HOMING SUCCESS IN WINTERING SPARROWS

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The ability of birds to return "home" after displacement is generally well known but poorly understood because of the multiplicity of variables that affect homing performance. These variables can include age and previous experience of the bird, as well as the timing and distance of the displacement. The phenomenon of homing is also difficult to interpret because, like other behaviors, its performance depends upon both motivation and ability. A deficiency in either component will preclude expression of the behavior.

In this study we attempted to determine the effects of age of birds and the date and distance of displacement upon homing success. We used in this study wintering sparrows of the genus *Zonotrichia*. From these data we wish to separate to some degree the motivational and ability components of homing performance.

Most previous work has dealt with displacements from the breeding grounds. Few studies have involved the wintering grounds, despite the usually longer residence there, often 5–6 months. The site tenacity of birds of the genus *Zonotrichia* to their winter home is well documented. Of birds captured at a banding station one winter, often 30 to 50% are recaptured the next (Linsdale 1949; Mewaldt 1956, 1963; Stokley and Stokley 1963; Ralph and Mewaldt 1975). Apparently most of those that survive return to the same wintering ground.

Environmental cues used to orient.—At least some species of passerine birds apparently have an innate ability to orient using celestial cues (Kramer 1952, Sauer 1957, Emlen 1967, Ralph 1975). Other hypotheses of orientation involving geomagnetism (Merkel and Wiltschko 1965), and wind (Gauthreaux and Able 1970) are being explored. In any case, such cues are probably secondary to celestial cues in most species (although see Wiltschko 1972). Evidence from homing experiments with Rock Doves (*Columba livia*) and Bank Swallows (*Riparia riparia*) (Graue 1963, Downhower and Windsor 1971) indicates that familiarity with landmarks can facilitate homing.

Factors influencing homing ability.—Several exogenous and endogenous factors apparently influence the ability of birds to home, and can provide clues to the mechanisms involved.

The age of a bird markedly affects its homing ability. Petersen (1953) found that wintering first-year gulls (*Larus r. ridibundus* and *L. c. canus*) showed poorer homing ability than adults. Schwartz (1963) moved 4 adult and 14 first-year Northern Waterthrushes (*Seiurus noveboracensis*) 10 to 65 km from their winter home in Venezuela and found that only the adults returned. Finally, of *Zonotrichia* displaced from their winter home one year, more adults than subadults returned to their home the next winter (Mewaldt 1964).

Related to the factor of age is the bird's previous migratory experience. An adult bird on the wintering grounds has made at least one round trip and has acquired a greater acquaintance with the topography and techniques involved.

Work on the effect of distance of displacement by Matthews (1963), Schmidt-Koenig (1964, 1966, 1970), and Wallraff (1967) has apparently shown that a hiatus in the accuracy of initial orientation of released Rock Doves exists between approximately 15 and 95 km from the home station. Within this distance, initial orientation is less accurate than either closer or farther from the home. This "dead belt" prompted Matthews to conclude that two different mechanisms are involved—one useful for short distances, the other for longer distances. He suggested that when birds are released at intermediate distances, neither mechanism is effective and initial orientation is less accurate. Under this hypothesis, in order to home from longer distances the birds must first take up the appropriate direction. Then they must have sufficient "directional momentum" to carry them across the hiatus into the zone where the short distance mechanism is effective. That is, they must be able to continue flying in the appropriate direction for a distance, despite a presumed lack of accurate information for navigation. However, Keeton (1970) and Graue (1970) were unable to confirm an intermediate zone of poor initial orientation of pigeon releases. It should be noted that the prior homing experience of their experimental birds may have been a factor in their results.

METHODS

We carried out a series of reciprocal displacements during the winter of 1964–65 involving 10 stations extending from Soquel in Santa Cruz County to Glen Ellen in Sonoma County, California, 160 km to the north (Fig. 1). Distances between stations varied from 5 to 160 km. For each displacement, birds were usually caught during the morning at each of the 10 stations and transported to every other station that afternoon. The number released at each station was arranged so that approximately equal numbers were displaced each distance. We displaced 905 individuals of

Fig. 1. Displacement localities in the vicinity of San Francisco Bay, California.

three taxa of migratory *Zonotrichia* as follows: Golden-crowned Sparrow (*Z. atricapilla*) 480, and White-crowned Sparrows (*Z. leucophrys gambelli*) 190, (*Z. l. pugetensis*) 235. All are known to be nocturnal migrants (Mewaldt et al. 1964). The relatively small samples of each of the three taxa preclude analysis of possible differences in performance among them. Additionally the taxa are very closely related and have similar migration routes, physiology, and habits (Mewaldt et al. 1964, Bent 1968).

All birds received bands for individual identification. Most were caught in wire mesh traps baited with cracked corn and wheat. Some were caught in mist nets near these traps.

The displaced birds were distributed randomly, but in predetermined quantities according to their displacement destination, and carried there in vented cardboard or wooden boxes. They remained relatively quiet during the several hours of travel by

TABLE 1

NUMBER OF BIRDS DISPLACED, RETURNED, AND REMAINED[1]

Distance displaced (km)	No. of stations		Date of displacement												Totals	
			28 Nov.		20 Dec.		9 Jan.		30 Jan.		13 Feb.		25 Feb.–6 March			
			Ad	Subad	Ad	Subad	Ad	Subad	Ad	Subad	Ad	Subad	Ad	Subad	Ad	Subad
1–20	5	No. displaced	12	29	10	11	2	4	6	8	15	13	6	2	51	67
		Return	7	5	2	3	1	0	2	3	3	0	0	0	15	11
		Remain	1	8	1	2	0	1	1	0	4	2	1	0	8	13
		2nd year	0	0	0	0	0	0	1	0	0	0	1	0	2	0
21–40	9	No. displaced	26	30	24	22	12	10	6	5	15	15	12	7	95	89
		Return	6	2	8	0	3	1	1	0	1	0	0	0	19	3
		Remain	1	2	2	2	1	2	0	0	2	1	0	0	6	7
		2nd year	0	0	0	0	0	1	0	0	0	1	1	0	1	2
41–60	9	No. displaced	11	34	16	18	11	22	14	7	19	13	11	9	82	103
		Return	3	0	6	2	3	0	1	0	1	1	0	0	14	3
		Remain	4	7	1	1	4	7	0	2	2	2	2	1	13	20
		2nd year	0	0	1	1	0	0	1	0	2	0	0	0	4	1
61–80	8	No. displaced	14	23	19	28	15	20	4	4	16	15	3	1	71	91
		Return	2	0	3	0	4	0	0	0	2	0	0	0	11	0
		Remain	3	8	4	8	1	4	0	1	3	2	1	0	12	23
		2nd year	0	0	1	0	0	0	0	0	1	0	0	0	2	0
81–100	6	No. displaced	9	13	7	18	11	13	4	4	3	2	0	4	34	54
		Return	3	0	2	0	1	0	1	0	0	0	0	0	7	0
		Remain	4	6	1	4	1	4	0	0	0	0	2	2	6	16
		2nd year	0	0	0	0	0	0	0	0	0	0	0	0	0	0
121–140	6	No. displaced	9	7	11	13	2	9	6	13	16	10	3	5	47	57
		Return	2	0	0	0	0	1	1	0	0	0	0	0	3	1
		Remain	1	0	2	1	1	0	0	2	0	0	0	1	4	4
		2nd year	0	0	0	0	0	0	0	0	0	0	0	0	0	0

TABLE 1.—Continued

Distance displaced (km)	No. of stations		Date of displacement												
			28 Nov.		20 Dec.		9 Jan.		30 Jan.		13 Feb.		25 Feb.–6 March		Totals	
			Ad	Subad	Ad	Subad	Ad	Subad	Ad	Subad	Ad	Subad	Ad	Subad	Ad	Subad
141–160	2	No. displaced	8	5	13	6	5	4	6	5	4	4	2	2	38	26
		Return	3	0	5	0	1	1	0	0	0	0	0	0	9	1
		Remain	0	1	0	0	0	0	0	2	0	1	0	1	0	5
		2nd year	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Totals		No. displaced	89	141	100	116	58	82	46	46	88	72	37	30	418	487
		Return	26	7	26	5	13	3	6	3	7	1	0	0	78	19
		Remain	14	32	11	18	8	18	1	7	11	8	4	5	49	88
		2nd year	0	0	2	1	0	1	2	0	3	1	2	0	9	3

[1]Abbreviations: Ad = adult, Subad = subadult, Return = number returning to home station, Remain = number remaining at new station, 2nd year = number remaining first year and returning the second.
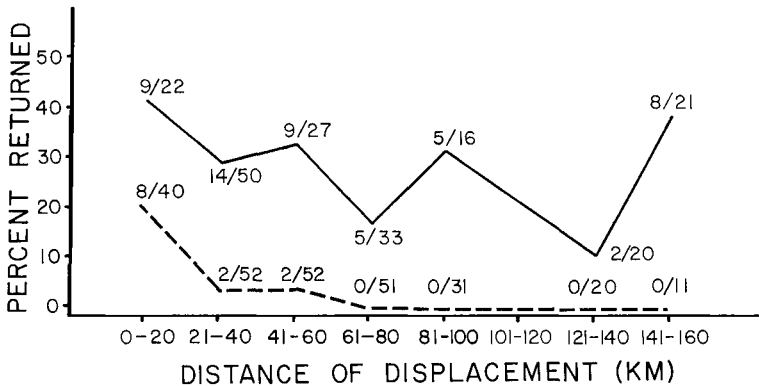
Fig. 2. Percent of adults (solid line) and subadults (dashed line) that returned to their home station by distance of displacement in November and December. By each point is the number of birds returned of those displaced.

automobile. After release many became at least temporarily attached to local flocks. A continuous trapping program was sustained at all 10 stations during the winter of 1964–65. More than 11,000 trap hours were expended during that season. Although equipment, methods, and intensity of effort varied among the stations, we believe the results were not significantly distorted by these variables.

For most analyses data are arranged by date of displacement or by distance of displacement grouped in 20-km distances. Tests of significance compared the equality of two percentages by the method involving the arcsine transformation (Sokal and Rohlf 1969: 607).

Birds were displaced within seven 20-km distances. For analyses, the central of these seven (61–80 km) was used for calculations of significance. This value includes the center of Matthew's (1963) and Schmidt-Koenig's (1964, 1966) zone of poor initial orientation, and also gives a maximum number of comparisons for calculations.

RESULTS AND DISCUSSION

Rates of return to home station.—The rate of return to the home stations during the same season (1964–65) varied with distance and time. Adults (those at least in their second winter) returned with greater frequency than did subadults (those in their first winter) at virtually all distances and all dates of displacement (Table 1, Fig. 2).

Adults displaced intermediate distances in November and December (Fig. 2) showed a somewhat poorer rate of return than those displaced the shorter distances and those displaced the longer distances (1–60 + 81–160 vs. 61–80 km, $P < 0.03$; 1–40 + 101–160 vs. 41–100 km, $P < 0.26$; 1–20 + 141–160 vs. 21–140 km, $P < 0.03$; all one-tailed tests). These results are only suggestive of a hiatal pattern. The hiatal pattern did not appear in the displacements made later in the season. In January
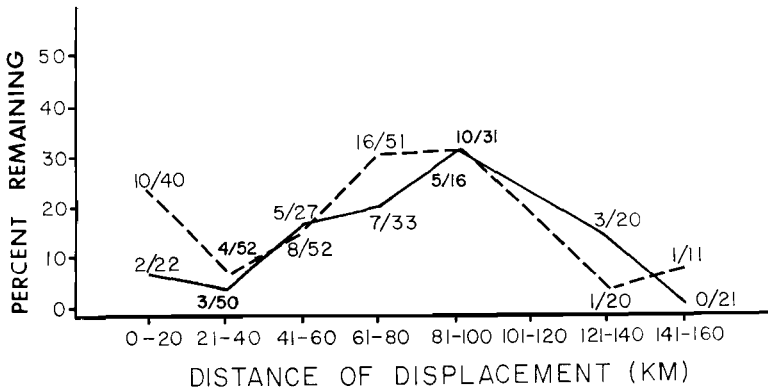
Fig. 3. Percent of adults (solid line) and subadults (dashed line) remaining at the displacement station more than 6 days by distance of displacement, from displacements made in November and December. By each point is the number of birds that remained of those displaced.

and February displacements, nearly as many adults returned from the shorter distances as in earlier displacements (Table 1); but the rate of returns steadily declined at distances greater than 100 km, in contrast to those birds displaced in November and December. Probably most adults displaced these longer distances in January and February did not try to return that season. No adults displaced in March returned during that season.

Subadults displaced during November and December did not return to the home station from distances greater than 60 km (Fig. 2). A comparison of those displaced less than 60 km with those displaced greater distances was highly significant ($P < 0.001$, one-tailed test). From displacements after December, a very few subadults did return from the longer distances, as well as from the shorter distances. None returned from intermediate distances. The return of these subadults from longer distances in the January and February displacements is probably related to the site fixation of the young birds onto their wintering ground (Ralph and Mewaldt 1975), and is further evidence of the existence of distance-related homing mechanisms with resultant effects in the predicted zone.

Rate of remaining at the new station.—In a homing experiment, the reciprocal of a bird returning to its home station would be its remaining at the new station. For example, if birds have a greater propensity to return from the shorter displacements, they should be less likely to remain at a new station close to the home station. Capture at a new station 6 days or more after release was the criterion we used to de-
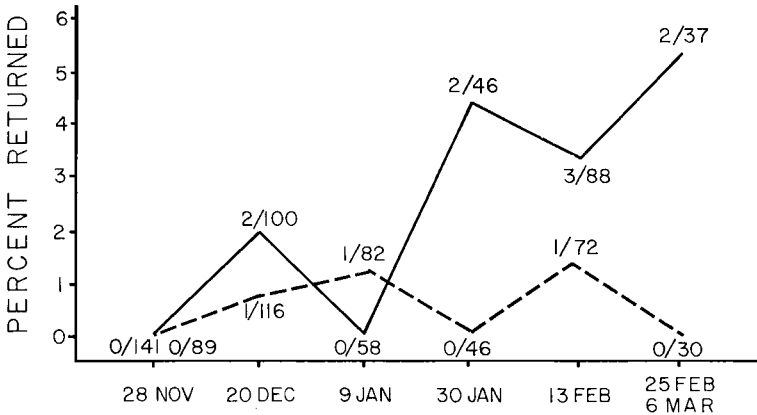
Fig. 4. Percent of adults (solid line) and subadults (dashed line) that returned to their home station in the second season, after remaining at the displacement station in the first season, plotted by date of original displacement. By each point is the number of birds so returning of those displaced. (Dates on the abscissa are ordered at regular intervals for clarity).

termine if the birds remained at the new station. The basis of this criterion was 9 birds captured at the new station that returned to the home station that same season. None of these was known to be at the new station more than 3 days after displacement.

For displacements in November and December the number of adults remaining at the new station was highest in the intermediate distances (Fig. 3). The differences were significant (1–60 + 81–160 vs. 61–80 km, $P < 0.08$; 1–40 + 101–160 vs. 41–100 km, $P < 0.001$; 1–20 + 141–160 vs. 21–140 km, $P < 0.01$; all one-tailed tests). In the January through March displacements the pattern tended to break down.

The pattern of subadults remaining at the new station is much like that of the adults (Fig. 3). This is in contrast to the pattern in those subadults returning to the home station (Fig. 2). A significant peak in numbers occurs in the intermediate distances for displacements made in November and December (1–60 + 81–160 vs. 61–80 km, $P < 0.006$; 1–40 + 101–160 vs. 41–100 km, $P < 0.005$; 1–21 + 141–160 vs. 21–140 km, $P < 0.30$; all one-tailed tests). Again, the displacements in January through March show little consistent pattern.

These results provide strong evidence for the hypothesis predicting a zone of minimum information in intermediate distances.

Rate of birds remaining the first season and returning the second.— A small but interesting proportion of the displaced birds are known to have remained at the new station in the first season and then returned
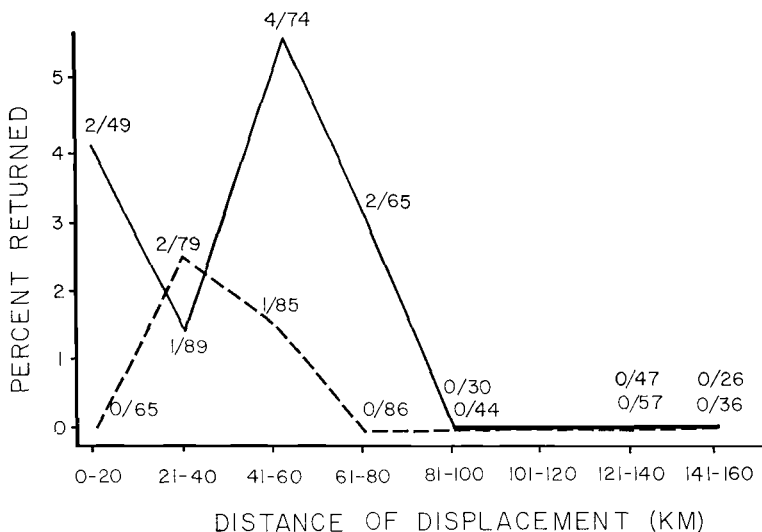
Fig. 5. Percent of adults (solid line) and subadults (dashed line) that returned to their home station in the first season, after remaining at the displacement station in the second season, plotted by distance of original displacement. By each point is the number of birds so returning of those displaced.

to their home station in the second winter season. These birds apparently had the ability to home, yet lacked the drive in the year of displacement. The proportion of adults that fulfilled these two conditions (Fig. 4) increased with some significance the later in the season their displacement occurred ($\leqslant$ December vs. $\geqslant$ 9 January, $P < 0.14$, $\leqslant$ 9 January vs. $\geqslant$ 30 January, $P < 0.025$; both two-tailed tests), but subadults showed no significant change in rate. The synergism of both the birds' drive to home and ability to home could explain the difference between adults and subadults. Subadult birds, as they become fixated onto their winter home, could concomitantly develop the ability to home there (Ralph and Mewaldt 1975), but the later in the season they are displaced perhaps the less drive they have to home in that season. It might well be disadvantageous to risk exposure to the hazards of homing late in the season in order to gain the advantages of a familiar place. The increasing level of ability and the decreasing level of drive over the course of a season could result in a constant level of birds remaining, as the data for subadults suggest. On the other hand, the drive of the adults to return (with a presumably constant ability to home) might decrease during the season. This would result in more remaining later in the season, as the data show.
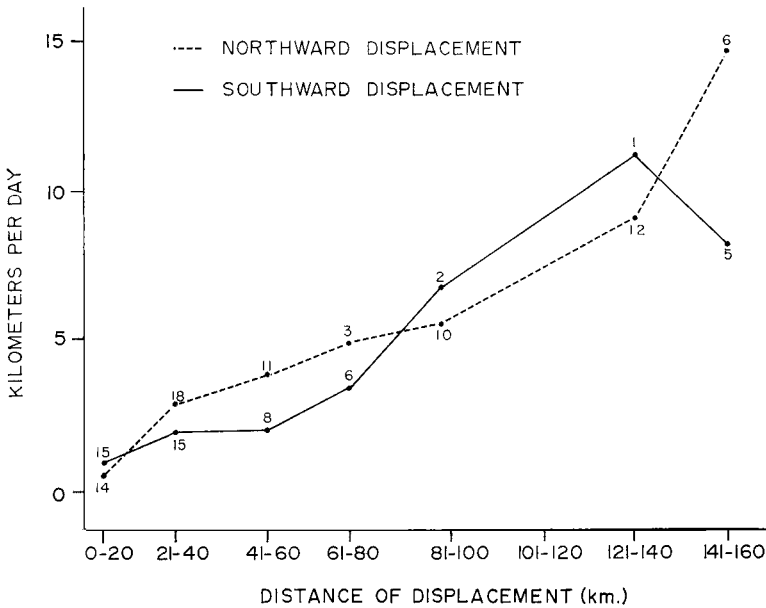
Fig. 6. Average rate of return to home station after northward or southward displacement as reflected by elapsed time between displacement release and recapture at home station. By each point is the number of birds returning that distance.

An additional observation involving these birds remaining at the new station the first season and returning home the second is of interest. These birds were all displaced the shorter distances of less than 80 km (Fig. 5). This effect of distance was highly significant ($P < 0.001$). Despite the caution engendered by the relatively few individuals involved, we may hypothesize that the birds displaced less than 80 km, although capable of homing, perhaps had less motivation to search for the home station. The birds displaced long distances might have more information of their displacement, through celestial or other cues, and thus be more motivated to attempt a return the first season. This is further evidence of distance-related homing mechanisms with resultant effects being demonstrated somewhere in the proposed zone of minimum information.

Speed of return.—The speed of return, as determined by time of recapture at the home station, was much slower than if they had returned by direct flight. Zonotrichia should be capable of flying 40 kph, which would enable them to return from even the most distant displacement in 4 h of flying time. The fastest returners were two birds recaptured after traveling apparently 40 km per day in a 160 km dis-

placement. The vast majority of birds returned at a rate of less than 10 km per day. Contrasting displacment to northward and southward localities (Fig. 6) we found no difference in speed of return. As the displacement distance increased, the speed of return increased proportionally. The normal lag time between recaptures at the home station, (even without displacement) is often several days. Even allowing for this, it appeared that birds displaced short distances spent proportionately more of their time searching for the home station than did long distance displacees. Although we have no direct evidence on the subject, conceivably these birds displaced long distances, presumed to have used some form of navigation, may have had some kind of directional momentum that carried them into the zone of familiarity near home and thus eliminated the need for random search. The data yield no evidence on whether the birds returned in a single flight or whether they flew during daylight or darkness.

Conclusions

Our data lead us to believe that a distance-related hiatus, a "dead belt," may indeed exist in the homing performance of *Zonotrichia*. The evidence indicates that the birds either are unable to home as accurately, or have somewhat less homing drive, or both, in the intermediate distances. The principal effects of the hiatus are apparently centered somewhere in (although not limited to) the 60–100 km range, a distance that agrees in general with previous results with Rock Doves.

The homing performances of adult and subadult birds differed markedly in the distances greater than 100 km. This indicates that the young birds in November and December probably either had not yet been fixated on the home station, or they did not yet have the ability to home from stations beyond the hiatus zone.

These findings lend some support to Matthew's hypothesis that birds employ two mechanisms of navigation, one for longer distances (inoperable in subadult *Zonotrichia* before site fixation) and one for shorter distances. At intermediate distances neither method of navigation might be particularly effective. In the shorter distances the birds might be stimulated to search for the home station by their familiarity with the terrain, using perhaps the type I navigation of Griffin (1955). In longer distances birds might possibly use true navigation (Griffin's type III), perhaps utilizing celestial cues. This is suggested by the greater rate of adult returns from longer distances than intermediate, and by the increased speed of return with longer displacement. At intermediate distances birds might not be stimulated to home either by familiarity with the terrain, as they might in the shorter distances, or

by the apparent change in the position of celestial cues, as would occur in the longer displacements.

SUMMARY

A total of 905 migratory sparrows of the genus *Zonotrichia* were displaced from their winter homes distances ranging from 5 to 160 km.

The time the birds took to return was much longer than one would expect of a direct flight. Adults were better homers overall than subadults, probably because of their greater experience and stronger site attachment.

The later in the season a bird was displaced, the less likely it was to return that season and the more likely it was to remain at the station of displacement, the advantages of returning to a known site possibly being offset by the hazards of returning.

The birds' behavior upon displacement apparently demonstrated a hiatus centered somewhere in the 60–100 km range, a zone of purported minimum information for navigation. This was indicated by three lines of evidence: a somewhat lower ability in certain groups of birds to return to their home stations, a higher propensity of some groups to remain at the station of displacement, and a difference in homing the year following the displacement. These results lend weight to the hypothesis that two methods are involved in homing. Homing from the shorter ranges might involve knowledge of the local terrain coupled with a search behavior, and homing over the longer ranges involves true navigation. Neither is apparently fully effective at the intermediate distances.

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