TIMING OF SITE FIXATION UPON THE WINTERING GROUNDS IN SPARROWS

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THE winter home of a bird, although vitally important in the study of adaptations, has received little attention as compared to various aspects of breeding. During the fall and winter much mortality occurs and may be the limiting factor in many populations (Mac Arthur 1971). We will explore the process of site fixation onto the winter quarters and its implications to the population.

Hilden (1965) gives many examples of tenacity to species-specific breeding habitat and is rather convincing as to the special nature of this phenomenon. Löhrl (1959) found that young Collared Flycatchers (*Ficedula albicollis*) do not fixate on their breeding area until 2 weeks prior to migration. Up to that time the birds could be displaced and would return to the new location in subsequent breeding seasons. Examples of the phenomenon on the wintering grounds are not common. However Sauer (1963) reported fixating American Golden Plovers (*Pluvialis dominica*) on a new winter home. He suggested the sensitive period to fixating followed fall migration (September–October) and was largely over by February. Schwartz (1963) moved 4 adult and 14 first-year Northern Waterthrushes (*Seiurus noveboracensis*) 10 to 65 km from their winter home in Venezuela. Only the adults returned, all within 12 days. Of the 14 first-year birds 7 remained in the displacement locality an average of at least 50 days (range: 15–126). Schwartz then hypothesized that first-year birds fixated upon their winter home about the time of spring departure, although he gave no direct evidence of this.

Studies of adaptations of fringillids to wintering grounds (e.g. Fretwell 1969) have largely bypassed the question of the timing of site fixation to winter quarters. These studies have generally assumed that a bird is best adapted for and will best survive in the habitat that it occupies early in the winter. It is important to document the existence and timing of site fixation because subadults may possibly range over a wider area than adults during the early winter, as Perdeck's (1964) data suggest. Thus a young individual may occupy one habitat in the early fall and, in the harshest part of the winter, quite another.

We chose to use the term site fixation with some reluctance. The phenomenon has much in common with imprinting, as several workers have stated (e.g. Löhrl 1959). Thorpe (1951) discussed applications of the concepts of imprinting and latent learning in birds to many events later in life, including territory recognition and homing responses. The phenomenon, as we will argue, is certainly at least a very special form of learning.

Methods

We displaced migratory White-crowned (*Zonotrichia leucophrys*) and Golden-crowned (*Z. atricapilla*) Sparrows from 10 stations in central California during the winter of 1964–65 as part of a homing experiment (Ralph and Mewaldt 1975). These displacements varied from 4 to 160 km and involved over 900 birds. The birds from any one station were displaced to each of the other nine stations. Approximately equal numbers were displaced each distance. Eight of the stations were operated the next winter season. This report discusses the data gathered the second winter. We were interested in determining whether the birds returned to their home station or to the new displacement station. Comparisons are also made with a population that was not displaced. The two species are very closely related and have similar migration routes, physiology, and habits (Mewaldt et al. 1964, Bent 1968). For these reasons we felt justified in grouping the results of the two species in order to increase the sample sizes for more meaningful comparisons.

All significance levels were tested by computing the normal deviate (z) derived from the approximation to the binomial (Snedecor and Cochran 1967: 220). We compared the probability of returns occurring: (1) before or after a given date, or (2) from more or less than a given distance.

Results and Discussion

The capture data in the second winter showed birds returning to their original home station, as well as birds returning to a new station, the station to which they had been moved the previous winter.

Fixation to a new site.—No birds displaced as adults were found at a new station the following winter (Table 1). On the other hand many adults displaced did return the following winter to the original capture station. These adults were apparently strongly fixated on their home station.

The subadults showed a strikingly different pattern. Some (12 of 424) returned to the vicinity of the new station the following year. These had all been displaced before mid-January. Of the birds displaced after this, none returned to the new station. The difference between the percentage returning from displacements before and after mid-January was significant ($P \leq 0.05$). Manifestly the earlier in the season a bird is displaced, the more likely it is to fixate onto a new location.

The low percentage (2.8%) of subadults returning to a new station, as opposed to the home station (8.3%), was probably due to our sampling techniques. To demonstrate fixation, a displaced bird must have (1) joined a flock near the new station, and (2) also have returned there the next winter. If a bird joined a flock whose home range did not

TABLE 1

NUMBERS OF SPARROWS RECAPTURED THE FOLLOWING WINTER[1]

	Date of displacement						
	28–29 Nov.	20 Dec.	9 Jan.	30 Jan.	13 Feb.	25 Feb.–6 Mar.	Total
Return new station							
Adults							
Displaced	85	101	46	52	92	33	411
Returned	0	0	0	0	0	0	0
Percent	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Subadults							
Displaced	125	105	78	39	54	25	424
Returned	8	1	3	0	0	0	12
Percent	6.4	1.0	3.8	0.0	0.0	0.0	2.8
Return home station							
Adults							
Displaced	85	98	48	40	80	33	384
Returned	11	13	6	5	25	5	65
Percent	12.9	13.3	12.5	12.0	31.2	15.1	16.9
Subadults							
Displaced	131	111	77	38	62	25	444
Returned	1	5	11	7	10	3	37
Percent	0.8	4.5	14.3	18.4	16.1	12.0	8.3

[1] The row totals differ because some stations were not in operation the second year. Therefore their data for returning to home station could not be used; however, their data could be used for returning to a new station if their birds were displaced to any station operating in the second year.

include the station, his return and his fixation would be unknown to us. These species' flock home ranges are approximately 20 ha (Ralph MS).

We found no significant ($P < 0.45$) effect of distance of displacement upon the numbers of subadults returning the following year to the displacement station (Table 2). This suggests that the degree of attachment to the home station might be important, not the ease or difficulty of return.

Birds returning to the home location.—In order to put the above data in perspective, it is appropriate to discuss those displaced birds that were not fixated upon a new site and returned to their original home in the second year. The later the subadults were displaced, the greater their tendency to return to their home station the following year (Table 1). Until late winter, this increase was significant ($P \leqslant 0.05$). Some subadults did return home from November and December displacements. This would not be expected if fixation does not generally occur until January. Those returning to the home station from early displace-

TABLE 2

NUMBER OF SUBADULTS RECAPTURED AT THE NEW STATION THE FOLLOWING WINTER

	Distance displaced (km)							
	1–20	21–40	41–60	61–80	81–100	121–140	141–160	Total
Displaced[1]	41	50	56	72	44	30	15	308
Returned	2	1	4	1	2	1	1	12
Percent	4.9	2.0	7.1	1.4	4.5	3.3	6.7	3.9

[1] Displacements are for 28 November through 9 January, the only displacements yielding returns.

ments were all displaced less than 60 km. In contrast, from the longer distances only those subadults displaced after January returned in the second year. Homing from shorter distances might reflect knowledge of the local area, whereas in the longer distances celestial or other forms of navigation may be involved (Matthews 1963, Schmidt-Koenig 1964, Ralph and Mewaldt 1975, but cf. Keeton 1970, Graue 1970). We have found (Ralph and Mewaldt 1975) that the development of ability to orient to a more distant site is apparently concomitant with fixation on that site. Subadults displaced in February returned next year to the home station equally well from all distances.

Adults showed a somewhat similar pattern. Those adults displaced later had a higher homing rate in the second year. The difference between those displaced before and after the end of January was significant ($P \leqslant 0.05$).

Three explanations of the increase in returning rate are possible, and all might well be involved:

(1) In the case of subadults this increase is presumably due to more individuals fixating upon the original home station (but see below). On the other hand, increase in the rate of adults returning during the second year might indicate a reinforcement of attachment to the winter home extending into the second year. Perhaps noteworthy is the finding that the frequency of return of adults displaced in November approximates the frequency of subadults displaced in March. It is as though returns of March subadults and November adults were part of a continuous trend, the rate increasing through two winter seasons, in both years being reinforced in January.

(2) The birds displaced earlier in the season may also have a greater drive to home that year (Ralph and Mewaldt 1975). If this is so, and if they attempted to return, they would be exposed to any hazards of the flight. This would result in fewer surviving to be recorded the second winter. This is in contrast to birds displaced later, which do not attempt to return that year.

TABLE 3

RETURN IN 1970–71 OF *ZONOTRICHIA*, HANDLED BY MONTH IN 1969–70

	Month captured 1969–70					
	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
Adults						
Captured	11	95	39	148	49	38
Returned[1]	4	43	16	71	21	23
Percent	36.4	45.3	41.0	48.0	42.9	60.5
Subadults						
Captured	44	261	117	299	108	50
Returned[1]	4	60	42	102	38	16
Percent	9.1	23.0	35.9	34.1	35.2	32.0

[1] This includes new captures and repeats, each individual was counted only once per month.

(3) A late displacee would have already survived most of the winter. In contrast, an early displacee has yet to experience such selection. Proportionally more of the late displacees will then survive into the next year. As in the case above, the increase in rate of return would be a sampling artifact.

Return rate of a nondisplaced population.—Partly to resolve these alternatives, we have more recently obtained survival information from a *Zonotrichia* population that was not being manipulated at the time. This provides comparative data to consider the question of site fixation (especially in the case of the subadults) vs. survival, as in the case of a seasonal increase in returns. These data, from the San Jose station, provide return rates in the 1970–71 winter from monthly captures in the previous winter (Table 3 and Fig. 1).

Of birds caught the previous October and November, returns the next year of subadults were substantially lower than returns of adults. This may be caused by local wandering prior to site fixation. The slight increase in return success of San Jose adults from the October through March captures may reflect expected mortality, though subadults originally caught at San Jose between December and March showed no such mortality. Thus mortality seems to be a slight factor in increasing rates of return.

The substantially lower level of the 8-station curves (Fig. 1) than the San Jose curve probably reflects less intensive trapping effort at some of the eight stations in the 1965–66 season.

Of primary importance is the very low return rates of subadults displaced in November and December. In contrast, by December the nondisplaced subadult population shows a stability in site attachment. The displaced November and December subadults had apparently not yet fixated on their home station. By January the subadult return rate had

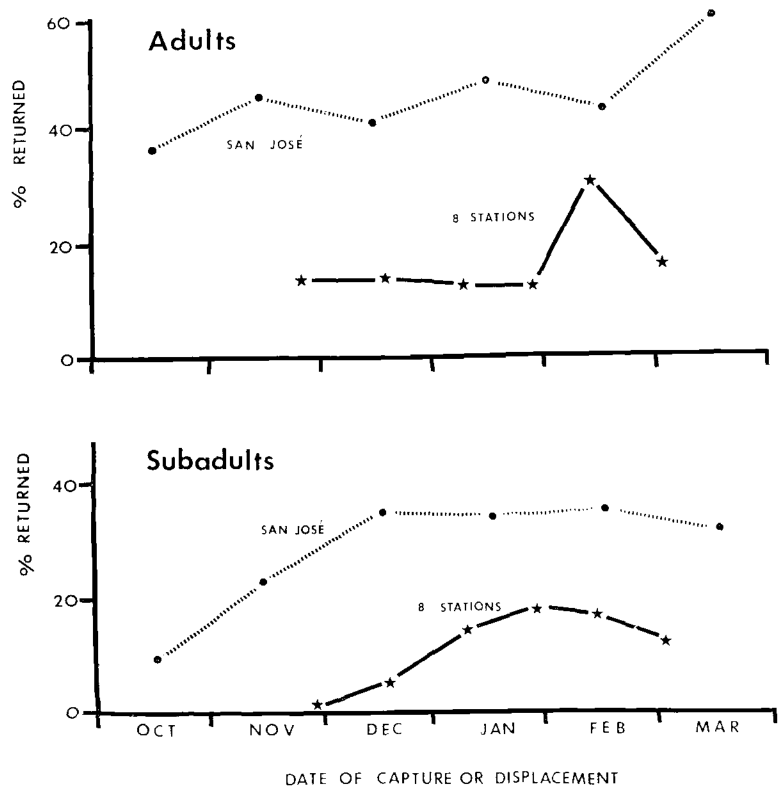

Fig. 1. Returns of adults and subadults to San Jose in 1970–71 by months handled in 1969–70 (solid circles) compared to returns of adults and subadults to eight home stations 1965–66, by approximate dates of displacement in 1964–65 (stars).

reached the plateau previously attained by adults in November. It thus seems that site fixation, and not mortality, causes the increase of returns and stability of site attachment. Although increased drive to return and thus increased mortality as discussed above cannot be ruled out, we feel it is of relatively minor importance.

Conclusions

The formation of site attachment to winter quarters as it occurs in some species of birds might meet the criteria of imprinting in a broad sense. These criteria are usually stated as involving: (1) a limited period in which imprinting can occur, (2) the stimulus is well defined, (3) the response is a fixation upon the stimulus, and (4) the fixation is irreversible. Although in our study the stimulus (the wintering area) is somewhat difficult to delimit or define, the response (the migration and homing to the area) is well documented. In addition site fixation seems irrevocable and somewhat time-limited. In this latter regard it is reasonable to propose that a period of a few hours in the first few days of a bird's life (in which it is possible to imprint upon a parental figure) could be compared to a period of several weeks during its first season on the wintering grounds. Although it is not our purpose to review the implications of the term imprinting as applied to site fixation, it is difficult to escape the conclusion that the phenomenon is, at the very least, a rather special form of learning.

The advantage in being able to return to a familiar home wintering ground is obvious. The delayed timing of such fixation in winter, as shown in this study, permits the dispersal of young and thorough utilization of the wintering grounds by the species. This could function to repopulate regions where temporary wintering failures had occurred previously. It also enables the young bird, before it becomes irrevocably fixated upon a specific site, to become familiar with a variety of possible areas and, in effect, to experiment with differing environments.

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SUMMARY

The apparent existence of time-limited and irrevocable site fixation to a winter home range is demonstrated in two species of *Zonotrichia* sparrows. Of more than 400 adults displaced varying distances, none returned the following year to the new station, while approximately 17% returned to their original home. Of more than 400 subadults displaced, 12 returned to the new station the following year and thus apparently were fixated upon it. No subadults displaced after mid-January returned to the new site. It is postulated that the mechanism of delaying site fixation until midwinter enables the young bird to explore differing environments early in the winter and tends to offset the effects of local wintering failures.

LITERATURE CITED

BENT, A. C. 1968. Life histories of North American Cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies, part 3. (O. L. Austin, Jr., Ed.). U.S. Natl. Mus. Bull. 237.

FRETWELL, S. 1969. Ecotypic variation in the non-breeding season in migratory populations: A study of tarsal length in some Fringillidae. Evolution 23: 406–420.

GRAUE, L. C. 1970. Orientation and distance in pigeon homing. Anim. Behav. 18: 36–40.

HILDEN, O. 1965. Habitat selection in birds, a review. Ann. Zool. Fennica 2: 50–75.

KEETON, W. T. 1970. "Distance effect" in pigeon orientation: an evaluation. Biol. Bull. 139: 510–519.

LÖHRL, H. 1959. Zur Frage des Zeitpunktes einer Pragung auf die Heimatregion beim Halbandschnapper (*Ficedula albicollis*). J. Ornithol. 100: 132–140.

MAC ARTHUR, R. A. 1971. Patterns of terrestrial bird communities. Pp. 189–221 *in* Avian biology, vol. 1 (D. S. Farner and J. R. King, Eds.). New York, Academic Press.

MATTHEWS, G. V. T. 1963. The orientation of pigeons as affected by the learning of landmarks and by the distance of displacement. Anim. Behav. 11: 310–317.

MEWALDT, L. R., M. L. MORTON, AND I. L. BROWN. 1964. Orientation of migratory restlessness in *Zonotrichia.* Condor 66: 377–417.

PERDECK, A. C. 1964. An experiment in the ending of autumn migration in Starlings. Ardea 52: 133–139.

RALPH, C. J., AND L. R. MEWALDT. 1975. Homing success in wintering sparrows. Auk, in press.

SAUER, E. G. F. 1963. Migration habits of Golden Plovers. Proc. 13th Intern. Ornithol. Congr.: 454–467.

SCHMIDT-KOENIG, K. 1964. Initial orientation and distance of displacement in pigeon homing. Nature 201: 638.

SCHWARTZ, P. 1963. Orientation experiments with Northern Waterthrushes wintering in Venezuela. Proc. 13th Intern. Ornithol. Congr.: 481–484.

SNEDECOR, G. W., AND W. G. COCHRAN. 1967. Statistical methods, sixth ed. Ames, Iowa State Univ. Press.

THORPE, W. H. 1951. The learning abilities of birds. Ibis 93: 1–52, 252–296.

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