (*Hirundo rustica*; Møller 1982). Mixed results have been found for European Starlings (*Sturnus vulgaris*), although differences in clutch size may have resulted from differences in age composition of females nesting in small and large boxes (Karlsson and Nilsson 1977, Karlsson 1978, Clobert and Berthet 1983). Box size had no effect on clutch size of Eastern Bluebirds (*Sialia sialis*; Pitts 1988). Great Tits, Pied Flycatchers, and Collared Flycatchers fledged more young from larger boxes (Löhr 1973, Gustafsson and Nilsson 1985). Thus, species appear to respond differently to box size, with smaller species responding the strongest and the largest species responding not at all to increases in box area (Karlsson and Nilsson 1977).

Few studies have compared reproductive parameters of bird species using nest boxes versus tree cavities. In this paper, we present data on nesting success, clutch size, productivity, and laying date for populations of four species of birds that use cavities and nest boxes. Studies of coexisting individuals eliminate biases of year, habitat, and geography. We also explored relationships between clutch size and bottom area of cavities.

STUDY AREA

This study was done at the San Joaquin Experimental Range in Madera County, California. The study area consists of relatively homogeneous foothill oak-pine woodlands ranging in elevation from 215 to 520 m. Winters are cool and wet, and summers are hot and dry. Annual precipitation averages 48.6 cm, with most falling as rain between November and March. Monthly mean air temperatures range from about 6°C in January to about 27°C in July. The study area has been lightly to moderately grazed by cattle since at least 1900. A "natural area" of about 29 ha has been ungrazed since 1934. Dominant overstory trees include a sparse cover of foothill pine (*Pinus sabiniana*), blue oak (*Quercus douglasii*), and interior live oak (*Q. wislizenii*). Understory species include buck brush (*Ceanothus cuneatus*), chaparral white-thorn (*C. leucodermis*), redberry (*Rhamnus crocea*), and Mariposa manzanita (*Arctostaphylos viscida mariposa*).

METHODS

From 1989 to 1991, we monitored 44 boxes on a 30-ha, gridded plot in the grazed portion of the study area. Distances between boxes ranged from 67 to 120 m. Boxes were placed on the suitable tree nearest to a designated grid marker, at a height of approximately 2 m. Boxes were placed on wooden posts ($n = 6$) when no tree was within 25 m of a designated marker. Equal numbers of boxes were oriented in each of the four cardinal directions. Half of the boxes had entrance diameters of 3.2 cm and half had diameters of 3.8 cm. These entrance diameters were chosen to assure use by most potential species but to exclude European Starlings. Boxes were constructed of redwood and had an average bottom area of $137 \pm \text{SD of } 7.1 \text{ cm}^2$ (range 105 to 147 cm^2). Boxes were checked every four to seven days. A small flashlight and mirror were sometimes used to determine nest contents.

We monitored 92 nest boxes from 1992 to 1994. Thirty-six were located on half of the ungrazed area; another 56 were located on half of the previously used grazed site, which was extended to accommodate them. All boxes were moved. Nest boxes were again placed on the suitable tree nearest to a designated grid marker, except in three cases in which wooden posts were used. The minimum distance between boxes was 90 m. We based this spacing, which we believe minimized the likelihood of multiple boxes in territories, on several years of spot-mapping data and a thorough knowledge of the distribution and density of these species in these sites. Therefore, we did not expect box density to affect bird densities. Equal numbers of boxes were randomly assigned to orientations in the four cardinal directions and equal numbers of the two entrance diameters were used. Nest boxes were checked approximately every four days.

Entrance holes of the boxes occasionally were enlarged by woodpeckers. We replaced doors on boxes with enlarged entrances before each breeding season, but not within a season. Boxes with enlarged entrances often were used by Ash-throated Flycatchers (*Myiarchus cinerascens*). No predator-exclusion devices were used, and nestlings were not banded or weighed. Contents of nest boxes were removed in the fall of each year.

Nests in cavities were located and monitored on both the grazed and ungrazed plots. Nests also were monitored in other grazed areas of the study area, especially in 1993 and 1994, to increase sample sizes for some species. Most cavities in this habitat were in live trees, primarily oaks, and lasted for many years. Some were natural cavities formed by limbs that had died and fallen out, and where heart rot resulted in a hollow stem. Others were excavated by primary cavity nesters, including Acorn Woodpeckers (*Melanerpes formicivorus*), Nuttall's Woodpeckers (*Picoides nuttallii*),

and Northern Flickers (*Colaptes auratus*). From 1989 to 1991, nests accessible by extension ladder were checked using an automotive inspection mirror and a small light bulb. Other nests were observed for activity but not checked directly. Nests were checked every four to seven days. From 1992 to 1994, we checked most nests by climbing trees and examining the nest contents with a flexible fiberoptic that allowed us to see clearly into the cavity and to count eggs and nestlings accurately (Purcell 1997). Nests that could not be examined directly because of an unstable nesting substrate were observed for activity.

Cavity depth was measured from the bottom of the entrance to the nest cup. The bottom area of cavities was estimated by placing a leaf of known size in the nest with a "pick-up" tool. The diameter was then estimated using the fiberoptic. When cavities were not circular, two diameters were estimated and area was computed as an ellipse. Volume was calculated as depth \times area.

We analyzed data only from nests in which at least one egg was laid. First-egg dates were determined by backdating, assuming one egg laid per day. When clutch size was unknown, the species' average clutch size was used for backdating. "Number hatched" and "number fledged" are based on nests that hatched at least one egg and fledged at least one young, respectively. Some of our data undoubtedly came from nests of the same individuals in multiple years. Because we did not find all of the nests each year, and annual survival typically is less than 50% in these species (Price 1936; Kendeigh and Baldwin 1937; Drilling and Thompson 1988; Martin 1988, 1993, 1995; Martin and Li 1992), we believe the influence of nonindependence was minimal.

Statistical analysis.—We estimated nesting success and daily mortality rates of nests based on Mayfield's methods (1961, 1975). Only the first nesting attempts were included, based on initiation dates and sequential occupancy of cavities and boxes. Values were calculated separately for all nest failures and for nests known to have been lost to predation. Variances were calculated following Hensler and Nichols (1981). Differences among daily mortality rates within species were tested using a chi-square statistic following Sauer and Williams (1989). In analyses of nesting success and nest predation rates, nests were pooled across years. Although we expect that year effects may exist, small within-year sample sizes and the low power of these tests precluded testing for them. Year effects and the corresponding interaction terms were included in analyses of laying date. We found significant differences across years for clutch size, number of eggs hatched, and number of young fledged for Plain Titmouse (*Parus inornatus*), although none of the interaction terms was significant for any species. For these measures of productivity, we standardized the data by testing deviations from the yearly means.

Variables were tested for normality using a Sha-

piro-Wilk statistic and for homogeneity of variances using Levene's test and the folded form of the *F* statistic (SAS Institute Inc. 1988: 943). Variables were transformed when appropriate.

Because we hypothesized that birds nesting in boxes would have higher reproductive success and productivity than birds nesting in cavities, power was calculated using one-tailed tests with $\alpha = 0.05$ (Abramowitz and Stegun 1964). We calculated power based on what we considered to be biologically meaningful differences. Power calculations based on observed differences are intrinsic to the data and, for a nonsignificant result, power can never be greater than 0.50 (J. Baldwin pers. comm.).

Regressions of clutch size on nest-bottom area and nest volume have no intuitive, biologically meaningful slope or effect size against which to test power. Values from the literature suggest a fairly constant slope of about 0.030 eggs/cm² for Great Tits, although higher values were found for Marsh and Willow tits, and lower values for Pied Flycatchers (Karls-son and Nilsson 1977, Löhrl 1980, van Balen 1984). This slope was used to determine effect size for power calculations for area relations. Two effect sizes for volume relationships were used: 0.0014 eggs/cm³ (calculated from van Balen's [1984] data on Great Tits) and 0.0003688 eggs/cm³ (W. Rendell pers. comm. for Tree Swallows).

RESULTS

Four bird species—Ash-throated Flycatcher, Plain Titmouse, House Wren (*Troglodytes aedon*), and Western Bluebird (*Sialia mexicana*)—used nest boxes in sufficient numbers to compare with natural nest sites. White-breasted Nuthatches (*Sitta carolinensis*) and Bewick's Wrens (*Thryomanes bewickii*) each made only two nesting attempts in boxes.

Box occupancy rates increased steadily from 25% in 1989 to 68% in 1994. This was due mainly to the fact that Plain Titmice initially did not use boxes in large numbers, perhaps due to site fidelity (see East and Perrins 1988). In 1989, titmice nested in only two boxes, representing only 18% of the boxes used. By 1991, they accounted for 71% of the boxes occupied. When boxes were relocated in 1992, use of boxes by titmice fell to 41% of all boxes used but increased to 89% by 1994. In contrast, use of boxes by Western Bluebirds remained fairly steady, ranging from 18 to 27% of boxes used. Use of nest boxes by House Wrens was variable, ranging from none in 1990 and 1991 to 12 (13%) in 1992 and 1993. The abundance of House Wrens also varied during this period (Verner et al.

TABLE 1. Mortality rates, predation rates, and nesting success (SD in parentheses) for Ash-throated Flycatcher, Plain Titmouse, House Wren, and Western Bluebird. Predation rates are based on failures from predation only. *P*-values compare differences between nest boxes and cavities.

Nest substrate	<i>n</i>	Daily mortality rate	<i>P</i>	Mayfield nesting success	Daily predation rate	<i>P</i>	Mayfield predation rate
Ash-throated Flycatcher							
Boxes	33	0.0134 (0.0040)	0.545	0.62	0.0098 (0.0034)	0.259	0.29
Cavities	52	0.0170 (0.0044)		0.55	0.0159 (0.0042)		0.43
Plain Titmouse							
Boxes	111	0.0117 (0.0017)	0.784	0.62	0.0068 (0.0013)	0.065	0.24
Cavities	171	0.0124 (0.0019)		0.60	0.0109 (0.0018)		0.36
House Wren							
Boxes	36	0.0050 (0.0020)	0.059	0.83	0.0050 (0.0020)	0.059	0.17
Cavities	47	0.0126 (0.0035)		0.63	0.0126 (0.0035)		0.37
Western Bluebird							
Boxes	47	0.0133 (0.0030)	0.033	0.59	0.0087 (0.0024)	0.035	0.29
Cavities	39	0.0297 (0.0071)		0.29	0.0227 (0.0062)		0.61

1997), and nest-box use reflected these trends. Use of boxes by Ash-throated Flycatchers dropped from 27% of boxes used in 1989 to 15% in 1994. In seven cases, Ash-throated Flycatchers used boxes in which other species had nested and failed earlier in the season; six of these instances occurred during the last two years of the study.

Nesting success.—Daily mortality rates were lower in boxes than in cavities for all four species, although significantly so only for Western Bluebirds and nearly so for House Wrens (Table 1). Nesting success followed the same pattern. Success of bluebirds nesting in boxes was more than twice that of bluebirds nesting in cavities; success of wrens nesting in boxes was 1.3 times that of wrens nesting in cavities. Daily predation rates also were lower in boxes than in cavities for all species, significantly so for Western Bluebirds, and marginally so for Plain Titmice and House Wrens (Table 1). Power to detect absolute differences of 0.10 in nesting success and predation rate, extrapolated back to the corresponding differences in daily mortality and predation rates, was low for all four species (0.20 to 0.48). Power to detect an absolute difference of 0.25 in nesting success and predation rate was high for Plain Titmice (0.94 and 0.98, respectively) but low for the other three species (0.55 to 0.73), indicating that biologically meaningful differences may have been undetected.

Laying date.—Laying dates differed across years between boxes and cavities for all four

species (Table 2). The average date of the first egg was earlier in boxes than in cavities for all four species, although significantly so only for Western Bluebirds (Table 2). Bluebirds were variable in their laying dates, but the difference was significant because it was large (18 days). Ash-throated Flycatchers also had a wide range of laying dates but a small difference between boxes and cavities (4.6 days earlier in boxes). Nesting of titmice and House Wrens was very synchronized; each species had a small difference in laying dates (ca. 2 and 4 days earlier in boxes, respectively). The four species responded differently to nesting in boxes, as indicated by a significant species \times nest type interaction ($P = 0.0002$) in a two-way ANOVA.

Productivity.—Based on data standardized across years, Plain Titmice and House Wrens laid larger clutches, hatched more eggs, and fledged more young in boxes than in cavities (Table 3). We detected no differences in clutch size, number of eggs hatched, or number of young fledged between boxes and cavities for Ash-throated Flycatchers and Western Bluebirds (Table 3). For both species, the power to detect a difference of one egg or nestling exceeded 0.99 in all cases. For Ash-throated Flycatchers, power to detect a difference of half an egg or nestling was 0.98 for clutch size, 0.93 for number of eggs hatched, and 0.88 for number of young fledged. The differences for the latter two, however, were in the opposite direction from that hypothesized. For Western Bluebirds,

TABLE 2. Results of two-way ANOVA testing effects of nest type (boxes vs. cavities) and year on laying date for boxes and cavities. *P*-values compare nest type, year, and nest type \times year interaction terms between nest boxes and cavities.

Nest type	Laying date ^a	<i>n</i>	Effects	<i>F</i>	<i>P</i>
Ash-throated Flycatcher					
Boxes	132.35 (10.35)	31	Nest type	0.11	0.740
Cavities	136.96 (14.66)	46	Year	4.31	0.002
			Nest type \times Year	0.25	0.862
Plain Titmouse					
Boxes	80.68 (8.16)	108	Nest type	0.08	0.784
Cavities	82.62 (9.48)	139	Year	11.30	0.000
			Nest type \times Year	0.94	0.456
House Wren					
Boxes	109.03 (5.33)	35	Nest type	2.09	0.153
Cavities	113.36 (7.78)	42	Year	4.57	0.003
			Nest type \times Year	3.71	0.029
Western Bluebird					
Boxes	88.48 (16.41)	40	Nest Type	5.39	0.024
Cavities	106.90 (16.93)	21	Year	6.35	0.000
			Nest type \times Year	1.46	0.230

^a Mean Julian date (SD in parentheses).

power to detect a difference of half an egg or nestling was 0.94 for clutch size, 0.77 for number hatched, and 0.67 for number fledged. Although the number of young fledged was only marginally significant for bluebirds (Table 3), the mean number fledged was higher in boxes in every year, and power calculations indicated a 33% chance of a Type II error.

The species \times nest type interaction term was significant in a two-way ANOVA that included all four species for number of eggs hatched ($P = 0.04$), and marginally so for number of young fledged ($P = 0.096$). Ash-throated Flycatchers nesting in boxes tended to hatch fewer eggs and fledge fewer young, whereas the other three species showed the opposite pattern.

If birds nesting in boxes begin nesting earlier, and there is a negative correlation between laying date and productivity, the higher productivity in boxes could be due to earlier laying dates in boxes. We examined this possibility using ANCOVA, including laying date as a covariate. Because none of the interaction terms in any of the models was significant, we used the simple models without interactions. Both nest type and laying date contributed to the higher productivity of Plain Titmice nesting in boxes (Table 4). For House Wrens, the larger clutches and greater number of young hatched in boxes were directly related to nest type (Table 4), and both nest type and laying date were linked to

the greater number of young fledged from boxes. Because Western Bluebirds nesting in boxes versus cavities did not differ in clutch size or number of young hatched, it is not surprising that nest type was not related to these measures of productivity, although laying date was (Table 4). Nest type, and not laying date, was responsible for the greater number of young bluebirds fledged from boxes (Table 4).

Relationships between clutch size and nest area.—The bottom areas of cavities used by Ash-throated Flycatchers averaged 65 ± 36.7 cm² (range 20 to 201 cm²); those of Plain Titmice averaged 62 ± 40.7 cm² (range 13 to 284 cm²); House Wrens averaged 48 ± 32.4 cm² (range 13 to 177 cm²); and Western Bluebirds averaged 73 ± 35.0 cm² (range 24 to 177 cm²). Regressions using data from cavities showed no significant relationships between bottom area of the cavity and clutch size (Table 5), number of eggs hatched, or number of young fledged. Power to detect a slope of 0.030 was high (>0.99) for clutch sizes for all species (Table 5). We also examined volume of nest cavities, which can influence clutch size (van Balen 1984, W. Rendell pers. comm.). All regressions of clutch size (Table 5), number of eggs hatched, and number of young fledged on volume of the nest cavity were nonsignificant. Power to detect a slope of 0.0014 was >0.97 for all tests (Table 5). Power to detect a slope of

TABLE 3. Standardized reproductive parameters (deviations from yearly means; $\bar{x} \pm SD$) for Ash-throated Flycatcher, Plain Titmouse, House Wren, and Western Bluebird for nest boxes and cavities. Number hatched includes only nests from which at least one egg hatched, and number fledged nests from which at least one young fledged. *P*-values compare standardized reproductive parameters between nest boxes and cavities.

	Ash-throated Flycatcher		Plain Titmouse		House Wren		Western Bluebird	
	Boxes	Cavities	Boxes	Cavities	Boxes	Cavities	Boxes	Cavities
\bar{x}	0.07 ± 0.80	-0.07 ± 0.58	0.15 ± 0.91	-0.27 ± 1.05	0.37 ± 0.80	-0.45 ± 0.18	0.05 ± 0.72	-0.14 ± 0.71
<i>n</i>	27	26	105	59	33	27	44	14
<i>P</i>		0.489	0.008			0.003	0.397	
\bar{x}	-0.04 ± 0.75	0.02 ± 0.83	0.39 ± 1.07	-0.43 ± 1.13	0.27 ± 0.97	-0.34 ± 1.09	0.09 ± 0.80	-0.15 ± 1.04
<i>n</i>	20	31	75	68	29	23	29	17
<i>P</i>		0.788	0.000			0.038	0.389	
\bar{x}	-0.07 ± 0.73	0.04 ± 0.83	0.36 ± 1.36	-0.28 ± 1.16	0.44 ± 1.39	-0.83 ± 1.25	0.17 ± 1.10	-0.38 ± 0.99
<i>n</i>	15	27	64	84	26	14	30	13
<i>P</i>		0.697	0.002			0.007	0.063	

0.0003688 ranged from 0.24 to 0.085 for clutch size (Table 5).

DISCUSSION

Studying avian life histories: Boxes versus cavities.—Our results revealed marked differences in several aspects of breeding ecology between birds nesting in boxes and those nesting in cavities. Not all species benefitted from nesting in boxes. Of the four species considered here, the resident Western Bluebird gained the most from breeding in nest boxes. Bluebirds readily occupied boxes and generally used them whenever they were available in a territory. Bluebird densities were low compared with the other three species, and their nesting was not synchronous. Bluebirds fledged more young from boxes even though clutch sizes did not differ between boxes and cavities.

Plain Titmice and House Wrens gained some benefits from nesting in boxes, e.g. larger clutches, more eggs hatched, and more young fledged, but not all differences were statistically significant. Although tests had low power, we suspect that the higher nesting success and lower predation rate for House Wren nests in boxes versus cavities (see Table 1) would have been significant with larger sample sizes. Because House Wrens are migrants and arrive after the resident species have established territories, cavity availability may be more limiting for them than for residents. If competition for nest sites is severe, migrants should be at a disadvantage because the best cavities would be occupied by earlier nesters (von Haartman 1957, 1968). In Finland, von Haartman (1968) found that no cavity nesters had very late breeding seasons, which he attributed to competition for nest sites. Other studies have shown that House Wrens are aggressive and destroy nests of conspecifics and other species, perhaps in an attempt to usurp nest sites (Ken-deigh 1941, Belles-Isles and Picman 1986, Finch 1990, Kennedy and White 1996).

In contrast, Ash-throated Flycatchers apparently gained no benefit from nesting in boxes compared with cavities. Ash-throated Flycatchers are late-arriving migrants that nested considerably later than other cavity nesters in the study area (Table 2), putting them at an even greater disadvantage in competition for nest sites. Cavities chosen by Ash-throated Fly-

TABLE 4. Results of ANCOVA and Type III sums of squares for standardized reproductive parameters (deviations from yearly means) that included nest type (nest boxes vs. cavities) and laying date (Julian date of first egg) for Plain Titmouse, House Wren, and Western Bluebird.

	Plain Titmouse		House Wren		Western Bluebird	
	F	P	F	P	F	P
Clutch size						
Nest type	5.05	0.026	6.07	0.017	0.09	0.761
Laying date	4.23	0.042	2.62	0.111	3.88	0.054
n	160		59		56	
Number hatched						
Nest type	17.39	0.000	3.35	0.073	1.07	0.308
Laying date	14.20	0.000	0.38	0.541	11.19	0.002
n	143		52		39	
Number fledged						
Nest type	8.66	0.000	8.93	0.005	4.27	0.047
Laying date	19.16	0.004	5.11	0.030	0.24	0.625
n	140		37		35	

catchers often were in very decayed wood with large openings that appeared to be unsuitable for other species and were highly susceptible to predation. Successful nests of Ash-throated Flycatchers had smaller entrance holes than depredated nests (Purcell 1995). The large size of this species and their aggressive nest defense may help to reduce predation (Murphy 1983, Martin 1992).

Although most studies have found higher reproductive success and/or lower nest predation in boxes versus cavities (e.g. Nilsson 1975, 1986; East and Perrins 1988; Kuitunen and

Aleknonis 1992), this is not always the case. For example, Robertson and Rendell (1990) found no difference in nesting success of Tree Swallows nesting in boxes versus cavities, which they attributed to predation by raccoons (*Procyon lotor*) and black rat snakes (*Elaphe obsoleta*) in boxes in the second year of the study. Nilsson (1984a) found lower predation rates in boxes for Great Tits and Pied Flycatchers but not for Blue Tits (*Parus caeruleus*) or Marsh Tits. Although we do not know why species differed in their response to nesting in boxes, the differences have biological relevance and need further study.

Differences in nesting success and nest predation rates between birds nesting in boxes versus cavities may be large, as we found for Western Bluebirds and House Wrens. Predation rates of Great Tits and Pied Flycatchers nesting in boxes were less than one-third those of birds nesting in cavities (Nilsson 1984b), and nesting success of European Tree-Creepers (*Certhia familiaris*) in boxes was nearly double that of birds nesting in cavities (Kuitunen and Aleknonis 1992). Similarly, clutch size tends to be larger among birds nesting in boxes. Great Tits laid smaller clutch sizes in boxes, although sample size was small (Nilsson 1975). For Pied Flycatchers, a nonsignificant difference in clutch size between boxes and cavities was attributed to later laying dates in boxes (Alatalo et al. 1990). First clutches of European Tree-Creepers did not differ in size between boxes and cavities (Kuitunen and Aleknonis 1992).

TABLE 5. Regressions of nest box bottom area and volume on clutch size for Ash-throated Flycatcher, Plain Titmouse, House Wren, and Western Bluebird. P-values test the significance of the regression of area or volume on clutch size.

	Slope	R ²	P	n	Power ^a	Power ^b
Ash-throated Flycatcher						
Area	0.007	0.078	0.232	20	1.000	
Volume	0.000	0.090	0.199	20	1.000	0.847
Plain Titmouse						
Area	0.002	0.004	0.709	41	1.000	
Volume	0.000	0.002	0.815	40	1.000	0.731
House Wren						
Area	0.002	0.003	0.815	22	1.000	
Volume	0.000	0.010	0.665	21	1.000	0.534
Western Bluebird						
Area	0.011	0.167	0.148	13	0.994	
Volume	0.000	0.001	0.930	14	0.970	0.238

^a Power based on a slope of 0.030 for area and 0.0014 for volume.

^b Power based on a slope of 0.0003688 for volume.

We have assumed that birds using cavities and boxes differ only in the type of nest site. This assumption may be violated if there is a preference for nesting in boxes, if the supply of boxes is limited, or if the birds nesting in boxes are older, more experienced, and/or in better condition than those nesting in cavities (Johnson and Kermott 1994). A review of age-related variation in reproductive performance of birds showed that first-time breeders generally bred later, had smaller clutches, and produced fewer fledglings than did older birds (Sæther 1990). Hatching success showed the least difference, with equal numbers of studies finding higher hatching success for younger and older females among passerines. The most pronounced differences were later laying dates for young females. Differences in reproductive performance between birds nesting in boxes versus cavities due to age and experience of breeders would be most important when the preference for boxes is strong and nest sites are limiting. In an area where nest sites were very limited, Robertson and Rendell (1990) found a ratio 4.8:1 of older to yearling Tree Swallows nesting in boxes. In an area without boxes, the ratio of older to first-year birds nesting in cavities was nearly equal. Because our birds were unbanded, we do not know whether older birds nested proportionately more often in boxes.

Our objective was to determine whether reproductive parameters differed between birds nesting in tree cavities and those nesting in boxes. Our study design did not allow us to address the mechanisms that caused these differences. Data comparing successful and depredated nests in cavities may provide some insight. Successful nests of Plain Titmice and House Wrens had smaller bottom areas, although the bottom areas of nest boxes are larger than those of most tree cavities (Purcell 1995). Successful nests of House Wrens and Western Bluebirds were lower than depredated nests (Purcell 1995), as were the nest boxes used here and in other studies. Obviously, many other factors could contribute to the observed differences, and studies designed to test specific hypotheses are needed.

Our results indicate that reproductive parameters estimated from nest-box studies may not be representative of birds nesting in tree cavities. Assumptions concerning reproductive ecology, life-history patterns, community structure,

and species' coexistence may need to be reconsidered. For example, cavity nesters generally are believed to have higher nesting success than open nesters (Lack 1954, Nice 1957, von Haartman 1957, Ricklefs 1969; but see Nilsson 1986, Martin and Li 1992). Because most of what we know about the reproductive ecology of secondary cavity nesters is based on studies using nest boxes, and because nesting success may be enhanced by nesting in boxes, this belief may be erroneous. In addition to the differences we have shown, the use of nest boxes may influence the frequency of extrapair copulations and egg dumping (Gowaty and Wagner 1988, Gowaty and Bridges 1991; but see Barber et al. 1996), competition for nest sites (Gowaty and Wagner 1988, Robertson and Rendell 1990, Merilä and Wiggins 1995), and dispersal.

We do not mean to invalidate studies based on nest boxes. On the contrary, nest-box studies have contributed greatly to our knowledge of the breeding ecology of secondary cavity nesters. Nest boxes are useful tools that facilitate the study of aspects of breeding biology that otherwise would be difficult to study, and there is no *a priori* reason to believe that behavioral responses to nesting in boxes are maladaptive (Koenig et al. 1992). Instead, we advise caution in designing and interpreting studies using nest boxes, and we encourage additional studies of birds nesting in natural situations and comparisons of birds nesting in boxes versus tree cavities.

Relationships between clutch size and nest area.—Based on other studies, the range of variability we observed in the area of cavity bottoms was sufficient for us to detect an effect on clutch size if one existed. We found no such relationship. In an analysis of several species, van Balen (1984) reported a steady increase in clutch size with bottom area up to about 150 cm². Studies using boxes with bottom areas of 314 cm² showed only a weak relationship between clutch size and nest area (Löhrl 1973, van Balen 1984). Because Great and Blue tits have large, variable clutch sizes, a correlation between clutch size and cavity size is more likely to be detected, although this relationship has been found in species with smaller clutch sizes.

Studies of clutch/area relations in cavities might be more informative, because adaptive responses to cavity size should have evolved in natural situations. Alatalo et al. (1988) also

found no relationship between clutch size and bottom area of cavities in Pied Flycatchers. Cavities in their study were larger than nest boxes. Alatalo et al. suggested that boxes typically used in nest-box experiments are outside the range of sizes of natural sites. In our study area and that of Nilsson (1984a), bottom areas of cavities averaged smaller than those of boxes, although variability was large. Perhaps factors other than bottom area (e.g. laying date, age, population density, food availability, predation risk) have a more important influence on clutch size.

Nest boxes and conservation.—Nest boxes have been used to augment nesting sites for a wide variety of bird species in many parts of the world. Although well intentioned and often highly successful, most of these efforts have proceeded without consideration of the effects of nest boxes on the rest of the bird community. For example, when nest boxes increase the productivity of bluebirds, do numbers of bluebirds increase to the detriment of other species? If we were concerned only with bluebirds, then putting up nest boxes would be an appropriate conservation measure. Our management concerns are rarely so uncomplicated, however, and generally they involve maintaining and protecting entire communities or ecosystems. Both Hogstad (1975) and Bock et al. (1992) reported increased abundances of cavity nesters and decreased abundances of open nesters after the addition of nest boxes on their study areas. Bock et al. (1992) suggested that diffuse competition influenced community composition. We are not aware of other studies that have investigated this question on a community-wide basis. Rare also are studies of possible changes in the composition of cavity-nesting species that may result from the addition of nest boxes to a habitat.

A differential benefit of nest boxes among cavity nesters would be likely if inter- and intraspecific competition for nest sites is strong and if preferred nest sites are obtained disproportionately. Although some studies (e.g. Haapanen 1965, Zarnowitz and Manuwal 1985, Wesolowski 1989) suggest that nest sites are not limiting in mature forests owing to a high density of nest holes, other studies have found that breeding densities of certain species are limited by nest-site availability, even in mature woodlands (Minot and Perrins 1986, East and

Perrins 1988). A previous study that involved blocking cavity entrances in our study area failed to show that cavities were limiting (Waters et al. 1990). We suspect, however, that limitation of nest cavities increased over the course of our study owing to an increase in the number of European Starlings. Point-count surveys from 1989 to 1994 indicate that starling numbers have more than doubled in our study area (unpubl. data), cavities formerly occupied by other species have been taken over by starlings, and aggressive interactions have been observed between starlings and other cavity-nesting species (K. Purcell pers. obs.).

Although the addition of nest boxes to a habitat may precipitate changes in the relative abundances of bird species (both cavity nesters and open nesters), we believe that nest-box programs generally are beneficial. We also believe that nest boxes may provide an opportunity, scarcely used in the past, to investigate questions of interspecific competition in bird communities.

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