POPULATION MOVEMENTS OF BIRDS

By Richard F. Johnston

This short paper is an exploratory discussion of three kinds of population movements of birds: dispersal, spacing, and migration. The last of these is of interest here only in its occurrence coincident with dispersal and spacing, and it is to the latter that chief attention is directed.

Dispersal refers only to movement, usually of young, from sites of birth to sites of breeding. "Effective distance of dispersal" refers to the least distance in an air line between site of birth and site (or sites) of subsequent breeding, and of course this is less in almost every instance than the distance actually traveled by an individual. The main significance of dispersal is ecological—by means of dispersal a species avails itself of suitable habitat within, peripheral to, or isolated from an occupied area. This general adaptation can be broken down into subcategories (Howard, 1960:157). There is, of course, important correlated function concerning movement of genetic elements through populations or between neighboring populations.

Spacing is the movement of birds that brings about territorial dispersion. Spacing is guided partly by configuration of their preferred vegetation and topography and partly by their territorial behavior. Territories of optimal quality tend to be occupied before those of suboptimal quality; consequently, a patchwork of occupied places can be established within a frame of generally suitable habitat. The routes that individuals follow in finding suitable places will reflect the fact that routes tend to be unknown beforehand, as are the locations of unoccupied places. Thus, the important elements of the environment in which spacing occurs are essentially distributed at random, as far as their influence on the direction and magnitude of spacing is concerned. For a population, therefore, spacing movements tend to cancel one another, that is, the vectorial sum of such movements approaches zero.

For a migratory bird, migration and dispersal (but not effective dispersal) more or less coincide in time. Additionally, terminal stages of migration and dispersal can merge with initial stages of spacing. Consequently, there is some reason for confounding these kinds of movement with one another; that we actually gain in distinguishing between them may be demonstrated in the following discussion.

DISPERSAL

There is general agreement that the chief means of dispersal in birds consists of movements by young individuals. Almost forty years ago Grinnell (1922) recognized that individuals that moved long distances (so-called distributional accidentals) were predominantly young-of-the-year; extralimital occurrence was almost always of young birds. Fisher (1955) adduced further evidence showing that such movement, which he called dispersal, was a function of young, mainly first-year birds. Howard (1960) discussed this kind of movement by young individuals of several kinds of vertebrates. Most significant is the evidence from studies on banded, sedentary bird populations (Nice, 1937; Erickson, 1938; Kluijver, 1951; Gibb, 1954; Johnston, 1956), which has demonstrated movement from sites of birth by young-of-the-year and remarkable constancy of adults in remaining at sites of breeding.

In sedentary bird populations, but not necessarily in non-sedentary ones, the difference in amount of movement recorded for adults *versus* first-year birds is so great that a qualitative difference in behavior seems to be involved. Moreover, there are data supporting the idea that certain first-year birds characteristically move long distances in the process of dispersal. Table 1 presents a summary of distances moved in the dispersal

of Song Sparrows (*Melospiza melodia*) of two, distinct populations. Earlier (Johnston, *op. cit.*:42), the correspondence in distances moved in the two samples had been noted. Curves drawn from these data are bimodal and differ from curves characteristic of random dispersal mainly near the extremes of the frequency distributions. In both samples, more individuals move relatively short distances and relatively great distances than are expected to do so on the basis of chance alone. Therefore, dispersal can be considered to be an organized or directed characteristic in Song Sparrows.

TABLE 1

DISTANCES OF DISPERSAL IN TWO POPULATIONS OF SONG SPARROWS

Population	Distance of dispersal in meters							
	100	200	300	400	500	600	700	800+
California[1]	39[3]	30	12	8	0	0	8	3
Ohio[2]	12	27	30	8	6	8	3	6

[1] From Johnston, 1956:42.
[2] From Nice, 1937:83.
[3] Per cent of total instances.

Studies on other kinds of sedentary animals have shown their dispersal qualitatively to resemble that of Song Sparrows. Bateman (1950) noted several examples of bimodal curves in the dispersal of flying insects in his analysis of "dispersal" of genes in populations. He concluded that "many if not most methods of gene dispersal produce such distributions," although he had no examples from terrestrial vertebrates at that time and he did not limit his conclusion to strictly sedentary populations. Bimodal curves of dispersal have been demonstrated for a leafhopper, *Macrosteles divisus* (Frampton, Linn, and Hansing, 1942), a weevil, *Bruchus pisorum* (Wakeland, 1934), a lizard, *Sceloporus olivaceus* (Blair, 1960), the House Finch, *Carpodacus mexicanus* (Thompson, 1960), the House Sparrow, *Passer domesticus* (Wagner, 1959), and a mouse, *Peromyscus maniculatus* (Dice and Howard, 1951). All available evidence indicates that such bimodal distributions are reflections of species-specific behavioral tendencies in dispersal; the preponderant fraction of the dispersing element is characterized by movement of relatively short distance (the "homing tendency" of Howard, *op. cit.*), and the lesser fraction of the dispersing element by movement of relatively long distance.

Thus, the tendency by subadults to move is evident in any fraction of this age class. Were there actually no tendency to move on the part of some individuals, the curves of dispersal would show a greater frequency of individuals staying at birthsites. Yet, few occur exactly at birthsites, and modal distances of dispersal for Song Sparrows, one of the most sedentary of bird species, are 200 to 400 meters. If it is necessary to emphasize one thing in order to establish dispersal as an innate tendency, the emphasis is properly placed on those young having the capacity to disperse long distances. Howard's review (*op. cit.*) has led him to a similar conclusion.

It is appropriate to note at this point that the genetic background for dispersal is complex. That only a small fraction of young disperse long distances is of adaptive significance. Also, there are different selective values for long-distance (or short-distance) dispersal in accord with whether the phenotype is present in centrally-located populations or at the periphery of the distribution of the species. Such fluctuating selective value on phenotypes (which may be composed of several genotypes) can, as Alden H. Miller has noted (personal communication), result in behavioral polymorphism. In such an instance, central populations would show a greater, and peripheral populations a lesser,

incidence of phenotypes dispersing long distances—conditions that could be demonstrated by appropriate intensive population studies.

SPACING

The fact that young individuals are the agents of dispersal provides one measure of the distinction between dispersal and spacing. Additionally, spacing, motivated in part by territorial behavior, results in the dispersion of breeding units in a population, and it would seem, to consider only two alternatives, that territorial aggression, rather than spacing itself, is the significant selective element in territorial behavior. It would also appear that spacing is not immediately related to dispersal.

Nevertheless, territorial spacing and dispersal have been associated causally (Fisher, 1955:440; Howard, 1960:152). The suggestions were that dispersal ("environmental dispersal" of Howard, *loc. cit.*) in sedentary (*ortstreuen*) bird species is attributable to the "territorial system." These suggestions were probably motivated by undue emphasis on the significance of territoriality. A tremendous amount of work in the past two decades and especially a paper by Pitelka (1959:253) serve clearly to point up the general conclusion that spacing of individuals or breeding units is the immediate adaptive advantage of territoriality; behavioral systems of territoriality result in ecologic systems of spacing. Indeed, the 31 functional categories listed by Carpenter (1958) chiefly have as their common denominator the phenomenon of spacing.

Territoriality in the northern hemisphere is a phenomenon chiefly of spring and summer; yet, by early spring (or autumn and winter for some species) dispersal has already been achieved. This is true almost without exception for sedentary, resident birds (Johnston, 1956:40), but it is less true for migratory species. In the latter, dispersal and migratory movement are identical, as has been noted previously; dispersal is thus nearly complete only when migration ceases. However, spacing functionally equivalent to dispersal occurs in early stages of territorial behavior. Effective distances of dispersal can consequently be increased or decreased depending on chance encounters of non-established birds with established birds. Such modification is the chief bearing of territorially-activated spacing movement on dispersal, and it should be clear that such bearing means little. The essential meaninglessness is emphasized particularly at the level of populations, in which as many individuals will be forced to move one way as another. In sedentary populations showing autumnal territoriality, the action of territorial aggression on juveniles that are dispersing would be evident in autumn, not spring, but the significance of territoriality in affecting meaningful modification of dispersal would be the same as that discussed for migratory species.

The term spacing is available and suitable for discussing movement resulting from territorial behavior, and it is here proposed that it be used as distinct from dispersal.

CONCLUSIONS

Dispersal, defined as movement from site of birth to site of breeding, is a mechanism that tends to ensure complete testing or investigation by a species of all suitable habitat within and beyond the area of established distribution of this species. This fragment of the population that disperses is the young; in birds such individuals are usually less than one year old. The genetic heritage of some of the individuals probably casts them in the roles of dispersers to long distances.

Spacing, resulting from territorial behavior of adults and responsible for dispersion of breeding units, does not effect, or in any meaningful way affect, dispersal. The capacities for these two types of movement exist independently of one another, in spite of the fact that some dispersal can occur coincident with spacing.

Migratory movement includes dispersal *in sensu lato*, but effective dispersal is independent of migration.

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