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LONG-DISTANCE HOMING BY NONMIGRATORY DARK-EYED JUNCOS¹

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In wild birds, as opposed to homing pigeons (*Columba livia*), convincing evidence of navigation, i.e., goal-oriented flight over unfamiliar territory, is rare (Able 1980). We here report instances of homing by Carolina Dark-eyed Juncos (*Junco hyemalis*) that seem likely to have involved navigation. Displaced males traversed distances that were great relative to the small size of the birds' lifetime home range. Furthermore, they did so at speeds inconsistent with the view that they simply searched until they came upon familiar cues and then homed over terrain known from previous experience.

MATERIALS AND METHODS

Studies were conducted from mid-May to mid-August in 1983 and 1984 at the University of Virginia's Mountain Lake Biological Station (near Pembroke, Virginia, 37°22'N, 80°32'W and approximately 1,158 m above sea level on Salt Pond Mountain). In 1983 we captured, displaced, and released five male juncos in the course of conducting an experiment unrelated to this report. Because some of these returned, we carried out a more structured displacement of males in 1984.

All subjects were mated and were captured at their nests on the day the eggs began to hatch or on the following day. All were banded with individually distinct combinations of color bands and with United States Fish and Wildlife Service numbered bands. The interval between capture and displacement (which was always immediately followed by release) varied, as shown in Table 1. Weights at the time of release were normal, as were other visible

indicators of physical condition. One junco (Bird F, Table 1) was equipped with a radio transmitter (Wildlife Materials, Carbondale, Illinois, weight 1.7 g) glued to its back (Raim 1978). Another (described both as Bird C and Bird H in Table 1) was displaced in both 1983 and 1984. No other individual was used twice. All distances referred to were calculated as rhumb lines, using air pilots' charts.

The birds were transported by automobile on days of fair weather. In 1983, some were placed in large, open, wire cages and others in individual, opaque, paper bags; in 1984, all were in individual, open, wire cages. During transport none could see other juncos, but, except for those in bags, no effort was made to deprive them of information en route.

Because returns were not anticipated in 1983, circumstances attending the releases, except those shown in Table 1, were not recorded. In 1984, three birds were driven for almost 4 hr on 7 June and let go one at a time (several min apart) at about 12:00 at the edge of a highway near Winchester, Kentucky. Each (including the one carrying the radio transmitter) flew into low, shrubby vegetation and disappeared. The remaining three were then driven for about another 4 hr on the same date to Bloomington, Indiana, and let go one at a time at 16:25 on the grounds of the aviary of Indiana University. There was no indication in either Kentucky or Indiana that the birds assembled after having been released.

RESULTS

Two of three males released in Virginia in 1983 returned to their territories 9 and 16 days later, respectively. Other males had claimed these territories during their absences but quickly withdrew. The third (Male D, Table 1), which had been displaced a shorter distance than the others, was not seen again. All these birds had been transported in paper bags. Two additional males were displaced in a cage to Bloomington, Indiana, in 1983. One returned—in 1984 he occupied a territory adjacent to his former territory—

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TABLE 1. Circumstances of capture, displacement, release, and homing by male Carolina juncos to breeding territories at Mountain Lake, Virginia.^a

Bird designation	Capture date	Release date	Release location, coordinates, altitude (m) ^b	Distance displaced (km) ^c	Return bearing ^c	Return (detection) date	Time elapsed, release to return (days) ^d	Rate of return (km/day) ^d
A	5/23/83	7/21/83	Bloomington, IN 39°10'N, 86°32'W 269 m	563	111°	none ^e	—	—
B	5/23/83	7/21/83	Bloomington, IN	563	111°	unknown ^e	unknown ^e	unknown ^e
C ^f	6/7/83	6/17/83	Charlottesville, VA 35°02'N, 78°30'W 144 m	195	248°	7/3/83	15	13.0
D	6/18/83	7/3/83	Roanoke, VA 37°16'N, 79°52'W 276 m	55	279°	none	—	—
E	6/23/83	7/17/83	Lynchburg, VA 37°25'N, 79°09'W 158 m	124	267°	7/26/83	8	15.5
F ^g	5/27/84	6/7/84	Winchester, KY 37°60'N, 84°11'W 296 m	328	104°	none	—	—
G	5/29/84	6/7/84	Winchester, KY	328	104°	6/21/84	13	25.2
H ^f	6/3/84	6/7/84	Winchester, KY	328	104°	6/29/84	21	15.6
I	5/12/84	6/7/84	Bloomington, IN	563	111°	7/11/84	33	17.1
J	5/28/84	6/7/84	Bloomington, IN	563	111°	7/4/84	26	21.7
K	6/4/84	6/7/84	Bloomington, IN	563	111°	none	—	—

^a Mountain Lake Biological Station of the University of Virginia is located at 37°22'N, 80°32'W at 1,158 m above mean sea level.

^b Altitudes are above mean sea level.

^c Return bearings were calculated with 0 located along meridians from grid north. Distances displaced were calculated as rhumb lines on air pilots' charts.

^d Time elapsed was the period beginning with the day following release and ending with, and including, the day before the bird was discovered back on its territory. That same number of days was used in determining mean rate of return per day.

^e There was no opportunity in 1983 to determine whether these individuals returned in that year. Bird B in 1984 defended a territory adjacent to the territory he had occupied in 1983. Bird A was not present in May 1984 or thereafter. It may have returned and died before May.

^f Birds C and H were the same individual.

^g This male was equipped with a radio transmitter weighing 1.7 g.

but we do not know when, because we left Mountain Lake soon after the displacement. We never saw the second male; it is possible that he too homed but died before we resumed our study in May 1984.

Two of the three males taken to Winchester, Kentucky, in 1984 homed to their territories, as did two of the three taken to Bloomington, Indiana (Table 1).

Birds that returned behaved conspicuously and aggressively, as do males establishing territories in spring, and we therefore believe we detected them no later than the first full day following their arrival. One Indiana bird was caught on the day he probably arrived at Mountain Lake; he was in normal, lean, breeding condition (20.7 g).

The fact that Male F was wearing a radio transmitter obscures the significance of his failure to reach home. If we assume that the failure was not attributable to the transmitter, and if we also count as a nonreturner the second bird taken to Bloomington in 1983 (Bird A, Table 1), then we conclude conservatively that seven of the eleven homed.

Table 1 estimates the mean daily rates of movement of the six males whose speeds we were able to determine, making the assumption that they moved in rhumb lines toward Mountain Lake every day between the day following release and the day before we found them on their territories, inclusive. However, two facts indicate that departure from the release point may not always have been as prompt as assumed. (1) A male released in 1984 at Bloomington was seen there on the day after release. (2) A male that we had planned to displace and were holding escaped at Mountain Lake, and although his territory was only 3 km distant he did not reappear there until 2 days later.

Figure 1 regresses the time required to reach Mountain

Lake against the distances between that location and the release sites, again on the assumption stated in the preceding paragraph. The regression is linear: $y = 0.046 + 3.239x$; $t = 4.521$; $P \approx 0.01$; $r^2 = 0.836$.

DISCUSSION

There can be little doubt that the birds were displaced to unfamiliar areas. Carolina juncos breed in the Appalachian Mountains above about 915 m from Maryland and West Virginia southward into South Carolina and Georgia and are commonest above 1,200 m (e.g., Miller 1941 p. 329, Rabenold 1978, Kendeigh and Fawver 1981). Some individuals, mostly males, remain on the breeding rounds in even the most severe winters, while others disperse short distances, moving to lower elevations in harsh winters than in moderate (Rabenold and Rabenold 1985). Members of the Virginia population that we study follow this pattern (Hostetter 1961). Thus, ornithologists long resident at Virginia Polytechnic Institute and State University in Blacksburg, Virginia, located 17 km from our study area and 16 km from the nearest breeding range at an altitude of 693 m, have never seen a Carolina junco in Blacksburg (C. Adkisson, J. Via, pers. comm.). Further, some members of our study population (all individually marked) are regularly seen at Mountain Lake throughout their first winter of life and subsequent winters (A. Hulbert, C. Ziegenfuss, pers. comm.; see also Hostetter 1961). Finally, the short distances separating the natal and first breeding site in this population suggest that most individuals spend their entire lives within a home range of a few km². (Of 55 banded young that left the nest in 1983, we found over 40% of the estimated survivors breeding within 2 to 3 km of their hatching sites in 1984 and/or 1985.)

Although we do not know the mechanism by which the

juncos homed, we can probably eliminate the possibility that they began by simply searching until they found familiar cues. Where homing is preceded by searching, the rate of success should be closely related to the ratio of the size of the familiar area to the distance separating that area from the release point (compare Griffin 1964, p. 96, Baker 1984, p. 20). Moreover, theoretical models predict that when birds employ random search patterns the proportion returning home will decrease with increasingly long displacement (Wilkinson 1952, Griffin 1964). Despite the small size of our sample, it is suggestive that four of six juncos homed from 328 km or less and three of five did so from 563 km. Finally, in the six cases in which we can estimate the mean distance traveled per day, extremes were 13.0 km and 25.2 km, which we view as low variation. Although independence of mean rate of movement and total distance traveled can in theory be reconciled with reliance on search patterns (Wilkinson 1952), the points in Figure 1 seem unlikely to have been produced by animals exploring over unfamiliar territory from different distances and in different directions from a faraway target.

Even the fastest average daily rate of homeward movement (Table 1) was much less than the distance a small migrating passerine can cover in a few hours, but such slow rates do not necessarily imply that homing was preceded by time consuming search for a familiar area. In the only reported case in which displaced wild passerines have been successfully radio tracked, Able et al. (1984) demonstrated that Wood Thrushes (*Hylocichla mustelina*) oriented consistently homeward after release, even though they made only short flights each day.

We are aware of noncomparable homing performance by so sedentary a bird. House Sparrows (*Passer domesticus*) and Eurasian Tree Sparrows (*P. montanus*), for instance, which may have lifetime familiar areas of about the same size as these juncos, did not return after displacement beyond 14.5 km (Wojtusiak et al. 1947, described in Matthews 1968). In migratory *Zonotrichia* spp. Mewaldt and associates have reported remarkable instances of long-distance homing by birds displaced from their wintering sites (Roadcap 1962; Mewaldt 1963, 1964a, 1964b; see also Manwell 1962). In most of these cases, displacement and recovery were separated by a long interval, so that it is likely that the birds migrated to the breeding range after displacement, and then in the following autumn migrated back to the place from which they had been taken during the preceding winter. In one instance, however, a *Zonotrichia leucophrys pugetensis* displaced far beyond the range of that race evidently homed directly to its winter site, covering about 3,000 airline km in approximately 70 days (Mewaldt 1963).

Nevertheless, between the homing of the Carolina juncos and that of the migratory sparrows there may be a difference of importance. Recent discussions of mechanisms of navigation have focused increasingly on the role of experience and learning in the development of the individual's orientational abilities (Baker 1978, 1984, Wiltschko and Wiltschko 1978, 1985, Papi 1982). It is proposed that movement over, and gradual enlargement of, a familiar area is accompanied by the perception of geophysical and other gradients that extend beyond that area. The result is that, as it moves about, the individual builds up and extrapolates a mosaic map of coordinates corresponding to the gradients it encounters, and this map then permits goal-oriented flight over terrain with which the animal has had no previous direct contact. This model is entirely consistent with the abilities displayed by Mewaldt's *Zonotrichia*, all of which had previously performed at least one seasonal migration. The sedentary juncos described herein had had far more limited experience. Even if they had formed a map based on gradients learned on their Virginia mountaintop, it is a long additional step to

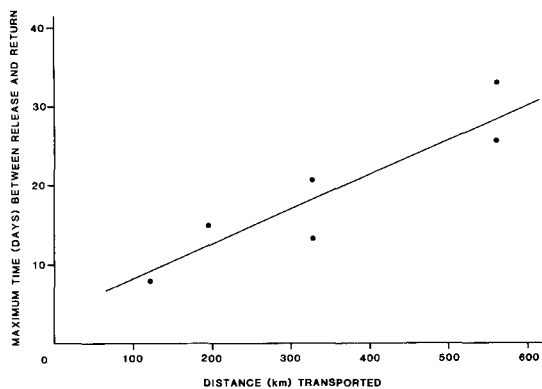


FIGURE 1. Relationship between distance transported and time required to return to territories by six juncos that homed. Distance is straight rhumb line between release site and home. Time is measured from day following release to day preceding detection on territory, inclusive.

suppose that the map would extend to Indiana and that it would be corrected for local variations and anomalies (Lednor 1982) that could distort its accuracy or interfere with its use.

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