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DISPERSAL AND POPULATION STRUCTURE IN THE EUROPEAN STARLING[1]

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Abstract. Dispersal in birds can be estimated in several ways, including the use of banding data and the indirect use of genetic data. This study uses both of these to estimate dispersal and genetic population structure in the European Starling (*Sturnus vulgaris*) in North America. Banding data imply that natal dispersal is quite high, and this finding is supported by the observed rapid colonization of North America. Genetic data, based on allozyme allele frequencies from populations in Virginia, Vermont, Colorado, and California, are consistent with a species with large demes and high rates of dispersal.

Key words: dispersal, European starling, population structure, Sturnus vulgaris.

Natal dispersal allows for the exchange of individuals among existing populations and provides individuals to colonize new areas. Thus, this process is integrally associated with the genetic structure of populations. Unfortunately, it is often very difficult to make direct and accurate estimates of natal dispersal. Banding data have offered important insights into both seasonal movements and dispersal. An alternative is the use of

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genetic estimates of population structure to infer dispersal parameters. This study uses both approaches to examine patterns of dispersal and population structure in European Starlings (*Sturnus vulgaris*) in North America. Different study populations were used for both approaches.

METHODS

BAND RETURN ANALYSIS

Banding data from the U.S. Fish and Wildlife Service (FWS) were examined for patterns of juvenile dispersal. Only records of starlings banded as nestlings and recovered during the breeding season (March–June) in a subsequent year were used. The banding and recovery location coordinates were used to calculate the arc distance in km between points. Results presented are means ± SD.

GENETIC ANALYSIS

Starlings were collected from four widely separated areas: California (n = 23), Colorado (22), Vermont (19), and Virginia (78). Tissue was stored in liquid nitrogen, and later used for electrophoretic analysis of enzymes. Seventeen enzymes were examined, yielding data on 22 loci. Procedures and techniques are detailed in Cabe (1998).

Putative genotypes were based on electrophoretic phenotypes. Genotypic frequency data for the 22 gene loci were analyzed using Genesys software (Corbin and Wilkie 1988), which provided calculations of allelic frequencies and F_{ST} values based on Wright (1978). Significance of the F_{ST} values was tested against the chi-square distribution (H_0: $F_{ST} = 0$, $\chi^2 = 2NF_{ST}$, df = (1 − number of populations sampled) = 5) for $P < 0.05$ (Neel and Ward 1972).

ESTIMATING POPULATION STRUCTURE AND DISPERSAL

The mean F_{ST} value was used to estimate Nm (Slatkin and Barton 1989) following Wright's (1951) equation:

$$F_{ST} \approx 1/(4Nm + 1)$$

where N is the effective population size of each deme and m is the proportion of each deme that are dispersers from other demes.

Natal dispersal estimates, in conjunction with population density estimates, also were used to produce an independent estimate of genetic population structure. With the variance in dispersal distance (V) and the density of breeding individuals (d), the effective size of the genetic "neighborhood" (N_n) was estimated using $N_n = 4\pi Vd$ from Wright (1946). This parameter for continuously distributed populations is equivalent to the quantity Nm (deme size times dispersal rate) used in models of populations composed of demes. This analysis is equivalent to others (Barrowclough 1980, Payne and Payne 1993) which examine the effective number of individuals in a circle of radius 2σ where σ is the root-mean-square dispersal distance. A density of about 10 pairs km^{-2} was assumed (Feare 1984).

RESULTS

From the suitable band returns, the average distance moved was 104 ± 307 km (n = 131). Of these records, 69 represent individuals recaptured in their natal area. The mean distance of natal dispersal for juveniles that actually moved (n = 62), as estimated from banding data, was 219 ± 419 km (range 12–2,623 km). The distribution of natal dispersal distances is both skewed and highly leptokurtic (Fig. 1). Most data came from the eastern seaboard (FWS flyway 1, 40 returns) and the Midwest (FWS flyway 2, 37 returns), with fewer returns from the Rocky Mountain and west coast states (FWS flyways 3 and 4, 12 and 10 returns, respectively. Additional returns (32) from Canada also were concentrated in the east (Ontario and Quebec). Mean dispersal distance did vary by region (108.6 km and 135.0 km for the east and Midwest, respectively vs. 24.2 km and 53.4 km for the Rocky Mountains and west coast, respectively), but the differences were not significant. In general, the differences were attributable to the one or two maximum dispersal distances in the east and Midwest. Potentially interesting comparisons of male and female dispersal could not be made due to lack of information.

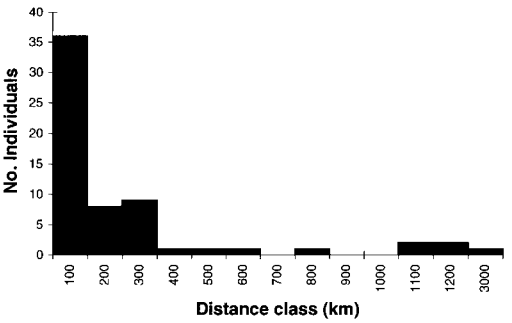

FIGURE 1. Frequency histogram of natal dispersal distances of juvenile starlings. Individuals recaptured where banded (n = 69) are not included. Note discontinuous distance scale. Distribution shows extreme kurtosis (g_2 = 37.1).

The electrophoretic analysis yielded 16 monomorphic loci and only 6 polymorphic loci which could be used to estimate F_{ST}. Five of these polymorphic loci showed no statistically significant population differentiation ($F_{ST} = 0$), and one locus showed a very minor level of population differentiation (F_{ST} = 0.04), giving an average over six loci of 0.007.

Effective size of genetic neighborhoods (N_n) was estimated using variance in dispersal distance (9.45×10^4) at about 2.38×10^7; even substantially lower densities would yield very large effective population sizes. The total population count of starlings in North America is probably in the hundreds of millions (ca. 2×10^8, Feare 1984), so this suggests little genetic substructuring of the population.

DISCUSSION

The rapid colonization of North America by starlings (Kessel 1953, Johnson and Cowan 1974) was primarily a result of natal dispersal. Adult starlings are highly philopatric; Kessel (1953) summarized available North American and European sources stating "[the data] of-

fer no evidence that a starling that has bred once in a given area has ever left that locality to breed at some distant place (over 20 miles)." Juveniles, however, may move long distances to breed, as the band recovery data indicate. The estimates from banding data are likely to be conservative (Moore and Dolbeer 1989). Although these data are too limited to quantify juvenile dispersal accurately, they do imply a high vagility for juvenile starlings.

The effective neighborhood size (2.36×10^7) is considerably larger (three orders of magnitude) than any reported in Barrowclough's (1980) survey, and also is dramatically higher than reported values for Indigo Buntings (*Passerina cyanea,* Payne and Payne 1993), but is consistent with the starling's high density and great propensity for dispersal. Studies of band return data from Common Grackles (*Quiscalus quiscula*) also have suggested long range dispersal (Moore and Dolbeer 1989), although mean dispersal distance was a third of that in starlings. Juvenile dispersal estimates from band returns in House Finches (*Carpodacus mexicanus*; Veit and Lewis 1996) showed an even higher mean dispersal distance (330 km); like Starlings, House Finches have a demonstrable ability for rapid range expansion.

In general, allozyme studies of avian species have revealed low levels of population structure, presumably due to high levels of dispersal (Barrowclough 1980, 1983). In areas of their native range, comparable allozyme analysis showed that starlings have a slight but statistically significant level of population subdivision ($F_{ST} = 0.0101 \pm 0.0017$). Introduced starlings in New Zealand exhibit a greater degree of subdivision ($F_{ST} = 0.0316 \pm 0.0103$), probably attributable to multiple introductions in different areas each with slightly different initial allelic frequencies due to founder effect (Ross 1983). This study found no statistically detectable population structure ($F_{ST} = 0$). Based on this statistic, the dispersal parameter *Nm* is infinity, implying that *Nm* is very large. This suggests large demes, high dispersal rates, or more likely, both. Estimates of population structure from the genetic data are completely consistent with estimates of population structure based on demographic data. Genetic neighborhoods of the size estimated from the banding data would predict F_{ST} values on the order of 10^{-8}, which would be indistinguishable from zero.

The genetic analysis presumes that the population structure in North America has reached an equilibrium, and this assumption is worth closer scrutiny. Starlings were introduced to New York City in 1890 and 1891 (see references in Cabe 1993), and have subsequently spread throughout North America. During geographic expansion, the population is unlikely to meet equilibrium expectations. Extensive computer simulations (Cabe 1994) suggest that equilibrium levels of differentiation are reached soon after the available geographic range has been colonized, especially if dispersal rates are high. As outlined above, natal dispersal rates are believed to be high, supporting the assumption of an equilibrium population structure.

The data suggest that the population of the European Starling in North America is nearly a single panmictic population. The high density of local populations (which limits drift) and the extreme vagility of juvenile dispersers (which blend local populations) produce a population which is genetically homogenous across its range.

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