AN ANALYSIS OF FACTORS GOVERNING PAIR-BONDING PERIOD AND THE ONSET OF LAYING IN INDIGO BUNTINGS

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Many factors, e.g., photoperiod, food supply, weather conditions, are thought to influence the timing of mating and nesting in birds (see Immelmann 1971, Skutch 1976, Murton and Westwood 1977 for reviews). Studies of such factors usually examine effects on the initiation of breeding activity; few studies have focused on the role of these factors in the time just after pair formation. Hamilton (1961) defined pair-bonding period as the interval between the time of meeting of the male and female of the pair and the time the female lays the first egg. I here present data on some factors that may affect the length of the pair-bonding period in Indigo Buntings (*Passerina cyanea*).

One assumption often made about the pair-bonding period is that selection would tend to make it very short, especially in late spring migrants such as the Indigo Bunting. The result would be a breeding season of maximal length. For example, Hamilton (1961) and Hamilton and Barth (1962) suggest that sexual dimorphism is stronger in long-distance migrant warblers and icterids as a mechanism facilitating rapid pairing (and nesting) at the beginning of their relatively short northern-latitude breeding seasons. Having found very long and variable pair-bonding periods in a population of Indigo Buntings, both within and between seasons (see Table 1), I became interested in identifying factors responsible for this variation and for what appeared to be unusual prolongation of the period.

STUDY AREA AND METHODS

Data were collected in 1973–1976 in conjunction with work on population dynamics and mating systems of Indigo Buntings. The study area, a rather homogeneous collection of old fields (20 ha), has been described in detail as the "high density" area in Carey and Nolan (1975, 1979) and Carey (1977). The fields are about 3 km north of the Indiana University campus, Bloomington, Monroe Co., Indiana. All fields were in early stages of secondary succession, having been cut over or cultivated only 3–5 years prior to the beginning of the study. Typical vegetation was a lush cover of forbs and grasses and scattered patches of blackberry (*Rubus*, spp.), roses (*Rosa multiflora*), and small saplings.

Nearly all breeding Indigo Buntings were mist-netted and banded with a numbered aluminum band and a unique combination of colored plastic bands. Over all years, 147 territorial males and 143 breeding females were marked. All territories were inspected daily from 1 May to 1 September to monitor behavior and population dynamics. As a result, individual histories were compiled for all Indigo Buntings residing on the study area for any period longer than a few days. Probably

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all nests were found (by observing behavior or by intensive search) and thereafter were checked at least daily.

Date of initial pairing, the beginning of the pair-bonding period, is the date a female was first observed on the territory within which she subsequently built a nest. This definition is crude because females were almost never seen until they were associated closely with a male. No more precise definition is practical, and the effect is that pair-bonding periods so defined were some days shorter than the period measured from the unknown date the male and female first met.

RESULTS

Pair-bonding periods for each year of the study are summarized in Table 1. Two features seem notable. First, the variation in duration is great, ranging from 5–34 days (pooled SD = 8 days). In comparison, Nolan's (1978) data for Prairie Warblers (*Dendroica discolor*) breeding in the same habitat showed a mean period (12 years pooled) of 12.6 days with extremes of 5 and 24 days and no annual SD greater than 6.3 days. Secondly, a distinct dichotomy is evident with 1973 and 1975 having relatively short mean periods and low variance, while 1974 and 1976 have a higher mean and greater variance. In a Kruskal-Wallis one-way analysis of variance of the pair-bonding periods for the 2 sets of years, $H = 5.2$, $P < .05$.

It may be instructive to calculate expected pair-bonding periods for Indigo Buntings to compare with the observed in Table 1. Events during the pair-bonding period can be conveniently subdivided into 3 parts: (1) the prebuilding period in which the pair forms and chooses a nest site; (2) the nest construction period during which the female builds a functionally complete structure; and (3) the post construction period, the time spent between completion of the nest and laying of the first egg. As stated above, the prebuilding period of these Indigo Buntings could not be determined precisely, but observations suggested that it was comparable to that of Prairie Warblers near Bloomington. The Prairie Warbler prebuilding period ranged from 0–17 days, with 80% of the cases falling within the range 0–6 days (Nolan 1978). I assume that 0–6 days is the normal expected range; the observed mean prebuilding period was 3.4 days. The nest construction period ranged from 4–10 days (mean, 6.7 days) for first nests of the year. The post construction period was almost always 1 day in length but rarely lasted 3 days. Summing the foregoing 3 parts, the expected mean for the Indigo Bunting's pair-bonding period is 11.1 days, and extremes for birds that breed promptly would range between 5 and 19 days. Conservatively, then, any female whose pair-bonding period exceeds 19 days can be considered to have delayed breeding or to have prolonged the period. Numbers and proportions of such females are shown in Table 1, and here the dichotomy between the sets of years is even more apparent. Obviously, something caused many females to lengthen the pair-bonding period.

One possibility to consider is that annual changes in weather might

TABLE 1. Means, extremes, and SD of Indigo Bunting pair-bonding periods (in days) according to year. Column ">19" is the number and percentage (in parentheses) of females having a pair-bonding period greater than 19 days, the maximum expected period (see text for discussion).

Year	n	Mean	Extremes	SD	>19
1973	10	13.3	5–23	5.9	2 (20)
1974	19	19.1	5–34	8.9	10 (53)
1975	21	14.0	5–34	6.9	3 (14)
1976	14	18.2	5–29	8.0	6 (43)
Pooled	64	15.8	5–34	8.0	21 (33)

explain annual changes in pair-bonding period. For example, a relatively cool or dry April and May could retard development of foliage, hence nest cover or insect food, and nesting might be delayed accordingly. However, mean April–May temperatures and precipitation levels show no relationship to the observed annual differences in mean pair-bonding period. Also, it is intuitively difficult to understand how annual weather changes could explain why one female had a pair-bonding period of 34 days, while a neighbor that paired at the same time had only a 5-day period. (Because the fields were relatively homogeneous, I would expect that microclimatic differences on them were minimal.)

A second possible factor is simply individual female differences; some may be inherently fast, others slow to nest. If this were true, the expectation would be that certain females consistently have long pair-bonding periods, others short. Table 2 presents data from individual females for which 2 or more pair-bonding periods could be determined. No individual trends are apparent.

Third, differences in initial pairing date among females could lead to different pair-bonding periods. For example, females pairing early may have relatively long periods as they wait for optimal conditions; later pairing females could begin nesting more promptly (e.g., see data of Nolan 1978). If so, I would expect a negative correlation between date of pairing and length of the pair-bonding period. Table 3 presents annual mean pairing dates and pair-bonding periods for yearling females (see below), old females, and all females pooled. No association between annual mean pairing date and mean pair-bonding period is apparent. Table 4 pools across years and presents mean pair-bonding periods of females according to date (5-day blocks) of pairing. Here a slight, significant ($r = -.28$, $P < .05$) decrease in pair-bonding period is evident as spring progresses. Despite the correlation, there is much variance within each 5-day date class, and on a yearly basis only 1974 showed a significant negative correlation. In fact, in 1976, the correlation coefficient was positive. Thus, while date of initial pairing may be a factor affecting length of pair-bonding period, it explains only 5% of the variation in pair-bonding period, and other factors must also be considered.

TABLE 2.   Pair-bonding periods of individual female Indigo Buntings whose periods are known for more than one year. A dash indicates that a female was resident in that year but that pair-bonding period could not be determined.

	Pair-bonding periods (days)			
Female	1973	1974	1975	1976
1	11	23		
2	22	—	15	—
3	18	26	23	
4		26	17	26
5		—	13	5
6		—	5	13
7		5	9	21
8		16	13	8
9		16	17	—
10			12	16

A fourth possibility is female age. Young, inexperienced females may be expected to have longer pair-bonding periods than older experienced females. No morphological criteria can be used to age female Indigo Buntings; however, relative ages after banding were known. Female site fidelity was 50% (Nolan et al. 1975). Since annual mortality in many small passerines is also around 50% (Cody 1971), it is probable that most surviving females are site faithful. Thus, because I was successful in banding almost all breeding females, I feel fairly confident that most unbanded females arriving on the study area were yearlings. Pair-bonding periods of these females can be compared to those of females banded in previous years and known to be more than one year old.

Table 3 compares pair-bonding periods of the 2 female age classes;

TABLE 3.   Mean Indigo Bunting pair-bonding periods (in days), according to year, date of initial pairing, and female age (see text for female aging method). Females could not be "aged" in 1973, the initial year of the study.

Year	Age	n	Mean pair-bonding period	Mean date of pairing
1973	Pooled	10	13.3	May 27
1974	Yearling	10	18.3	May 26
	Old	9	19.9	May 21
	Pooled	19	19.1	May 25
1975	Yearling	13	13.8	May 28
	Old	8	14.2	May 13
	Pooled	21	14.0	May 22
1976	Yearling	5	21.0	May 29
	Old	9	16.7	May 21
	Pooled	14	18.2	May 24

TABLE 4. Mean, extremes, and SD of Indigo Bunting pair-bonding periods (in days), according to date of initial pairing. All years pooled.

Date of pairing	n	Mean pair-bonding period	Extremes	SD
6–10 May	8	18.7	13–33	6.7
11–15 May	6	18.3	5–34	12.0
16–20 May	14	19.1	7–34	7.9
21–25 May	11	16.1	5–26	7.1
26–30 May	8	16.5	9–22	5.6
31 May–4 June	8	16.7	7–26	7.4
5–9 June	8	12.4	6–29	7.3
After 9 June	4	6.0	5–7	1.1

there are no significant differences. Table 2 also shows no trend toward reduction in period length as individual females aged. However, Table 3 does show that yearling females pair at a significantly later date than old (all years pooled, $H = 10.4$, $P < .01$). This can lead to a possible interaction between pairing date and age, both ultimately affecting pair-bonding period. The late-pairing females were usually young and had relatively short pair-bonding periods, as expected. However, early pairing yearlings had extremely long pair-bonding periods; all periods longer than 30 days were those of such females. Thus age also appears to be a factor important in determining individual pair-bonding periods.

A fifth factor possibly leading to prolonged pair-bonding periods is predation. Nest predation was very high early in the breeding season and then fell sharply (see also Nolan 1978). Over all years, Indigo Bunting success in nests receiving eggs prior to 2 July was 7%; of nests receiving eggs after 2 July, 51% were successful. Over 80% of failures were due to predators, primarily snakes (see Nolan 1978 for supporting evidence). Prolongation of the pair-bonding period could aid in avoiding this almost total early nest loss. However, snakes apparently locate nests by random search and immediately eat their contents (Nolan 1978). This random search and the concealment of the snakes would make it very difficult for individual buntings to predict predation. Thus, I would expect that if predator avoidance were an important factor, all females would prolong the pair-bonding period until after the general threat had abated. The high variance in pair-bonding period thus argues against predation as an important factor.

The sixth and final factor to be considered is Brown-headed Cowbird (*Molothrus ater*) parasitism. Cowbird females are most active early in the breeding season (see Nolan 1963, 1978). Of 23 parasitized Indigo Bunting nests, only 3 received cowbird eggs after 15 June and none later than 26 June. I never found a cowbird egg laid in any host nest later than 1 July. Over all years 46% (19 of 41) of nests receiving first eggs on or before 15 June were parasitized by cowbirds. In contrast only 14%

(3 of 22) later nests in June were parasitized. Thus, by delaying laying at least until mid-June, Indigo Buntings can avoid the brunt of cowbird parasitism. Also, since cowbirds appear to locate nests primarily by observing construction (Friedmann 1929, Norman and Robertson 1975), it is possible that individual bunting females, upon noticing cowbird attention, would interrupt nesting and postpone activity as long as cowbirds were present on the territory. Individual females that do not detect cowbirds may continue activity, thus giving rise to individual female differences in pair-bonding period. If this reasoning is correct, I would also expect that annual changes in cowbird population sizes would lead to annual changes in mean pairing-bonding period.

Table 5 presents 2 measures of cowbird pressure on the study area according to year and relates them to annual changes in mean pair-bonding period. One indirectly looks at cowbird population size by noting the proportion of nests parasitized. Indigo Bunting nests are excluded from this sample. If it is assumed that buntings are delaying breeding to avoid cowbird parasitism, then percent of bunting nests parasitized may not be related to cowbird population size. The other uses cowbird capture rates on the study area as a relative measure of population size. As the table shows, both measures indicate high cowbird population size in 1974 and 1976, the two years with a high proportion of prolonged pair-bonding periods. Both measures are relatively low in the 2 years with short periods. Thus it also appears probable that cowbirds exerted some effect on the pair-bonding period of Indigo Buntings.

DISCUSSION

To begin the discussion, the data must be acknowledged to be quite preliminary and limited. This is due to the fact that they were not collected for the purpose to which this paper puts them. With this caveat in mind, the following tentative conclusions are proposed.

One surprising result is the apparent lack of a weather effect on the pair-bonding period. A possible reason for this is the very late date of initial pairing in this population, mid-May through June. In almost all other small passerines on the study area, nesting was well under way while the Indigo Buntings were still pairing (see Nolan 1963, 1978; Thompson and Nolan 1973). Nest cover was well developed and food was probably abundant when the buntings began to pair. Weather could then have had little effect on Indigo Buntings. It is also probable that my weather data, i.e. monthly mean temperatures and precipitation levels, are not refined enough to show any effects on pair-bonding periods calculated as annual means. That is, short periods of cool weather or heavy precipitation might have effects on the pair-bonding periods of individual females, as Nolan (1978) found to be the case with Prairie Warblers. In sum, it appears that weather conditions do not affect annual mean pair-bonding periods of bunting populations; further study is needed to learn if there are any individual effects. The data also

TABLE 5.   Mean Indigo Bunting pair-bonding periods and measures of cowbird popu-
           lation size according to year.

Year	Mean pair-bonding period	Cowbird capture rate[1]	% of nests of species other than Indigo Bunting receiving cowbird eggs[2]
1973	13.3	3.5	28
1974	19.1	21.4	40
1975	14.0	4.6	30
1976	18.2	23.9	53

[1] Denotes the number of cowbirds captured per 1000 mist-net (20 m) hours, 1 May–1 July.

[2] Includes all nests discovered on the study area, 1 May–1 July. Species, ordered according to abundance in the sample are: Field Sparrow (*Spizella pusilla*) n = 20, Prairie Warbler n = 17, Yellow-breasted Chat (*Icteria virens*) n = 12, Common Yellowthroat (*Geothlypis trichas*) n = 5, Red-winged Blackbird (*Agelaius phoeniceus*) n = 3, and White-eyed Vireo (*Vireo griseus*) n = 2.

indicate that individual female differences and predation rates had little or no effect on the pair-bonding period.

The three factors that appear to have some importance in determining the length of the pair-bonding period, date of initial pairing, female age, and cowbirds, probably interact on the individual female. The reduction in pair-bonding period with advancing date of pairing could be attributable to increased cover, more abundant food, or physiological (e.g., hormonal) changes. Modifying this decrease due to pairing date are the longer pair-bonding periods associated with yearling females, many of which pair late in the spring. Although these date and age trends are seen in the present data, they are for the most part non-significant. It is possible that larger sample sizes will reveal the separate effects of these two factors on pair-bonding period.

Date of initial pairing and female age, along with the level of cowbird pressure, do appear important in determining individual differences in pair-bonding period. However, age and pairing date had no apparent relationship to annual changes in the mean period (see Table 3). Cowbird pressure seems to be the factor that best explains these annual changes (see Table 5). This proposed effect of the cowbird on the pair-bonding period is of special interest because delayed breeding as a cowbird avoidance mechanism has rarely been mentioned in the literature and never, so far as I know, as a proximate timer of female breeding activity (see Rothstein 1975, Robertson and Norman 1976, and Payne 1977 for discussions of cowbird avoidance mechanisms). One reason for this lack of mention is that delayed breeding may not be a useful mechanism for many northern species. In order for delayed breeding to be beneficial, a pair must have a sufficiently long breeding season to enable

successful late nesting. In Indiana, the Indigo Bunting is one of the few such species. I observed many pairs still laying in mid- to late August, and young were still being fed in late September. These dates are much later than those given for other comparable species by Nolan (1963). Breeding delay may not be a reasonable strategy for these other species. The only other person to mention cowbirds as affecting nesting date is Middleton (1977, 1979). He suggested that cowbird avoidance may be a factor in postponing young American Goldfinch (*Carduelis tristis*) nesting, another species that continues nesting into the late summer. I suggest that other species that nest into late summer might also show a relationship between cowbird pressure and pair-bonding period.

SUMMARY

Some Indigo Bunting females appear to spend extremely long periods of time on a male's territory before completing a nest and laying in it, e.g., they have prolonged pair-bonding periods. The data presented indicate that three factors are important in determining the length of this period. (1) The later the date of initial pairing, the shorter the period tends to be; (2) yearling females have longer periods than older females; (3) annual changes in cowbird population size correlate best with annual changes in pair-bonding period. It is proposed that individual females postpone nesting activity in the presence of cowbirds in order to reduce the probability of being parasitized.

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