Polygyny in Indigo Buntings: A Hypothesis Tested

Abstract. *A test of a model for the evolution of avian polygyny revealed that 10 percent of male indigo buntings had two mates simultaneously and some had none. Old males acquired territories first, and yearlings moved into leftover space. Yearling males that obtained mates tended to form brief, monogamous bonds. Females mated to polygynists produced as many young as females mated to monogamists.*

The evolution of avian mating systems continues to be the subject of much attention (*1*), with particular interest attaching to polygyny because of its infrequency (*2, 3*). A model extensively cited to explain the origin of polygyny has been suggested by Verner and Willson (*4*) and fully developed by Orians (*5*). We have made what is, to the best of our knowledge, the first test of this model's ability to predict that a bird species is polygynous (*6*); this report is of evidence supporting that hypothesis. Success in obtaining and keeping mates varied greatly among male indigo buntings (*Passerina cyanea*); factors associated with success were age of the birds and character of the vegetation on the territory.

The rarity of avian polygyny, especially among nidicolous species (*2, 3*), is attributed to the lowered fitness ordinarily anticipated for the female that chooses to pair with an already mated male. A male having two or more altricial broods simultaneously dependent on him will probably of necessity curtail parental attention to each; added disadvantages to his mates may arise from density effects, such as attraction of predators to the territory or depletion of its food resources. However, according to the Verner-Willson-Orians hypothesis, these disadvantages may be compensated for if critical resources are distributed sufficiently unequally. Given the regular occurrence of a wide enough range in the quality of territories, a female's expected reproductive success may be greater if she chooses a mated male rich in resources rather than an impoverished bachelor. Polygyny, once established under these circumstances, will intensify male competition for mates and lead to the evolution of characteristic displays such as prolonged vocal advertisement, strong sexual dimorphism, drastic reduction or elimination of male parental care, and, if young males tend to lose in the competition for mates, delayed maturation of characters employed in attracting females and competing with other males.

Preliminary study of the indigo bunting at Bloomington, Indiana, led us to predict polygyny in that population for the following reasons. The species occupies diverse habitats, from grassy and herbaceous fields to regenerating forests whose canopies have begun to close; we suspect territories vary greatly in food resources and nest sites. Males appear to sing much more than most passerines, for about 30 percent of the day throughout the season and regardless of mating status. Sexual dimorphism is striking; old males are bright blue, females are dull brown, and yearling males, which are recognizable in the hand by their brown greater primary coverts, range between these extremes and are usually somewhat mottled. We have never seen males feed nestlings despite many efforts to observe this behavior, and they appear to tend fledglings only when females begin the nest of a second brood before the first brood has become independent. Thus the variety in territories appeared likely to satisfy the hypothetical requirements for the situation in which polygyny can be expected, and the buntings have many of the behavioral and morphological characters that the model predicts will evolve under the selective influence of that mating system.

Study areas chosen were a series of nearly adjoining old fields of various ages, on some of which we had long experience in studying other passerine species. One group of tracts 18 hectares in area had been abandoned 25 to 30 years before 1973, when we started the investigation. On this, the low-density field, the population of indigo buntings has declined steadily for at least the past 10 years; the largest number of males holding territories simultaneously during 1973–1974 was 8, or 44 in each 100 hectares. The nearby high-density field was 16 hectares in area; here 19 males were on territory simultaneously, or 119 per 100 hectares (*7*). All parts of this field had been cultivated or cut over quite recently; two segments, for example, were mowed the year before the study began. Typical of the low-density field were thickets of sapling trees with the canopies closing and large eroded areas supporting only sparse ground cover. Patches of luxuriant forbs and grasses constituted less than 20 percent of the area of this field, whereas a lush layer of forbs and grasses 1 to 1.5 m high covered the high-density field.

We visited the fields daily in 1973 and 1974 and regularly operated mist nets (nets of a very fine mesh) to capture indigo buntings. Most bunting inhabitants were caught and marked with color-coded bands within a few days after arriving. We believe that we found nearly every nest built and all young that left nests, and that we know the reproductive histories of all individuals during their residence. Many males were present for one or both full seasons; at the other extreme, some stayed only a few days or weeks. Males were regarded as resident if they held territory for at least 3 weeks, about one quarter of the period during which territories are acquired (May to July). We classed as transients males caught only once in the year of banding and not seen again that year.

Most male residents of the low-density field were yearlings; in the high-density field fewer than one-fourth of the residents were yearlings (Table 1; $\chi^2_{\text{adj}} = 6.38$; $P \sim .01$). Although old males and yearlings arrived at about the same time, old males were the first to take up territories. Yearlings settled later, sometimes weeks later, on unoccupied land. One old and two yearling territory holders moved from the low-density field in 1 year to the high-density field in the next; no male returned and made the opposite shift into the low-density field. In addition to these relocations at the beginning of the season, some yearling males made futile efforts in midseason to acquire territories by encroaching on holdings in the high-density field.

Table 1. Frequencies of pair bonds, according to the population density of the field and the age of the male.

Pair bond	Low-density field		High-density field		Fields pooled		Total	
	Old	Yearling	Old	Yearling	Old	Yearling	*N*	%
Polygyny	1	1	4	0	5	1	6	10
Monogamy								
Season-long	3	1	13	2	16	3	19	30
Successive	1	1	9	0	10	1	11	17
Short-term	0	5	11	7	11	12	23	37
Unmated	0	1	0	3	0	4	4	6
Totals	5	9	37	12	42	21	63	100

In the low-density field, ownership of some territories changed several times during a season as yearlings took possession and held them for varying periods, abandoned them, and were replaced. These birds exhibited normal territorial behavior, singing often and usually responding aggressively to tape-recorded songs and to mounted specimens of indigo buntings. Parallel to such changes in territory occupancy were the movements of transients; of

13 caught after breeding was well under way, 11 were yearlings, and unbanded males that appeared briefly were almost all yearlings. We therefore think it probable that significant numbers of young males never settled anywhere very long and never mated. In one such case a male was territorial intermittently in the low-density field for much of 1973 and once associated for a few days with a female that left him without nesting. He also failed in two vigorous efforts to seize part of a territory in the high-density field; he returned next year, obtained that territory, and bred successfully.

We considered a male mated if he had a female that built at least one nest. Polygynous males were those mated to two females simultaneously, for whatever period. Some monogamous males had only one mate per season; we classed their bonds as either season-long or, when bonds lasted less than three-quarters of the season, short-term. Males that had more than one mate but with no overlap in the periods of association with them we called successively monogamous. Short-term monogamous bonds were evenly distributed over the season, a point of importance because the rate of nest success varied greatly according to calendar date. One factor evidently associated with the variety of pair relationships was the high rate of nest predation, especially in the spring (*8*). Only about one-fifth of all nests, and fewer than one-twentieth of nests built in the first half of the season, produced fledglings. Most females nested repeatedly after nest failure, but some switched mates before doing so.

Of 63 resident males, 6 were polygynous (Table 1). Judged by Verner and Willson's (*3*) criterion that polygyny is regular rather than casual when at least 5 percent of males are polygynists, our expectation for this indigo bunting population was fulfilled. As predicted by the model, female buntings paired with already mated males even though unmated males were present and advertising. Also as predicted (*9*) those males that were preferred, the polygynists and season-long monogamists, obtained females earlier in the season than did successive and short-term monogamists. In this comparison we considered pair-formation dates only of males that acquired territories at the beginning of the season, before 1 June (Wilcoxon two-sample test, one-tailed, $t_s = 2.50$; $P < .01$).

We calculated mean productivity of each sex, according to the form of the pair bond, on the basis of the number of young leaving the nest for each adult participating in the bond (Table 2). If a female switched males, her production with each male was regarded as an independent case and counted separately. For males, polygyny was most successful and short-term monogamy least successful. As expected under the hypothesis being tested, mates of polygynists suffered no disadvantage: Six females that paired with mated males produced an average 1.5 young that left the nest; this equaled the production of the first mates to pair with the same males and was about the same as the production of mates of season-long monogamists.

Table 2. Reproductive success per individual, according to the form of its pair bond. Values are the number of young leaving the nest divided by the number of participants in the bond.

Pair bond	Male	Female
Polygyny	3.0	1.5
Monogamy		
Season-long	1.6	1.6
Successive	1.7	1.0
Short-term	0.9	0.9

Old males were more successful than yearlings in acquiring and keeping mates (Table 1). Of the 6 polygynists, 5 were old, and 16 of 42 old birds but only 3 of 21 yearlings were season-long monogamists. Among short-term monogamists, yearlings predominated, and four yearlings but no old males were unmated. In a test of independence, age of males and form of the bond were significantly associated; the test compared polygynists and season-long monogamists pooled with other resident males pooled ($\chi^2_{\text{adj}} = 4.38$; $P < .05$).

Within each field reproductive success of mated males was the same without respect to age, but unmated males, all of which were yearlings, were not considered in this comparison. In the high-density field, an average of 1.6 fledglings were produced per old male and 1.8 fledglings per mated yearling; in the low-density field, average production was 0.6 fledgling for each age class. Clearly, then, reproductive success differed between fields. When each mated adult is counted only once in a season regardless of the multiple pair bonds of some females, 98 adults (46 males, 52 females) in the high-density field produced 79 fledglings, or 0.8 per adult. In the low-density field 28 adults (13 males, 15 females) produced 8 young, or 0.3 per adult, a significantly lower productivity ($\chi^2_{\text{adj}} = 7.53$; $P < .01$).

The absence of age-associated differences in productivity of mated males appears inconsistent with evidence (i) that for males the forms of pair bond varied in productivity and (ii) that old males participated more frequently than yearlings in the most productive forms of bond. Another apparent inconsistency is that bonds of mated males were distributed very similarly in the two fields despite the between-field difference in male ages (Table 1). How can these points be reconciled? If the question is simply a logical one—can all these results come out of the same investigation?—the answer lies in sample sizes. The large difference in number of males per field, the small number of yearlings that obtained mates in the high-density field, and the few nest successes, especially in the low-density field where successes numbered only three, interact to reduce samples greatly in certain comparisons and probably to magnify chance effects. Thus, a single case of successive monogamy by a yearling whose second mate produced fledglings in the low-density field has important effects on the comparison of fields with respect to pair bond and the comparison of productivity of the two age classes in the low-density field; it has much less influence on the comparison of age classes with respect to pair bond.

When the question about interrelationships of the variables is not logical but biological, answers cannot yet be proposed. Considerable work will be necessary before sample sizes let us ask about interaction of age and habitat on the form of the pair bond and about the separate effects of these three variables on reproductive success. However, our results so far suggest that habitat parameters are the key factor (*10*), as the model that we tested assumes and requires.

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References and Notes

1. J. R. King, in *Avian Energetics*, R. A. Paynter, Ed. (Publication 15 of the Nuttall Ornithological Club, Harvard Univ., Cambridge, Mass., 1974), pp. 4–70; H. Wiley, *Q. Rev. Biol.* **49**, 201 (1974).
2. About 2 percent of bird species are polygynous (8 percent of nidifugous species and 1 percent of nidicolous species), according to D. Lack [*Ecological Adaptations for Breeding in Birds* (Methuen, London, 1968), pp. 149–150].
3. J. Verner and M. F. Willson, *Mating Systems, Sexual Dimorphism, and the Role of Male North American Passerine Birds in the Nesting Cycle* (Ornithological Monogr. 9, American Ornithologists' Union, Washington, D.C., 1969), pp. 1–76.
4. J. Verner, *Evolution* **18**, 252 (1964); ——— and M. F. Willson *Ecology* **47**, 143 (1966).
5. G. H. Orians, *Am. Nat.* **103**, 589 (1969).
6. Thus C. J. Krebs [*Ecology* (Harper & Row, New York, 1972), p. 575] discusses the model and concludes: "At the present . . . we must be content with after-the-fact analysis rather than prediction. . . . [W]e are unable to predict what the mating system of an unstudied species . . . will be like." However, simply because of the male's prolonged singing throughout the nesting cycle, Verner and Willson (*4*) correctly predicted that dickcissels (*Spiza americana*) are polygynous.
7. In 1974 the high-density area was enlarged to 20 hectares by including a previously unstudied field. Male numbers per unit area remained unchanged.
8. Nest predation in the low-density field is discussed by V. Nolan Jr., *Ecology* **44**, 305 (1963).
9. G. H. Orians, in *Proceedings of the 15th International Ornithological Congress*, K. H. Voous, Ed. (Brill, Leiden, Netherlands, 1972) pp. 389–398.
10. Compare with the results of C. H. Holm [*Ecology* **54**, 356 (1973)].
11. We thank P. A. Randolph, R. C. Richmond, and C. F. Thompson for reading an earlier version of the manuscript. Contribution No. 1017 from the Department of Zoology, Indiana University.

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