ANNUAL PRODUCTIVITY AND ITS MEASUREMENT IN A MULTI-BROODED PASSERINE, THE EASTERN BLUEBIRD

BENEDICT C. PINKOWSKI

*Ecological Sciences Division, NUS Corporation, 1910 Cochran,
Pittsburgh, Pennsylvania 15220 USA*

ABSTRACT.—Breeding and demographic parameters are examined for 434 Eastern Bluebirds (*Sialia sialis*) attempting 324 nests in southeastern Michigan during 1968–1977. Nesting birds spent an average of 10.4 weeks (63.9% of a 16.2-week season) in the study area. Only 154 (35.5%) of the nesting birds remained for entire breeding seasons; these season-long residents averaged 2.14 nests/season and had a higher success rate (68.4%) and presumably greater productivity (5.6 young·pair^{-1}·season^{-1}) than other birds because site fidelity depends on nesting success.

Although two seasonal peaks for egg-laying were observed, only 75 of 357 birds (21.0%) successfully raised two broods. Evidence is presented to suggest that birds observed for only part of a season initiated nests at the same rate while in and not in the study area, so that an average annual productivity value of 5.0 young·pair^{-1}·season^{-1} is calculated for all nesting birds from the observed success rate (57.1%) and mean length of stay in the area. Estimated average productivity of yearlings (4.3 young·pair^{-1}·season^{-1}) was lower than that of adults (5.7 young·pair^{-1}·season^{-1}) although nesting success rates were similar in the two age groups. *Received 12 June 1978, accepted 29 March 1979.*

DESPITE a wealth of information on certain readily obtained parameters of avian demography such as clutch size, nesting success, and survival rate (Hickey 1952, Nice 1957, Ricklefs 1969), little information is available on some other parameters, especially annual production of young (young fledged·pair^{-1}·season^{-1}). Ricklefs and Bloom (1977) indirectly calculated mean annual productivity for several avian species by employing the more readily obtained parameters, and for some species it may be possible to calculate productivity from changes in the sex ratios over a period of time (Dale 1952, Hanson 1963). Productivity has also been directly observed in tractable, relatively closed populations of sedentary species with short breeding seasons (Austin 1977). Most passerines, however, are not sedentary, and many have long breeding seasons, considerations that make following individual birds over long periods of time difficult or even impossible. Moreover, in some species nest site and territory fidelity are dependent on nesting success (Nolan 1966, Darley et al. 1977, Pinkowski 1978), so that individual birds remaining in an area for prolonged periods of time are apt to be more productive than an entire population.

During recent investigations of a breeding population of Eastern Bluebirds (*Sialia sialis*), I found that the birds present in the study area at any time were the result of earlier movements of birds into and out of the area (Pinkowski 1977). Analysis of arrival and departure data suggested that many of the late arrivals may have had intraseasonal nesting histories similar to those of the departing birds. If this hypothesis is correct, then it is possible that mean annual productivity of all birds using the study area at one time or another could be estimated by projecting values based on individuals present and observed for only part of a season.

In this report I summarize Eastern Bluebird breeding parameters obtained during the 10-yr study, present evidence supporting the symmetry of intraseasonal nesting histories of birds entering and leaving the study area after the start of a season, and estimate mean annual productivity of all birds breeding in the study area at one

time or another. A categorization of nesting birds into four demographic groups is suggested as a useful approach for analyzing population data for bluebirds and other multi-brooded passerines.

MATERIALS AND METHODS

The study area, 200 km² of old fields and oak (*Quercus* spp.) woodlands in Macomb County, Michigan has been described in detail elsewhere (Pinkowski 1975, 1976, 1977). Approximately 50 nest boxes were available for each breeding season, and bluebirds nested in these as well as natural cavities present in the area. Nest boxes were placed on posts in relatively open areas and checked every 1–3 days during the breeding season. A thorough search for birds and natural nests was made in areas containing nest boxes at least once or twice each week, and a bird's length of stay in the study area was always known to the nearest week. I found it easy to determine bluebird arrival and departure dates because this species forages in relatively open terrain. Unmated males sing loudly from conspicuous perches to advertise for a female, but they become less vocal after females arrive and pairing takes place; these behaviors also facilitated keeping track of the birds' movements in and out of the study area.

A few of 28 nests in natural cavities were inaccessible; otherwise, all adults and their young were color-banded. Birds that were banded in the study area in previous seasons could be aged as yearlings (birds in their first breeding season) or adults (birds in at least their second breeding season); ages of unbanded birds were unknown. Many adults attempted 2 broods while in the study area, and a few individuals attempted 3 or more, but no birds successfully reared more than 2 broods (Pinkowski 1977). All double-brooded pairs initiated clutches in a very synchronous Spring nesting period (6 April–14 May) and a less synchronous Summer nesting period (7 June–23 July); pairs breeding in an Intermediate period (15 May–6 June) reared one successful brood per season at most. All birds entering the study area without juveniles before 7 June, the earliest date on which independent fledglings were observed, were presumed to have not reared a previous brood; criteria for determining whether other birds nesting in Early Summer (7 June–9 July) had previously reared a brood (*Group PRB*) or not (*Group NPB*) are summarized by Pinkowski (1977). Birds initiating clutches in Late Summer (after 9 July) either had a previously successful nest in the study area or their histories were unknown.

Nesting birds were classified into four demographic groups according to length of stay in the area. In assigning birds to demographic groups I considered an individual as present at the start of the season if it was seen before 15 May; birds were considered present at the end of a season if they were observed after 23 July. Season-long residents (*Group SLR*) were birds present at both the start and end of breeding seasons. Birds that were present in the study area before 15 May but left before 23 July were considered as present at the start of the season only (*Group SSO*), and birds that entered the study area after 15 May but remained until after 23 July were classed as present at the end of the season only (*Group ESO*). Some birds entered the study area after 15 May and left before 23 July and thus were present at neither the start nor the end of the season (*Group NSE*).

Members of a nesting pair of adults were often in different demographic groups or age classes. In making comparisons between groups and age classes I counted each nesting attempt and outcome (success or failure, number of young fledged) as a separate record for both nesting adults. This procedure was considered preferable to dividing each nest record between the two adults, because it permitted me to express productivity in terms of young·pair⁻¹·season⁻¹ and to avoid meaningless results involving partial nests or young. Although some bluebirds nested in the study area for as many as five different seasons (Pinkowski 1978), I considered one individual as a bird present for any part of one season, and the same bird present for two seasons as two birds, etc. Nonbreeders were omitted from the analysis, and birds killed during a season were considered present for the remainder of the season because the aim of this analysis was to determine the number of young produced by the breeding population present at the start of the season. Approximate length of the breeding season was calculated from MacArthur's (1964) formula: $B = 30 \exp(-\Sigma\, p_i \ln p_i)$, where B is the season length in days adjusted for an unequal distribution of breeding intensity, and p_i is the proportion of clutches initiated during the ith month (Ricklefs and Bloom 1977).

RESULTS

Group composition.—A total of 434 birds nested in the study area during 1968–1977. More of these birds were females (227, 52.3%) than males (207, 47.7%) because after nest failures some males remain on their territories while females leave (Pinkowski 1977). Males comprised 81 of 154 (52.6%) of the birds in Group SLR, and

TABLE 1. Yearly variation in nesting parameters of a population of Eastern Bluebirds.

Year	Number of birds	Number of nests	Eggs laid[a]			Successful nests		Young fledged		
			Number of eggs	Number of nests	Number per nest	Number	Per-centage[b]	Number of young	Number of nests	Number per nest
1968	14	8	38	8	4.8	8	100.0	35	8	4.4
1969	29	19	79	19	4.2	6	31.6	21	6	3.5
1970	40	27	109	27	4.0	9	33.3	35	9	3.9
1971	49	34	130	34	3.8	20	58.8	64	19	3.4
1972	56	38	155	38	4.1	22	57.9	84	21	4.0
1973	52	36	145	35	4.1	23	63.9	75	22	3.4
1974	49	39	136	37	3.7	20	51.3	67	19	3.5
1975	58	49	182	44	4.1	34	69.4	123	32	3.8
1976	58	49	190	48	4.0	24	49.0	88	22	4.0
1977	29	25	103	24	4.3	19	76.0	68	19	3.6
Total	434	324	1,267	314	4.0	185	57.1	660	177	3.7

[a] Includes partially completed clutches.
[b] Percentage of nests resulting in at least one young fledged.

although females predominated in Group SSO (68 females:60 males), Group ESO (66:53), and Group NSE (20:13), none of the differences in sex composition of the four groups is significant (χ^2, $P > 0.2$ in each case).

Banding returns permitted limited insight into the age and origin of some members of the various demographic groups. More of the 89 birds that returned to the study area after having been banded there in an earlier season were in Group SLR (56, 62.9%) than the other groups combined (33, 37.1%; $\chi^2 = 29.2$, df = 1, $P < 0.001$). Twenty-seven of 35 (77.1%) banded adult males were in Group SLR, so adult male returns were more likely to be season-long residents than members of other groups ($\chi^2 = 21.2$, $P < 0.001$); a similar but less pronounced tendency existed for yearling males (10 of 15, 66.7%; $\chi^2 = 4.7$, $P < 0.05$) and adult females (12 of 22, 54.5%; $\chi^2 = 5.0$, $P < 0.05$), but not yearling females (7 of 17, 41.2%; $\chi^2 = 1.3$, $P > 0.2$). Adult males were more frequent in Group SSO than Group ESO (6:2), whereas the reverse was true for yearling males (1:4). Adult and yearling females, however, occurred in Group SSO and Group ESO at nearly equal frequencies (3 adults and 5 yearlings in Group SSO and 6 adults and 4 yearlings in Group ESO). Only 2 birds of known age, 1 adult female and 1 yearling female, were found in Group NSE. Thus more of the birds that arrived in the study area after the start of a season were unbanded and new to the area (134 of 152, 88.2%) than was the case for birds present at the start of a season (211 of 282, 74.8%; $\chi^2 = 8.6$, df = 1, $P < 0.01$).

Nesting success.—Of 324 nests attempted in the study area, 185 (57.1%) were successful in that at least one young fledged. Annual variation in success ranged from 31.6% (1969) to 76.0% (1977, Table 1). An average of 4.04 eggs was laid per nest, and the average completed clutch contained 4.48 eggs. A mean 3.73 young was fledged per successful nest, so for all seasons combined, $(0.571) \cdot (3.73) \div (4.04) = 52.8\%$ of the eggs laid resulted in fledged young.

There was no significant difference in the proportion of birds breeding in the study area that were in Groups SLR, SSO, and ESO (Table 2; $\chi^2 = 4.9$, df = 2, $P > 0.1$). Members of Group SLR, however, were responsible for a larger number of the nests observed in the study area ($\chi^2 = 116.4$, df = 2, $P < 0.001$) and an even greater number of the successful nests observed in the area ($\chi^2 = 139.8$, df = 2, $P < 0.001$). On the other hand, none of the relatively small number of birds in Group NSE nested successfully in the study area.

TABLE 2. Composition and nesting success of the four demographic groups.

	Demographic group								
	SLR		SSO		ESO		NSE		
	Num-ber	Per-centage	Num-ber	Per-centage	Num-ber	Per-centage	Num-ber	Per-centage	Total number
Number of birds	154	35.5	128	29.5	119	27.4	33	7.6	434
Number of nests[a]	329	50.8	154	23.8	129	19.9	36	5.6	648
Number of successful nests[a]	225	60.8	43	11.6	102	27.6	0	0.0	370
% success	68.4		27.9		79.1		0.0		57.1
Mean brood size[b]	3.83		3.81		3.43		0.0		3.73

[a] Each nest is counted twice, once for each adult; see text.
[b] Young fledged/successful nest.

Annual variation in population size.—The number of nests per season and the number of successful nests per season increased during the first 5 yr after nest boxes were provided (Table 1). Thereafter, the number of nests per season remained rather stable until 1977, when a sudden decline occurred. There was no corresponding increase in the number of bluebirds breeding in Michigan during 1968–1972, as determined from USFWS Breeding Bird Survey data (Adams and Pinkowski in press). The reduction in 1977, however, was attributable to a harsh winter in 1976–1977; bluebird populations breeding throughout Michigan decreased by approximately 50% in 1977 compared with 1976 (Pinkowski 1979).

The number of birds present in the study area at the start of each season was positively correlated with the number present at the end of that season ($r = 0.87$, $P < 0.01$). This correlation would be expected because of the presence of season-long residents at both the start and end of each season. Nevertheless, season-long residents accounted for only about one-third of all breeding birds (Table 2), and there was much movement in and out of the area by birds that did not remain for entire seasons. I found no correlation in the number of birds leaving and the number entering after the start of breeding, i.e. in the number of birds in Group SSO and the number in Group ESO ($r = 0.32$, $P > 0.5$) and in the number of birds in Group SSO and the number in Groups ESO and NSE combined ($r = 0.46$, $P > 0.2$).

During 1968–1972, the number of season-long residents increased at a slower rate (approximately 3–4 birds/season) than was the case for the total number of birds that used the area (approximately 10–11 birds/season) (Fig. 1). In 1972–1975 the total number of birds using the area was relatively constant, but the number remaining for entire seasons continued to rise. In 1975–1977 the total number of birds decreased at a more rapid rate than the number of birds remaining for entire seasons. As a result of these trends, the annual variation in the proportion of birds nesting in the study area that remained as season-long residents increased from 14.3% (1968) to 58.6% (1977) and was positively correlated with year of study ($r = 0.93$, $P < 0.01$). The pattern of steady increase was broken only in 1976, when a decline in nesting success compared with the previous season (Table 1) evidently contributed to a reduction in the proportion of birds remaining for the entire season.

Nesting attempts and productivity of Group SLR.—All breeding parameters, including number of young fledged during an entire nesting season, were known for 147 of the season-long residents. Most of these birds attempted 2 (102 birds, 69.4%)
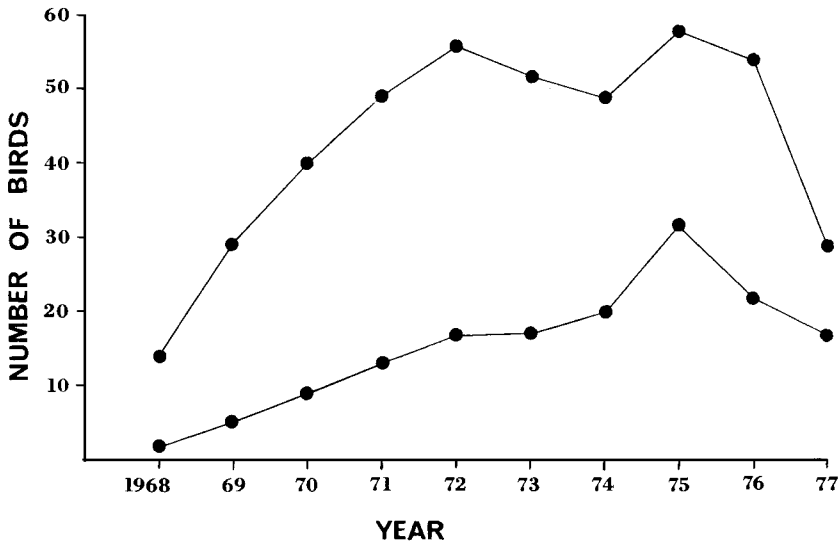
Fig. 1. Number of birds using the study area during any part of a season (all groups, top) and number present for the entire season (Group SLR, bottom).

or 3 (28, 19.0%) nests ($\bar{x}$ = 2.14). Fourteen birds (9.5%) attempted only 1 nest, but 3 of these as well as 2 of the birds attempting 2 nests were females killed by predators. Only 2 birds attempted 4 nests per season and 1 attempted 5, and all 3 of these birds were males.

Except for four of the five females killed by predators, all season-long residents reared at least one successful brood. Seventy-four season-long residents reared one brood, and 69 reared two broods; the average number of successful nests per season was 1.44, and the number of young reared pair^{-1}·season^{-1} ranged to a maximum of 10 ($\bar{x}$ = 5.6, SD = 2.0). Four or 5 eggs were laid in more clutches than any other number (Pinkowski 1977), and more season-long residents produced 4 young·pair^{-1}·season^{-1} (23) or 5 young·pair^{-1}·season^{-1} (39) than any other number.

Nesting attempts and productivity of Groups SSO, ESO, and NSE.— Mean numbers of nesting attempts in the study area were similar for all birds in Group SSO (1.20), Group ESO (1.08), and Group NSE (1.09), despite considerable variation in the nesting success rates of these groups (Table 2). The average number of attempts by members of all three groups was near unity, because most of these birds (128 of 153, 83.7%) left the study area if their nests failed before 23 July.

All but 17 birds in Group ESO, the most successful group except for season-long residents, nested successfully while in the study area. Consequently, the average number of successful nests in the study area by members of Group ESO was quite high (0.86). While in the study area, most birds (115/119 = 96.6%) in Group ESO attempted their first nests during the Intermediate (42 birds) or Early Summer (73 birds) nesting periods. None of the birds nesting in the Intermediate period and only six of the birds nesting in the Early Summer period had reared a previous brood. Thus 109 (91.6%) of the birds in Group ESO certainly did not rear an earlier brood. Annual productivity for all members of Group ESO, then, was only slightly higher than the observed average of 2.9 young·pair^{-1}·season^{-1} raised by members of this group while they were in the study area.
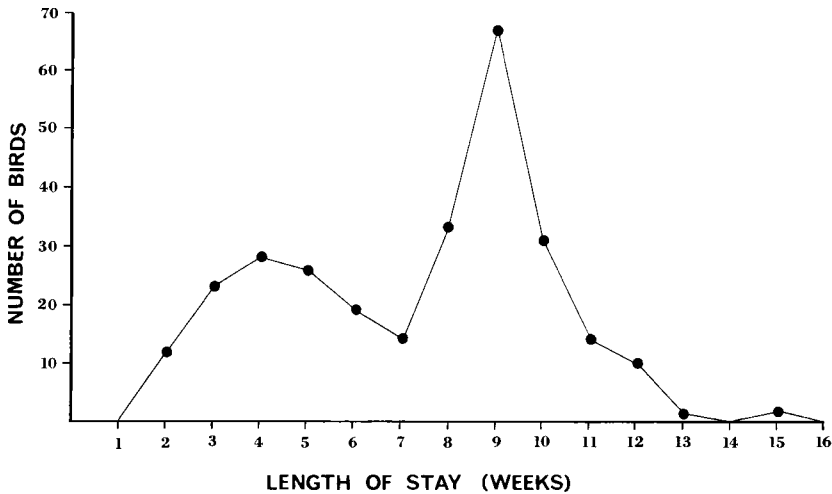
Fig. 2.   Length of stay in the study area in weeks for all birds that were not season-long residents.

Birds in Group NSE did not raise any young while in the study area. Nine (27.3%) of the birds in Group NSE began nesting in the Intermediate period, and 24 (72.7%) were birds that began nesting in Early Summer but had no previous brood. Thus none of the birds in Group NSE raised a brood before entering the study area. Birds arriving in the study area after the start of the season and remaining until it was too late for a possible renesting elsewhere were classed in Group ESO, so all birds in Group NSE could have reared a brood after leaving the area.

Only 43 (33.6%) of the birds in Group SSO nested successfully before leaving the study area. The average number of successful nests per season by birds in this group was quite low (0.34). Thirty (35.3%) of the unsuccessful birds left the study area before 15 May, early enough to rear two broods elsewhere; 55 (64.7%) left after 15 May and, like the successful birds, could have reared only one brood after their departure. Thus average annual productivity of Group SSO may have been much greater than the mean of 1.3 young·pair^{-1}·season^{-1} reared while these birds were in the study area.

Rate of nest initiation.—The only birds that raised two successful broods in the study area were classed as season-long residents. A plot of the mean length of time spent in the study area by birds that were not season-long residents (Fig. 2) shows two peaks corresponding to the mean duration for birds involved in no successful nests ($\bar{x}$ = 5.0 weeks) and one successful nest ($\bar{x}$ = 9.4 weeks). Expectedly, the median length of time spent in the area varied among groups according to the rate of nesting success; it was significantly greater in Group ESO (9 weeks) than in Group SSO (7 weeks; χ^2 = 16.2, P < 0.001 by median test) and significantly greater in Group SSO than in Group NSE (4 weeks; χ^2 = 42.2, P < 0.001). If all season-long residents are presumed present for entire 113.7-day (16.24-week) seasons, then the mean length of time that all birds spent in the area averaged 10.38 weeks or 10.38 ÷ 16.24 = 63.9% of a season.

The rate at which nests were initiated (nests·pair^{-1}·season^{-1}) in the study area was (324)·(2) ÷ (434) = 1.49. Birds that were not season-long residents, however, undoubtedly attempted many nests while not in the study area. If birds in and not in the study area initiated nests at the same rate and followed the same pattern of

seasonal variation in nest initiation, then the overall rate of nesting was $[(324) \cdot (2)$ $\div (434)] \div (0.639) = 2.34$ nests$\cdot$pair$^{-1}\cdot$season^{-1}. Expectedly, this rate is greater than that observed for season-long residents (2.14) because the latter were breeding at a higher rate of success and presumably initiated fewer new nests per season than other birds.

Estimation of annual productivity.—Mean annual productivity (young$\cdot$pair$^{-1}\cdot$season^{-1}) for all birds using the study area at one time or another would be equal to that observed in season-long residents if the following breeding parameters were equal: (1) the number of young fledged/successful nest, (2) the proportion of nests succeeding, and (3) the rate at which nests were initiated. Productivity (P) is related to these three parameters as follows:

$$P = \text{(young fledged/successful nest)} \cdot \text{(\% success)} \cdot \text{(nests/season)}.$$

Using the values obtained for Group SLR, $P = (3.83) \cdot (0.684) \cdot (2.14) = 5.6$ young, which is in agreement with the value obtained by field observations on these birds. Using the values obtained for all birds nesting in the study area at one time or another, $P = (3.73) \cdot (0.571) \cdot (2.34) = 5.0$ young.

Annual productivity has also been estimated indirectly from the daily rate at which young are fledged (Ricklefs and Bloom 1977) by employing the following parameters: P_s, the probability of nesting success (0.571); r_s, the interval until a new clutch is begun after a successful nesting (19.5 days, Pinkowski 1977); r_f, the interval until a new clutch is begun after an unsuccessful nesting (13.0 days, $n = 44$; this study); C, the mean clutch size (4.48); T, the length of the breeding cycle (37.6 days; Pinkowski 1975, 1977); S, the proportion of eggs resulting in fledged young (0.528); and B, the approximate length of the breeding season adjusted for unevenness (from MacArthur 1964, 113.7 days; this study). Using these parameters I calculated values for the rate of nest initiation (=0.023 clutches$\cdot$pair$^{-1}\cdot$day^{-1}), the rate at which young are fledged (=0.053 young$\cdot$pair$^{-1}\cdot$day^{-1}), and the nest mortality rate (=0.015 nest failures/day). Two of the calculated values are related to productivity, P, in that $P = \text{(young fledged}\cdot\text{pair}^{-1}\cdot\text{day}^{-1}) \cdot \text{(length of breeding season)} = (0.053) \cdot (113.7) = 6.0$ young$\cdot$pair$^{-1}\cdot$season^{-1}. This figure is higher than the estimate of 5.0 young$\cdot$pair$^{-1}\cdot$season^{-1} calculated above; more importantly, it exceeds the value of 5.6 young$\cdot$pair$^{-1}\cdot$season^{-1} observed for the highly successful Group SLR and therefore overestimates productivity of the entire population. Part of the overestimation may result from the length of the breeding season approximation and part may be based on the invalid assumption that all pairs attempt another nest after a first brood is raised. The estimate of 5.0 young more closely agrees with field observations and will be used in the following calculations.

Demographic implications.—Throughout most of this study the population of birds under investigation was either increasing or remained stable; it decreased only in the final year of study (Table 1). Consequently, the average annual productivity of 5.0 young$\cdot$pair$^{-1}\cdot$season^{-1} was evidently more than would have been required had the population been stable. Nevertheless, a number of instructive demographic calculations follow from the annual productivity estimates.

Production requirements of a stable population of birds are dependent on survival rates (Henny and Wight 1969). Summers-Smith (1956) estimated survival rates of 30% and 58% for yearling and adult House Sparrows (*Passer domesticus*), respectively, and from these values Henny et al. (1970) calculated a productivity requirement of 2.8 young per breeding female. Survival rates have been estimated for

bluebirds as follows: 82% between fledging and independence, 33% between independence and the start of the breeding season (1 April), and 50% annually thereafter for adults (Pinkowski 1971, 1977). The productivity necessary to balance these survival rates is given by $[2 \cdot (1 - 0.5)] \div [(0.33) \cdot (0.82)] = 3.7$ young (Henny and Wight 1969, Henny et al. 1970). Thus, production in the study area evidently averaged about $(5.0 - 3.7)/3.7 = 35\%$ more than would have been required had the population not been increasing during 5 of the 10 yr of study.

Three male bluebirds that returned to the study area did not breed as yearlings (Pinkowski 1977). These birds were among 592 young fledged in the study area in 1968–1976 (Table 1). Thirty-one other yearlings returned, so only $34/592 = 5.7\%$ of the fledglings returned to the area. The nonbreeders accounted for $3/34 = 8.8\%$ of all yearlings in the study area. Returning yearlings comprised $(0.057) \div [(0.33) \cdot (0.82)] = 21\%$ of all surviving yearlings, and $1 - 0.21 = 79\%$ of the surviving yearlings went elsewhere for their first breeding seasons.

Productivity of adults and yearlings.—Among season-long residents of known age, adults reared more $young \cdot pair^{-1} \cdot season^{-1}$ ($\bar{x} \pm SD = 6.1 \pm 1.8$) than did yearlings ($4.9 \pm 1.5$; $t = 2.2$, $P < 0.05$). This difference is not attributable to significant differences in brood size or rate of nesting success in the two age groups but instead occurs because adults attempt more nests per season than do yearlings (Pinkowski 1977). Nevertheless, productivity estimates for adults and yearlings in Group SLR are probably higher than what is true for each age class because of the higher rate of success of Group SLR (Table 2).

Relative production of young by all adults and yearlings can be estimated more accurately when data on birds in Group SLR are combined with data on birds that were not in Group SLR but whose annual productivity was nevertheless known from the timing of their arrival in the study area. One female of known age in Group ESO entered the study area very late and may have reared an earlier brood elsewhere. All other birds of known age in Group ESO did not raise a brood prior to their arrival in the study area. When Group ESO birds of known age whose histories were known are combined with birds of known age in Group SLR, the adults still reared more $young \cdot pair^{-1} \cdot season^{-1}$ (5.7 ± 2.1) than did yearlings (4.3 ± 1.6, $t = 2.7$, $P < 0.01$), although the resulting estimates are probably closer to the absolute values for each age class than are estimates using only Group SLR birds. If adults and yearlings are equally represented in the breeding population, as might be expected if adult survivorship is about 50%, then it is noteworthy that the combined average productivity of adults and yearlings in Groups SLR and ESO was $(5.7 + 4.3)/2 = 5.0$, a figure that is identical to that estimated for the entire population.

DISCUSSION

Population dynamics.—One of the aims of population study is to understand the dynamics of populations under changing conditions (Ricklefs 1973). Nest site availability and nesting success appeared to be the principal determinants of the demographic parameters measured in this study. The number of birds nesting in the study area gradually increased after the initial provision of nest boxes, apparently because young birds that were reared in the area were returning there to breed and adults that were successful in the area were returning there for subsequent nestings. Returning birds were more likely to remain for entire seasons than were recent arrivals to the study area, which resulted in a steady increase in the annual proportion of

birds in Group SLR. These trends reflect the dependency of site fidelity on nesting success in bluebirds.

Variation in site fidelity was affected by nesting success and made possible the a posteriori classification of the breeding population into four demographic groups. This classification resulted in a method of analyzing mean annual productivity that is based on an assumed symmetry in rate of nest initiation for birds in and not in the study area. Admittedly this assumption would not be as serious for an open-nesting passerine as it is for a secondary (nonexcavating) cavity-nester studied in an area supplied with artificial nest sites. Birds outside the study area may have initiated nests at a slower rate than those inside the study area if a limited number of cavities prevented some birds from nesting in areas where nest boxes were not available. The gradual and not sudden increase in the number of birds nesting in the study area after nest boxes were provided argues against a serious cavity shortage outside the study area, however, as does the lack of a correlation between the numbers of birds entering and leaving the study area after the start of breeding seasons. Moreover, birds in Groups SSO and NSE often left the area after nest failures and did not return; this would not be expected if nest sites in adjacent areas were limited. Finally, although the rate of nest initiation depends on the rate of nesting success, which could differ in the nest boxes used in the study area and the natural cavities used elsewhere, the success rate in natural cavities in the study area (55.6%) was nearly identical to that in nest boxes (55.5%, Pinkowski 1977). Thus I could find no reason why birds in the study area might be nesting at a very different rate than those not in the study area.

If birds in and not in the study area were symmetrical with respect to opportunities for breeding and rate of nest initiation, then it is instructive to look upon birds outside the study area as spatial and temporal complements to those in the population under investigation. A bird that was present in the study area at the start of a season but left before the end of that season would be classed in Group SSO in the study area but would be in Group ESO (especially if successful after it left the study area) or Group NSE (especially if unsuccessful) in the area in which it subsequently settled. Similarly, members of a Group SSO in another area could become members of Group ESO or NSE in the study area after leaving their first nesting areas, where they were likely to have nested unsuccessfully. Birds successful in other areas would tend to remain in those areas for entire seasons, comprising a local Group SLR. Thus birds entering the study area after the start of nesting (Groups ESO and NSE) were often unbanded and new to the area because they had previous nests elsewhere or had been raised in another area. Site fidelity is strongest in adult males, and it is probable that most males in Groups ESO and NSE were yearlings; females in these groups may have been entering the study area after nest failures elsewhere, however, because females often leave territories without their mates after nest failures.

Bioenergetic considerations.—Birds presumably allocate energy available for reproduction so as to raise the greatest number of young over a given period (Ricklefs 1974). Although at northern latitudes the bluebird exhibits a bimodal egg-laying pattern and is often considered a double-brooded species (Peakall 1970), in this study only 75 of 357 individuals (21.0%) for which productivity was directly observed or indirectly inferred succeeded in rearing two broods. If a single brood represents the maximum productivity of most pairs of a species with a long breeding season, then

selection should favor relatively great reproductive effort by pairs rearing a first brood rather than favoring a strategy entailing less reproductive effort because of a possible (but unlikely) second successful brood.

In a demographic analysis of the Prairie Warbler (*Dendroica discolor*), an open-nesting species with a somewhat shorter breeding season than the bluebird, Nolan (1978) concluded that a 65% annual survival rate was characteristic of both adult males and adult females. This rate is higher than the 50% adult survivorship that is typical of passerines breeding in the north Temperate Zone (Lack 1954, Farner 1955, Gibb 1961, Cody 1971), and it exceeds the 50% adult survivorship that has been suggested as an average for male and female bluebirds. Part of the annual mortality of adult bluebirds reportedly results from costs incurred while raising young (Pinkowski 1977). A cavity-nesting species may tolerate a reduction in physiological condition and hence experience increased mortality for the sake of a brood because its nest sites are limited; selection may not have favored this tolerance in open-nesting species that are more likely to find another site in the event of nest failure. Also, cavity-nesters may incur greater costs in raising a brood because their broods are generally larger than those of open-nesters (Lack 1968). In any case, the young of cavity-nesters fledge in a more developed state and have a higher post-fledging survival rate than young of open-nesters (Haartman 1957, Ricklefs 1974). Differences in post-fledging survival may demographically balance any difference in mortality rate of breeding adults.

Equal survival rates for various age classes of breeding passerines are often assumed in life table analyses (Lack 1946, Nolan 1978). One important consequence of the unequal numbers of young raised per season by adult and yearling bluebirds, however, is that the cost of breeding and hence mortality related to these costs may be greater in the older birds that raise more young per season. In at least one other cavity-nester, the Pied Flycatcher (*Ficedula hypoleuca*), the survival rate has been reported to decrease from 74% in yearlings to 65% in second-year birds to 30% in third-year birds (Berndt and Sternberg 1963, *in* Lack 1966). Observations such as this indicate the need for more long-term investigations to elucidate bioenergetic and demographic relations.

LITERATURE CITED

ADAMS, R. J., & B. C. PINKOWSKI. 1979. The Michigan U.S. Fish Wildl. Serv. breeding bird survey, 1967–1977. Jack-Pine Warbler in press.

AUSTIN, G. T. 1977. Production and survival of the Verdin. Wilson Bull. 89: 572–582.

BERNDT, R., & H. STERNBERG. 1963. Ist die Mortalitatsrate adulter *Ficedula hypoleuca* wirklich unabhangig vom Lebensalter? Proc. 13th Intern. Ornithol. Congr.: 675–684.

CODY, M. L. 1971. Ecological aspects of reproduction. Pp. 461–512 *in* Avian biology, vol. 1 (D. S. Farner and J. R. King, Eds.). New York, Academic Press.

DALE, F. M. 1952. Sex ratios in pheasant research and management. J. Wildl. Mgmt. 16: 156–163.

DARLEY, J. A., D. M. SCOTT, & N. K. TAYLOR. 1977. Effects of age, sex, and breeding success on site fidelity of Gray Catbirds. Bird-Banding 48: 145–151.

FARNER, D. S. 1955. Bird banding in the study of population dynamics. Pp. 397–449 *in* Recent studies in avian biology (A. Wolfson, Ed.). Urbana, Univ. Illinois Press.

GIBB, J. A. 1961. Bird populations. Pp. 413–446 *in* Biology and comparative physiology of birds (A. J. Marshall, Ed.). New York, Academic Press.

HAARTMAN, L. VON. 1957. Adaptation in hole-nesting birds. Evolution 11: 339–347.

HANSON, W. R. 1963. Calculation of productivity, survival, and abundance of selected vertebrates from sex and age ratios. Wildl. Monogr. No. 9.

HENNY, C. J., W. S. OVERTON, & H. M. WIGHT. 1970. Determining parameters for populations by using structural models. J. Wildl. Mgmt. 34: 690–703.

————, & H. M. WIGHT. 1969. An endangered Osprey population: estimates of mortality and production. Auk 86: 188–198.

HICKEY, J. J. 1952. Survival studies of banded birds. U.S. Fish Wildl. Serv. Spec. Sci. Rep.-Wildl. 15.

LACK, D. 1946. Do juvenile birds survive less well than adults? Brit. Birds 39: 258–264.

————. 1954. The natural regulation of animal numbers. London, Oxford Univ. Press.

————. 1966. Population studies in birds. Oxford, Oxford Univ. Press.

————. 1968. Ecological adaptations for breeding in birds. London, Methuen.

MACARTHUR, R. H. 1964. Environmental factors affecting bird species diversity. Amer. Natur. 98: 387–397.

NICE, M. M. 1957. Nesting success in altricial birds. Auk 74: 305–321.

NOLAN, V., JR. 1966. Fidelity to the breeding site in Prairie Warblers, *Dendroica discolor*. Abstracts 14th Intern. Ornithol. Congr.: 90–91.

————. 1978. The ecology and behavior of the Prairie Warbler *Dendroica discolor*. Ornithol. Monogr. No. 26.

PEAKALL, D. B. 1970. The Eastern Bluebird: its breeding season, clutch size and nesting success. Living Bird 9: 239–255.

PINKOWSKI, B. C. 1971. An analysis of banding-recovery data on Eastern Bluebirds banded in Michigan and three neighboring states. Jack-Pine Warbler 49: 33–50.

————. 1975. Growth and development of Eastern Bluebirds. Bird-Banding 46: 273–289.

————. 1976. Use of tree cavities by nesting Eastern Bluebirds. J. Wildl. Mgmt. 40: 556–563.

————. 1977. Breeding adaptations in the Eastern Bluebird. Condor 79: 289–302.

————. 1978. Five years of observations of a male Eastern Bluebird. Jack-Pine Warbler 56: 161–163.

————. 1979. Effects of a severe winter on a breeding population of Eastern Bluebirds. Jack-Pine Warbler 57: 8–12.

RICKLEFS, R. E. 1969. An analysis of nesting mortality in birds. Smithsonian Contrib. Zool. 9: 1–48.

————. 1973. Fecundity, mortality and avian demography. Pp. 366–447 *in* Breeding biology of birds (D. S. Farner, Ed.). Washington, D.C., Nat. Acad. Sci.

————. 1974. Energetics of reproduction in birds. Pp. 152–297 *in* Avian energetics (R. Paynter, Jr., Ed.). Cambridge, Massachusetts, Publ. Nuttall Ornithol. Club No. 15.

————, & G. BLOOM. 1977. Components of avian breeding productivity. Auk 94: 86–96.

SUMMERS-SMITH, D. 1956. Mortality of the House Sparrow. Bird Study 3: 265–270.