DISPERSAL IN WHITE-CROWNED SPARROWS: A COMPUTER SIMULATION OF THE EFFECT OF STUDY-AREA SIZE ON ESTIMATES OF LOCAL RECRUITMENT

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ABSTRACT.—Consideration of the problem of sampling a population within a finite study area suggested that recruitment results might be related to the size of the study area. Specifically, the proportion of recruits observed within a defined study area that originate in that area (local recruits) should be a function of the proportion of the population that the study area represents. Computer simulations of dispersal, using Nuttall's White-crowned Sparrow (*Zonotrichia leucophrys nuttalli*) as a model, were designed to test this hypothesis, and the effect of territory size and population size on this relationship. The simulations confirmed that local recruitment is a function of the proportion of the population sampled in the study area. Additionally, these simulations demonstrated that by holding the distribution of dispersal distances constant, local recruitment for a given proportion of the population sampled increased with territory size and population size. These latter results, however, are artifacts of the simulations and have no biological significance. Finally, the proportion of local recruits predicted for a natural population was remarkably close to that obtained from fieldwork. I suggest that conclusions about dispersal and population structure should not be drawn from proportions of local recruitment within finite study areas, and require more detailed analysis of dispersal. *Received 7 December 1984, accepted 11 July 1985.*

ANALYSES of dispersal (Howard 1960), and the attendant gene flow (Wright 1940, 1943, 1946, 1951; Murray 1967; Crumpacker and Williams 1973; Powell et al. 1976; Endler 1977), are important to understanding population structure and evolutionary processes (Barrowclough 1978, Greenwood and Harvey 1982, Shields 1982). Conclusions about dispersal are often not derived from observed zygote-to-zygote dispersal distances. Instead, a study area is defined within a population and an attempt is made to mark all individuals produced within that study area. In subsequent breeding seasons, the study area is censused to determine what proportion of the breeding adults originated within the study area. From such "local turnover," inferences are drawn about the magnitude of dispersal among study populations (Petrinovich et al. 1981). Petrinovich and Patterson's work (1982; see also Baptista and Morton 1982) on the stability, recruitment, and population structure of Nuttall's White-crowned Sparrows (*Zonotrichia leucophrys nuttalli*) is an example of this latter approach.

Estimating dispersal from local turnover has an inherent problem: the proportion of "local" recruits (i.e. those produced within the study area) is related to the proportion of the breeding population sampled in the study area. Consider a small hypothetical study area including only a single territory, and a dispersal rule that individuals cannot settle within their natal territory. Clearly, the proportion of recruits to the study area that originated there (local recruits) will be zero. At the other extreme, a study area encompassing the entire breeding population will necessarily contain 100% local recruits. Most study areas lie somewhere between these extremes, representing some portion of the population of interest.

To demonstrate the relationship between local recruitment and the proportion of a population sampled, I designed a computer simulation of dispersal and sampled defined study areas. To make this simulation representative of a natural population, I drew the necessary parameters from the literature on the demog-

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raphy and dispersal of Nuttall's White-crowned Sparrow. The general conclusions from this analysis should, however, be applicable to essentially any population of dispersing organisms. Finally, I simulated Petrinovich and Patterson's (1982) study conditions to see if the proportion of local recruits predicted from my model would be comparable to their empirical result.

COMPUTER SIMULATIONS

Simulations were programmed in Applesoft BASIC on an Apple II+ computer. The first simulation was designed to determine the relationship between local recruitment and the proportion of a population sampled, and to determine the effect of territory size on that relationship, for a given dispersal distribution. The population was defined as a square array of 625 territories, 25 on a side. This approximates the size of a song dialect population at Point Reyes National Seashore, California (300-800 pairs/dialect, Baker 1981; pers. obs.). The population was stored in computer memory as a two-dimensional array and treated as a hexagonal array by manipulation of the addresses (Page and Didday 1980). The advantage of the hexagonal arrangement was that each territory (with the exception of boundary territories) was surrounded by six neighboring territories whose centers were equidistant from the center of the territory they bounded. In nature, the spatial arrangement of territories may be highly variable, but an approximation to hexagonal packing is common (Nice 1937, Lack 1966, Leuthold 1966, Grant 1968, Southern 1970, Barlow 1974, Wilson 1975, Ligon and Ligon 1982). Study areas were defined as square arrays centered within the population and represented samples of the population ranging from approximately 5% to 95% at approximately 5% intervals.

Each simulation began by establishing the status of all territories within the population. A survivorship test determined whether each territory was occupied by a surviving adult or was available to a recruit. Survivorship was 50% for each adult generation (Mewaldt 1964, Baker et al. 1981). For simplicity, each territory was occupied by a single individual rather than a pair [simulating pairs would have required running the program twice (once for each sex, assuming the sexes disperse independently) and averaging the results to obtain a single proportion], and recruitment was limited to first-year birds, i.e. adult movement was not considered.

Dispersal began by randomly selecting a territory of origin from the entire population, then determining a target territory by randomly generating a dispersal direction and distance. Dispersal directions were chosen randomly to be along one of the six axes through the six neighboring territories. Dispersal distances were selected probabilistically from a two-parameter gamma distribution fitted by Baker and Mewaldt (1978) to dispersal data for both sexes from White-crowned Sparrow populations at Point Reyes, California. For this distribution, gamma = 0.89352 and the two parameters were calculated to be alpha (α) = 0.6 and beta (β) = 366.8. Alpha is a shape parameter and beta is a scale parameter, where the mode = $\alpha\beta$ and the mean = $(\alpha + 1)\beta$ (Johnson and Kotz 1970, Hastings and Peacock 1975). Dispersal distances were calculated in meters and converted into territorial units by dividing that distance by the territorial diameter. Hexagonal polygons have two diameters, side-to-side (minimum) and corner-to-corner (maximum). All simulations in this study used minimum diameters for territory diameters.

Dispersing individuals were moved to the target territory, determined by the dispersal direction and distance, using the hex address manipulation. If the territory was available (not occupied by a surviving adult or previously dispersed juvenile), the dispersing juvenile occupied that territory; if the territory was occupied, the dispersing juvenile searched the six neighboring territories and occupied the first available territory encountered. Once the dispersing juvenile settled, it was noted whether it had originated from within or from outside the study area. Following this, or if the disperser was not able to settle in the target territory or one of the six neighboring territories, a new territory of origin was randomly selected and dispersal of a new individual was initiated in like manner. The populations defined in these simulations were finite, and the boundaries were absorbing; i.e. if a dispersing juvenile contacted a boundary he was eliminated, and dispersal of a new juvenile was initiated. The number of juveniles that could disperse from a given territory was not limited (White-crowned Sparrows may produce more than one clutch/season with up to 4-5 young/clutch), but on each iteration the territory of origin was again chosen randomly. Dispersal iterations continued until all territories within the study area were occupied. The study area was then censused to determine the proportion of recruits that originated within the study area.

This simulation used four different territory diameters (20, 40, 80, and 160 m) and 16 study-area proportions (from about 6% to 92% at approximately 5% intervals). The simulation was repeated 20 times for each of the combinations of territory diameter and study-area proportion. This range of territory diameters was chosen because it brackets those reported for Nuttall's White-crowned Sparrow. The smallest territories were reported in San Francisco and averaged 1,127 m^2 (Patterson and Petrinovich 1978, Petrinovich and Patterson 1982). The minimum diameter of hexagonal territories of this area would be

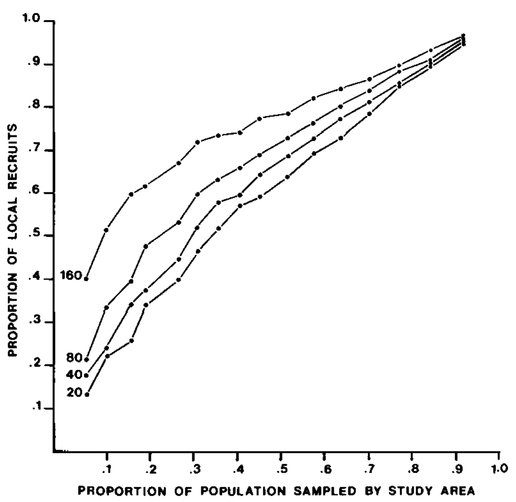

Fig. 1. Proportion of local recruits as a function of the proportion of the population sampled in the study area. Each curve represents the plotted means of 20 runs for each of 16 study-area proportions, for territory diameters of 20, 40, 80, and 160 m. The population size was 625 territories, and the dispersal parameters were: alpha = 0.6, beta = 366.8, and gamma = 0.89352.

approximately 36 m. The average territories at Point Reyes range in size from 2,360 m^2 (Ralph and Pearson 1971) to 4,452 m^2 (Chamberlain 1972). These figures produce minimum diameters of hexagonal territories in the range of 52–72 m.

A second simulation was performed to compare the proportion of local recruits predicted from my model with an empirical result (Petrinovich and Patterson 1982). The Presidio study area of Petrinovich and Patterson represented approximately 15% of the Presidio dialect area (as determined by measurements taken from Fig. 1 of Petrinovich and Patterson 1982) and contained about 31 territories. Assuming the population density of the entire dialect area was the same as in the study area, the population of the Presidio dialect included about 203 territorial pairs. For the purpose of simulation, the nearest square array of territories, representing the Presidio dialect population, is a 14 × 14 array of 196 territories. Because Petrinovich and Patterson did not provide a dispersal distribution for their study population, I assumed dispersal followed that reported by Baker and Mewaldt (1978). I used 40 m as the territory diameter because it approximated the diameter of a Presidio territory (for a hexagonal territory of 1,127 m^2, min. diam. = 36.1, max. diam. = 41.7). The simulation was repeated 20 times for each of 11 study-area proportions (from about 5% to 86% at approximately 5–10% intervals). Finally, by comparison with the results from the previous simulation, which used the same dispersal distribution and territory diameter, I was also able to determine the effect of population size on the proportion of local recruits observed within a study area.

TABLE 1. Power-curve regression coefficients for dispersal simulations.[a]

Population size (territories)	Territory diameter	Median territories dispersed	*a*	*b*
625	20	18.75	1.0156	0.6942
625	40	9.38	1.0175	0.6090
625	80	4.69	1.0220	0.5082
625	160	2.34	0.9797	0.2932
196[b]	40	9.38	1.1349	0.8432

[a] Power function: $y = ax^b$; median dispersal distance = 375 m; dispersal parameters: alpha = 0.60, beta = 366.8, gamma = 0.89352.

[b] Simulation comparable to the field study by Petrinovich and Patterson (1982).

RESULTS AND DISCUSSION

Two clear relationships emerged from the first simulation. First, the proportion of local recruits is an increasing function of the proportion of the breeding population that the study area encompasses (Fig. 1). The shape of these curves suggests a simple power function of the form: $y = ax^b$, where a and b are constants. Theoretically, for this particular problem, y (the proportion of local recruits) should equal 1.0 when x (the proportion of the population sampled in the study area) is 1.0. The simulation confirms this (Fig. 1). Thus, the constant a should equal 1.0, and the power function reduces to $y = x^b$. Within the range of parameters used in this simulation, the exponent b should assume some value between 0.0 and 1.0. For each of the four territory diameters used in this simulation, I fitted power curves to the mean values of the 20 runs for each study-area proportion, and the theoretical point of x = 1.0, y = 1.0. The theoretical point of x = 0.0, y = 0.0 could not be included because of logarithms in the curve-fitting program. In all four cases the coefficient a was within 3% of the expected value of 1.0 (Table 1).

The second relationship suggested by this simulation is that for a given distribution of dispersal distances and a given proportion of

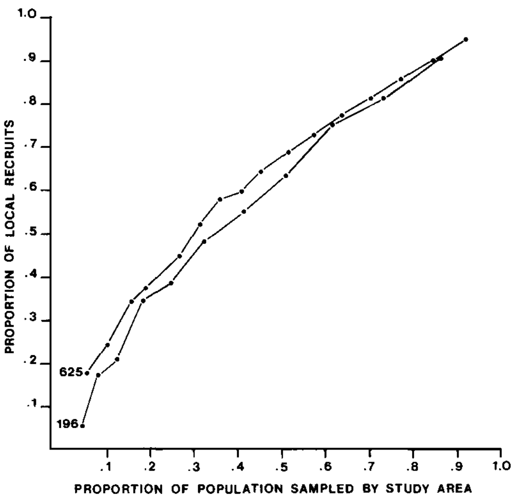

Fig. 2. Proportion of local recruits as a function of the proportion of the population sampled in the study area. The curves represent the plotted means of 20 runs for each of 16 (upper curve) and 11 (lower curve) study-area proportions, for populations of 625 (upper curve) and 196 (lower curve) territories. The territory diameter was 40 m, and the dispersal parameters were: alpha = 0.6, beta = 366.8, and gamma = 0.89352. The upper curve is from the first simulation and is also shown in Fig. 1.

the population sampled in the study area, the proportion of local recruits increases with increasing territory diameter (Fig. 1). That is, for a given distribution of absolute dispersal distances, as the territory diameter increases, the number of territories dispersed decreases (Table 1). The second simulation, with dispersal distribution and territory diameter held constant, indicated that, for a given proportion of the population sampled, the proportion of local recruits increased as the size of the population increased (Fig. 2). Both of these results are purely artifacts of the simulations, and for the same reason. As the area occupied by a population increases, either because territory size or population size increases, the study area must likewise increase to sample the same proportion of the population. If the dispersal distribution remains constant and the study-area size is increased, then fewer of the individuals produced within the study area disperse beyond its boundaries. It is important to keep these relationships in mind when considering these simulations, as they influence the absolute values of the dependent variable (proportion of local recruits), but they should not change the general trends in the relationships described here.

The result of decreasing dispersal (higher local recruitment) with increasing territory size (Fig. 1), in addition to being an artifact of the simulation, probably does not apply to natural populations. Dispersal is a discrete rather than a continuous process because territorial species disperse from territory to territory and not simply absolute distances (Shields 1982). In natural populations, we would expect that as territory size increases so will absolute dispersal distances, because individuals are forced to move longer distances while crossing the same number of territories. With regard to population size, Nuttall's White-crowned Sparrow presents some special problems because this subspecies is subdivided by song dialects. In this study I assumed that song dialects represent distinct populations; however, this has been a point of some debate (for review see Baker and Cunningham 1985). If song dialects are not (relatively) distinct populations, the actual population size would be much larger. This would change the position of the recruitment curve, as demonstrated by the second simulation (Fig. 2). In natural populations the dispersal distribution itself is an important determinant of the "effective" population size (Wright 1943, 1951; Baker 1981); for dialect species, such as the White-crowned Sparrow, the effective population size will depend upon both the dispersal distribution and the effect of dialect boundaries (Baker and Mewaldt 1978, Baker 1981).

The more important objective of the second simulation was to compare the proportion of local recruits predicted from the model with that observed previously (Petrinovich and Patterson 1982). Petrinovich and Patterson reported that only 16% of all recruits were produced within their study areas. Elsewhere (Petrinovich et al. 1981) they concluded, from this low proportion of local recruits, that there must be significant cross-dialect dispersal. They counted adults that moved into their study areas as recruits, as well as first-year birds. In my simulations, I considered only juveniles as recruits. For comparison I used only the first-year birds (nestlings, fledglings, and first-year brown crowns) from Petrinovich and Patterson's (1982) data. Of the 182 first-year birds that settled in their study areas, 51 had been banded there as nestlings, giving a local recruitment of 28%. These recruitment figures are combined data from two study sites, the Presidio and Twin Peaks, but the authors stated that the data were treated separately only in those instances in which the results were different for the two study areas. I assumed that the data from the Presidio and Twin Peaks were similar. It is difficult to determine what proportion of the San Francisco dialect population the Twin Peaks study area represented, because the San Francisco dialect population is highly fragmented in an urban area, and the full extent of the dialect is not shown on the map provided (Petrinovich and Patterson 1982). However, the Presidio dialect area is indicated (see also Petrinovich et al. 1981), and the Presidio study area represented about 15% of the dialect area.

The results of the second simulation are plotted in Fig. 2 (lower curve), and the power-curve regression coefficients are given in Table 1. This regression was not as close to the theoretical asymptote, where the coefficient $a = 1.0$, as the regressions in the previous simulation (Table 1). Using the simplified power function, $y = x^b$, the predicted proportion of local recruits was 20% for a study area containing 15% of the population, but this curve did not fit the data well and yielded predicted values almost 12% below that of the fitted power curve. The power function using the calculated coefficient (a) of 0.1349 provided a better fit than the simplified function, but the fit still was not good because it predicted values less than the observed means for x in the range of 8–41% and greater than the observed means for x in the range of 51–100%. Using this fitted power curve, the predicted value for a study area containing 15% of the population was 23%. The observed means (from 20 computer runs) for study areas containing 13% and 18% of the population were 21% and 35%, respectively. Linear interpolation between these values for a study area containing 15% of the population yields 27% local recruits.

All three of the predicted values for the proportion of local recruits, from a study area containing about 15% of a population of 196 territories, were close to the 28% local recruits observed by Petrinovich and Patterson (1982), the third being remarkably close. This close correspondence between observed values of local recruitment and those predicted by my model suggests that there may be nothing surprising about the findings of Petrinovich and Patterson, and inferences about interdialect exchange made from these data (Petrinovich et al. 1981) might be invalid. In fact, neither these simulations nor the results of Petrinovich and Patterson directly address the issue of interdialect dispersal. Some qualifications are in order because there are a number of complicating factors that render this simulation only an approximation of the population that Petrinovich and Patterson studied.

Because of the lack of detailed dispersal data from the Presidio population, I used the dispersal distribution parameters from the Point Reyes populations (Baker and Mewaldt 1978). This distribution is given in absolute distances rather than number of territories moved. The territories at the Presidio tend to be only 25–50% as large as those at Point Reyes. If birds disperse by territorial units rather than by absolute distance (Shields 1982), and if dispersal is similar at the Presidio and Point Reyes, then the dispersal distances should be proportionately shorter for the Presidio population. A distribution of shorter dispersal distances should increase the proportion of local recruits for a given-size study area.

The physical habitat at the Presidio is quite different from that at Point Reyes (Baker and Mewaldt 1981; pers. obs.). In the Presidio, suitable breeding habitat is patchy, crossed by major highways, and fully within an urban area, while Point Reyes provides larger tracts of continuous breeding habitat in a natural "wilderness" area. Thus, birds at the Presidio commonly may have to disperse across areas of unsuitable habitat before locating an available territory. A patchy distribution of breeding habitat would tend to increase the absolute dispersal distances, thus decreasing the proportion of local recruits, perhaps counteracting the effect of smaller territory size.

The results of my simulations support the argument that the proportion of local recruits observed within a study area depends on the proportion of the breeding population encompassed by that study area. This relationship can be described by a simple power function. While my simulation only roughly approximates the conditions at the Presidio, it suggests that the proportion of local recruits observed there might not be unexpectedly small; it does not necessarily indicate that "a sizable proportion of banded nestlings dispersed out of the Presidio" (Petrinovich et al. 1981). In fact, the proportion of local recruits observed within a study area is a function of the size of the study area in relation to the dispersal distribution itself, which is the important determinant of the "effective" population size. Reliable conclusions about dispersal and population structure cannot be made from proportions of local recruitment in finite study areas. To evaluate the structure of natural populations, detailed analyses of dispersal are needed that consider the territorial nature of the population, the effects of social interactions (e.g. dialect effects), and the distribution of suitable habitat.

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