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NATAL DISPERSAL, AREA EFFECTS, AND EFFECTIVE POPULATION SIZE

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Abstract.—The effects of long-distance natal dispersal, dispersal within a finite study area, and variance in reproductive success on estimates of population size were compared. By including the observed long-distance banding recoveries in Kendeigh's (1941) population of House Wrens (*Troglodytes aedon*), the root mean squared dispersal distance, σ, is increased from 1.3 to 84 km, from Barrowclough's (1978) model estimate. Taking into account local and regional population densities and the revised estimate of σ, neighborhood size N_1 and effective population size N_e are increased by a factor of 18. The effect of long-distance dispersal was considerably greater than the adjustment for a finite area effect on local dispersal. The magnitude of long-distance dispersal overwhelmed the adjustments suggested for variance in reproductive success and for a non-normal distribution of distances. Estimates of dispersal should use all recovery data even when the proportion of banded birds that are recovered is low, especially for birds banded as nestlings, and should include the proportion of breeding birds that were born in the same area.

DISPERSIÓN NATAL, EFECTO DE ÁREA Y TAMAÑO EFECTIVO DE UNA POBLACIÓN

Sinopsis.—Se comparó el efecto de la dispersión natal a larga distancia, dispersión dentro de un área de estudio definida y la variación del éxito reproductivo solore los estimados del tamaño poblacional. Al incluir el movimiento a larga distancia de individuos de *Troglodytes aedon* informado por Kendeigh's (1941) a través del recobro de bandas, el promedio de la raíz cuadrada de la distancia de dispersión (σ), aumenta en el modelo de estimados de Barrowclough's (1978) de 1.3 a 84 km. Tomando en consideración densidades poblacionales locales y regionales y el estimado revisado de σ, el número de individuos en una vecindad (N_1), y el tamaño efectivo de la población (N_e) aumenta en un factor de 18. El efecto de la dispersión a larga distancia resultó ser considerablemente mayor que el ajuste para un área definida de una dispersión local. La magnitud de la dispersión a large distancia sobrepasa el ajuste sugerido para la varianza en el éxito reproductivo y para una distribución de distancia no-normal. Los estimados de dispersión deben utilizar toda la información del recobro de bandas aún cuando la proporción de aves anilladas recobradas sea baja particularmente de pájaros anillados como polluelos. Los estimados deben incluir, además, la proporción de aves reproductivas que nacieron en la misma área.

Dispersal and population size are central to the biological species concept and to a conservation theory of viable population size (Lande and Barrowclough 1986, Koenig 1988, Mayr 1963, Templeton 1989). A biological species is a cohesive and inclusive population to the extent that individuals in different areas disperse and exchange genes in breeding (Mayr 1963, Templeton 1989). Natal dispersal, between the site of birth and site of breeding, determines the extent of gene flow and population structure. Effective population size determines the importance of stochastic processes in evolutionary change. The size and genetic variation of a population are important in long-term demographic survival and in retaining diversity in respect to loss of variation by sampling error or genetic drift (Lande 1988, Lande and Barrowclough 1986).

Wright (1969) developed a genetic concept of population size. First, the number of individuals in a neighborhood, or N_1, can be estimated from the distribution of parent-offspring distances, that is, from natal dispersal. The more individuals that are potential mates, the larger the population. N_1 reflects the ideal population size from which mates are drawn as if at random. N_1 is derived from 2σ, where σ is the root mean squared natal dispersal distance. In a statistically normal distribution of dispersal distances, an area with a radius of 2σ accounts for about 86.5% of the observed cases (Wright 1969:303).

Second, the genetically effective population size, or N_e, is a function of N_1 and other factors that take into account the variance in reproductive success. The genetic variance observed at any time may reflect historically small sizes rather than current size, and other factors may affect genetic diversity within a population (Wright 1969). An abstract genetic concept, N_e includes both dispersal and variation among individuals in transmitting genes across generations. N_e can be estimated from gene frequencies as well as from dispersal data.

Dispersal data from local field studies of several species have been used to estimate N_1 and the genetic equivalent, N_e (e.g., Barrowclough 1980, Rockwell and Barrowclough 1987). A limitation of local study areas was pointed out by Barrowclough (1978): birds may disperse from their birth site and breed just beyond the boundary, especially if they were born near the edge. As a result observed σ distances will be less than the actual σ. Barrowclough developed a model to adjust dispersal distances for a finite area by using an integral approximating the study area with a circle of diameter determined by the observed local distances. This adjustment has been used in estimating population size in several species (Barrowclough 1980, Koenig and Mumme 1987, Rockwell and Barrowclough 1987).

Barrowclough (1980:790) used only the distances observed within a study area, "Because dispersal is only of interest here if it leads to gene flow (Mayr 1963), only those studies were used in which young were banded at or near their nests, and then were recovered at their breeding sites. . . . This limited the study to intensive field projects and eliminated general recoveries of banded birds." The reasoning implies that birds do not breed if they do not breed within the study area. However, gene flow may occur over a wider region (Mayr 1963) and the degree to which birds breed at distances remote from their natal site is exactly what is to be determined in estimating gene flow.

Here I test the contribution of longer dispersal distances to estimates of N_1, and show that the full set of natal to breeding site distances gives substantially larger estimates of dispersal and population size than distances observed within a local area. I also compare the effects of long-distance dispersal, variance in reproductive success, and non-normal distributions of dispersal distances.

DISPERSAL DISTANCES AND POPULATION SIZE IN HOUSE WRENS

Barrowclough (1978) developed the model of area effect using the shorter local dispersal distances observed in a population of House Wrens, *Troglodytes aedon* (Kendeigh 1941). Kendeigh banded 7375 nestling House Wrens in a study area, "Outfield," of 4 km^2 in Ohio. Of these, 154 (2.1%) returned to breed in the area. By comparing birth and survival rates of adult wrens, Kendeigh and Baldwin (1937) estimated that about 11.5% of the surviving birds that were banded as nestlings returned to their natal area, suggesting that more than 80% dispersed elsewhere to breed. An additional 28 nestlings (0.4% of those banded as nestlings) were recovered in a later breeding season outside this area (Kendeigh 1941), showing the occurrence of long-distance natal dispersal.

Barrowclough (1978) suggested that by considering the geometry of the study area, the natal dispersal σ observed in "Outfield" would be increased over the directly calculated σ by 23%. The adjusted σ was 1.32 km. Using σ and an estimated adult survival of 0.5, he calculated an effective population size N_1 of 7679 birds (Barrowclough 1980).

This analysis did not include the nestlings that were recovered at greater distances beyond "Outfield" (Table 1). The wren that moved the longest distance was caught in summer at a nest site (Kendeigh 1941:18); all were thought to have been on breeding sites. Since the longer distances have a disproportionate effect on σ, the full data indicate more dispersal and a larger population size than the within-area dispersals, regardless of a finite area effect. Including all natal dispersal distances for the wrens, $\sigma = 83.6$ km. This difference in estimated dispersal is large, 64 times greater than Barrowclough's 1978 estimate, compared with the 23% difference of unadjusted and adjusted σ within the area. For the 28 long-distance recoveries alone, σ was 210.6 km, or 2.5 times greater than σ for all distances. A few long-distance recoveries contributed more to the magnitude of σ than did the larger number of returns from the same population.

Barrowclough's (1978) model provided a solution to the bias created when some birds may disperse just outside a study area, at distances within those observed within the area. As he noted, it does not address the problem of dispersal distances at a larger scale. In the House Wrens, the effect of long-distance dispersal is to increase the estimate of σ by a factor of 64. N_1 would increase by σ^2, but the following analysis develops a more moderate estimate of N_1.

Neighborhood population size, or N_1, was estimated from σ and population density. Breeding Bird Surveys (BBS) recorded an average of 6.4 House Wrens per route in Ohio (Robbins et al. 1986). Population density of birds can be estimated when their detection distance is determined (Emlen 1977). If half the birds present were detected within 100 m of each sample site, then the 50% detection distance r would be 100 m. If all these were singing males, then each stop effectively sampled an area of about πr^2, or π 0.5 ha, and the 50 stops in a route effectively sampled

TABLE 1. Summary of natal dispersal distances (km) of House Wrens at "Outfield" (from Kendeigh 1941:17). Distances within the "Outfield" study area were used in Barrowclough's (1978) estimate and were given in classes of 1000 feet; the midrange was used here. Longer distances were given in miles.

Area	n	Min	Max	Mean	σ	Skew	Kurtosis
Within area	154	0.0	3.5	1.06	0.78	0.87	0.24
Beyond area	28	4.0	1126	5.91	210.6	4.96	22.7
Total	182	0.0	1126	9.34	83.6	13.2	173.7

a total area of about 4 km^2. House Wrens are distributed unevenly in the midwest and are concentrated in towns (Graber and Graber 1963). The population density of House Wrens would be 6.4/4 km^2, or 1.6 wrens per km^2, fewer than in "Outfield" where nestboxes were supplied but representative of the larger region. N_1 would be $4 \pi \rho \sigma^2$, where ρ = the density of birds per km^2 (Wright 1969:303). Estimated from the local returns and banding recoveries from Kendeigh (1941), N_1 for House Wrens is about 141,527 birds. This estimate of N_1 is 18 times that of Barrowclough (1980).

EFFECTIVE POPULATION SIZE

Effective population size, or N_e, is a population genetics construct. It can be estimated in different ways from dispersal data and includes demographic and other factors that tend to decrease the estimate of N_1. The variance effective population size N_e differs from N_1 by adjusting for variances in individual genetic success, including survival and breeding (Barrowclough 1980, Chepko-Sade and Shields et al. 1987, Koenig 1988, Lande and Barrowclough 1986, Wright 1969). Koenig (1988) estimated the decrease in N_e from N_1 as the product of factors for overlapping generations, variance in reproductive success, and non-normal distributions of dispersal distances in four species other than House Wrens for which data were available. In his analysis, N_e averaged 34% of N_1. These factors would also lower the estimate in House Wrens.

However, these factors may exaggerate the difference between N_e and N_1. First, the observed dispersal distances were for nestlings surviving until the breeding season, so the data include the minimal survival required for an estimate, in contrast to the approach of Barrowclough (1980). Second, survival and breeding success show little change with age in small songbirds, and relative variance in lifetime reproductive success (LRS) often is similar to variance in annual success when entire cohorts are considered (Newton 1989). Mean breeding success in a year per pair of House Wrens in Kendeigh's 6 ha core area "Hillcrest" was 4.82 with a variance of 9.46 (Payne 1984). Adjustment for variance in breeding success, as in Chepko-Sade and Shields et al. (1987) and Koenig (1988), decreases N_e by 51% of N_1 in the House Wrens.

Finally, the distribution of dispersal distances away from the natal site generally are lacking. In most studies, including those in Koenig (1988), no banding recoveries were reported. For the Acorn Woodpecker (*Melanerpes formicivorus*), estimates from demography suggest that more than 20% of the surviving females emigrate beyond the study area (Koenig and Mumme 1987). Without information on dispersal outside the study area, kurtosis cannot be calculated, though the effect of a non-normal distribution of distances on N_1 may be minor. Estimates of γ^2 have a large confidence interval (Moore and Dolbeer 1989). In Kendeigh's data the degree of kurtosis, or γ^2, was 173.7, and beyond "Outfield" it was 22.7 (Table 1). Wright (1969) estimated the effect of kurtotic distributions on σ and N_1. Within a range of γ^2 of 0 to 30, leptokurtosis decreased N_1, but even a γ^2 of 104 (the highest value used by Wright 1969:304) affected N_1 by a factor of 2.3, a low effect in relation to that of long-distance dispersal.

To place into perspective the significance of long-distance dispersal, estimates of N_1 based on local dispersal are effective inasmuch as local dispersal accounts for immigration and emigration. The proportion of birds returning to the natal area or recovered elsewhere in the House Wrens is low (2.5%) compared with the number of young needed to replace the nonsurviving adults (67%, Kendeigh and Baldwin 1937). A more direct test of whether the dispersal distances observed in an area account for overall natal dispersal is the proportion of birds that were born there. In long-term local studies where all nestling songbirds were banded in migratory, partly migratory, and some resident populations, from 1% to 50% of the breeding birds of one or both sexes were born there (Bairlein 1978, Bauer 1987; Baumer-März and Schmidt 1985; Bulmer and Perrins 1973; Cohen et al. 1989; Harvey et al. 1988; Kneis 1985; Marzluff and Balda 1989; Payne et al. 1987; Schmidt 1983; Winkel 1981, 1982, 1989; Winkel and Frantzen 1989; Zeh et al. 1985). The proportion would vary with size of the area, which is usually determined by observer effort rather than by biology of the birds. The studies cited were in areas of 10 km^2 or less and within widespread and continuous populations. That is, they were populations described by a spatially continuous or isolation by distance model, and not by an island or steppingstone model (Wright 1969).

In one species, estimates of population size can be compared with both dispersal and genetic data. Moore and Dolbeer (1989) calculated dispersal σ for Red-winged Blackbirds (*Agelaius phoeniceus*) from the banding recovery file of the Bird Banding Laboratory (BBL). The data were biased towards long-distance recoveries, as local returns were excluded. Most recoveries of yearlings were within 20 km of the site where they were marked; some birds of the year were banded after they had fledged and may have dispersed from their natal site. For yearling blackbirds, σ was 68.4 km. Assuming detectability as in the wrens, a mean density of 7.8 birds per BBS route in North America (Robbins et al. 1986) leads to an estimated N_1 of $4 \pi \rho \sigma^2$, or 4.6×10^5. Genetic data in the blackbirds suggest an N_e of 3.7×10^4 (Avise et al. 1988). The genetic data are consistent with inference from banding recoveries of a large N_1, but the recoveries were not necessarily natal dispersals because free-flying birds of the year were included. The differences in estimates of N_1 and N_e may be due to sex-specific variances in breeding success (Orians and Beletsky 1989, Payne 1984), to a non-normal distribution of natal dispersal distances (Moore and Dolbeer 1989), and especially to historically lower population sizes (Avise et al. 1988).

Population studies that do not account for the individuals that breed well beyond a local area will lead to underestimation of dispersal and population size, regardless of minor adjustments for dispersal observed within a finite area or for demography. Few birds banded as nestlings are recovered in regional banding programs (Baillie and Green 1987, Brownie et al. 1985, North 1887). Nevertheless, analysis of all natal banding recoveries is more likely to lead to true estimates of dispersal distances and population sizes in birds than local returns, and both should be considered.

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Association of Field Ornithologists Annual Meeting 21–24 March 1991

(Tentative schedule)

21 March			Arrival; Council meeting
22 March	0700		Local field trips
	0915		Welcome
	0930		Symposium—Avian Conservation: Problems and Solutions
		0930	Recent population trends—Scott K. Robinson
		1030	Coffee break
		1100	Preservation of staging areas of shorebirds—Brian A. Harrington
		1200	Lunch
		1330	Recovery of hawk populations—Tom J. Cade
		1430	Conserving the tropics—Carlos Quintela
		1530	Coffee break
		1600	Considering the future—Frances C. James
	1700		Reception
	1900		Dinner
	2000		Wildlife and landscape of frontier Ohio—Robert C. Glotzhober
23 March	0700		Local field trips
	0900		Symposium—History of North American Ornithology—William E. Davis and Jerome A. Jackson
	1030		Coffee break
	1100		Symposium (cont.)
	1200		Lunch
	1300		AFO business meeting
	1400		Contributed papers
	1700		Reception, poster papers
	1900		Banquet
	2000		Avian chamber music—COSO String Quartet
24 March			Field Trips

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