
Wintering site fidelity of migrant passerines in El Salvador, Central America

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Faithfulness to wintering sites — wintering philopatry — is well known in certain species that winter north of Mexico, especially the much-studied *Zonotrichia* sparrows. For the latter, recapture rates up to 50% have been recorded in years subsequent to banding (Ralph and Mewaldt 1976). Continued site tenacity has been demonstrated at long-existing banding stations such as that of Fisk (1974, 1978, 1979) in south Florida, where individual Painted Buntings (*Passerina ciris*) have been recaptured year after year for 10 years, and Indigo Buntings (*P. cyanea*) for 8 years. But wintering philopatry is not universal. Dolbeer (1978), studying band recovery data, concluded that Red-winged Blackbirds (*Agelaius phoeniceus*) are not faithful to the same roosting area in subsequent winters. Possibly, birds that flock in winter, such as red-wings and shorebirds, must be flexible because of variations in food supplies; they may even develop regular, widespread movements as seasonally abundant foods become exhausted.

South of Mexico relatively few banders have been operating and data are scant. Van Tyne (1932) banded Indigo Buntings in Guatemala during March-April 1931, 6 being retaken in April 1932; he interpreted the recaptures as evidence that the buntings, "migrating as a unit," had returned to the identical wintering grounds. Nickell (1968), during 6 expeditions to Belize and Honduras in March-April, 1960 through 1965, obtained almost 200 returns which he considered indicative of faithfulness to "winter quarters." It should be pointed out that another interpretation of these data, while admitting the possibility of local wintering, recognizes that in March and April migra-

tion is at its height and that recaptured birds may have wintered farther south; there are reported instances of transients being retaken at banding stations on their migratory routes (Nisbet 1969; Goodpasture 1979). In contrast, Ely (1973) and Ely et al (1977) netted in southern Mexico during December-January only; their recaptures were without doubt wintering locally.

Loftin (1977) summarized the returns of banded birds thus far reported for the Neotropics. Some of the data support the hypothesis of wintering philopatry but some are susceptible to other interpretations. The most conclusive evidence was provided by Schwartz (1964) in color-banding studies of Northern Waterthrushes (*Seiurus noveboracensis*) in Venezuela, where one marked bird was seen in 5 successive winters, another in 3 winters, and 2 in 2 winters. Unfortunately, not all reports give dates of banding, recaptures during the same season, and recaptures during subsequent seasons, so one cannot always evaluate the data and/or the interpretation of the data.

During the 10 years we have been netting and banding in San Salvador, we have recaptured a small percentage of our banded migrants as "returns" (as defined by the North American Bird Banding Manual, Vol. 1); most of these are reported elsewhere (Thurber and Villeda, 1972, 1974, 1976). Some of our recaptures indicate a certain degree of fidelity to our banding sites. After reading Spofford's note (1976) about the paucity of information on the wintering habits of warblers, we thought it worthwhile to examine our data with the subject of philopatry in mind.

Table 1. Migrants banded in El Salvador and recaptured at the same stations after one or more intervening breeding seasons.

Species	Location ¹	Status ²	Banded	Recaptured
Black-and-white Warbler (<i>Mniotilta varia</i>)	Los Pinos	A 2	21/1/72	15/1/73; 24/2/74
	Cerro Verde	B 1	20/10/71	12/10/72
Tennessee Warbler (<i>Vermivora peregrina</i>)	Los Pinos	A 1	25/1/72	6/3/73
		A 1	25/1/72	18/1/73
		A 1	25/1/72	17/1/73
	Cerro Verde	A 2 (5)	16/10/71	7/12/72; 20/11/77
		A 1 (2)	22/10/71	3/2/74
		A 1	2/3/72	13/10/72; 14/10/72; 6/12/72
		A 1	7/3/72	9/12/72
		A 2	24/11/71	7/3/72; 8/10/72*; 3/2/74
		A 1	7/3/72	9/12/72
		A 1	14/11/73	30/1/74; 7/10/74
A 1	5/2/74	8/10/74		
A 1 (2)	22/10/75	18/11/77		
Nashville Warbler (<i>Vermivora ruficapilla</i>)	Cerro Verde	B 1 (2)	23/10/75	6/3/78
Yellow Warbler (<i>Dendroica aestiva</i>)	Los Pinos	A 1	16/1/73	24/2/74
		A 1	26/1/72	18/1/73
		A 1	17/1/73	20/2/74
		A 1 (3)	18/1/73	3/2/76
Magnolia Warbler (<i>Denroica magnolia</i>)	Los Pinos	A 1	15/1/73	23/2/74
		A 1	18/2/76	16/11/76
		A 1	20/2/74	17/2/75
Townsend's Warbler (<i>Dendroica townsendi</i>)	Cerro Verde	A 1	24/11/71	1/3/72; 17/10/72
		A 1	27/9/73	3/10/74; 26/1/75
		B 1 (2)	7/10/74	27/9/76
		B 1	1/3/72	17/10/72
B 1	9/9/77	26/9/78		
Ovenbird (<i>Seiurus aurocapillus</i>)	Cerro Verde	B 1	21/4/71	17/10/71
		B 1	4/3/72	17/10/72
		A 2	4/3/72	5/12/72; 23/11/73
		B 1	29/9/73	8/10/74
		A 1	16/2/75	31/1/76
	Las Minas	A 1	23/10/74	19/2/76
	Los Pinos	A 1	20/2/75	6/2/76
MacGillivray's Warbler (<i>Oporornis tolmiei</i>)	Cerro Verde	B 1	19/4/71	4/3/72
		A 2	20/4/71	2/3/72; 20/11/73; 3/2/74
		B 1 (2)	2/3/72	3/10/74; 8/10/74
		A 1 (2)	7/10/74	31/1/75; 27/9/76
Yellowthroat (<i>Geothlypis trichas</i>)	Los Pinos	A 1	25/1/72	19/1/73
		A 1	25/2/74	16/2/75
Yellow-breasted Chat (<i>Icteria virens</i>)	Los Pinos	A 1	22/2/71	29/1/72
		A 1 (2)	24/1/72	1/3/74
	Las Minas	A 2	19/10/74	18/2/76; 16/11/76
Hooded Warbler (<i>Wilsonia citrina</i>)	Las Minas	A 1 (2)	21/10/74	23/11/76
Wilson's Warbler (<i>Wilsonia pusilla</i>)	Cerro Verde	A 1	8/1/71	24/11/71; 1/3/72**
		B 1	22/4/71	3/3/72
		B 1	17/10/71	2/3/72
		B 1	2/3/72	15/10/72
		A 1	19/11/73	29/1/75
		A 1	13/10/72	19/11/73; 20/11/73
		A 2 (3)	4/10/74	31/1/75; 27/10/75; 14/11/77; 5/3/78
	Montecristo	A 1	17/11/74	27/11/75

Species	Location ¹	Status ²	Banded	Recaptured
Rose-breasted Grosbeak (<i>Pheucticus ludovicianus</i>)	Montecristo	A 1	20/11/74	24/11/75
Painted Bunting (<i>Passerina ciris</i>)	Los Pinos	A 1	21/2/71	25/1/72
		B 1 (3)	21/2/71	24/2/74
		A 1	21/2/71	26/1/72
		A 2 (3)	30/1/72	6/3/73; 17/2/75
		A 1	2/3/74	17/2/75
		A 1	20/2/75	5/2/76
		A 2	17/1/73	1/3/74; 15/2/75

¹ Banding stations: Los Pinos (Hacienda Los Pinos), Usulután, 50 m elev.; Las Minas (Las Minas de San Cristóbal), Morazán, 300 m elev.; Cerro Verde (Parque Cerro Verde), Santa Ana, 2000 m elev.; Montecristo (Planes de Montecristo), Santa Ana, 1850 m elev.

² Status. Left column: A, an almost certain winter resident; B, a possible winter resident but possibly a bird-in-passage. Right column: number of certain autumnal returns to the banding site as determined by recaptures (number in parenthesis denotes number of probable autumnal returns inferred by assuming unvarying winter philopatry).

* This bird recaptured 8 times in October 1972 and once again in December 1972.

** This bird recaptured 4 times in March 1972.

Methods and results

We selected from our banding records those instances of birds which were retaken after at least one breeding season intervened. We noted also any additional recaptures of these birds. The results are given in Table 1. Each bird was recaptured at the same site where banded, some in the same nets or clusters of nets where first captured. We have indicated with the letter "A" those birds that were present between 15 November and 15 February, such birds being probable winter residents (the more contacts the more certain this is). We indicate with "B" the birds present outside this period; such birds might have been winter residents or they might have been birds-in-passage following the same routes with regular stop-over sites.

Discussion

Knowledge of migrants wintering in the Neotropics is quantitatively and qualitatively scant. That which we present and which others have presented show that at least a few birds return to the same sites again and again, in some instances for the better part of, or all of, their lives, thus displaying strong wintering philopatry. But we do not know whether these birds represent the rule for their respective species or whether they are exceptions. For all we know, most migrants shift

their wintering grounds from year to year and/or wander widely each winter. Present evidence does not justify broad generalizations.

Considering the limited evidence for wintering territoriality, we are justified in asking whether, out of all the millions of migrants, some might reappear at a banding site through pure chance. For example, what is the probability that a Wilson's Warbler (*Wilsonia pusilla*) banded at Cerro Verde in El Salvador, will happen again upon that identical site? The probability that a certain event will occur by chance is one in the number of possibilities — $1/N$ where N is the number of possibilities. The probability that our Wilson's Warbler might arrive again by chance one more time is $1/N_w$ where N_w equals all the suitable sites within the wintering range of the species, in this case, between central Mexico and northern Panama. Obviously, N_w is a very large number and $1/N_w$ correspondingly small. Thus the probability of the bird's return by chance is slight. That some of our netted birds have returned to the banding sites in 2 or more successive years reduces the probabilities of chance occurrence to vanishingly small values.

With chance eliminated as an explanation, we can look for some internal control that might bring this warbler back in subsequent years. It is tempting to invoke "instinct" which in this case implies genetic information that guides a bird to a specific win-

tering locality. Such an explanation would require of each wintering population some form of reproductive isolation while on the breeding grounds to avoid mixing of genetic information. Otherwise, offspring of our Wilson's Warbler and some bird that winters elsewhere, say in Guatemala, would have information that might guide to both places. Within a few generations of crosses between birds from different wintering sites, the genetical information would be greatly diluted and some might be lost.

Another explanation requires that a bird learn a route. By this hypothesis, our Wilson's Warbler first arrived at Cerro Verde through the influence of some factor such as a storm, or followed other migrating birds, or was overtaken by fatigue. Our warbler either learned the route by which it came or the route by which it returned to its breeding grounds. Thereafter, it retraced the route each year.

We use here the term "route" as applied to the travels of an individual bird which performs its own navigation. The concept of a definite, fixed migratory flyway is now considered simplistic (see discussion in Thompson 1964, p. 468). Some ornithologists avoid using the term "route." Ralph and Mewaldt (1975) spoke of "site-fixation"; Schwartz (1963) used "orientation." But site-fixation implies a goal, and orientation is "taking up a direction" (Matthews 1968). A goal and orientation are essential for navigation but are not sufficient; there must also be a course. The course, or route, may or may not coincide with that of others of a species and, by the route-learning hypothesis, is learned by each individual bird.

Limited experimental evidence supports the suggestion that individual migrants learn routes while returning to the breeding grounds. Schwartz (1963) displaced Northern Waterthrushes from a banding site in Venezuela and found that only birds which had spent a previous winter at the banding site returned. He concluded, "What a bird learns on its first trip south does not enable it to orient to its new winter home . . . but once having flown north . . . the bird . . . is thereafter able to return to its winter home."

Ralph and Mewaldt (1975) carried out a more elaborate experiment in California using over 900 migrant *Zonotrichia* sparrows. They released equal numbers of adults and subadults at netting stations remote from the "home" stations where captured. The next year 17% of the adults were recaptured at the "home" stations; apparently they had learned the route during previous migrations. About 3% of the subadults reappeared at the re-

lease stations, suggesting that they had learned the new route while returning to the breeding grounds.

The hypothesis of route imprinting during the spring migration can be used to explain certain extensions of wintering range we noted following Hurricane Fifi in September 1974. (For details see Thurber 1980.) Several unusual migrants appeared in El Salvador in 1974 and some reappeared in succeeding years. Nashville Warblers (*Vermivora ruficapilla*), previously unreported, reappeared in 1975-76, 1976-77, 1977-78, and 1979-80; a bird banded in 1975 was retaken in 1978. Hermit Thrushes (*Catharus guttatus*), also previously unreported, were present again in 1975-76 and 1976-77. Lincoln's Sparrows (*Melospiza lincolni*), only 4 birds reported before 1974, became locally common in 1974-75 and 1975-76. A Hooded Warbler (*Wilsonia citrina*), a species reported only twice before, was banded in 1974 and retaken in 1976. Seemingly, some of the birds displaced by Fifi memorized the route to El Salvador during their return north.

Evidence supporting route-imprinting is scant but not negligible. Our data and those of others such as Schwartz (op. cit.) show that some birds navigate with pinpoint accuracy to their wintering sites in successive years. Accurate navigation back to their breeding grounds is also well documented; recaptures show that many adults "routinely" return to breed in the same area where they bred in previous seasons (Emlen 1975).

The recapture of transients, mentioned above, shows that at least a few migrants utilize the same stopping places while enroute. Such feats of navigation can be explained by the hypothesis of route learning. However, massive amounts of recapture data are needed to substantiate or deny the hypothesis, data that are presently lacking, especially for species migrating into the Neotropics. Quoting Lof-tin (op. cit.) on this subject: "This subject [of homing to Neotropical winter quarters] certainly demands more attention than has heretofore been given, and it underlies the fact that ornithologists know very little about boreal-breeding migratory species for the five or more months of each year when they are out of sight of North American birdwatchers." ❖

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