

BREEDING ADAPTATIONS IN THE EASTERN BLUEBIRD

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The Eastern Bluebird (*Sialia sialis*) is a secondary (non-excavating) cavity-nesting species that readily accepts nesting boxes, and many studies (Laskey 1943, Thomas 1946, Peakall 1970, White and Woolfenden 1973) have reported on breeding phenology, clutch size, and nesting success in various parts of its range. In the northern United States some bluebirds are double-brooded; first nests are usually begun in early spring and second nests are initiated during summer (Peakall 1970). Many bluebird pairs, however, rear only a single brood in either the spring or the summer, and do not attempt second nests (pers. observ.), perhaps because of a limited number of suitable nest sites (Lack 1968:176, Stewart 1973).

In this paper I examine bluebird nesting adaptations, particularly those relating to the temporal organization of the breeding season, and compare nesting performance in yearling and adult birds. To test the hypothesis that breeding costs energy and reduces the physiological condition of the adults (Ricklefs 1974:261), I also compare nesting success of bluebirds breeding in summer—those who reared a spring brood vs. those who did not. Such a comparison has not been made in studies of other multi-brooded, cavity nesting species (Kessel 1957, Summers-Smith 1963, Will 1973, Risser 1975).

METHODS

I observed 299 bluebird nests in natural and artificial cavities near Washington, Macomb Co., Michigan during 1968–1976. The study area consisted of old fields containing shrubs, small trees, and mixed herbaceous perennials (Pinkowski 1975a, 1977). Nest boxes were placed on posts in relatively open areas and checked every 1 to 3 days during the nesting season. Because clutch size of one cavity nester, the Great Tit (*Parus major*), is known to be influenced by the size of the nest cavity (Nilsson 1975), all nest boxes had the same dimensions: a 13 × 13 cm floor, and a 3.8-cm diameter entrance, the bottom of which was 15 cm from the floor. Most natural nests were located in oaks (*Quercus* spp.) or American elm (*Ulmus americana*) stubs (Pinkowski 1976a). A few natural nests were inaccessible; they account for those successful nests where clutch size or number of young fledged was unknown.

Both male and female Eastern Bluebirds feed the young; only the female builds the nest, incubates the eggs, and broods the nestlings. Early in the season female bluebirds often build nests in several cavities, then select one to deposit the eggs in (Pinkowski 1974a). In counting nests, I did not include partial

structures built in the abandoned cavities unless an obvious disturbance (predation, inclement weather, conflict with other species) appeared to have prompted the move to a new site.

I banded 909 bluebirds with a standard aluminum band (size 1B) and one to three plastic, colored leg bands. Nestlings were banded when 8 to 12 days old. Adult birds were captured with mist nets and a variety of manual and automatic traps attached to nest boxes. Although a few birds were caught and banded throughout the breeding period, most unbanded adults were captured as soon as possible after their arrival in March and April. Banding early in the season was necessary in order to obtain complete breeding histories because bluebirds may change territories and nest sites in early spring (e.g., four different pairs successively occupied a single nest box between 3 April and 13 May 1976).

Most bluebirds left the study area in winter; arrival dates for these birds (migrants) are the dates of initial sightings in the study area. An arrival date is not necessarily the date of territory establishment (males) or date of pair bond formation (males and females). A few bluebirds (non-migrants) wintered in and around the study area; I considered their arrival dates as the earliest dates after which I regularly saw them in the breeding areas.

Clutch size refers to completed clutches only; I followed Zwickel (1975) in considering clutches complete "if incubation was underway, or in a very few cases, almost certainly underway" provided there was no subsequent increase in the number of eggs present in the nest. Date of onset of general laying (GLD) is defined as the earliest date of a season on which two or more females laid their first eggs, and the mean GLD date is the average of the general laying dates for the nine years of study. I divided the nesting season into three successive periods: spring, intermediate, and summer. The spring period was further divided into a pre-mean GLD period (clutches initiated before the mean GLD), an early spring period, and a late spring period. The summer period was divided into an early summer period and late summer period.

I considered a nest successful if at least one young fledged. Inclement weather and predation were the common causes of nesting failure. Predation pressure (P_p) is the average number of nests lost to predators per day per year (Robertson 1973); weather pressure (W_p) is the average number of nests lost to inclement weather per day per year. I computed the average daily rate loss (m) for each nesting stage from Ricklefs' (1969) formula:

$$m = -(\log_e P)/t,$$

where P is the proportion of nests still active after each stage to the number of nests active when each stage begins, and t is the length of each stage in days.

All birds were aged by reference to the date of banding, and age designations follow standard banding terminology. Second year (SY) birds are yearlings in their first full breeding season after hatching, and after-second-year (ASY) birds are those in at least their second full breeding season. For summer-

nesting adults, I distinguished between birds that previously reared a brood to fledging (group PRB) in the same breeding season and those that did not previously rear a brood to fledging (group NPB).

The sex of nestlings was determined by the amount of blue on the primaries, secondaries, primary coverts, and rectrices, and the extent of the white edging on the outer rectrices (Bent 1949, Pinkowski 1974a). The primary sex ratio (proportion of sexes at fertilization) is the sex ratio in nests where all eggs hatched and all nestlings survived until the date of sexing (12–18 days after hatching), and the secondary sex ratio (proportion of sexes at hatching) is the sex ratio in nests where all young that hatched survived to the date of sexing (Kessel 1957). The fledgling sex ratio is the proportion of the sexes at the time of nest departure (18–22 days after hatching).

I determined survival rate by following family groups from fledging until independence of the young at an age of 35–40 days (Pinkowski 1975a). Familial attachments are strong in bluebirds during the post-fledging period, and juveniles out of the nest form cohesive units (Pinkowski 1975b, 1976b); these considerations greatly facilitated analysis of fledgling survival. Juveniles were counted on three separate occasions for each brood during a 48-h period and, if the counts agreed, I accepted this number as the number of survivors. Sample size was limited by time availability (all spring broods fledge at about the same time), terrain (fledglings in more wooded areas were more difficult to count than those in open areas), and adult behavior (some adults moved out of the study area at about the time the young became independent).

I obtained ten bluebirds from the study area and bred them in captivity during 1970–1973. These captive birds were obtained as nestlings from different nests and hand-reared to independence. The breeding cages and food of the captive birds are described elsewhere (Pinkowski 1975c, 1976c). Two of 24 nests in captivity were artificially terminated to study the subsequent behavior of the adults; seven other nests failed when the female deserted for no apparent reason. Fifteen nests were successful, and all but 1 of 50 young fledged survived to independence. Juveniles reared in captivity were left with their parents until self-feeding was established, but most adult birds began new nests well before the young were independent.

Unless otherwise stated, I compare pairs of mean clutch and brood sizes by the Mann-Whitney U-test and two-tailed *P*-values are given. Intra-seasonal (spring, intermediate, and summer) clutch sizes and inter-seasonal (1968–1976, inclusive) clutch sizes are tested for significant differences by a chi-square analysis on the pooled frequency distributions of clutches larger than average (5–6 eggs) and smaller than average (2–4 eggs). Chi-square values are corrected for continuity. Data expressed as proportions are examined for a linear trend by a test described by Snedecor and Cochran (1967:246–248). Temporal analysis of arrival and egg-laying dates was accomplished by assigning a day number to each sampled event (Robertson 1973). Descriptive data are expressed in the form " $\bar{x} \pm SD$."

RESULTS

ARRIVAL CHRONOLOGY

Each year some bluebirds wintered in the study area and others migrated, apparently to

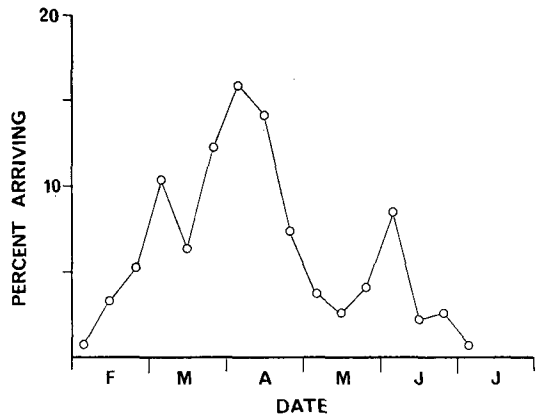


FIGURE 1. Percentage of Eastern Bluebirds arriving in the study area over 10-day periods, 1969–1976, based on 270 birds whose arrival dates were known (± 1 day).

the southern United States (Pinkowski 1971). Of 61 birds with known histories breeding in the study area, 18 (29.5%) were non-migrants and 43 (70.5%) were migrants. During winter, non-migrants occasionally roosted in the nest boxes available in the study area, but I seldom saw them in the areas used for nesting except when they entered and left roost sites.

The greatest influx of birds into the study area occurred between 20 March and 20 April (Fig. 1). A large influx also took place in early June, when young of first broods left the nest. Most non-migrants arrived on territories between 20 February and 10 March (range, 6 February–18 March); migrants first appeared in early March (earliest, 29 February) but were not common until late March and early April. Thus, relatively few birds entered the study area in mid-March and non-migrants arrived earlier than migrants.

Previous nesting success was important in determining attachment to an area on an inter-seasonal basis. All adults that returned to breed in the study area for a second consecutive year had nested successfully in the first year ($n = 47$, including 10 non-migrants).

Bluebirds arriving in the study area after 20 April came from areas adjacent to the study area and did not appear to be returning migrants. ASY males rarely appeared after 20 April (Table 1), but females and SY males did arrive after that date; some of the late arrivals (especially ASY females) undoubtedly had already attempted nests elsewhere because after 20 April some bluebirds left the study area following nest failures.

Arrival dates of birds of known age appearing before 20 April did not differ for ASY and SY males (mean dates, 22 March and 21

TABLE 1. Arrival chronologies of second year (SY) and older (ASY) bluebirds.

	No. arriving before 20 April		No. arriving after 20 April	
	SY	ASY	SY	ASY
Males ^a	20	35	5	1
Females	8	9	7	7

^a Proportions of two age classes arriving before and after 20 April is significantly different (Fisher exact test, $P < 0.05$).

March, respectively) or females (24 March and 18 March). The similarity of arrival dates for SY and ASY birds is not surprising because some adults wintered with their offspring and entered the study area as a family group. Two ASY males, for example, arrived in the company of male offspring as early as 14 February 1976 and 26 February 1974.

All ASY males established territories immediately after their arrival. Four SY males, however, arrived before 20 April but established territories after that date. Consequently, the proportion of ASY males among males establishing territories was significantly greater before 20 April than afterward ($\chi^2 = 13.6$, $P < 0.01$), and the mean date of territory establishment for SY males (24 April) occurred 33 days after the mean date of territory establishment for ASY males (22 March).

Male bluebirds are not always invincible on their territories (Thomas 1946, Krieg 1971: 83). On three occasions I observed a male arrive in the spring and drive out one that had arrived earlier. In each case an ASY male returned to the territory it had occupied the year before and reclaimed the area. SY males were not seen usurping territories in spring, but in summer they sometimes drove off other males (observed once) or claimed territories that were abandoned by males that already nested successfully (observed three times).

Most females became paired and thus entered the breeding population soon after arrival; for SY females the mean pairing date was 17 April, one week earlier than the mean date of territory establishment by SY males. Three SY birds, all males, remained in the study area but did not establish territories and breed for an entire season; at least two of them had male broodmates who bred as yearlings. Thus, despite individual variation in the onset of breeding among males and similar migration chronologies of yearling males and females, female bluebirds entered the breeding population earlier than males.

Mating status upon arrival was known for 134 males, 71 (53.0%) of whom were paired

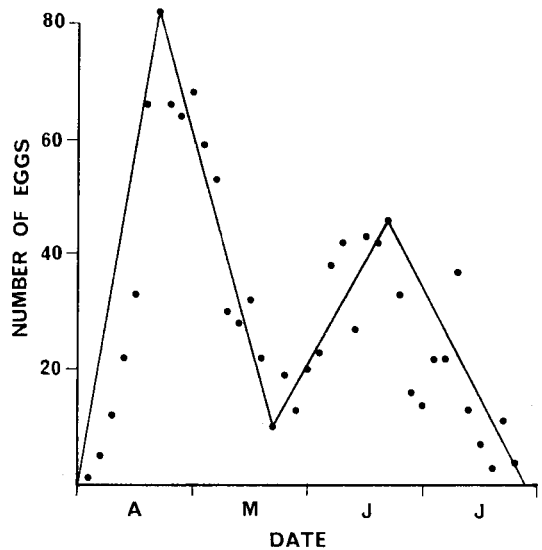


FIGURE 2. Number of eggs laid per 3-day period, 1968–1976, including incomplete clutches ($n = 1,348$ eggs). The lines connect extreme values.

before they arrived. Males arriving before the peak influx of migrants (1 April) were paired when they arrived less often (43.5%) than males arriving later (63.1%; $\chi^2 = 4.5$, $P < 0.05$). For 16 males of known age that arrived unpaired, pairing occurred an average of 8.4 days after territory establishment and initiation of mate searching behavior (singing from high perches; Pinkowski 1974a). The interval between arrival and pairing was significantly longer for SY males (12.8 days) than ASY males (5.6 days, one-tailed t -test, $P < 0.05$).

PHENOLOGY OF THE BREEDING SEASON

No bluebirds in my study area reared three broods, although some females laid three sets of eggs. Clutches were initiated over a 108-day period between 6 April (1973) and 23 July (1974).

Two peak periods of egg-laying centered on about 23 April and 21 June (Fig. 2), reflecting the tendency towards two broods per season. The overall shape of the egg-laying curve is similar to the curve for percentage of nests found measured against time in Pennsylvania by Peakall (1970), although his ratio of spring to summer peaks for nests was nearer unity (approximately 1.0:0.87) than mine (1.0:0.56). The peak for spring clutches was high and narrow, indicating good synchronization. As discussed below, the summer peak was short and broad due to: (1) the staggered arrival of new birds late in the season; (2) the asynchronous reneating of pairs whose previous nests had failed; and (3) unequal

periods of time between successful spring nests and the initiation of second nests by different adults.

The average date of the first egg laid per season was 14 April (range, 6–26 April), and the mean GLD occurred 6 days later on 20 April (range, 11–28 April). All bluebirds who raised two successful broods started their first clutches in the spring nesting period (6 April–14 May) and second clutches in the summer nesting period (7 June–23 July). In some years (1972, 1974, 1975) I observed two distinct peaks for egg-laying, and these occurred in the early and late spring periods.

Birds who nested during the intermediate period (15 May–6 June) had not already nested successfully (some had previously attempted nests and others had not); they did not rear a second brood if they were successful, and although two pairs attempted to do so, both of the exceptions were unusual in other respects. One female began a successful clutch on 17 May, laid a single egg in a summer nesting, and then deserted; the other began a successful clutch on 19 May and then laid three infertile eggs in summer.

The average date on which the final clutch of the season was begun was 14 July (range, 30 June–23 July). I found no difference in the variances of dates on which first and last clutches of each of the nine seasons were initiated ($P > 0.3$). Also, dates on which first clutches of a season were begun did not correlate with dates on which final clutches of the same season were begun ($P > 0.5$). In view of the wide range of dates for the onset and termination of breeding, however, the intermediate period was remarkably constant from year to year.

I divided the spring breeding period into three time intervals on the basis of the nesting history of the adults and their subsequent behavior in the event of a nest failure. The pre-mean GLD period consisted of nests attempted by females laying before 20 April. The eight known instances of nest failures in which the adults subsequently reared two broods (and hence re-nested before 15 May) occurred in this period. Two females that laid incomplete clutches in the pre-mean GLD period re-laid in the early spring period; six females that laid complete clutches in the pre-mean GLD period and re-nested in spring began replacement clutches in the late spring period. By contrast, all adults nesting in the early spring period (20–28 April) and late spring period (29 April–14 May) re-nested after 15 May if their nests failed and thus reared one brood at most.

The summer period was divided into an early summer period (7 June–9 July) and a late summer period (10–23 July) with reference to arrival dates of the nesting adults. New birds were still entering the study area during the early summer period (Fig. 1), but not in the late summer period. All birds nesting in late summer had previously attempted nests in the study area, and 21 (87.5%) of those whose histories were known had previously nested successfully.

SY birds predominated in the late spring period; ASY birds predominated in the two earlier spring periods. SY birds comprised 3 (13.0%) of those birds of known age nesting in the pre-mean GLD period, 6 (30.0%) in the early spring period, and 14 (53.8%) in the late spring period; the linear trend in the proportion of SY to ASY birds nesting during the successive spring periods is significant ($P < 0.01$). Consequently, the mean date of the first egg of spring-nesting SY females was 30 April compared with 19 April for ASY females, and the difference of 11 days is similar to a corresponding figure of 9 days observed for bluebirds nesting in Tennessee by Laskey (1943).

The rapidity with which a female began nesting in spring appeared to be influenced by the age of the male. Two SY sibling females appeared in the study area in early March 1976. One of the females paired with a four-year-old male and began laying on 14 April; the other female paired with a SY male and did not lay her first egg until 7 May. Altogether, females mated to SY males began laying six days later (mean date = 28 April) than females mated to ASY males (22 April).

RATE OF LAYING AND CLUTCH SIZE

Although Eastern Bluebirds normally lay one egg per day (Hartshorne 1962), White and Woolfenden (1973) observed an interval of more than one day between successive eggs of some clutches and noted that this was most common early in the season. For nests I checked daily from before to after the egg-laying period, 3 of 20 females (15.0%) laying before mean GLD laid one egg, ceased laying for a time (2–10 days), and then laid the complement of a normal clutch (4 to 6 eggs). Irregular egg-laying occurred in only 2 of 74 clutches (2.7%) begun after mean GLD and thus was most common in early spring when short-term food (insect) shortages were most likely to occur.

Mean clutch size was nearly identical in the three spring periods, decreased slightly

TABLE 2. Variation in bluebird clutch size with nesting period.

Nesting period	Number of clutches with					Mean \pm SD (n)
	2 eggs	3 eggs	4 eggs	5 eggs	6 eggs	
Pre-mean GLD	0	2	6	20	3	4.77 \pm 0.72 (31)
Early spring	1	1	6	30	1	4.74 \pm 0.68 (39)
Late spring	0	2	10	31	4	4.79 \pm 0.66 (47)
Intermediate	0	0	17	16	1	4.53 \pm 0.57 (34)
Early summer	1	8	48	21	1	4.17 \pm 0.67 (79)
Late summer	1	4	3	0	0	3.25 \pm 0.89 (8)
TOTAL	3	17	90	118	10	4.48 \pm 0.75 (238)
% of all clutches	1.3	7.1	37.8	49.6	4.2	

in the intermediate period, and declined rapidly in the summer periods (Table 2). Although the frequency distributions of clutch sizes were significantly different in the spring, intermediate, and summer periods ($\chi^2 = 49.9$, $P < 0.001$), mean annual clutch sizes were fairly constant (4.28–4.75) and the annual frequency distributions in clutch sizes were homogeneous ($\chi^2 = 1.8$, $df = 8$, $P > 0.9$). White and Woolfenden (1973) also noted that bluebird clutch size varied little from one year to another.

I found no difference in the mean clutch size of SY females (4.53, $n = 19$) compared with ASY females (4.72, $n = 25$; $P > 0.3$). Laskey (1943) obtained similar results for female bluebirds nesting in Tennessee, where both age groups averaged five eggs per clutch. Also, I found no difference in the mean clutch size of females paired with SY males (4.69, $n = 16$) and females paired with ASY males (4.49, $n = 53$, $P > 0.3$). Finally, no significant difference ($P > 0.1$) was found in the mean clutch size of females that were hatched or had nested in the study area in previous seasons (4.63, $n = 38$) compared with females spending their first season in the study area (4.46, $n = 200$), and mean clutch size was nearly identical in females paired with males that did (4.54, $n = 69$) and did not (4.46, $n = 169$) spend a previous season in the study area ($P > 0.7$). Thus, clutch size did not vary according to age class or length of time spent in the study area.

NESTING SUCCESS, SEX RATIO, AND FLEDGLING SURVIVAL

Nesting success was greater in the intermediate period than in the spring and summer periods (Table 3); it was lowest at the extremities of the breeding period, i.e., in the pre-mean GLD period (11 of 36 nests successful, 30.6%) and the late summer period (6 of 13 nests successful, 46.2%). Brood size, however, was largest in spring and declined thereafter.

Thus, despite the lengthy season and the lower success rate in the spring period than the intermediate period, most young (296 of 590, 50.2%) were fledged from clutches begun during the spring period, which made up but 39 days (36.1%) of the season.

Predators were the principal cause of nesting failures. Of all nest failures, 31 (23.3%) were attributable to House Wrens (*Troglodytes aedon*), who often entered the cavity and punctured or removed the eggs. Twenty-five (18.8%) of the failures occurred because of predation by raccoons (*Procyon lotor*) and other mammals, and 19 (14.3%) were attributable to inclement weather (cold conditions most common early in the season).

Seasonal patterns of predation are known to influence the timing of breeding in single-brooded species (Robertson 1973), but their effect on a multi-brooded species like the bluebird is more complex. Predation pressure (P_p) increased during the three consecutive spring periods ($P_p = 0.030$, 0.037, 0.056, respectively) and was greatest in early summer (0.114) when most (83.9%) House Wren predation occurred. Thus, an early start in breeding may be selectively favored to minimize predation, but weather pressure (W_p) was greatest early in the season ($W_p = 0.119$, 0.062, and 0.072 for the consecutive spring periods and 0.000 thereafter). Combined weather and predation pressure ($W_p + P_p$) was lower in the intermediate period (0.024)

TABLE 3. Bluebird nesting success compared with nesting period.

Nesting period	No. nests	No. success-ful	Percent successful	Brood size	
				Mean \pm SD	(n)
Spring	141	74	52.5	4.11 \pm 1.17	(72)
Inter- mediate	39	27	69.2	3.76 \pm 1.05	(25)
Summer	119	65	54.6	3.28 \pm 1.08	(61)
TOTAL	299	166	55.5	3.73 \pm 1.13	(158)

TABLE 4. Frequency of bluebird nesting failures compared with stage of nesting cycle.

Nesting stage	Failures		Length of stage ^b	Daily rate loss (m) ^c
	No.	% ^a		
Nest-building	10	7.5	10.6	0.0
Egg-laying	41	30.8	3.5	4.4
Incubation	58	43.6	15.3	1.7
Nestling	24	18.0	18.8	0.7

^a Percentage of all failures recorded.

^b Given in days; see text for length of egg-laying stage (mean clutch size minus one) and Pinkowski (1974a, 1975a) for lengths of others.

^c Defined by Ricklefs (1969).

than in spring (0.086) or summer (0.085). Evidently more young can be reared with double broods although they entail more failure at the onset ($W_p > P_p$) and termination ($P_p > W_p$) of the season, than with single broods because most pairs of bluebirds are double-brooded.

Daily rate of nest loss was highest in the egg-laying stage and decreased in the incubation and nestling stages (Table 4). Such a trend is advantageous in permitting the birds to renest if a failure occurs early in the cycle before considerable time and energy have been expended (Klimstra and Roseberry 1975). The paucity of nest failures in the nest-building stage mostly reflects a lack of predator activity around nests not containing eggs or young. However, nest-building may be temporarily suspended early in the season during periods of inclement weather (Pinkowski 1974a:178); this also tends to minimize rate loss during the nest-building stage.

Natural nests comprised 27 (9.0%) of all nests observed. Although the success rate in natural nests (55.6%) was identical to that in nest boxes (55.5%), natural nests decreased in frequency as the season progressed; they accounted for 27.8% of the nests in pre-mean GLD period, 8.3% in early spring, 8.8% in late spring, 5.1% in the intermediate period, 5.7% in early summer, and 0.0% in late summer. The linear trend in decreased usage is significant ($P < 0.01$) and presumably reflects increased competition from other cavity-nesting species such as the Starling (*Sturnus vul-*

garis), Tree Swallow (*Iridoprocne bicolor*), and House Wren as the season progresses.

The lack of any correlation between clutch size and age of adults suggests that young birds may be able to rear as many young per brood as older birds. Of 48 nests involving SY birds (24 males and 24 females), 31 (64.6%) were successful, raising an average of 3.71 ± 1.18 young ($n = 28$) per brood. Fifty-eight of 95 nests of ASY birds were successful (61.1%), with the mean of 3.94 ± 1.28 young ($n = 54$) reared per successful nest not significantly different from that of SY birds ($P > 0.3$). Despite the slightly higher success rate of SY birds, none of 3 SY birds (2 females, 1 male) nesting in the pre-mean GLD period was successful although 9 of 20 ASY birds nesting in that period were successful.

Females outnumbered males by approximately 1.3:1 in each of the three computed sex ratios (Table 5). No significant difference was noted in the proportion of females in the primary ratio compared with the proportion of females at fledging ($P > 0.5$), indicating equal mortality to males and females between fertilization and fledging. The proportion of females among birds fledged in spring (53.2%), intermediate (51.1%), and summer (58.9%) periods did not differ significantly ($P > 0.3$). Of 31 unisexual broods fledged, containing an average of 3.0 ± 1.3 young each, 17 (54.8%) consisted of females and 14 of males.

A total of 154 of 189 fledglings (81.5%) from 48 broods survived to independence. At least one young survived from 46 (95.8%) of the broods. This survival rate is higher than has been reported for open-nesting passerines and near that of other cavity nesting species (Ricklefs 1972:374). Heavy rains occurred on day-of-departure for the two cases having no survivors; these involved broods with three and five young. Survival rate was highest (94.1%, $n = 17$ birds) for unusually small broods containing one or two young, but did not depend on brood size (χ^2 , $P > 0.5$). Also, I found no significant difference ($P > 0.9$) in the survival rate of 132 young fledged by SY and ASY adults.

TABLE 5. Sex ratios of nestling bluebirds.

	No. nests	No. males	No. females	% Females	P^a
Primary sex ratio	72	127	177	58.2	<0.01
Secondary sex ratio	91	152	208	57.8	<0.01
Sex ratio at fledging	142	224	282	55.7	<0.05

^a The probability that the observed ratio differs significantly from a 50:50 ratio (chi-square).

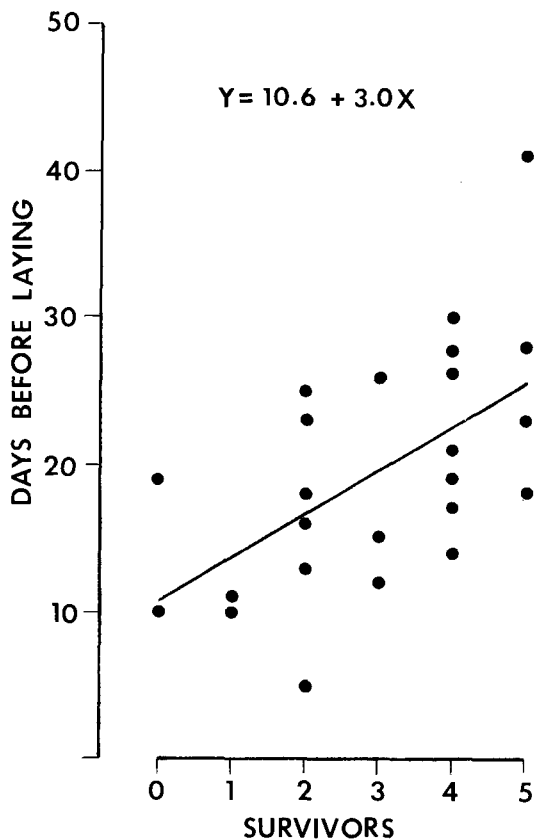


FIGURE 3. Relationship between the number of surviving juveniles in spring broods and the number of days elapsing before egg-laying began in summer. The slope of the regression is significant ($F = 11.0$, $P < 0.01$). Only pairs for which vacant nest sites were available from fledging to laying are included in the analysis.

BEHAVIOR OF ADULTS AFTER NESTING IN SPRING

Spring broods fledged between 21 May and 17 June (mean = 4 June, $SD = 7.0$ days, $n = 71$); the earliest date when I saw independent juveniles was 7 June. Adult birds who reared a spring brood renested in summer after an interval of 5 to 41 days ($\bar{x} = 19.50 \pm 8.05$ days, $n = 24$) between the fledging of the spring brood and the onset of laying. I observed females in the wild and in captivity feeding young during the nest-building stage of a subsequent nest, but not after egg-laying had begun.

Adults renested more rapidly if fewer rather than more fledglings survived (Fig. 3). Only 33.4% of the variation in the speed of re-nesting, however, was explained by the fitted regression, suggesting that other variables (such as habitat quality, weather, food availability, number of non-survivors) also influence the rapidity with which second nests are begun.

Although Nice (1930) implied that taking new mates between broods was not uncommon among bluebirds, I found that adults nesting successfully in spring usually remained paired and attempted summer nests in the same area (Table 6). Thirty-eight (77.6%) of the renestings by previously successful pairs were in the same site, including both instances where no fledglings survived, and 11 (22.4%) were in a different site. Except for one instance when the adults left the study area but the juveniles stayed, and another in which the female disappeared (Pinkowski 1976b), all young remained with the female parent (typically both parents) until mid-June or later. In one of the four cases of mate changes, both adults renested with a new mate; in the others the male renested and the female did not. All of the birds that changed mates, except the one female mentioned above, remained in the general area of the spring nesting. Thus, 139 of 140 adults nesting successfully in spring either remained paired, stayed in the same territory, or remained in the company of the juveniles.

Following an unsuccessful spring nesting, at least one adult usually left the study area (Table 6). Both adults left the study area together on 16 occasions and separately (the male's departure always followed the female's) on 8. The percentage of females departing after a nest failure in spring ($40/61 = 65.6\%$) was greater than that of males ($24/61 = 39.3\%$; $\chi^2 = 7.4$, $P < 0.01$) because in no instances did the female remain in the study area after a nest failure while the male departed; females left the study area while males stayed and renested on 16 occasions. When the pair bond persisted and both adults re-nested in the study area together, 17 (81.0%) of the renestings were in a different site and 4 were in the same site; these figures are significantly different from those of birds nesting successfully in spring ($\chi^2 = 18.6$, $P < 0.001$).

Longevity of the pair bond in bluebirds clearly depends upon previous nesting success (Table 6). At least 34.4% (21/61) and no more than 60.7% (37/61) of the unsuccessful pairs renested together, and between 70.0% (49/70) and 84.3% (59/70) of the successful pairs renested together. (The exact percentages depend upon the subsequent behavior of those birds that left the study area together.) Interestingly, if a pair of bluebirds was successful in spring and then failed in a summer nest, the pair bond was invariably preserved. This occurred in eight instances in which the pair renested, and in each case a new site was selected.

TABLE 6. Behavior of adult bluebirds following successful and unsuccessful spring nests.

Behavior of adults	Outcome of spring nest ^a	
	Successful (n = 70)	Unsuccessful (n = 61)
Remain paired and renest	49 (70.0%)	21 (34.4%)
Both leave the study area	10 (14.3%)	24 (39.3%)
At least one renews with new mate	4 (5.7%)	16 (26.2%)
Remain together but neither renews	7 (10.0%)	0 (0.0%)

^a Percentages of each behavior following successful and unsuccessful nests are significantly different ($P < 0.01$; Sokal and Rohlf 1969:607).

I obtained little information on the distances traveled by adults, especially females, after a nesting failure. A few males moved up to 3–5 km to a new territory in a new portion of the study area. None of the females that left a territory after a nesting failure in spring, however, was seen again, suggesting that they move a considerable distance and the trip is irreversible. L. Kibler (pers. comm.) found a female Eastern Bluebird that moved 19 km after deserting a nest, and Scott (1974) reported a female Mountain Bluebird (*S. currucoides*) that traveled 208 km in one week after deserting a nest.

CRITERIA FOR DETERMINING NESTING HISTORY OF BLUEBIRDS BREEDING IN SUMMER

As already noted, some bluebirds breeding in the study area during summer had previously reared a brood (group PRB), whereas others had no previous brood (group NPB). We would expect relatively few summer pairings of PRB × NPB birds because of mate tenacity in PRB birds, and NPB birds would be expected to predominate among late arrivals entering the study area to breed in summer because of site tenacity in PRB birds.

The history of 147 (61.8%) of the birds breeding in the study area in summer was known with certainty because these birds had been followed since their arrival in early

spring. To determine whether birds entering the study area to breed in summer had previously reared a brood, I used the following criteria: (1) birds arriving before 7 June and not in the company of juveniles were categorized as NPB; (2) birds arriving paired and with juveniles after 7 June were categorized PRB; (3) females arriving alone (not in the company of a male or juveniles) after 7 June were categorized NPB. Histories of birds not satisfying these criteria were considered unknown. None of the criteria was violated by birds with known histories serving as “test cases.” I was able to determine the nesting history of 89 of 91 (97.8%) late arrivals that entered the study area to breed in summer.

EFFECT OF NESTING HISTORY

Of 236 adults with known histories involved in the 118 summer nests, 127 (53.8%) were PRB. PRB birds included more males (67) than females (60) because of eight PRB male × NPB female pairings and only one NPB male × PRB female pairing. All but six (95.3%) of the PRB birds reared their spring broods in the study area. By contrast, only 26 NPB birds (23.9%), 20 males and 6 females, previously attempted nests in the study area.

The annual proportion of PRB birds nesting in the two summer periods (Table 7) varied from 79.4% in 1975, when the greatest number of successful spring nests (19) occurred, to 14.3% in 1969, when the fewest number (1) of successful spring nests occurred. The number of PRB birds nesting per summer was significantly correlated with the number of successful spring nests in the same year ($r = 0.917$, $P < 0.001$). Although we might expect more NPB birds during summers in which fewer PRB birds nested, I found no correlation ($P > 0.3$) in the annual numbers of PRB and NPB birds during 1970–1976, when the total number of summer nests was relatively constant. Some PRB males were observed maintaining territories and guarding nest sites even though they did not nest again, a behavior tending to negate any correlation between the relative PRB and NPB annual densities.

TABLE 7. Nesting history of bluebirds nesting in the two summer periods.

Group	Year								
	1968	1969	1970	1971	1972	1973	1974	1975	1976
Previously reared a brood (PRB)	2	2	12	17	12	14	22	33 ^a	16 ^b
No previous brood (NPB)	4	12	14	17	14	6	14	7	18

^a Includes four adults that entered the study area with juveniles.

^b Includes two adults that entered the study area with juveniles.

TABLE 8. Clutch size of females that had not previously reared a brood (NPB) and those that had (PRB) nesting in early summer.

Group	Number of clutches with					Mean ^a ± SD (n)
	2 eggs	3 eggs	4 eggs	5 eggs	6 eggs	
NPB	0	2	22	14	1	4.36 ± 0.63 (39)
PRB	1	6	26	7	0	3.98 ± 0.66 (40)

^a Means significantly different (Mann-Whitney U-test, $P < 0.05$).

PRB females predominated in the late summer period and thus laid later in the summer than NPB females. Although clutch size and nesting success declined as the summer nesting period progressed, nesting parameters can be compared for NPB and PRB females nesting in early summer because both groups occurred with near-equal frequencies throughout the early summer period. The mean dates of clutch initiation for NPB females (20 June) and PRB females (23 June) nesting in early summer were not significantly different ($t = 1.5$, $P > 0.1$).

For NPB and PRB females nesting in the early summer period, the mean clutch size of NPB females was significantly greater than that of PRB females (Table 8). PRB females laid more smaller clutches (2, 3, and 4 eggs) and fewer larger clutches (5 and 6 eggs) than NPB females.

Crowding and breeding density are known to influence clutch size in some species (Kluyver 1951, Perrins 1965, Risser 1975). If such an effect occurred among the bluebirds I observed, it may explain the different clutch size in PRB and NPB females because of the varying annual proportions of each group and the different annual breeding densities of the two groups combined. The mean clutch size of PRB females, however, did not exceed that of NPB females in any of the nine different years (they were equal in 1968, when only three clutches were recorded for both groups combined), and mean clutch size did not correlate with the total number of nesting pairs in either PRB ($P > 0.1$) or NPB ($P > 0.3$) females. The lack of a relationship between breeding density

and clutch size is not surprising because of the relative constancy of clutch size from year to year.

Nesting success was nearly identical in NPB and PRB females nesting in early summer (Table 9). PRB males were less successful than NPB males, however, mainly because PRB males did poorly in heterogeneous pairings. Of 7 PRB male × NPB female nests, only 2 were successful with 2 young fledged in each case; the only NPB male × PRB female nest was successful and 4 young fledged. Also, the only NPB male nesting in late summer was successful (4 young fledged) but only 5 of 11 PRB males nesting then were successful (average brood = 2.80 young). A single heterogeneous pairing in late summer involved a PRB male and NPB female and it was unsuccessful.

The lower success rate of PRB males was particularly surprising because NPB males appeared to be relegated to poorer habitats than PRB males. NPB males nested in 29 different sites, PRB males in 25 different sites, and 18 sites were used by males belonging to both groups. Considering only sites used by both NPB and PRB males in early summer, NPB males had greater success (82.6%, $n = 23$ nests) than PRB males (52.6%, $n = 38$ nests; $\chi^2 = 4.4$, $P < 0.05$).

It is possible that SY and ASY birds contribute unequally to the nesting composition and reproductive performance of the PRB and NPB groups. SY males and females comprised 10 of 23 NPB birds (43.5%) of known age nesting in early summer and 5 of 28 (17.9%) PRB birds. Although the difference approaches significance ($\chi^2 = 2.9$, $0.05 < P < 0.1$), the success rate of ASY birds (55.6% for 36 nests) was similar to that of SY birds (60.0% for 15 nests).

After rearing a spring brood, 21 ASY birds and 4 SY birds attempted summer nests in the study area. SY birds accounted for five of six PRB adults of known age that remained in the study area but did not reneest and three of four PRB birds of known age that left after a successful spring nest. Most birds that left

TABLE 9. Nesting success of PRB (previously raised a brood) and NPB (had not raised a brood) males and females in early summer.

Sex	Group	No. nests	No. successful	Percent successful	Brood size Mean ± SD (n)	Young fledged per attempt
Female	PRB	50	28	56.0	3.35 ± 1.02 (26)	1.88
	NPB	55	31	56.4	3.31 ± 1.20 (29)	1.87
Male	PRB	56	29	51.8	3.22 ± 1.05 (27)	1.67 ^a
	NPB	49	30	61.2	3.43 ± 1.17 (28)	2.10 ^a

^a Difference significant (Mann-Whitney U-test, $P < 0.02$).

TABLE 10. Clutch size and brood size in captive bluebirds.^a

Female number	Season ^b number	Brood		
		First	Second	Third
1	1	5(0)		
	2	5(4)	5(2)	
	3	5(5)		
2	1	5(0)	4(4)	
	2	4(3)	4(4)	
	3	5(4)	5(2)	4(3)
3	1	5(0)	5(4 ^c)	5(0)
	2	5(0)	6(0)	
4	1	5(4)	4(4)	
	2	5(0)	5(4)	
5	1	5(3)	4(0)	6(5)
Mean clutch size		4.91 ± 0.30	4.67 ± 0.71	5.00 ± 1.00

^a Clutch size with brood size in parentheses. A "0" for brood size indicates that the nest failed; all failures occurred before or on hatching day.

^b Bird is 1 year old in season 1, 2 years old in season 2, etc.

^c Includes one young that died shortly after fledging.

after rearing one brood apparently did not re-nest because vacant nest sites were available on the territories of eight of the ten departing pairs and more PRB birds were among all birds leaving the study area in late spring and summer (23.8%; Table 6) than among those entering to nest (6.7%; $\chi^2 = 8.6$, $P < 0.01$). If the four PRB birds of known age that left the area after a successful spring nest did not re-nest, then the proportion of ASY birds attempting second broods (91.3%) was significantly greater ($\chi^2 = 10.3$, $P < 0.01$) than of SY birds (33.3%).

COMPARISON OF WILD AND CAPTIVE BIRDS

Although aviary programs do not duplicate natural conditions (Zwicker 1975), many studies (e.g., Jenkins et al. 1965) have shown how instructive conclusions can be drawn when birds kept in captivity under standard conditions are compared with birds observed under variable natural conditions.

Clutches were completed in 23 of 24 bluebird nests in captivity; the mean clutch size was 4.83 ± 0.58 eggs, significantly greater ($P < 0.05$) than the mean clutch size observed in the wild. All captive SY birds nested, and I found no difference in the mean clutch size of SY (4.82) and ASY (4.83) females.

Risser (1975) observed that successive clutches of captive Starlings did not decrease in size and suggested that the failure of cap-

tive broods to survive to fledging might permit females to respond with greater physiological effort in subsequent nestings. I observed a similar trend in clutch size among bluebirds (Table 10), although many nests were successful and young reached independence. The failure of clutch size to decline seasonally in captive birds explains much of the overall difference in mean clutch size of wild and captive birds (Tables 2 and 10).

Analysis of successive clutch and brood sizes for captive birds attempting at least two broods during a season indicated that mean clutch size was significantly greater if the previous nest was unsuccessful (5.20 ± 0.84 , $n = 5$) than if the previous nest was successful (4.43 ± 0.53 , $n = 7$); despite the small samples, the difference approaches significance ($P < 0.1$), reminiscent of the results obtained from PRB-NPB birds in the wild.

All but 1 of 50 young fledged in captivity survived to independence, and the survival rate of fledglings reared in captivity (98.0%) was greater than that of fledglings reared in the wild ($\chi^2 = 7.2$, $P < 0.001$). Evidently most mortality in fledglings exposed to natural conditions is due to environmental factors, especially weather. The interval from fledging to egg-laying between successive broods in captivity ranged from 4 to 11 days and averaged only 7.86 ± 2.91 days, significantly less than that observed in the wild (Mann-Whitney U-test, $P < 0.001$). One captive female (number 2; Table 10) reared three broods during one breeding period although this was not observed in the wild.

DISCUSSION

BREEDING STRATEGY

Natural selection would seem to favor an early start in bluebird nesting because: (1) nests in the spring are more productive than those in the intermediate or summer periods; (2) nest sites become increasingly scarce as the season progresses; (3) only pairs nesting early (before general laying) can still rear two broods in the event of a nest failure; and (4) predation pressure is less early in the spring period than late in spring and in summer. The greater nesting success of ASY than SY birds nesting in the pre-mean GLD period and the earlier breeding of ASY birds suggest that older birds are better able to exploit the advantages of early breeding and are less affected by poor weather, the cause of most nest failures early in the season. Accordingly, ASY birds rear two broods more often than SY birds, but nesting parameters are nearly

equal in SY and ASY bluebirds compared on a nest-for-nest basis.

SY males establish territories later than most ASY males. Lack (1968:304) suggested that this occurs to prevent "young males from occupying places from which they will later be dispossessed by the returning owners." Among bluebirds, however, nest site tenacity is very dependent on previous nesting success, both on an inter- and intra-seasonal basis. The delayed breeding by SY males and the dependency of site tenacity on previous success may function to assure the most successful males of a previously successful nest site, thereby maximizing reproductive output. Although pair bond longevity also depends on previous success, severance of a pair bond by the female is more interpretable as a rejection of a territory (toward which some males are more attached than others) than rejection of a mate.

Morton (1976) suggested that selection may favor an early migration in bluebirds because this species has a limited number of nest sites. Unexplained, however, is the early arrival and occasional non-migratory behavior of yearling males that breed relatively late, and the fact that some bluebirds migrate and others do not. Individual bluebirds may migrate in some years but not others (Pinkowski 1976b), and I found that adult bluebirds wintered in the same area used for nesting during the previous year only if they had nested successfully. These non-migrants, therefore, are also reflecting the dependency of site tenacity on previous success. Moreover, non-migrants are assured of a nest site because they are able to establish territories before migrants arrive.

SY non-migrants usually spend the winter with their parents and may remain with the adults until nesting begins in spring (Pinkowski 1974b). If yearlings are not as efficient as adults at obtaining food, roosting sites, etc., then the SY birds may benefit from an association with older birds during winter and early spring, when extreme weather conditions are most likely to occur.

Pair bonds involving SY males form less rapidly than those involving ASY males, suggesting that females pair with males who are most ready to breed. That some SY males breed whereas others, including siblings of breeders, do not breed suggests that external factors such as weather and the availability of territories and nest sites may influence the speed with which young males enter the breeding population. All yearling males would be expected to breed under ideal nesting conditions (abundant nest sites, vacant

territories, favorable weather) because all captive males breed as yearlings.

BIOENERGETIC AND DEMOGRAPHIC EFFECTS

The nesting history of multi-brooded species has not hitherto been demonstrated as one of the many factors influencing clutch size (Lack 1954, 1966, Cody 1966, Ricklefs 1968, 1972, Klomp 1970, Fretwell et al. 1974). The larger clutch size of NPB than PRB females appears unrelated to age structure, breeding density, and date of laying, factors that explain about 70% of clutch size variability in the Great Tit (Perrins 1965, Perrins and Jones 1974).

Female bluebirds who do not rear a brood early in the season are presumably able to lay more eggs (as told by their larger clutches) than females who have already raised a brood. This may occur if females not rearing an early brood are in better physiological condition than females that already reared a brood, but other possible explanations exist for the different clutch sizes. Habitat quality, for example, may affect clutch size. Although the habitats of PRB birds may have been inferior to those of NPB birds, this is not supported by the nesting success data on PRB and NPB males using the same nest boxes. Furthermore, it is contrary to the generally accepted hypothesis that the earliest arriving birds choose the best habitats (Glas 1960, Brown 1969, Welsh 1975). The earliest arriving bluebirds, which later in the season comprised most PRB birds, exhibited greater selectivity than late arrivals in choosing nest sites (Pinkowski 1977) and evidently chose sites located in the best habitats. NPB females (and males) arrived relatively late in the season and occupied poorer habitats than PRB females. Furthermore, NPB females may have been at a disadvantage compared with PRB females because they were less familiar with their territories, but I found no evidence for this inasmuch as clutch size did not depend on whether or not adults had spent a previous season in the study area.

Food availability is known to affect clutch size (Cody 1966, Lack 1966), and although prey could be reduced on the territories of PRB birds because juveniles of spring broods usually remain with the female until a new clutch is begun, this seems unlikely. Bluebird foods differ in spring and summer (Pinkowski 1978) and, in the aviaries, clutch size declined after a brood was raised even though food was abundant and juveniles were fed until the onset of egg-laying. Moreover, blue-

birds do not respond to food shortages early in the season by reducing clutch size.

It also seems unlikely that clutch size is adaptively reduced in PRB females because of future time and energy demands placed on the parents by the young of the first brood. Female bluebirds cease caring for the first brood when a new clutch is begun and males rarely feed juveniles of a first brood after the young of the second brood have hatched. Juveniles often leave the natal territory (Pinkowski 1974a) by the time young of the second brood hatch or, if they remain, they may even assist in feeding the young of the second brood (Wetherbee 1933, Laskey 1939, Pinkowski 1975b).

The bluebird, like many passerines, is a determinant species that lays only a limited number of eggs per clutch (Nash 1942, Pinkowski 1974a). Holcomb (1974) raised the question of whether determinant species also have a limited number of ova that will develop into eggs for an entire nesting season. Were this the case, it would explain the larger clutches of some NPB females who may have been attempting their first nests of the season. However, if the number of ova available to form eggs is limited, clutch size would be reduced in females reneesting after a failure. I found that eight females reneesting after failures laid the same number of eggs in the second clutch as in the first; one female increased and another decreased the number of eggs by one. Thus, the NPB-PRB clutch size difference is probably not attributable to a difference in egg-laying capability related to the number of ova available to form eggs.

The hypothesis that breeding costs energy and reduces the physiological condition of adults is, therefore, supported by my data. By rearing an early brood, PRB females incur time and energy expenses additional to those involved in self-maintenance; these expenses are not incurred by NPB birds. The physiological condition of PRB birds is thereby reduced and clutch size declines. Although nesting success and failure are not sharply defined categories in a bioenergetic sense, most unsuccessful bluebird nests fail early in the cycle and most fledglings survive to independence, considerations which sharpen the dichotomy between success and failure.

If female bluebirds that reared an earlier brood are not able to lay as many eggs as females that did not, then it follows that the species has an inheritable tolerance of a reduction in physiological condition for the sake of reproduction. Such a tolerance has been indirectly demonstrated (mostly by weight

change) for several species (Breitenbach et al. 1963, Hussell 1972). It appears phenotypically in bluebirds in the form of reduced clutch size of PRB females and would seem more advantageous in secondary cavity-nesters than primary (excavating) cavity-nesters or open-nesting species. A breeding pair of a secondary cavity-nesting species occupies one of a limited number of nest sites, the distribution of which is somewhat fortuitous. Selection may favor behavior resulting in a greater reproductive effort by these birds (Williams 1966).

Female bluebirds respond with greater effort than males to factors (such as mate disappearance) that increase the hunger of the young (Pinkowski 1974a:240, 248). This observation, together with the reduced clutch size of PRB females and the relatively low success of PRB males compared with PRB females and NPB males, suggests that female bluebirds may be more tolerant than males of impaired physiological condition for the sake of reproduction.

Reproductive performance is often related to adult survival in that any physiological strain resulting from breeding is reflected in decreased adult survivorship (Kessel 1957, Anthony 1970, Ricklefs 1974). Reduced survivorship as a result of breeding in female bluebirds compared with males may occur because of energetic strain on the female resulting from egg-laying (King 1973), incubation (Kendeigh 1963, Drent 1970), or the female's greater role in the care of nestlings (Pinkowski 1978). If the differential expense of breeding between male and female bluebirds is reflected in a lower survival rate in females, it appears to be partially compensated for by an unbalanced sex ratio. Moreover, an earlier entry of females into the breeding population has been equated (Cody 1971) with a greater cost of reproduction to females and a resulting higher turnover of females than males. These demographic considerations support the thesis that the reduced PRB clutches result from bioenergetic expenses involved in raising a brood.

SUMMARY

Adaptations in the breeding of Eastern Bluebirds were studied in southeastern Michigan during 1968–1976. No temporal differences were found in the arrival pattern of yearlings compared with adults, but yearlings (especially males) began nesting later, sometimes ceased breeding earlier, and reared fewer young per season than adults. Otherwise, nest-

ing parameters (clutch size, nesting success, brood size, and fledgling survival) were not significantly different for the two age groups.

Females not rearing a brood earlier in the same season laid larger clutches than those having a previous brood. Nesting success was equal in females that did and those that did not have an earlier brood. Males that did not have an earlier brood had greater success although they appeared to be restricted to poorer habitats. The reduced clutch size of females already successful may result from impaired physiological condition, a consequence of rearing an earlier brood. Tolerance for reduced physiological condition for the sake of reproduction would seem desirable in secondary cavity-nesters, although it does not appear to be as great in male bluebirds as in females.

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