

A LONG-TERM STUDY OF THE BREEDING SUCCESS OF EASTERN BLUEBIRDS BY YEAR AND CAVITY TYPE

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Abstract.—Annual variation in the breeding success of Eastern Bluebirds (*Sialia sialis*) nesting in five types of cavities was assessed over 27 yr near Green Bay, Wisconsin. We found slight but statistically significant variation in clutch size, the fraction of young hatched, banded, and surviving from hatching to banding, and the percentage of banded young that returned to the study population. Breeding success was significantly greater in Open Top than in Standard boxes for all measures except return rate. Success improved slightly over the course of the study in Standard boxes, probably because of gradual improvements in box design. Total nest failure was the main factor influencing nesting success, and House Wrens (*Troglodytes aedon*), House Sparrows (*Passer domesticus*), cats (*Felis domesticus*), and raccoons (*Procyon lotor*) were the major causes. Total nest failure was significantly lower in Open Top boxes than in Standard boxes, probably because sparrows and wrens prefer cavities with closed tops. As a result, where these two box types are used together and sparrows and wrens are common, bluebirds are probably being produced at lower rates than could be obtained if only Open Top boxes were employed.

ESTUDIO DE LARGO ALCANCE SOBRE EL ÉXITO REPRODUCTIVO DE *SIALIA SIALIS* EN DISTINTOS TIPOS DE CAJAS DE ANIDAMIENTO

Sinopsis.—Se llevó a cabo una evaluación, de 27 años de datos, sobre la variación anual en el éxito de anidamiento de individuos de *Sialia sialis* utilizando cinco tipos de cavidades. El trabajo se llevó a cabo en Green Bay, Wisconsin. Encontramos una pequeña, pero significativa variación, en el tamaño de la camada, la fracción de huevos eclosionados, el número de individuos anillados y que sobrevivieron desde que nacieron hasta que fueron anillados, y el porcentaje de individuos anillados que regresaron al área de estudio. El éxito reproductivo fue mayor en cajas de tope abierto que en cajas estándar, para todas las medidas excepto para la tasa de regreso al lugar de origen. El éxito de anidamiento mejoró un poco a lo largo del estudio en las cajas estándar, debido, probablemente, a mejoras en el diseño de éstas. El fracaso total de nidos, fue el factor que más influyó en el éxito de anidamiento. Los principales responsables del fracaso de nidos los fueron *Troglodytes aedon*, *Passer domesticus*, *Felis domesticus* y *Procyon lotor*. El fracaso total de nidos fue significativamente menor en cajas con el tope abierto que en cajas estándar, probablemente por que las dos aves competidoras

prefieren cajas cerradas. Como resultado, cuando se usan ambos tipos de cajas, y están presentes reyezuelos y gorriones, probablemente se producirá una menor proporción de individuos de *Sialis sialis*, que sí se utilizaran solamente cajas abiertas.

Eastern Bluebirds (*Sialia sialis*) are secondary cavity nesters that experienced a population decline during the latter part of this century (Zeleny 1976). This decline is thought to have been caused by reductions in the availability of natural nesting cavities via habitat destruction, forest practices that included the removal of snags, and competition with introduced cavity-nesters (House Sparrows, *Passer domesticus*, and European Starlings, *Sturnus vulgaris*; Wallace 1959, Zeleny 1976). In response to this decline, nest-box programs have been initiated throughout North America (e.g., Kibler 1969), and many different types of nest-boxes have been designed in an effort to increase bluebird productivity and population size.

Many studies have focused on which nest-box designs bluebirds prefer (Lumsden 1986, 1989; Munro and Rounds 1985; Pitts 1988; Van Horn and Bacon 1989). Fewer studies, however, have been conducted to determine which box types are the most productive. This is an important point because it is conceivable that bluebirds may not prefer box types that produce the most young. If preferred boxes are not the most productive, the overall goal of increasing population size may not be achieved, or, worse, bluebirds may be lured into boxes that provide poor protection from predators or competitors at the nest.

In this study, we report on variation in clutch size, hatching success, nestling survival, and predation rate in four types of nest-boxes erected for the production of Eastern Bluebirds from 1968–1994, near Green Bay, Wisconsin. We also report the rate of recruitment of young bluebirds to the local breeding population. Because our study spans 27 yr, and comprises over 2600 nesting attempts, our results also offer valuable long-term information on annual variation in reproductive success in this species.

METHODS

Study area and procedure.—Between 1968 and 1994 one of us (VMB) erected and monitored ca. 500–700 nest-boxes in Brown and Oconto counties near Green Bay, Wisconsin, with the help of many other amateur ornithologists. Nest-boxes were located near houses or on fences adjacent to fields, pastures, or orchards. In most cases, boxes were placed in what was considered prime bluebird habitat, as described by Zeleny (1976), Munro and Rounds (1985) and Lumsden (1989).

Nest-boxes were checked for occupancy every 7–10 d each year, beginning in mid-March. Boxes were checked more frequently after eggs were laid, and nestlings were banded with a USFWS metal band at about ten days of age. Adults were also trapped and banded at this time, using the Bauldry bluebird trap (Anonymous 1989). When predation occurred, the predator responsible was identified either by direct observation or using

a method similar to Pinkowski's key to nest-box predators (Pinkowski 1975).

Types of nest-boxes.—Four different nest-box types were used during the study: Open Top, Standard, Tin Can, and Hollow Post. The majority of boxes used in the study were Open Tops. These boxes were designed by VMB to mimic natural nest sites in hollowed-out fence posts or broken tree tops. They are 29-cm deep, have a 10 cm × 10 cm interior base, and are made of 2-cm rough lumber. Open Top boxes have a predator guard (a 2-cm block of wood placed over the entrance hole to extend the side entrance) and a circular, screened opening in the roof measuring 9 cm in diameter. Detailed plans can be requested by sending a self-addressed, stamped envelope to VMB.

Standard boxes were the second most numerous in the study area and included a variety of styles, with most modeled after Zeleny (1976). These boxes are typically 18–21 cm in depth with a 10 cm × 13 cm base, and are often constructed with thinner lumber than the Open Top box. Most Standard boxes had sloping roofs, and many lacked predator guards early in the study period. Tin Can nest-boxes were constructed from a one gallon can placed horizontally. One end of the can was replaced by a wooden front with a predator guard. Hollow Posts, also designed to mimic hollowed-out fence posts, were the least common of the artificial cavity types monitored in this study. These cavities were made by drilling-out the center of new, large posts with a hole measuring 10 cm in diameter and 36-cm deep. The top was left open and unscreened, and there was no predator guard over the side entrance, which nevertheless averaged 2–5 cm in depth, depending on the diameter of the post. Both Hollow Post and Tin Can boxes were used in only 15 of 27 years of the study. In addition to these artificial nest cavities, seven nesting attempts by bluebirds were also recorded in natural tree cavities over four years.

Data analysis.—We used five variables to quantify bluebird productivity and survival. *Clutch size* was the maximum number of eggs observed in each nest. We divided the total number of young that hatched or were banded by clutch size in order to control for the effect of clutch size on productivity, and to obtain two related estimates of egg and nestling survival, respectively. Thus, the *fraction hatched* equaled the fraction of eggs that survived from the time of laying to hatching in each nest. The *fraction banded* was the number of eggs that hatched and survived as nestlings to banding age. The *fraction survived* was the fraction of young that survived from the time of hatching to banding age, and was thus an estimate of survival from 0–10 d. *Juvenile return rate* was the number of birds returning to the study site that were banded as a nestling, divided by the total number of nestlings banded in a given nest, cavity type or year, depending on the analysis.

We also assessed the success of each box type by tallying the fraction of nests in which at least one egg did not hatch or did not survive to banding age. Nests in this category were divided further into two classes: (1) partial failures, wherein some but not all eggs or young were lost; and

(2) complete failures, wherein all eggs or young died prior to banding. For all complete failures we also tallied the fraction of boxes where predation by House Wrens (*Troglodytes aedon*), House Sparrows, raccoons (*Procyon lotor*), domestic cats (*Felis domesticus*), or snakes occurred.

We used Systat (Wilkinson 1989) for all statistical analyses and parametric tests for most comparisons. Whenever graphical analyses (e.g. normal probability plots of the raw data or residuals of regressions) suggested that the data were not normally distributed, we transformed the data to improve the shape of the distribution for analysis (e.g., log or arcsin-square-root). In a few cases transformation did not improve distributions, so we conducted parallel non-parametric tests to see if our results were sensitive to the type of test employed. Perhaps because of the large sample of nests and years used, however, we found no case where the statistical significance of a result differed markedly based on the type of test used. We therefore report only the results of parametric tests in this paper.

We used general linear models to check for statistical interactions between year and box type, and for consistent increases or decreases in nesting success over the study period. We used one-way ANOVA to test for significant variation between years in nesting success, where each nesting attempt was used as a datum. The only exception to this was for the analysis of juvenile return rate, where, because of the overwhelming number of zero young returning from individual nesting attempts, we used a Log-likelihood Ratio test to analyze categorically the number of attempts with zero versus one or more returning young per year.

To assess the relative performance of cavity types, we compared the mean nesting success in each cavity type and year using paired *t*-tests. We used means because the sample of nests in each cavity type and year varied widely. We also included only mean values based on five or more nesting attempts, because we judged those with fewer attempts as less reliable.

We focused our analyses of success on comparisons between Open Top versus Standard boxes, Tin Cans, and Hollow Posts. We did this because our main goal was to test if Open Tops out-performed other cavity types. We also wished to minimize the total number of statistical tests and experimentwise error rates (cf. Chandler 1995). For example, because three paired comparisons were made for each estimate of success (Open Top vs. Standard, Open Top vs. Hollow Post, Open Top vs. Tin Can), the accepted level of statistical significance for each test should be adjusted to 0.0125 (0.05/3). A further downward adjustment is probably also warranted because three of the variables that we compared are not independent (survival from laying to hatching, hatching to banding, and laying to banding). Thus, a conservative approach would be to use a final level of statistical significance of $0.05/9 = 0.0056$ for these tests. Comparisons of the causes of predation in Open Top versus other box types also warrant lower levels of acceptance, depending on the number of comparisons made. For all these analyses, we report significance levels to three places and leave it to the reader to decide what level of statistical significance is appropriate in each case.

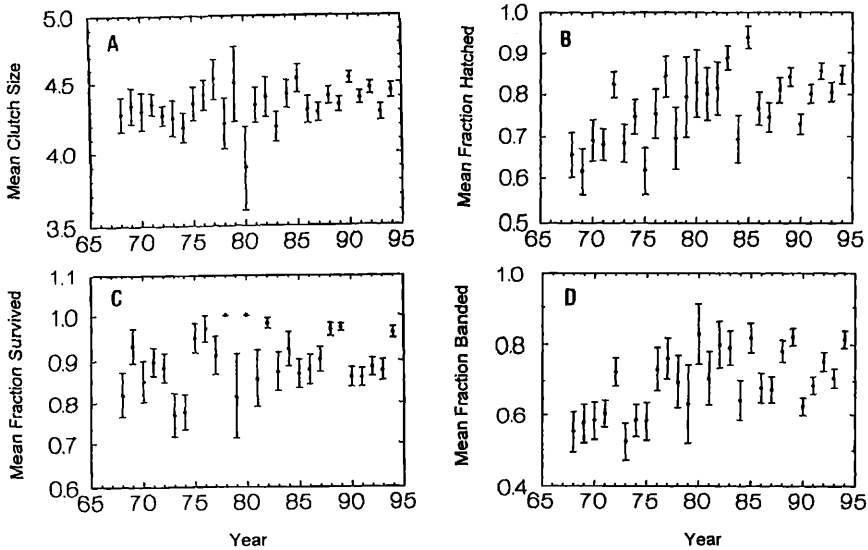


FIGURE 1. Annual variation in nesting success as mean a) clutch size, b) fraction of eggs hatched, c) fraction of young surviving from hatching to banding, and d) fraction of eggs surviving to banding age. Plots give the mean values as solid circles ± 1 SE. We found significant variation across years in each measure of success (clutch size: $F = 1.67$, $df = 26, 2628$, $P = 0.018$; fraction hatched: $F = 4.36$, $df = 26, 2626$, $P < 0.0001$; fraction banded: $F = 4.79$, $df = 26, 2621$, $P < 0.001$; fraction surviving hatching to banding: $F = 3.19$, $df = 26, 2240$, $P < 0.001$).

Frequency tables were tested using the G-statistic of the Log-likelihood Ratio test with the Williams correction. Complete data on nesting attempts from laying to banding were available for 1506 Open Top boxes, 1066 Standard boxes, 29 Hollow Posts, 36 Tin Cans, and 7 Natural Cavities, for a total of 2644 attempts. This is slightly fewer than the total number of attempts recorded ($n = 2654$) because data were incomplete in some cases.

RESULTS

Annual variation in productivity.—Annual variation in clutch size was slight, but, because of the large number of nests used, we did find that it varied significantly over the study ($F = 1.67$, $df = 26, 2628$, $P < 0.02$; Fig. 1a). Mean clutch size varied from 4.2–4.6, except in 1980, when it equaled 3.9 (Fig. 1a). One clutch of nine eggs was incubated by two females in 1973.

The mean annual fraction of young hatched, banded, and surviving from hatching to banding all varied widely and significantly among years (Fig. 1b–d). The fraction of young hatched varied by about 50%, being as low as 0.62 in 1969 and 1975, and as high as 0.94 in 1985 ($F = 4.36$, $df = 26, 2626$, $P < 0.0001$; Fig. 1b). The mean fraction of young that

survived from hatching to banding ranged from 0.77 to 1.00 ($F = 4.79$, $df = 26$, 2621, $P < 0.0001$; Fig. 1c). The mean fraction of young banded varied from 0.52 and 0.82 ($F = 3.19$, $df = 26$, 2240; Fig. 1d). Juvenile return rate varied by a factor of ten, from 0.54 to 5.14, and over all years this variation was statistically significant ($G = 35.37$, $df = 25$, $P < 0.01$).

We found a tendency for all measures of productivity to increase over the period of the study, but in most cases the effect was small. The measured increase in clutch size, for example, amounted to less than 0.2 eggs in 1994 as compared to 1968. Nevertheless, this difference was statistically significant because of the large sample of nests used ($r^2 = 0.003$, $F = 8.65$, $df = 1$, 2653, $P = 0.003$). We also found that the fraction of eggs hatched increased over the course of the study, but this also amounted to an increase of about 0.2 young in 1994 as compared to 1968 ($r^2 = 0.016$, $F = 43.07$, $df = 1$, 2651, $P < 0.0001$). The fraction of young banded also increased over the study, and this amounted to a slightly greater difference of about 0.3 young in 1994 as compared to 1968 ($r^2 = 0.015$, $F = 1.56$, $df = 1$, 2646, $P < 0.0001$). The fraction of young surviving increased by less than 0.1 young in 1994 as compared to 1968. However, this increase was also statistically significant ($r^2 = 0.002$, $F = 4.87$, $df = 1$, 2265, $P = 0.028$). In contrast, there was no significant increase in juvenile return rate ($r^2 = 0.001$, $F = 2.03$, $df = 1$, 2646, $P > 0.05$).

Interaction between box type and year.—A multivariate analysis revealed a significant statistical interaction between cavity type and year ($F = 8.72$, $df = 4$, 2641, $P < 0.001$). Exploratory analyses of the data indicate that this occurred because the performance of Standard boxes improved slightly throughout the study, while performance of other cavity types remained about constant.

Variation in productivity among cavity types.—Mean clutch size varied slightly among box types ($F = 3.17$, $df = 4$, 2638, $P = 0.013$; Fig. 2a). Clutches were slightly larger in Open Top than in Standard boxes ($t = 3.32$, $df = 25$, $P < 0.002$; Fig. 2a), but they were about equal to those laid in Tin Cans and Hollow Posts (both P s > 0.05 ; Fig. 2a).

The mean fraction of eggs hatched equaled 0.82 (SE = 0.01, $n = 27$) for Open Tops, 0.72 (SE = 0.03, $n = 27$) for Standards, 0.67 (SE = 0.10, $n = 15$) for Tin Cans, 0.79 (SE = 0.07, $n = 16$) for Hollow Posts and 0.93 (SE = 0.07, $n = 3$) for Natural Cavities. Overall, the mean fraction of eggs hatched varied significantly by cavity type ($F = 8.52$, $df = 4$, 2636, $P < 0.001$; Fig. 2b), and it was significantly greater in Open Top than Standard boxes ($t = 3.82$, $df = 25$, $P < 0.001$; Fig. 2b). Comparisons between Open Tops and other cavity types were not significant (P s > 0.05 ; Fig. 2b).

The mean fraction of young surviving from hatching to banding was 0.93 (SE = 0.01, $n = 27$) for Open Tops, 0.87 (SE = 0.02, $n = 27$) for Standards, 0.79 (SE = 0.11, $n = 12$) for Tin Cans, 0.93 (SE = 0.04, $n = 15$) for Hollow Posts and 0.50 (SE = 0.29, $n = 4$) for Natural Cavities. It also varied significantly by box type ($F = 11.99$, $df = 4$, 2631, $P < 0.001$; Fig. 2c). Survival from hatching to banding was also significantly higher

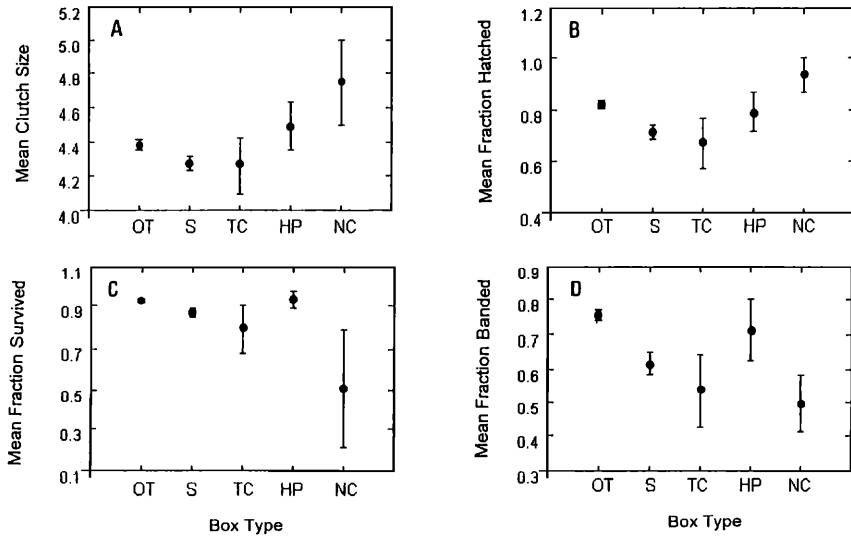


FIGURE 2. Variation in nesting success by cavity type. Each dot represents the mean (\pm SE) a) clutch size, b) fraction of eggs hatched, c) fraction of young surviving from hatching to banding, and d) fraction of eggs surviving to banding age, over all years of the study. Number of years = 27 for Open Top (OT) and Standard (S) boxes, 16 for Tin Cans (TC), 15 for Hollow Posts (HP), and 4 for Natural Cavities (NC).

in Open Top than Standard boxes ($t = 2.90$, $df = 25$, $P < 0.005$; Fig. 2c), but comparisons between Open Tops and other cavity types were not significant ($P_s > 0.05$; Fig. 2c).

The mean fraction of young banded was 0.76 (SE = 0.02, $n = 27$) for Open Tops, 0.62 (SE = 0.03, $n = 27$) for Standards, 0.53 (SE = 0.11, $n = 15$) for Tin Cans, 0.72 (SE = 0.09, $n = 16$) for Hollow Posts and 0.50 (SE = 0.29, $n = 4$) for Natural Cavities. This also varied significantly by cavity type ($F = 5.05$, $df = 4$, 2231, $P < 0.001$; Fig. 2d) and was significantly greater in Open Top than Standard nest-boxes ($t = 5.27$, $df = 25$, $P < 0.001$; Fig. 2d). Again, however, comparisons between Open Tops and other cavity types were not significant ($P_s > 0.05$; Fig. 2d).

Finally, juvenile return rate averaged 2.12% for Open Tops, (SE = 0.35, $n = 26$ yr), 2.40% for Standards (SE = 0.53, $n = 26$ yr), 1.60% for Tin Cans (SE = 0.93, $n = 15$), and 5.20% for Hollow Posts (SE = 2.87, $n = 15$). No young from Natural Cavities returned. Overall, annual return rate varied significantly among cavity types ($F = 12.82$, $df = 4$, 78, $P < 0.005$), but, in this case there were no significant differences between Open Tops and the three other common box types.

Nest failure.—Partial failure occurred when a fraction of the eggs that were laid did not hatch, or when some nestlings died or went missing. Overall, however, partial failure occurred about equally often in all cavity types over all nesting stages (Table 1).

TABLE 1. The number of occurrences (percent) of partial or total nest failure by nesting stage and box type over all years. Partial failures from egg to banding are less than the sum of partial failures during the egg and nestling stages combined because 67 nests suffered partial losses in both stages, but were counted only once from egg to banding. Number of attempts = 1506, 1066, 29, 36, 7 for Open Top, Standard, Hollow Post, Tin Can and Natural Cavity, respectively.

	Cavity type					Total
	Open Top	Standard	Hollow Post	Tin Can	Natural Cavity	
Partial Failure						
Egg Stage	374 (24.9)	244 (22.9)	7 (24.1)	4 (11.1)	1 (14.3)	630
Hatching to Banding	87 (5.6)	59 (5.5)	1 (3.5)	0	0	147
Egg to Banding	424 (28.2)	274 (25.7)	7 (24.1)	4 (11.1)	1 (14.3)	740
Total Failure						
Egg Stage	164 (10.9)	202 (19.0)	7 (24.1)	7 (19.4)	0	380
Hatching to Banding	81 (5.4)	94 (8.8)	2 (6.9)	5 (13.9)	2 (28.6)	184
Egg to Banding	245 (16.3)	296 (27.8)	9 (31.0)	12 (33.3)	2 (28.6)	564

In contrast, total failure prior to hatching occurred about half as often in Open Tops than in other types of nest-boxes, except that there were no failures prior to hatching in seven attempts in Natural Cavities (Table 1). Total failure between hatching and banding also occurred in Open Tops at 30–60% of the rate at which failure at this stage occurred in other cavity types (Table 1). Overall, therefore, the failure rate from the egg to banding age in Open Tops was about half of that in Standard boxes ($G = 49.95$, $df = 1$, $P < 0.0001$), Tin Cans ($G = 7.35$, $df = 1$, $P < 0.01$), or Hollow Posts ($G = 4.48$, $df = 1$, $P < 0.04$). Natural Cavities experienced the highest level of total failure (57.1% of 7 nests).

Nest failure as a result of predation or the take-over of cavities by com-

TABLE 2. Number (percentage) of bluebird nests with no young surviving to banding age by nest type and cause of failure (see Methods; samples sizes as for Table 1).

Cause of failure	Cavity type					Total
	Open Top	Standard	Hollow Post	Tin Can	Natural Cavity	
Domestic Cat	19 (1.3)	17 (1.6)	0	0	0	36 (10.2)
Raccoon	1 (0.1)	39 (3.7)	1 (3.5)	0	1 (14.9)	44 (12.6)
Red Squirrel	1 (0.1)	0	0	0	0	1 (0.3)
Snake	6 (0.4)	4 (0.4)	2 (6.9)	1 (2.8)	0	13 (3.7)
House Sparrow	47 (3.1)	57 (5.2)	0	2 (5.6)	0	106 (30.0)
House Wren	48 (3.1)	83 (7.8)	0	7 (19.4)	0	138 (39.1)
Starling	0	1 (0.1)	0	0	0	1 (0.3)
Tree Swallow	2 (0.1)	1 (0.1)	0	0	0	3 (0.9)
Weaseal	1 (0.1)	0	0	0	0	1 (0.3)
Unknown	1 (0.1)	6 (0.6)	3 (10.3)	0	0	10 (2.8)

petitors also varied markedly by cavity type (Table 2). House Wrens, House Sparrows, cats, and raccoons were the major causes of nest failure. Wrens caused 38.8% of total nest failures, but they accounted for less than half as many failures in Open Top as compared to Standard boxes ($G = 27.27$, $df = 1$, $P < 0.0001$), and only about 15% as many failures in Open Tops as compared to Tin Cans ($G = 13.58$, $df = 1$, $P < 0.0001$; Table 2). No wrens were observed to have caused failures in Hollow Posts or Natural Cavities.

House Sparrows caused 29.5% of failures overall. As found for wrens, however, House Sparrows accounted for only about two-thirds as many failures in Open Top as compared to Standard boxes ($G = 8.03$, $df = 1$, $P = 0.005$; Table 2). There was no significant difference between the incidence of House Sparrows causing predation in Open Tops versus Tin Cans, and House Sparrows caused no failures in Hollow Posts or Natural Cavities (all P s > 0.05 ; Table 2).

Nest predation by raccoons and cats was uncommon in all cavity types (Table 2). When the cause of nest failure was broken down as being related to predation on adults versus nestlings and eggs, we found that 94.5% of predation by cats involved adult bluebirds.

DISCUSSION

Our results show that it may be more important to consider which boxes are most productive, rather than which are occupied preferentially, if increasing the size of bluebird populations is the main goal of erecting nest-boxes. Zeleny (1976) noted that in the absence of alternatives, bluebirds accept almost any type of cavity in which to nest. However, our results show that in Wisconsin, Open Top boxes were significantly more productive than other box types commonly used and sold to the public.

In the discussion that follows, we focus on the mechanisms responsible for the observed differences in the performance of boxes monitored in this study. However, we limit our discussion primarily to Open Top and Standard boxes because these were the most common box types used in our study, and because the latter type is commonly offered for sale in retail outlets.

Nest failure and interactions with other species.—The differences in nesting success that we observed between box types resulted more from total than from partial nest failure (Table 1). Predation and the take-over of active nests by competitors were the main causes of total failure, and Standard boxes suffered from this twice as often as did Open Tops (Table 2).

House Wrens were the primary cause of total failure in our study (Table 2). This occurred even though most boxes were maintained at high densities in an attempt to reduce competition for nest sites, and they were placed in areas thought to be less favored by wrens (e.g., Kibler 1969). Several other authors have also noted that House Wrens present problems for nesting bluebirds because they often destroy the nests of other birds even after they have secured a box of their own (Lumsden 1986, Petersen 1969, Pinkowski 1975, Zeleny 1976). Pinkowski (1977) found that wrens

caused the majority of the failures he recorded (23.3% of 133 attempts). We observed that wrens caused nest failures at similar rates to those reported by Pinkowski (1977) in Standard boxes, but that they caused nest failure much less often in Open Top boxes (Table 2). Although we do not know why this difference occurred, it seems reasonable to conclude that wrens avoided Open Top boxes.

House Sparrows also destroy bluebird eggs and nestlings (Lumsden 1989, Wallace 1959), and they occasionally kill adults (Gowaty 1984). Because House Sparrows are often winter residents, and roost in boxes maintained for bluebirds (Zeleny, 1976), they may gain an advantage over migratory bluebirds in competition for nest sites. Our results show that nest depredation by House Sparrows was less common in Open Top than in Standard boxes (Table 2). We suggest that Open Top boxes may have discouraged occupation by House Sparrows because the hole allows heat to escape and renders the boxes unsuitable as winter roosts.

Mammalian predators, mainly raccoons and cats, also caused nests to fail (Table 2). Predator guards and deep boxes are known to reduce mammalian predation (Zeleny 1976), and this finding was borne out in our study. Both Zeleny (1976) and Petersen (1969) stated that raccoons were a major predator of bluebirds. We observed that raccoon predation was rare in Open Top boxes, but was common in Standard boxes (18.8%; Table 2), where it occurred at a rate equal to that reported by Pinkowski (18.8%; 1977). This attests to the effectiveness of the predator guard and increased depth of Open Top boxes. Predator guards were absent from most Standard boxes, which were also several inches shallower than Open Tops on average.

Cats caused nest failure mainly by killing one or both of the adults, but overall they accounted for only 10.2% of all nest failures. Only two instances of cats preying on nestlings were recorded, and these both occurred at Standard boxes.

Partial nest failure resulted when birds laid infertile eggs or when there was a shortage of food for nestlings. Thus we did not expect these causes to be influenced by nest-box type. As expected, we found that partial failure in Open Top and Standard nest-boxes occurred at rates within three percentage points of each other at each nesting stage (Table 1).

Productivity.—In preference tests conducted by Bacon (1987), bluebirds rarely chose Open Top boxes when given a closed-top box as a nearby alternative. We found that in Wisconsin, however, Open Top boxes were consistently more productive than the closed-top nest-boxes considered here, primarily because bluebirds that used Open Top boxes suffered lower rates of total nest failure.

Bluebird enthusiasts may not have noted this effect previously because it has been conventional to report only the number of young banded or fledged per successful nest (reviewed in Bauldry et al. 1995). However, this method of reporting results excludes nests where total failures have occurred and thus inflates the apparent rate of nesting success overall.

Overall, therefore, our results suggest that the use of closed-top boxes

may result in the production of fewer bluebirds than if Open Top designs were adopted, particularly where House Sparrows and House Wrens are present. It is possible that where these competitors are uncommon or absent, the advantages of Open Top boxes relative to others may be less than reported here. This cannot be assumed to be true, however, until comparable studies are conducted where these nest competitors are absent.

We also observed slight but statistically significant increases in breeding success over the 27 years of this study. However, when broken down by box type, we found that this increase occurred only in Standard boxes. We expect that this occurred as a result of gradual improvements in the design of typical Standard nest-boxes that have been commercially available in recent years, such as the increased use of predator guards.

Although it is generally assumed that increasing the number of available nest-boxes in breeding areas has the greatest positive effect on bluebird population size, severe winter weather is also a major limiting factor (Zeleny, 1976). In the late 1950s, and again in the late 1970s, bluebird numbers dropped to extremely low levels following three severe winters in the Southeast and South Central portions of the U.S (Pinkowski 1979, Sauer and Droege 1990, Wallace 1959, Zeleny 1976). We suggest that increasing the average nesting success of bluebirds will help to provide larger populations of potential recruits each year, and thus help to rebuild populations more quickly following severe winters.

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UPCOMING MEETINGS

Association of Systematic Collections.—24–26 Apr. 1997, Atlanta, Georgia. Held jointly with Association of Science Museum Directors. Contact ASC, 1725 K St., NW Suite 601, Washington, D.C. 20006-1401 (202)-835-9050; fax 202-835-7334; asc@ascoll.org; <http://www.ascoll.org>).

Fifth International Congress of Vertebrate Morphology.—12–17 Jul. 1997, University of Bristol, United Kingdom. Contact J.V.M. Rayner, School of Biological Sciences, University of Bristol, Woodland Rd., Bristol BS8 1UG (fax +44 117 925 7374; ICVM97@bristol.ac.uk; <http://www.bio.bris.ac.uk/icvm.html>).

Society of Caribbean Ornithology.—1–6 Aug. 1997, Aruba, Dutch West Indies. Contact Joseph M. Wunderle, President, SCO, P.O. Box 507, Palmer, Puerto Rico 00721.

Forum on Wildlife Telemetry.—21–23 Sep. 1997, Snowmass, Colorado, immediately preceding the 1997 Annual Conference of The Wildlife Society. Contact Jane Austin, National Biological Service, Northern Prairie Science Center, Jamestown, ND 58401 (701-252-5363; fax 701-252-4217; jane_austin@nbs.gov).