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# Can Experience Alter the Avian Annual Cycle? Results of Migration Experiments with Indigo Buntings

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*With 2 figures*

## Abstract

Field experiments were conducted during 2 years testing whether premature release on their familiar, perennial breeding territories would cause indigo buntings (*Passerina cyanea*) to delete spring migration from their annual cycle. In the first year, male buntings were captured on their breeding territories in summer and held indoors for the winter on the photoregime that they would have encountered in nature as fall migrants and winter residents. The following spring they were released at the time buntings begin spring migration from the subtropics. Half were released on their breeding territories, to which they would normally have returned; half were released far to the south. Some of the males released on their territories remained and passed into breeding condition without having migrated, while some of those released to the south returned north to their territories. The results suggest that endogenous or photoperiodic mechanisms controlling the timing and occurrence of migration in this species can be overridden by experience. In the second year we tested alternative explanations for these results. Our second year's results seem to indicate (1) that birds that deleted migration in year one did not do so because of unfavourable weather and (2) that the birds that returned to their breeding sites in year one were actually migrating and not simply retracing their outward journey.

## Introduction

Research has revealed two types of physiological mechanism controlling the timing of migration and other annual cycle events in birds. Some species (reviewed by FARNER et al. 1983) respond directly to seasonal changes in photoperiod. Spring moult, gonadal enlargement, migratory fattening, migration and eventual reproductive activity take place sequentially in response to increasing daylength. Autumn moult and migration are thought to follow as internally coupled events in delayed response to long vernal days. Short days in winter are necessary to reset the photoperiodic response mechanism for the following spring. Other species (reviewed by GWINNER 1986) possess an endogenous, circannual rhythm. When these species are held on constant daylength, seasonal

moults and indices of spring migratory, reproductive and fall migratory physiology cycle in their natural sequence with a period of approximately 1 year. The annual progression of daylengths experienced in nature is thought to adjust the period to precisely 1 year, much as daily photoperiod entrains circadian rhythms. It is possible that photoperiodic and endogenous timing mechanisms have evolved independently in many avian taxa (FARNER & GWINNER 1980).

The possible role of experience in altering annual cycle timing has received little experimental attention (GWINNER 1986, KETTERSON & NOLAN 1987 a, b). Many birds return yearly to specific wintering and breeding sites, and experience is necessary for the formation of attachment to such sites (LÖHRL 1959). Year-to-year differences in individual arrival times (e.g. NOLAN 1978, ch. 4) indicate that experience possibly mediates the precise timing of termination of migratory behaviour. How much plasticity in timing and duration of migratory behaviour, and hence in the annual cycle, can experience confer upon birds? In this paper we report two years of field experiments on this question. In these experiments we placed birds in potential conflict between the stimulatory influence of seasonal migratory physiology and the possible suppressive influence of experience.

An ideal test of the importance of experience would involve capturing birds just before migration and transporting some of them prematurely to their familiar destinations; temporal information would then conflict with any response to presence at the destination. Unfortunately it is rarely possible to know both the breeding and wintering sites of individual migrants, and thus experimental subjects must be obtained in some other way. Adult male indigo buntings (i.e., those breeding for at least the second time; hereafter old males) return each spring to the same breeding territory (CAREY & NOLAN 1975, 1979). By capturing old males on their territories during the breeding season and holding them through the winter, we produced experimental subjects whose migratory destinations were known the following spring. At the onset of spring migration we released these subjects simultaneously at two locations. Buntings in experimental groups were released on their territories; those in control groups were released to the south, at the northern edge of the species' winter range. The hypothesis that experience can substantially alter the annual cycle predicted that birds released at their destinations should remain on their territories and those released to the south should migrate. Primacy of physiological timing mechanisms, however, predicted that all birds should migrate regardless of where they were released. Thus if experimentals deleted migration from their annual cycle and remained on their territories while controls returned to theirs in the normal manner, we could conclude that photoperiodic or endogenous timing mechanisms in indigo buntings can be greatly modified, and even overridden, by experience.

## Initial Experiment: 1985

### Study Species and Methods

The indigo bunting breeds in old field and second growth habitats in the eastern United States from Canada to the Gulf Coast and winters largely in Central America, Cuba and the Bahamas (BENT 1968) (Fig. 1). In the laboratory buntings grow fat and restless during the seasons of migration; the

Fig. 1: Map of North and Central America showing approximate breeding and wintering ranges of the indigo bunting, site of capture of buntings in 1984 (Bloomington, Indiana), and sites of release in 1985 (Bloomington, Indiana and Pensacola, Florida)

BLOOMINGTON, IN

PENSACOLA, FL
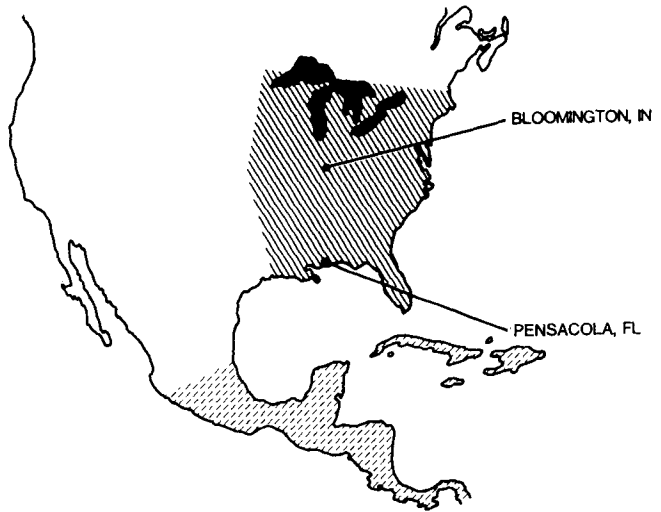
timing of this state can be manipulated photoperiodically (EMLEN 1969). Preliminary evidence from our laboratory suggests that the species may possess an endogenous, circannual rhythm controlling the development of a secondary sex character indicative of reproductive physiology (the cloacal protuberance of males) and the occurrence of seasonal moults and periods of migratory physiology at appropriate times of year in the absence of seasonal daylength changes (SNIEGOWSKI, unpubl. data).

Male buntings can be aged by plumage inspection as yearlings or older birds. At our principal study site near Bloomington, Indiana 62 % of old males breeding in one year return to the same territory to breed in the next (CAREY & NOLAN 1975). Because annual survivorship of small migratory passerines that breed in the Nearctic and winter in the Neotropics averages approximately 60 % (data from GREENBERG 1980), it appears that almost all old male buntings return to the same breeding site as long as they live.

During summer 1984, a total of 46 old male buntings were captured near Bloomington, Indiana and uniquely colour-ringed. 22 (hereafter, territorial males) were taken from their breeding territories using song playback and a live or mounted male as a lure. The remaining 24 (hereafter, supplemental males) were netted from the same areas, but at a later date; the exact locations of their territories were unknown.

Throughout captivity the buntings were given free access to food (commercial wild bird seed mix supplemented with turkey starter mash, grit, and occasionally mealworms) and water (with vitamins added). Subcutaneous fat level, moult, body mass, and general condition were recorded at 2-week intervals.

All subjects were initially housed communally in a large outdoor aviary at Indiana University. During Sep., after all had moulted into the brown basic plumage, they were transferred indoors to two windowless flight rooms in which the daily photoperiod (morning civil twilight to evening civil twilight) was adjusted at three-day intervals to simulate that encountered by freeliving buntings migrating to and wintering in Central America at latitude 15° N. By mid-March 1985, all birds had begun and some had completed the pre-alternate moult into the blue breeding plumage. We next placed each of the territorial males in an individual activity cage in which any incipient spring migratory unrest (Zugunruhe) could be monitored nightly by microswitch-equipped perches attached to a computer (described in KETTERSON & NOLAN 1983, 1987b). By late March, around the time when free-living indigo buntings begin spring migration (BENT 1968), 3 of the territorial males were showing Zugunruhe and 16 of the total 46 captives were carrying fat, indicating the onset of migratory condition.

We next randomly partitioned the 22 territorial males into two groups, experimentals and controls, consisting of 11 birds each. On 28 March we released each of the experimentals on its Bloomington, Indiana breeding territory, and on 29 March we released each of the controls

individually near Pensacola, Florida, approximately 1000 km due south of Bloomington (Fig. 1). (Controls were transported from Indiana to Florida by automobile on the night of 28 March. In this way the timing of their daily photocycle was kept as similar as possible to that experienced by the experimentals.) We emphasize that since the dates of release were near the vernal equinox — 22 March in 1985 — civil daylengths at release in Indiana and Florida were very similar (Bloomington, Indiana: 13 h, 25 min; Pensacola, Florida: 13 h, 8 min; data from 1985 Nautical Almanac). We then visited the territories of all subjects, experimental and control, daily between 1 April and 20 May.

On 30 March, immediately after release of the territorial males, we moved the 24 supplemental males from the windowless flight room to individual activity cages in a room with windows in which they could experience the natural daily Indiana photoperiod. Activity cages were positioned so that the birds received ample light from the windows but could not see outside. We quantified *Zugunruhe* in the supplemental males for the nights of 10 and 17 April by recording the number of 5-min intervals between 21.00 and 04.30 h during which each bird activated its microswitch perch at least once.

## Year One Results

Four of the males we released in Indiana remained there and 5 of those released in Florida returned. All of these males successfully reclaimed their territories in early to mid-May; aggressive behaviour and song were typical of breeding male indigo buntings at this time of year. All were still present on territory in mid-July when we quit following them. None of the remaining 13 birds released was sighted again.

Of the 24 supplemental males retained in captivity on Indiana daylength, 23 showed *Zugunruhe* in the typical pattern, indicating that the daylengths in Indiana at this time were not inhibitory to migration. Excluding the one inactive bird, which was underweight and possibly sick, mean scores for 10 and 17 April were 17 and 24 5-min units with activity, respectively, out of a possible 90. High scores were 67 and 73; the average of the higher of the two nights' scores for all birds was 27. All birds were active on at least one night.

## Discussion of Year One Results

Because birds held in the laboratory on natural Indiana daylength showed physiological readiness to migrate, it is unlikely that the slight difference in photoperiod between Indiana and Florida caused the observed difference in behaviour between the 4 birds that remained in Indiana (experimentals) and the 5 that returned from Florida (controls). Thus the data from 1985 strongly suggest that, in the 4 males that remained after release in Indiana, some response to presence at the breeding territory predominated over the migratory state characteristic of indigo buntings in early spring. We therefore interpret these results as consistent with the hypothesis that experience alters the annual cycle.

It is perhaps impossible, in field experiments of this type, to account for all birds released. We cannot know whether some birds released in Bloomington migrated and some released in Florida remained. It is possible, however, that some of these birds died after release. Release in unfamiliar territory and attempted migration after long captivity may have killed some of those that did not return from Florida. In Indiana, weather conditions in late March, when we released the birds, are harsher and less predictable than in late April when indigo buntings begin arriving in the area. For 1985, in particular, we consider it

remarkable that as many as 4 of the birds released in Indiana survived, as an unexpectedly heavy rainstorm began 6 h after their release on 28 March and continued for more than 48 h thereafter. Precipitation during this storm amounted to 16.1 cm compared to the long-term monthly March average of 9.7 cm (Climatological Data 1985).

## Followup Experiments: 1986

### Objectives and General Methods

In 1986 our objective, in addition to confirmation of the 1985 result, was to test the most likely alternative explanations for the behaviour of the 5 controls that returned to Indiana and 4 experimentals that remained in 1985. It was plausible that the controls had merely homed to Indiana following displacement to Florida (i.e., retracted their outward journey) rather than migrated there as if freeliving. For the experimentals, it seemed possible that cold early spring weather had prevented them from acquiring sufficient energy reserves to migrate before they advanced out of migratory and into reproductive condition.

To address the alternative explanation for the controls that returned, we held for the winter at Bloomington a group of birds whose territories were east of Bloomington, then in early spring released half at their breeding territories and half to the south. If the birds released to the south returned to their breeding territories rather than to Bloomington where they had been held for the winter, we could conclude that they, and hence probably also the controls in 1985, had migrated as if freeliving rather than homed after southward displacement. To address the alternative explanation for the experimentals that remained in Indiana, we released at Bloomington in early spring a group of birds whose breeding territories were north of Bloomington. If these birds migrated to their more northerly breeding territories, then early spring weather at Bloomington probably could not inhibit migration in the manner proposed above.

In 1986 also we repeated the 1985 experiment at Bloomington, this time, however, equipping the birds with radiotransmitters. We hoped by this to learn more about the movements and eventual fates of birds after release and thereby to account for a greater number of individuals.

## Methods

We obtained 39 territorial adult male buntings from three different locations during summer 1985: 16 from Bloomington, Indiana, 16 from Pembroke, Virginia, and 7 from Niles, Michigan. Pembroke, Virginia is located 1030 km due east of Bloomington; Niles, Michigan is 330 km due north (Fig. 2). Birds from Michigan and Virginia were transported to Indiana shortly after capture, and all birds were held in Indiana for the winter. Methods of capture and treatment in captivity were identical to those described for the 1985 experiment.

Releases in 1986 took place between the dates of 4 and 10 April. 9 of the 16 birds from Virginia were released on their territories near Pembroke, Virginia. The remaining 7 were released 300 km to the southwest at Clemson, South Carolina (Fig. 2). The 7 birds from Niles, Michigan, were released at Bloomington, Indiana.

For the repetition of the 1985 release experiment at Indiana and Florida, we equipped half of the Indiana buntings with radiotransmitters (Wildlife Materials, Inc.) and the other half with dummy units (containing no circuitry) of the same weight and shape (attachment according to RAIM 1978). Real transmitters were placed on birds released on their breeding territories in Indiana; Florida releases were given dummy units since their average return time to Indiana in 1985 — 39 days — exceeded the battery life of a live unit. The total mass of each unit and its attachment device was approximately 1.5 g, or about 12 % of male indigo bunting summer body mass. Although the general practice in avian telemetry is to limit radiotransmitter load to $\leq$ 5 % of lean body mass, this standard is an informal one (COCHRAN 1980). Allometric and aerodynamic considerations (CACCAMISE & HEDIN 1985) and the fact that indigo buntings often carry fat equal to over 50 % of lean body mass
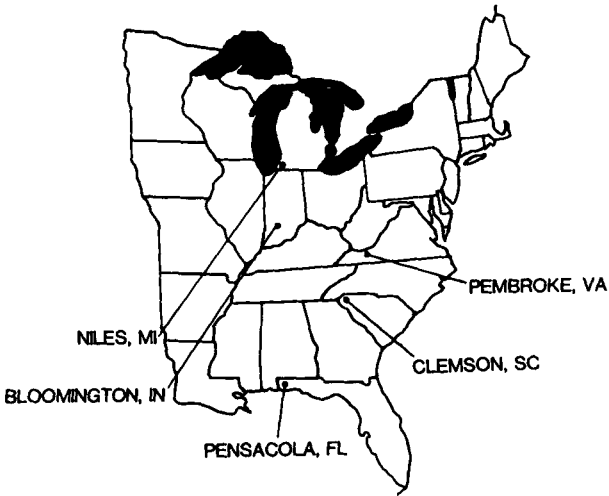
*Fig. 2:* Map of eastern USA, showing sites of capture of buntings in 1985 (Bloomington, Indiana, Niles, Michigan, and Pembroke, Virginia) and release in 1986 (birds were released at all sites shown except Niles)

during spring migration (JOHNSTON & DOWNER 1968) suggested that buntings might successfully migrate with a load of 1.5 g.

Following release, we made daily efforts to locate and track males released on territory at Bloomington using hand-held Yagi antennas and portable receiver units (Merlin 24, Wildlife Materials, Inc.) having an effective range of approximately 800 m in flat, open country (pers. obs.). During May and early June, we searched for released birds on their territories in Michigan, Virginia, and Indiana.

## Results

Three of the 7 Michigan breeders were found on their Michigan territories. Three of the 7 Virginia breeders released in South Carolina were found on their Virginia territories, but only 1 of the 9 males released on territory in Virginia was subsequently found there.

Of the 8 birds released on their territories in Indiana carrying transmitters, 1 was located alive and remained near its territory, 3 were found dead nearby within five days of the release date, and the remaining 4 were not seen again or detected. Of the 8 birds released in Florida carrying dummy units, only 1 was subsequently found on its Indiana territory, where we first noticed it on 16 May.

We followed the 1 transmitter-bearing male we could locate after its release in Indiana closely on an almost daily basis. Early in April it spent little time on its territory; rather it foraged nearby (within 1000 m) in loose association with other granivores. This foraging behaviour is similar to that described in wintering and migrating indigo buntings (BENT 1968). In late April it began restricting activity to the immediate area of its breeding territory; singing and territorial behaviour were first detected on 29 April.

## Discussion

The return of three buntings to Michigan suggests that early spring weather at Indiana does not necessarily inhibit migration. We therefore think it unlikely that the 4 experimentals that deleted migration in 1985 did so because weather conditions held them in Indiana until they passed out of migratory condition.

The alternative explanation for the return of 5 controls to Indiana in 1985 — that they homed rather than migrated as if freeliving — is also unlikely, since 3 of 7 birds from Virginia returned to their Virginia breeding territories after long captivity in Indiana and southeastward displacement from Indiana to South Carolina.

It was disappointing that only 1 of the birds released in Virginia was later detected on its territory. As in 1985, nothing can be said with certainty about birds never seen again. However, two observations suggest that at least some unaccounted-for birds may have died or made small moves after release that made their presence undetectable. First, in both 1985 and 1986 the buntings were relatively lean at release because they had refused to eat and lost body mass when placed in activity cages before release. In both years this drop in body condition may have decreased the chances of survival after release. Second, the degree of site fidelity to breeding territories may vary geographically. For example, at Niles, Michigan, old male buntings return to their territories of the previous year at a rate of approximately 58 %, whereas at the E. S. George Reserve near Ann Arbor, Michigan, old males return at the lesser rate of approximately 51 % (R. B. PAYNE, unpubl. data). In this study, one of the three males that returned to Niles after release in Indiana established its 1986 territory over 0.5 km from its 1985 site. In Virginia, any experimental or control birds that relocated in this manner during 1986 would very probably have not been found, since their original territories were along roadsides in a mountainous area where extensive offroad searching was almost impossible.

Mortality and movement may also account for the low recovery of Indiana buntings in 1986. Three of 8 were found dead near their territories within a week after release, as indicated, possibly because the transmitter load was too great. However, one survived release in Bloomington and one returned from Florida, indicating that the transmitters did not completely preclude survival and migration. Since the one that we are certain survived release in Indiana was sometimes found as far as 1 km from its territory, it is possible that buntings we never found made similar movements and died beyond the 800 m range of our receiving equipment.

In sum, the results obtained using transmitters suggest that mortality, and perhaps movement, occurred in all of the experiments reported here and were partially responsible for birds for which we could not account after release.

## General Discussion

KETTERSON & NOLAN (1983, 1987a, b) have reported suppression of autumn migratory physiology in experienced dark-eyed juncos (*Junco hyemalis*) confined during spring and summer at their perennial wintering site. The experiments reported here provide some evidence of a possible similar effect of experience on spring migration. If our interpretation of the data is correct, premature presence at the familiar breeding territory can delete spring migration from the annual cycle of the indigo bunting.

Although these experiments were designed to test the importance of experience in controlling whether spring migration occurs, we believe the results are also relevant to the question of what stimuli serve to terminate spring migration once it has begun. In contrast to autumn, spring *Zugunruhe* in most species, including the indigo bunting, continues well beyond the time when freeliving conspecifics have stopped migrating (GWINNER & CZESCHLIK 1978; WILTSCHKO et al. 1980). GWINNER & CZESCHLIK (1978) have proposed that reproductive activity provides the terminating stimulus to spring migration in freeliving birds. In contrast, our data for the indigo bunting suggest that experience can provide the terminating stimulus through the perception of familiar cues at the breeding site. Reproduction in indigo buntings in Indiana does not begin until females arrive in mid-May (CAREY & NOLAN 1979), yet males in these experiments deleted migration when released on their territories in late March and early April.

Induction of seasonal migratory physiology and behaviour is thought to follow from hormonal state (EMLEN 1969; review by MEIER & FERRELL 1978; FARNER & GWINNER 1980; MEIER & RUSSO 1985). The possible effect of experience in deleting or terminating migration may be hormonally mediated. A useful analogy in this regard would be that of hormonally mediated parental behaviour, which is elicited, sustained, and terminated by the interaction of internal state, response to external stimuli, and experience (e.g., SILVER 1980, 1983; MICHEL & MOORE 1986; compare KETTERSON & NOLAN 1987a). In a similar fashion, the interaction of seasonal internal state and perception of familiar external cues may determine when birds terminate migration and even, as our data suggest, whether migration occurs at all.

## Acknowledgements

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