

1980

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Recommended Citation

Stewart, Paul A. (1980) "Further Research Needed on Present-day Bird Movements As a Clue to the Evolution of Bird Migration," *North American Bird Bander*. Vol. 5 : Iss. 1 , Article 2.
Available at: <https://digitalcommons.usf.edu/nabb/vol5/iss1/2>

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Further research needed on present-day bird movements as a clue to the evolution of bird migration

Paul A. Stewart

With Sibley and Spendelow (1977) daring to ask, "What's wrong with migration studies?" I am emboldened to express a concern that I have been struggling with for more than twenty years. I think that ornithologists are failing to make full use of available data on recoveries of banded birds. While these data have furnished the basis for many important research publications, I think that their fuller use could be made to the benefit of ornithological science. I would particularly like to see more analyses of bird banding and recovery records as they relate to the movements of different species, for I think that such analyses might help toward explaining the evolution of bird migration.

In the discussion that follows, the word *evolution* is used as a name for the process in which birds have developed their present patterns of geographic movements relative to their hatching or nesting places. *Migration* is the seasonal movement in which birds travel from their nesting to their wintering grounds and back again. *Dispersal* is the movement of birds from their hatching or nesting localities, basically into all compass directions, soon after completion of the reproductive season. *Dispersion* is the distribution of birds over their breeding grounds, but it does not involve the movement resulting in that distribution.

The explanation of the evolution of bird migration can be facilitated by comparing the movements of different species as to how these movements relate to the two separate movements, (1) post-breeding dispersal and (2) regular fall migration. Showing the relationship of the dispersal movements to the evolution of bird migration can be enhanced also by use of a schematic representation of the dispersal movements. In my early work (Stewart 1958) with banding and recovery records of Wood Ducks (*Aix sponsa*) I found movements into all compass directions from the nesting localities and thus have represented, schematically, those movements as radial dispersal (Stewart 1977a;

1977b; 1977c; 1979). I see post-nesting dispersal as involving movements into all compass directions from the nesting localities when the movements are not influenced by a lack of suitable habitat in any direction and thus being basically a radial movement.

Consideration of the relationship of dispersal movements to the evolution of bird migration can be facilitated, also, by a change in the definition of the word *dispersal*. As presently defined, dispersal results in dispersion or in the distribution of birds from their hatching to their nesting places (Berndt and Sternberg 1968). This definition defines dispersal solely relative to the starting and finishing points, and dispersal thus does not relate to a movement but to two separate points. With some birds, as for example Black-capped Chickadees (*Parus atricapillus*), dispersal may lead to dispersion (Weise and Meyer 1979). However, with many migratory birds, although excluded by definition, southward and northward migrations are parts of the movements made by birds traveling from their hatching to their nesting places. Dispersal should be defined as the movement made by birds soon after completion of the nesting season away from their hatching or nesting places, and this is the meaning of dispersal as used in this paper.

Radial dispersal or movements into all compass directions from the nesting place soon after the nesting season is a widespread phenomenon among birds, involving most but not all species. However, these movements among some species are viewed in a different light so that their basic nature as dispersal is obscured. With the "white herons" in the southeastern United States, movement soon after the nesting season is a well-known phenomenon but, because of the lack of suitable habitat to the south, the movements expressed and seen are largely northward, and they have come to be recognized as northward wanderings. When one considers that the basic pattern of movement after the nesting season, with habitat permitting,

involves flight into all compass directions, the northward movement of "white herons" after the nesting season can be seen as an outgrowth of radial dispersal.

Similarly, in the northern part of North America, many birds, including many shorebirds and warblers, start their southward migrations soon after completion of the nesting season. Here, because of the lack of suitable habitat to the north, most of the movements are southward. These movements, starting as dispersal movements, come to be seen and recognized as fall migration.

Whereas the northern warblers and shorebirds make only the dispersal movements which come to be recognized as fall migration, the "white herons" and some Wood Ducks travel in both the dispersal movements and the fall migration. However, differences as to whether birds of a species are involved in both the dispersal movement and fall migration occur within as well as among species; as I have shown (Stewart 1979), Wood Ducks nesting in the southern part of their range may participate in the dispersal movement but not in the later fall migration. Whether or not Wood Ducks are involved in the fall migration in addition to the dispersal movement may depend on the success of individual birds in finding suitable habitats in which to spend the winter after they have made the dispersal movement. Thus, some few scattered Wood Ducks spend the winter north to Idaho (Low 1952) and Ontario (Bailie 1951) although most of them travel to the southern United States.

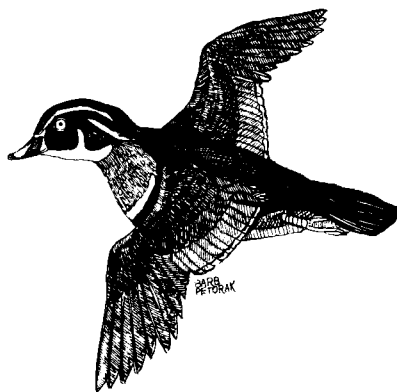
With fall migration among some species developing or being an outgrowth of radial dispersal, patterns of movements take on importance as possibly having characteristics distinguishing radial dispersal from fall migration. Thus, birds in dispersal movements sometimes make relatively

long-distance flights in short periods of time, suggesting direct non-stop flights. Such a case was found with a Wood Duck banded in New York on 30 August 1972 and shot in Florida three days later (Stewart 1977b). A flight of this type might have been the basis for establishment of the Hawaiian Islands as a wintering grounds for American Golden Plovers (*Pluvialis dominica*) nesting in Alaska.

Whereas rapid flights are sometimes made in dispersal movements, leisurely movement may be a characteristic of fall migration. Thus, Wood Ducks were found moving steadily southward from Vermont and New York toward Florida throughout November and December (Stewart 1977a; 1977b), suggesting that the movements might be related to weather conditions. Also, I found in mid-January weather-related southward movement of Common Grackles (*Quiscalus quiscula*) from a roosting site in Kentucky (Stewart 1978), the birds moving southward in association with a heavy snowstorm.

Another important characteristic of dispersal movements as distinguished from regular fall migration is the time of initiation of the movements. Dispersal movements characteristically occur soon after the nesting season. Among Wood Ducks I found dispersal occurring in late August and early September, with fall migration starting in late October or early November (Stewart 1977a; 1977b).

Still another characteristic of the dispersal movement is the suddenness with which the movements are initiated. In daily observations of roosting congregations of Wood Ducks in Maryland, I found (unpublished notes) the birds present one day and mostly gone the next day. Weise and Meyer (1979) also noted an abrupt initiation of dispersal movements among Black-capped Chickadees in Wisconsin.



With dispersal and fall migration starting as two distinct movements, the motivation for initiating the movements can be suspected of being different. While fall migration seems to be at least partly dependent on weather conditions, I think that the tendency for dispersal after the nesting season may presently occur as an inherited behavior pattern. Berndt and Sternberg (1968) also considered dispersal to be an inherited behavior pattern. In their dispersal movements individual birds within species travel widely different distances, and Johnston (1956) suggested that even the distances traveled by individual birds is an inherited characteristic. Thus, the inheritance of variable patterns in the distances traveled by individual birds now appears to occur with advantages to the birds, perhaps advantages in the development of migratory behavior.

But if the movements of birds are to be more than dispersal away from their nesting grounds, the birds must return to their nesting grounds for reproduction. The capability and tendency for homing to the nesting grounds for purpose of reproduction is then a necessary attribute of migratory behavior. Perhaps originally forced on the progenitors of birds by the need to return to water for egg laying, returning to the hatching place for egg laying and hence homing ability early became an inherited tendency among birds or their progenitors.

How then did bird migration develop? Early in the evolution of birds or their progenitors, reproduction outpaced the carrying capacity of the immediate area occupied. Environmental factors permitting, dispersal into all compass directions resulted until dispersal after the nesting season became an inherited behavior pattern. But, as with frogs and toads today, the early progenitors of birds could not reproduce without returning to their hatching place in the water, and homing to the hatching place for reproduction was forced and also became an inherited behavior pattern. With the possibility recognized that birds carry an inherited tendency for dispersal from their hatching places soon after the nesting season and an inherited tendency to return to their hatching place for reproduction, studies of their present-day movements will show how each species has developed its specific pattern of migratory behavior in testing habitats seasonally favorable and unfavorable for their use.

In the concept of the evolution of bird migration espoused in this paper, I see migratory behavior as a continuing adjustment to habitat use. However, to

the extent that birds making successful movements are preserved and others eliminated, patterns of movement, including migration routes and locations of wintering grounds, have become somewhat established.

Dorst (1962) noted that, "The origin of bird migrations is such an important question that it dominates all other aspects of ornithology, but every 'solution' must remain in the realm of pure conjecture, as it cannot be substantiated by observation or experiment." Also, Gadgil (1971) noted that dispersal of birds is one of the most important and least understood factors of population biology. When analyses are completed of the present-day movements of many species of birds, I think that a blueprint will be available of the courses taken by the different species in evolving migratory behavior. This better understanding of the evolution of bird migration can be used to make more meaningful future research into problems of the operation of migratory behavior. 🐦

Acknowledgment

I am grateful to David E. Stewart for many stimulating discussions which aided my thinking in preparation of this manuscript and for helpful suggestions toward improvement of the manuscript.

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(Ed. Note: This is a condensation of a longer unpublished paper, "Radial Dispersal and the Evolution of Bird Migration," by Dr. Stewart. Anyone interested in reading the longer version may request a copy from the EBBA editor. Dr. Stewart is sponsoring some grants for research into this subject through the Wilson Ornithological Society.)

Paul A. Stewart Awards

The Paul A. Stewart Fund for Ornithological Research has been established by donations from Paul A. Stewart. Income from this endowment will be awarded annually to support research in ornithology, especially studies in bird movements based on banding and analyses of recoveries and returns and investigations pertaining to economic ornithology.

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(Dr. Stewart is a life member of EBBA. This award is handled by The Wilson Ornithological Society.)

We regret that several lines were omitted from Table 2 of Peter Homman's article, "Wintering bird returns in north Florida (1979. NABB 4:155) Below is the correct table.

Table 2. Repeats and returns of wintering birds

	0			1			2			3			4		
	n	rep		n	ret	*	n	ret	*	n	ret	*	n	ret	*
Y.-b. Sapsucker 4 (2-1-0)	19	13 (5)		19	2	11	13	2	15	9	1	11	-	-	-
Common Flicker 7 (7-0-0)	43	11 (9)		36	6	17	24	1	4	9	0	0	-	-	-
E. Meadowlark 5 (5-0-0)	50	7 (7)		45	3	7	38	2	5	21	0	0	10	0	0
Am. Goldfinch 2 (2-0-0)	315	8 (7)		297	1	.3	256	1	.4	79	0	0	21	0	0
Savannah Sparrow 5 (5-0-0)	54	13 (12)		48	4	8	24	1	4	-	-	-	-	-	-
White-cr. Sparrow 2 (2-0-0)	34	11 (6)		20	2	10	10	0	0	-	-	-	-	-	-
Wh.-thr. Sparrow 24 (16-2-0-1)	131	27 (24)		119	23	19	77	6	8	47	1	2	21	1	5
Field Sparrow 31 (19-6-0)	211	54 (41)		144	25	17	110	11	10	64	0	0	40	1	3
Song Sparrow 7 (5-1-0)	60	9 (9)		49	5	10	28	1	4	12	1	8	-	-	-
Y.-rumped Warbler 29 (25-2-0)	1375	128 (106)		1306	23	2	1165	4	.3	942	4	.5	596	0	0
Ruby-cr. Kinglet 4 (4-0-0)	53	16 (7)		48	3	6	38	0	0	27	1	4	5	0	0

Legend: Below the name of the bird is given the total number of returns, and in parentheses the number of individuals returning once, twice, three times, etc., in that order. In the first column (year 0 = banding year) the total number of captured birds is given, then the number of repeats (rep) during the same winter, followed by (in parentheses) the number of repeating individuals (the totals include returning, previously banded individuals and their repeats, resp.). In the other columns, the number n designates the "possible returns" (see text for additional explanations), followed by the number of returns (ret) and its percentage of n.