BREEDING OF THE EASTERN BLUEBIRD IN CENTRAL FLORIDA

By Susan C. White and Glen E. Woolfenden

This study of reproduction by the Eastern Bluebird (*Sialia sialis*) in central Florida is based on the analysis of 495 nest records obtained during seven consecutive years, 1966-1972. Other published studies were based on records from nest boxes in the central portion of the species' range in Massachusetts, New York, Illinois, Tennessee, and Arkansas. Only Peakall's (1970) analysis includes nest records from the Coastal Plain. One-third of the records we have analyzed are of nests built in natural cavities; the others are from nest boxes. In our analyses we have emphasized comparisons between breeding in Florida, where the endemic *S. s. grata* resides (AOU Check-list, 1957), and elsewhere in North America as well as comparisons between natural-cavity and nest-box breeding.

STUDY AREA

The nest boxes are located north of Tampa, Florida, along state road 581 where it crosses the Hillsborough-Pasco County line (Figs. 1 and 2). The boxes extend 6.6 miles south of the county line into Hillsborough County, and, originally, 1.0 miles north into Pasco County. As of 1970 the boxes were extended 5.1 miles into Pasco County making the entire line 11.7 miles long.

The study area is characterized by a subtropical climate. Freezes are uncommon and cold spells occur only a few days during the year. Maximum temperatures are about 97°F in the summer months when frequent thundershowers provide relief from prolonged high temperatures. Average daily temperature is 62°F in January and 82°F in August. Mean annual rainfall is about 50 inches, 60 per cent of which falls in the four summer months. The spring months are generally dry.

The terrain of the study area is flat and low lying with elevations varying between 40 and 60 feet above sea level. The soil is of the Leon-Plummer association, strongly acid and poorly drained. Pine woods occur on the Leon soils and cypress stands, in shallow ponds on the Plummer soils of the slough-like depressions (U.S.D.A., 1950, 1969).

At present most of the area is open cattle range. The only developed land is a golf course built in 1968 which borders one mile of the road. Ranchers manage the open pine woods for pasture by controlled burning every one to three years. This temporarily removes palmettos and accumulated underbrush and encourages the growth of native wire grasses. The scattered trees are mostly longleaf pines (*Pinus palustris*) with a few slash pines (*P. elliottii*) and live oaks (*Quercus virginiana*). Logging of the pines and cypress is frequent. The most abundant shrub of the pine understory is saw palmetto (*Serenoa repens*), with saltbush (*Baccharis halimifolia*), rusty lyonia (*Lyonia ferruginea*), and gallberry (*Ilex glabra*) also abundant. Spanish moss (*Tillandsia usneoides*) is a con-

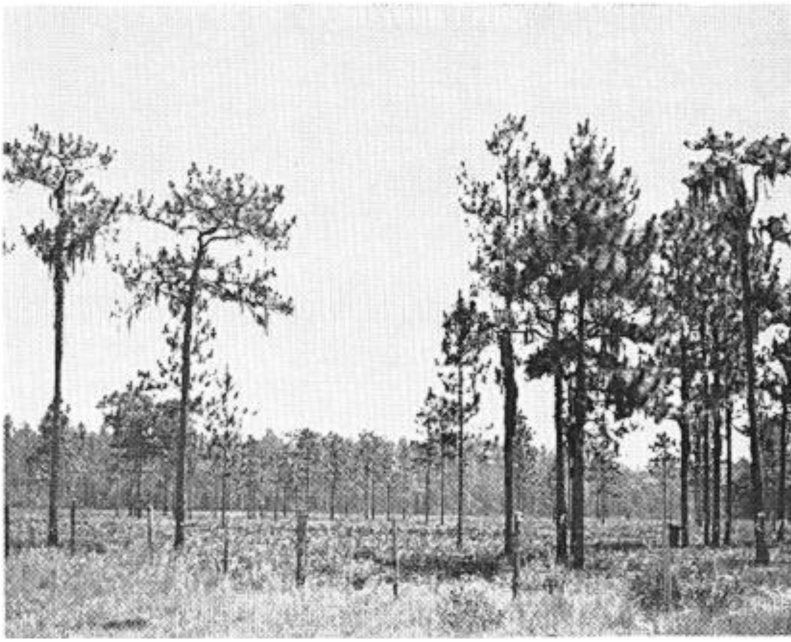


FIGURE 1. Open pine woods north of Tampa, Florida in Hillsborough County. A bluebird nest box is in the right foreground.

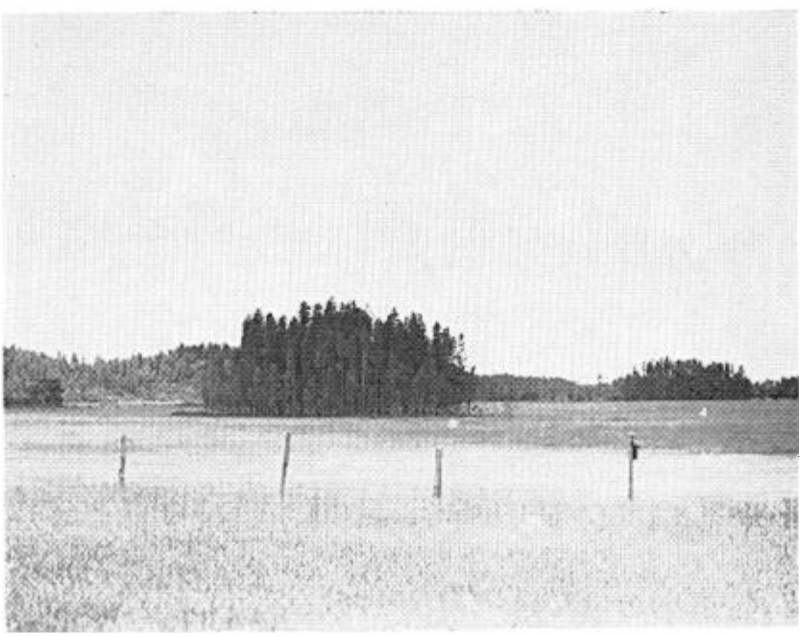


FIGURE 2. Improved pastureland north of Tampa, Florida in Pasco County. Areas formerly covered by pines have been converted to grasses. Cypress stands, their extent often reduced by logging, dot the landscape.

spicuous epiphyte. Large areas in Pasco County have been cleared of pines and shrubs to produce open pasture.

The wet depressions are dominated by bald-cypress (*Taxodium distichum*) or by oaks including live oak, laurel oak (*Quercus laurifolia*), and water oak (*Q. nigra*). Southern red maple (*Acer rubrum*) and cabbage palm (*Sabal palmetto*) are found in some depressions.

The wide road shoulders are mowed regularly and dominated by herbs. Some of the roadside ditches and depressions contain Southern willow (*Salix caroliniana*) and wax myrtle (*Myrica cerifera*).

The varied wet and dry parts of the study area support a rich herpetofauna. Several non-poisonous terrestrial snakes are potential predators on bluebird nests. Two species, the corn snake (*Elaphe guttata*) and the yellow rat shake (*E. obsoleta quadrivittata*) have been observed robbing nests. Of the breeding avifauna in the study area, those that occasionally nest in the boxes include the Yellow-shafted Flicker (*Colaptes auratus*), Red-bellied Woodpecker (*Centurus carolinus*), Great Crested Flycatcher (*Myiarchus crinitus*), and Carolina Chickadee (*Parus carolinensis*). Mammals that might rob bluebird nests include the raccoon (*Procyon lotor*) and opossum (*Didelphis marsupialis*) and man. Three failures in which nest material was pulled upward to the hinged roof of the nest box suggested mammalian predation.

PROCEDURES

Members of the Tampa Audubon Society erected 50 bluebird nest boxes early in 1966. Most boxes were nailed to the west sides of fence posts on the west side of the road and about 0.2 miles apart. Eight boxes on the east side of the road were spaced between those on the west. The nest boxes added in 1970 were 0.25 miles apart. The boxes were constructed of 3/4 inch exterior plywood, with a hinged roof of 1/2 inch plywood covered with a roofing shingle. Floor space was 4.5 inches square and the entrance hole 1.5 inches in diameter. No boxes had anti-predator devices.

Visits to active nests were brief, with as little disturbance as possible except in 1971 when most chicks were weighed and measured daily. Chicks were banded at 8 to 12 days of age in 1967, 1969, 1970, and 1971. Thirty breeding adults were banded during the study, mostly in 1971.

Data from seven years, 1966 through 1972, are included in the various analyses. In every year except 1968 observations began before the first clutch was laid. In 1966 Dorothy Teschner and Herbert W. Kale II checked the 50 new boxes, and in 1967 Chet E. Winegarner checked the 41 boxes still present. In 1968 Fred E. Lohrer and others checked the 36 intact boxes, and in 1969 they were checked by White and Ralph W. Schreiber. New nest boxes were built by Eagle Scout David Ryan, and in December 1969 the line was extended by the addition of 13, and in February 1970 numerous boxes damaged or destroyed were replaced making the total 53. These 53 were checked in 1970 and 1971 by White and the remaining 43 were checked in 1972 by Woolfenden and others.

In 1968 and 1969 Dr. Arnold Moorhouse found and made sporadic observations of 166 bluebird nests built in natural cavities. These nests were scattered in an area of approximately 1,100 square miles in Hillsborough, Pasco, Hernando and Sumter counties adjacent to and northeast of the Tampa study area. Various of the analyses that follow include these important data.

It is important to note that all of the Moorhouse records and the first four years of records from the Tampa study (1966 to 1969) were used by Peakall (1970) in a computer analysis of Eastern Bluebird reproduction throughout much of its breeding range. Seventeen other bluebird nest records from Florida collected by observers other than Moorhouse also were included in Peakall's analysis but not in ours.

THE NESTING CYCLE

Various of our analyses of reproduction require careful determination of the average duration of each of the five stages in the nesting cycle: building, egg-laying, incubation, hatching, and nestling. These are explained below.

The duration of the building stage was recorded for 28 nests. Building, which is done entirely by the female, requires only two to three days, but sometimes work is interrupted by inclement weather. Cold fronts might prolong this stage to nine days.

Based on records at 31 nests, an interval of from 2-20 days occurs between the building and egg-laying stages. This interval is longest early in the year and decreases as the season advances. The time lapse was more than five days in 26 of 28 nest records from March and early April, and was two days for all three records after mid-April.

Normally one egg is laid each day, and the duration of the egg-laying stage is one day less than the number of eggs in the clutch. In 5 to 10 per cent of the clutches, one or more days elapse between the laying of consecutive eggs. This occurs most often early in the breeding season and between the laying of the last two eggs of large clutches. When it was necessary to extrapolate laying dates, the laying of one egg per day was assumed and if clutch size was uncertain, four eggs were assumed.

The duration of the incubation stage was determined by the common practice of counting the number of days from the last egg laid to the last egg hatched for clutches in which all eggs hatched. Records from six clutches in which not all eggs hatched also are included because the eggs were marked as they were laid so that the hatching date of the last egg is known. Of the 49 usable nest records, most come from data in 1970-1971 and all are based on daily visits through the hatching stage.

For these 49 nests, the incubation period was 13 days in 6 cases, 14 days in 30, and 15 days in 13, with a mean of 14.1. No seasonal variation was detected, so 14 days is considered the length of the incubation period for extrapolations. Burns (1915) gives an incubation period of 12 days, but no subsequent worker reports an incubation period this short. Thomas (1946) gives incubation as 13 to 15 days, commonly 14 days; and Laskey (1940) and Kibler (pers. comm.) give 13 to 14 days. Bent (1949) apparently obtained his value of 12 days from Burns.

The duration of the hatching stage in Florida bluebirds varies. Early in the breeding season clutches hatch in one day, but as the season progresses an increasing percentage of clutches require two and rarely three days for all to hatch. Observation of marked eggs revealed that the duration from laying to hatching remained constant for the last egg of each clutch, but that the eggs laid earlier were hatching earlier. Perhaps summer ambient temperatures are high enough to initiate some embryonic development during the laying stage.

Duration of the nestling stage is defined as the age of chicks in days on the last day they were seen in the nest before fledging, provided the nest was visited daily. The first day of a chick's existence is considered day zero. Chicks were found dead in the nest on day 15 in three instances and no cases of fledging before 15 days of age are known. Several cases of fledging at 15 days were verified by chicks seen later or recovered as road kills; therefore, attainment of this age is considered sufficient evidence for fledging unless knowledge to the contrary exists. In 1970, fledging occurred in nine instances at 15 days, in seven at 16 days, in fourteen at 17 days, and in nine at 18 days. This is not an unbiased distribution of natural fledging ages. Any disturbance might induce fledging, although daily minor disturbances are less likely to initiate early fledging than less frequent visits. Undisturbed chicks probably remain in the nest 17 or 18 days.

Thomas (1946) reports the normal fledging age as 17 to 18 days. Laskey (pers. comm.) states most chicks fledge at 16 days but some remain in the nest longer. Hamilton (1943) observed fledging at 14 to 16 days, and Kibler (pers. comm.) reports fledging might occur at any age from 14 to 22 days depending on depth of the box and degree of disturbance to the nest.

Total length of the nest cycle appears to decrease slightly from south to north. The normal period from the start of incubation to fledging in Arkansas (Thomas, 1946) and Florida is 30 to 32 days. In Tennessee, it is 29 to 30 days (Laskey, pers. comm.) and in New York 27 to 30 days (Hamilton, 1943; Kibler, pers. comm.).

BREEDING SEASON

Banding has shown that bluebirds breeding in the Tampa area are permanent residents. They associate in winter flocks until February, when they establish territories and form pairs. For all seven years, building has begun in March following a warm spell when daytime temperatures reach about 80°F. In 1971 and 1972, abnormally warm weather, including successive days with 80°F plus temperatures, occurred in early February, but building still did not begin until March. Egg-laying begins about a week after nest completion. If cold weather precedes egg-laying, the first eggs are not laid until warm weather recurs.

Bluebirds produce two broods in Florida as indicated by the bimodal distribution of clutches through the season in Figure 3. Clutches were completed over a period of 138 days from 7 March (1972) to 13 July (1971). The high and narrow first peak indicates a highly synchronized first brood. Later in the season synchrony is much reduced because of the laying of repeat clutches following failures as well as second clutches following successes. Color-banding of adult bluebirds in 1971 proved three broods are raised by some individuals, but two broods appear typical of the population. In the text that follows we refer to the first and second peaks of breeding as the spring and summer breeding periods respectively.

CLUTCH SIZE

Daily visits from late in the laying stage to early incubation are optimum for determining clutch size; however, only 87 of our 495 Florida bluebird nest records showed visits this frequent. We enlarged the sample by including nests observed in the incubation stage for which laying had ended. These additional nests fall into three categories:

a) Nests visited at least once during the laying stage and again after sufficient time had elapsed for clutch completion (159 nests).

b) Nests observed at least twice with no increase in the number of eggs noted (127 nests).

c) Nests observed only once during incubation, but again after hatching with the interim less than the incubation stage (35 nests).

Loss of single eggs from clutches is rare. The possibility of undetected losses does exist, and five nests that fit one of the latter two categories were excluded because, when first visited late in incubation, they had only two eggs, a clutch size never observed in 247 nests visited during laying. As implied above, nests seen only once or only after hatching were excluded. Using these criteria, the distribution of clutch sizes for 300 nests from seven years of observation at Tampa is similar to the distribution for the 110 nest records of Moorhouse as shown below:

Clutch size	3	4	5	6
Tampa records	26 (8.7%)	131 (43.7%)	137 (45.7%)	6 (2.0%)
Moorhouse records	8 (7.3%)	48 (43.6%)	51 (46.4%)	3 (2.7%)

Clutch size generally shows one of two seasonal patterns of variations in passerines. With few exceptions, in single-brooded species mean clutch size decreases throughout the breeding season, and in multi-brooded species it increases to a peak at mid-season and then decreases (Klomp, 1970). The bluebird, typically double-brooded in Florida, shows the latter pattern modified by a decrease before peak mean clutch size is attained at mid-season (Fig. 3). This initial decrease appears in certain years with large sample sizes, but is most evident when data from all years are combined (Fig. 3). The mid-season peak is evident for six of the seven seasons when examined separately. The exception is 1966, when only 14 nests were observed. In 1971, observations on color-banded females showed that the individuals that laid large clutches and laid earliest in the season also were responsible for the large clutches at mid-season. These same females also were most likely to attempt third broods, with a smaller clutch than before.

Plotting the number of clutches of each size at five-day intervals, based on date of completion, illustrates the nature of this seasonal pattern (Fig. 3). Five-egg clutches predominate early in the season and between the spring and summer breeding periods, but decrease after mid-May. Four-egg clutches predominate during the summer period. Three-egg clutches are infrequent before mid-May and thereafter form an increasing proportion of the clutches. Six-egg clutches are rare; the nine recorded occurred in the spring period.

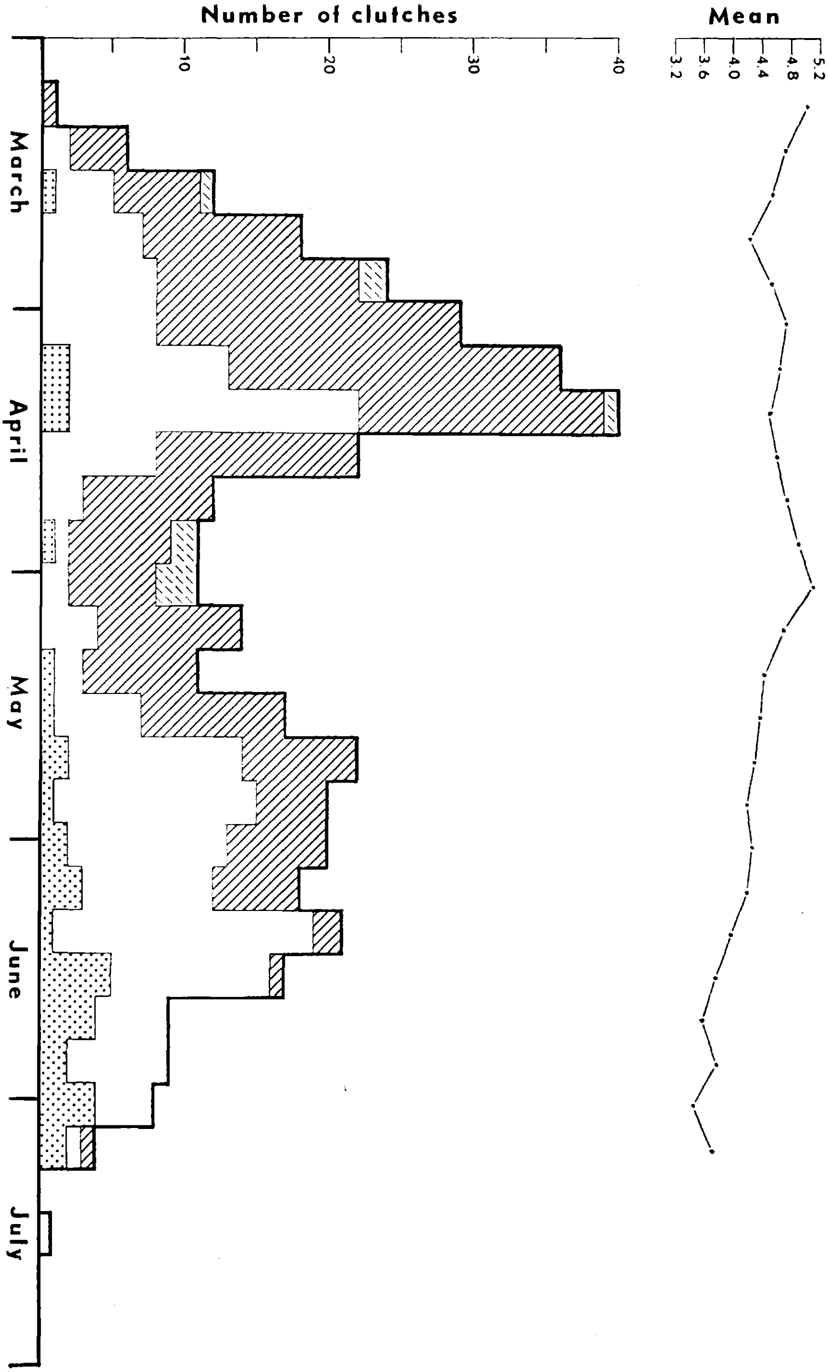
Mean clutch size for the entire season is remarkably stable from year to year (Table 1) with the difference between the largest and smallest means only 0.20 eggs per clutch. No significant difference between years can be shown for this sample by the *t*-test. However, the small difference between 1968 and 1969 for the Tampa data also exists for the Moorhouse data.

TABLE 1. Annual mean clutch size for the Eastern Bluebird in central Florida, 1966-1972.

Year	Tampa data $\bar{x} \pm SD$	(n)			Moorhouse data $\bar{x} \pm SD$	(n)
1966	4.33 ± 0.65	(11)				
1967	4.35 ± 0.75	(26)				
1968	4.38 ± 0.63	(40)			4.38 ± 0.86	(21)
1969	4.47 ± 0.59	(45)			4.47 ± 0.62	(90)
1970	4.34 ± 0.67	(65)				
1971	4.41 ± 0.75	(64)				
1972	4.53 ± 0.68	(57)				
All data			4.42 ± 0.67	(410)		

Peakall (1970) gives a slightly smaller mean clutch size (4.33) for Florida than we found (4.42). Perhaps this is because he included abnormally small clutch records when an adult was present on the nest. We rejected this criterion because adults were found on nests at all times of day during the laying period and in one case before laying began.

FIGURE 3. Clutch size records plotted by 5-day intervals for the Eastern Bluebird in central Florida, 1966-1972. The histogram shows number of clutches of 3 (stipple), 4 (open), 5 (diagonal complete lines), and 6 (diagonal dashes) eggs for each interval, with mean clutch size for the interval plotted above.


Number of clutches
10
20
30
40
Mean
3.2
3.6
4.0
4.4
4.8
5.2
March
April
May
June
July

NEST SUCCESS

Nest success is compared between the seven years, and between the box-nests of the Tampa area and the natural-cavity nests in the adjacent counties. In addition, the Tampa data are analyzed with respect to the pattern of success within the breeding season. Unfortunately, in 1968 visits to the nest boxes did not begin until 4 April when half of the spring period nests were near hatching. As nesting is especially successful early in the season, the late start in 1968 probably accounts for this season's low estimate.

In this study, nest success is defined as the proportion of nests with complete clutches that fledge at least one young. Successful fledging is assumed when chicks are present in the nest at 15 or more days of age. Conversely, nest failure is assumed when chicks are absent on or before day 15 of the nestling stage. This criterion of success is the most accurate one possible for the population under study, but it means that the fates of some nests must be regarded as unknown except in 1970 and 1971 when all nests were observed to completion. Any direct calculation of nest success would be biased by either the exclusion or inclusion of these nests (Mayfield, 1960; Snow, 1954). To avoid these biases, we calculated nest success using a modification of the exposure method described by Mayfield (1960). In this modification, exposure of the nests that failed was calculated as half the number of nest-days they would have existed had they succeeded, minus the number of nest-days they existed before they were found. This partially corrects for the assumption of equal rates of loss through the nest cycle that is intrinsic to the procedure.

As shown in Table 2, nest success for the Tampa study area, years 1966-1967 and 1969-1970 are 15 per cent higher than for the nests found by Moorhouse. The major difference between these sets of data is that the Tampa study is based on a line of boxes whereas all of Moorhouse's records are of nests built in natural cavities (mostly in woodpecker holes in fence posts). The greater success in boxes supports the suggestion of Lack (1954) that nest-box studies of reproduction might not represent the species as a whole because the birds are subjected to less competition for nest sites. The high nest success in 1966, when boxes were first erected, might be due to an initial low density of adult bluebirds or by chance because of the small number of nests (14) and infrequent observations. Support of the first supposition comes from the fact that in 1970 when about 20 new nest boxes were available, high success occurred again, and in this year a large sample size and particularly complete data were obtained. This interpretation is not altogether satisfying, because boxes might hold other advantages for breeding birds and the 1970 season might have been singularly successful because of unusually favorable environmental factors.

Analysis of nesting success through the breeding season, all Tampa data combined, shows a steady decrease from March until June (Fig. 4). The great increase from June to July might be an artifact of the small sample of only nine nests for the latter month.

TABLE 2. Fate of nests and nest success by year for the Eastern Bluebird in central Florida. Except for 1970, when success was calculated directly, nest success was calculated by the modified exposure method given in the text. The nests of unknown fate are divided into those for which young were last seen when less than 11-days old (< 11) and when more than 11, but less than 15 (< 15).

							Moorhouse records	
Year	1966	1967	1968	1969	1970	1971	1972	1968	1969
Successes	2	12	10	19	38	37	19	10	37
Failures	4	12	21	20	17	28	23	11	57
Unknown (< 11)	5	0	4	2	0	0	9	10	20
Unknown (< 15)	8	2	15	6	0	0	18	39	34
Exposure	233	578	801	956	—	1469	1298	430	1901
Success	60.8	54.8	46.8	54.5	69.1	57.5	59.8	47.6	41.9

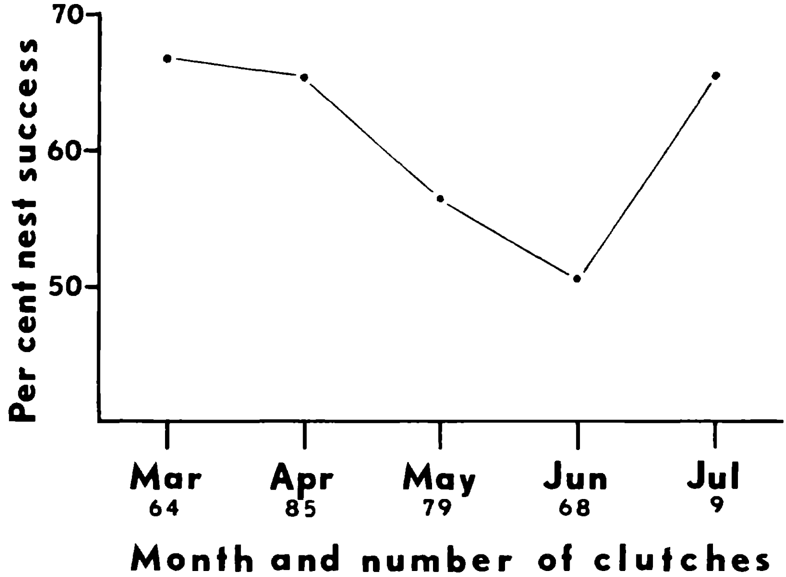


FIGURE 4. Nest success plotted by month in which clutch was begun for Eastern Bluebirds at Tampa, Florida, 1966-1972.

Regardless of the situation in July, clearly early nests contribute disproportionately to overall annual productivity, and strong selection might exist for early annual breeding by the Eastern Bluebird in Florida.

Of the 45 nest failures in 1970 and 1971, only 19 occurred during the incubation period whereas 26 came during the nestling stage. Peakall (1970) also found greater losses during the nestling stage but felt his results might have been biased. Our data are convincing and lead us to wonder if increased activity by parents and young increases the level of predation on nests with young because the majority (18) of the nestling-stage failures occurred when the chicks were eight or more days of age. At this age their eyes are open, their feathers are emerging, and their activity and noise sharply increase. Often they jump up to the nest entrance and call to their approaching parents. The approach of an observer, however, elicits complete silence and cowering. The relative safety of cavity nests compared to open nests appears to reside in their relative inconspicuousness as well as relative inaccessibility to certain predators.

INDIVIDUAL MORTALITY

Most individual bluebird eggs or young are lost as part of the destruction of complete clutches or broods. The 1970 data, which are the most complete, show that 29 eggs were lost from 7 complete clutches (excludes one nest in which all 4 eggs failed to hatch) and 45 nestlings from 9 broods. These 74 individuals constitute 65 per cent of all losses for the season. Predation appears to be the primary cause of these losses. For two of the brood-losses the nest material was pulled upward and for one of these an adult secondary feather was found beneath the box, suggesting mammalian predation. No signs of disturbance were noted at the other 14 nests that failed. Snakes might have cleaned out many of these boxes because on numerous occasions through the seven years of this study snakes were seen in the boxes (two yellow rat snakes in 1969 and one corn snake in 1972; both disgorged nestlings when handled).

Discounting hatching failure, which is discussed below, loss of individuals from otherwise successful nests is unusual. In 1970 when no eggs were lost from 48 clutches that reached the hatching stage, and only 5 young were lost from 38 broods that fledged young, such losses accounted for only 4 per cent of the total. Two of the 5 young were siblings found dead and emaciated in their nest, the other three disappeared.

HATCHING SUCCESS

Based on 1064 eggs that were present the day before the hatching date that could be accounted for thereafter either as chicks or unhatched eggs, hatching success has varied from 74 to 82 per cent annually (Table 3) with a low overall average of 80.9. Peakall's (1970) analysis reveals hatching success is lower in Florida than elsewhere for Eastern Bluebirds, but his figure is higher (87.9 per cent) and is closer to that of other passerines from eastern North America. Hatching success for the Scrub Jay (*Aphelocoma coerulescens*) in Florida is 92.4 per cent (Woolfenden, unpubl.), for the Cedar Waxwing (*Bombycilla cedrorum*) it is 95.4 per cent (Putnam, 1949) and for the Song Sparrow (*Melospiza melodia*) 93.9 per cent (Nice, 1937).

TABLE 3. Hatching success for the Eastern Bluebird at Tampa, Florida, 1966-1970. Percentages based on eggs known present at beginning of hatching stage that could be accounted for as chicks or as unhatched eggs after the hatching stage.

Year	Per cent hatching success	Number of eggs	Number of nests
1966	78.6	42	10
1967	75.6	86	22
1968	74.1	166	38
1969	82.3	141	31
1970	82.4	195	47
1971	81.8	192	43
1972	80.9	184	41

Further analysis of our data reveals that hatching success for the Tampa area bluebirds is much lower for late clutches than early clutches. If 1 May is used as the break between the spring and summer breeding periods, per cent hatching success is 87.7 in spring, whereas it is 71.6 in summer. Musselman (1935) found a decrease in hatching success for summer nestings in Illinois, but no continent-wide pattern was evident in Peakall's (1970) analysis by months.

Summarizing, low hatching success is not a species characteristic of the Eastern Bluebird because outside of Florida only 10 per cent or less of the eggs fail to hatch, a figure which is typical of some other passerines. Furthermore, hatching success decreases dramatically from spring to summer. These values lead us to suspect that high environmental temperatures might cause the frequent hatching failures. In June and July maximum ambient temperatures reach 88-92°F in the shade, and boxes in the sun become several degrees hotter. Nest temperatures up to 102°F were recorded in June 1971. Thus high summer temperature might be selectively advantageous for early breeding by Florida bluebirds.

CONCLUSIONS

Eastern Bluebirds in central Florida are permanent residents and nest from early March to mid-July. Two broods are characteristic of the population. Laskey (1939) in Tennessee and Thomas (1946) in Arkansas commonly observed three broods and sometimes four whereas Musselman (1935) in Illinois, Low (1934) in Massachusetts, and Hamilton (1943) in New York found two broods were normal. Krug (1941) in Ontario, a northern extreme, found only about half as many second as first broods and no third broods. Thus, the breeding season is longest in the center of the species' range and decreases north and south.

According to Peakall (1970), clutch size shows a similar geographical pattern. The mean size for Florida is 4.42 eggs (range, from 3 to 6) and generally decreases from first to later clutches. We found no differences in clutch size between data from nest boxes and natural cavities in Florida.

Nest success, calculated using a modified exposure method, has varied from 55 to 69 per cent in nest boxes during seven consecutive years. In natural cavities for two years success was 42 to 48 per cent, a difference we consider real, boxes being safer for nesting than natural cavities. Because success is influenced by the source of data and the method of calculation, further work is needed to substantiate Peakall's conclusion that no geographical cline in nest success is exhibited by the Eastern Bluebird.

Both biological and physical environmental factors influence the duration of breeding in Florida. Nest success decreases through the breeding season because of increased predation, which normally results in the loss of complete clutches or broods. Within clutches, success also decreases through the season because an increasing percentage of eggs fail to hatch. Hatching failure during the spring breeding period is 12.3 per cent, which is higher than is known for the Eastern Bluebird elsewhere in its range and for a few other passerines from eastern North America. By the summer breeding period hatching failure has reached an extremely high 28.4 per cent. The high and seasonally increasing hatching failure might be because ambient temperatures reach levels fatal to developing embryos.

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Department of Biology, University of South Florida, Tampa, Florida 33620.
(Present address of White: Department of Biology, University of Pennsylvania, Philadelphia, Pa. 19104.)

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