

## BEHAVIOR OF MIGRATORY DARK-EYED JUNCOS FOLLOWING RELEASE IN THE WINTER RANGE DURING THE BREEDING SEASON

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In this paper we report the behavior of Dark-eyed Juncos (*Junco h. hyemalis*) detained in their winter range near Bloomington, Indiana (39°N, 87°W), which lies about 600 km south of the nearest breeding sites in Michigan (Wood 1951, Zimmerman and Van Tyne 1959), and set free there during the breeding season. In 1981, at least 2 unintentionally released juncos remained and bred at Bloomington, while at least 1 migrated about 1000 km to its former Canadian breeding site. Subsequent intentional releases in 1982 and observations on captives gave results that also indicated that some individuals were ready to breed outside their normal range while others were not. In both years, those that failed to migrate were either juveniles when first captured at their natal site in Canada or, if adult, were released well after breeding had begun in free-living birds. The only individual known to have migrated was an adult when captured and was released early in the breeding season. We shall attempt to interpret these observations in light of current views regarding the regulation and timing of avian migration and reproduction.

### THE STUDY SUBJECT AND METHODS

*The Dark-eyed Junco.*—Eastern migratory Dark-eyed Juncos breed primarily in spruce-fir forests of Canada and winter throughout the eastern U.S. (e.g., Bent 1968, Ketterson and Nolan 1976). Bloomington winter-resident juncos (i.e., those caught repeatedly in December–February) seldom are seen there beyond about 5 April (Ketterson and Nolan 1983a). Migrant flocks made up mostly of females are numerous until mid-April. Studies in the breeding range usually state that nesting begins in early May (e.g., Bent 1968). Fidelity to the breeding site is probably complete in males that have bred at least once (Ketterson and Nolan 1983a). Females are much less faithful than males to the exact home range of the preceding breeding season. Almost nothing is known regarding fidelity to the natal site, but if it is typical of passerines it is not highly specific.

*1981 escapes and releases.*—Between 2 and 4 May 1981, 36 color-banded captives that had been held for periods of 3–19 months in a large outdoor aviary at Bloomington escaped. All had been weighed and examined recently and had appeared to be in good health and good plumage. These birds, all members of the eastern migratory race, fell into 3 groups that differed according to the season in which and location at which they had been captured, as follows:

Group A: 4 immatures (i.e., birds hatched during the preceding breeding season) that probably were or had recently been

migrating when caught in early October 1980 near Kalamazoo, Michigan (42°N, 86°W);

Group B: 4 adults and 16 still dependent and/or newly independent juveniles that were captured on the breeding grounds near Wawa, Ontario, Canada (49°N, 85°W) in July 1981;

Group C: 10 adults and 2 immatures that were captured on their winter home ranges in Bloomington in December–February 1980–1981.

Members of groups A and B were transported to Bloomington immediately after being caught. Age in groups A and C was determined by degree of skull pneumatization, in group B by plumage. (Hereafter we shall continue to refer to individuals according to their age at first capture.) Sex was established by methods we have previously described (Ketterson and Nolan 1976); in addition, adult females and males of group B had brood patches and cloacal protuberances, respectively.

On 24 May we deliberately released an apparently healthy young female with a history like that of the group A juncos.

Beginning 7 May we looked for juncos at the aviary nearly daily until mid-September, except for the period 17 June to 9 July. During the latter period, we returned to the capture site of 8 of the group B juncos (including that of 1 adult male, 1 adult female, 4 juvenile males, and 2 juvenile females). There we netted intensively and checked all singing males for color bands.

*1982 releases.*—On 21 May 1982, we released 1 male and 1 female whose histories were the same as those of the group B juveniles, except for the additional year they had been in captivity and the fact that they had been subjects of a Zugunruhe study and housed during the intervening fall and spring in small registration cages. Both had shown normal vernal nocturnal restlessness and had accumulated typical levels of migratory fat. Their plumage was more frayed than that of free-living juncos as the result of life in the small cages; in other respects they appeared to be in normal healthy condition.

On 15 June 1982, we released 2 males with histories identical to those of the group B adults and whose prior treatment and condition were like those of the juncos released on 21 May. On 9 July we released 9 similarly treated females (2 with histories like those of group B juveniles, 3 like group B adults, the others caught at Bloomington in the winter of 1982).

As in 1981, daily visits were made to the aviary after releases, except for another period (18 June–8 July) when we were in Ontario.

*Observations on captives.*—The juncos that were subjects of the Zugunruhe study referred to in the last section were studied in the spring of 1981 and 1982 and had histories like the group B juncos. The females among them were checked every 7–10 days from 1 March to early June 1981 and 1982 for the presence or absence of a brood patch. Thereafter they were housed communally with group B males in the large outdoor aviary.

## RESULTS

*1981 escapes and releases.*—Several of the escaped birds, all of them juveniles from group B, remained near the aviary. We recaptured 4 of them by 7 May, too soon after release to conclude anything about whether they would have stayed throughout the breeding season. Recapture efforts stopped on 7 May because we observed a female carrying nest material; she was followed by a male with which she copulated. These birds, also group B juveniles, built 3 nests and the female laid eggs in the first and third of these; the second was not used. Nest 1 and its 2 eggs were destroyed by a predator before incubation had begun. On 20 May, the female was killed by a predator after laying 2 eggs in nest 3 and again before having had the opportunity to incubate.

The male resumed advertising but was unable to attract the female released on 24 May; she disappeared. This advertising continued until at least 17 June, when we departed for Ontario. In mid-July, when we resumed observations, the male, still present, was in mid-molt. He was not seen after 9 September, despite near-daily capture efforts in the vicinity during the next 10 months.

Only one other 1981 subject was seen again at Bloomington. On 25 May a second group B (juvenile, uniquely color-banded) escaped male appeared at the aviary for about 10 min. We conclude from the fact that 3 weeks had passed since his escape that he did not migrate.

In Canada, we found the only escaped adult male that had previously bred at the Canadian study site and soon recaptured (and released) him. We next saw him with a female, on 6 and 7 July. Both were feeding young whose size and behavior indicated that they had left the nest 6 or 7 days before, and we assume the male was their parent. Estimating the time required to produce these fledglings and supposing that the period between territory establishment and the laying of 4 eggs took a minimum of 8 days, the male had arrived on his territory no later than 31 May. Therefore, he had taken at the most 27 days to cover some 1000 km, assuming he moved in a straight line. This same male was also seen frequently and netted at Wawa in June and July of 1982, at the precise location he had occupied in 1980 and had returned to in 1981.

*1982 releases.*—The first-released male sang frequently at the aviary for 9 days after release and was not found thereafter. Considering the date (30 May) of his disappearance and the duration of his territorial behavior prior to his disappearance, we think it likely that he did not migrate, but rather that he made a local movement or died. The first-released female was seen frequently for only 4 days prior to her disappearance but there were no observed interactions with the male. We draw no conclusion regarding her fate.

Of the males released on 15 June, 1 was not seen again at Bloomington or at Wawa, where we searched for him between 19 June–7 July. The other stayed at the aviary, behaved very aggressively for several days toward male juncos that were still caged, sang until late July, and re-

mained until at least mid-September. Only 1 of the 2 juvenile females released 9 July stayed at the aviary, where until at least 1 August she associated with the male that had remained as though they had formed a pair. On 22 July she persistently gave alarm calls at us like those of breeding adults when an intruder approaches nests or young, but on 23 July she and the male fed quietly together for long periods and showed no alarm. We could find no nest, but junco nests are well concealed on the ground and exceedingly difficult to find after the pair has quit using them.

*Observations on captives.*—Nine females caught at Wawa, Ontario, as juveniles in the summer of 1980 developed brood patches by May of 1981 or 1982, while 11 of 13 Wawa adults did not (adj. chi square = 4.95,  $df = 1$ ,  $P < .05$ , individuals studied in both years counted only in the first year). On 9 July we found an empty junco's nest inside the aviary. A fresh junco egg lying 2 m distant had been opened by cuts whose shape suggested that a mouse was responsible for them. The identities of the nest builder and/or the egg-layer are not known. (cf. Swanson 1975, who reports egg laying by juncos held in small individual cages.)

#### DISCUSSION

We discuss only the 7 juncos whose status after release is known or can be inferred with some assurance. Two adult males, both from Wawa, differed in that 1 migrated to his former breeding site, whereas 1 attempted (possibly successfully) to breed at the aviary without migrating. The migrant escaped at the very beginning of the breeding season; the non-migrant was freed only after the breeding season was more than half over. Four juvenile males and 2 juvenile females, all from Wawa, probably did not migrate after releases ranging from the beginning of the breeding season to quite late in that period. It is known with certainty that two of these bred.

Recognizing that our observations are incomplete, we attempt nevertheless to interpret them in light of current views regarding regulation of the transition between the migratory and the reproductive conditions (Gwinner and Czeschlik 1978). In birds that have a strong tendency to reoccupy the former breeding site (as male juncos do), arrival at that site probably plays some role in terminating the migratory state (compare Gwinner and Czeschlik's 1978 review of hypotheses to explain prolonged vernal *Zugunruhe* in captive birds). However, the relative importance of the stimuli associated with the migratory goal, as compared to those emanating from the bird's internal sense of time, is poorly understood. For example, whether an adult male transported prematurely to its breeding territory of the preceding year would settle immediately on that territory is not known. (However, we do know that juncos held for almost a year at the wintering site of the preceding year and then monitored there from late in the following summer through autumn do not fatten normally or exhibit normal levels of *Zugunruhe*;

Ketterson and Nolan 1983b.) Neither is it known whether an adult male detained along its route, and thus prevented temporarily from reaching the breeding home range, would exhibit a delayed transition from the migratory to the reproductive condition and therefore complete its journey. The male junco that returned to Wawa suggests that such a delay is possible, since he was able to migrate about 1000 km in a period during all or most of which he would normally have been engaged in reproductive behavior at Wawa. Wolfson (1940, 1942), who detained juncos in the winter range until June, reports that they migrated nonetheless. Still, an indefinite delay seems unlikely, and this view is supported by the case of the Wawa adult male that took as his territory the aviary grounds after being freed in mid-breeding season. Earlier readiness to migrate by this bird had been indicated by his intense spring Zugunruhe.

If perception of the familiar breeding site normally interacts with information about the time-advance of the season to terminate the migratory state of experienced birds, a similar model can be applied to young juncos arriving on the breeding range for the first time. It seems very likely that fledgling juncos, like young of many species (e.g., Bellrose 1958, Löhrl 1959, 1962, Berndt and Winkel 1979), form an attachment to next year's potential breeding sites sometime before they begin autumn migration, and arrival at these the following spring could have the consequences that we suggest the former breeding site has on more experienced birds. However, our juvenile group B juncos probably did not have a normal opportunity to form such an attachment to the breeding ground before we took them from it. If so, then when set free they may have possessed only the information that the season for migration had passed, and this could explain why the 5 that we know about did not migrate (cf. Rüppel and Schein 1941). The fact that significantly more juvenile than adult females from Wawa developed incubation patches toward the end of the spring Zugunruhe experiments may also reflect the readiness of inexperienced birds to become reproductive on the basis of temporal information alone, regardless of location. An alternate hypothesis—that the Wawa juveniles passed through a sensitive phase at Bloomington (i.e., were imprinted and developed site attachment there)—seems less likely, considering that in some species freedom to move about has been found to be necessary to forming attachment to a location (Löhrl 1959, 1962), but that hypothesis cannot be rejected.

One final note regarding the junco that returned to Wawa after having been transported to Bloomington by automobile the preceding summer. Considering the great size of the junco's winter range, it is highly unlikely that this bird had ever been in Bloomington while free-living, and his relatively rapid return to his breeding territory might suggest that he had employed navigation and not random search over at least part of his course between Wawa and Bloomington (see Able 1980 for current views on the importance of navigation to migrants). Homing following long-distance displacement has been reported in passerines many times

(e.g., Hamilton 1962, Mewaldt 1964, Southern 1968, Demong and Emlen 1978, Nastase 1982), but the present case is unusual because of the long delay between transport and release, coupled with the promptness of return to the capture site.

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