

A PARAMETRIC METHOD FOR COMPARING DISPERSAL DISTANCES¹

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Since Greenwood's work relating dispersal patterns to mating systems (1980, 1983; Greenwood and Harvey 1982), many studies have sought to distinguish philopatric from dispersed individuals, and the dispersing sex from the non-dispersing sex. Although Greenwood's scheme has received some criticism, (e.g., Ostfeld [1987] criticized use of mating-system categories), dispersal concepts have been unchallenged. My first objective is to argue that discrete categories separating philopatry from dispersal, and the dispersing sex from the non-dispersing sex are arbitrary, and they generally confuse, rather than clarify, the complex ecological patterns present in nature. Gender, population, and species comparisons should be made strictly in terms of dispersal distributions and distances from the natal site. I make this point by presenting information on juvenile premigratory movement patterns. My second objective is to present a simple parametric test for comparing dispersal distributions.

PHILOPATRY OR DISPERSAL?

How close to a natal site must a yearling breed to be considered philopatric, and how distant to be considered dispersed? If breeding on an individual's natal territory were the strict definition of philopatry, the distinction between philopatric and dispersed individuals would be clear. However, the boundary between philopatry and dispersal is an arbitrary distance from the birth site (e.g., Shields 1983) and, in practice, study-site boundaries are often arbitrary delimiters for dispersal boundaries. Selecting arbitrary boundaries, however, often ignores how individuals perceive their environment and what processes determine return to a study site and movement within a site.

The case for non-migratory species is relatively straightforward. Individuals breed at some distance from their natal sites, and individuals of both sexes might disperse to breed. In some cases the distance dispersed is zero, but this is part of a continuum of distances. In principle, there is no reason to divide dispersal distances arbitrarily and presume it has ecological meaning. One exception might be primates that live in troops, where only a single sex ever leaves the troop (examples in Pusey and Packer 1986). However, even in these cases, fission-fusion group dynamics re-

sults in some dispersal of both sexes (Melnick and Kidd 1983, Pusey and Packer 1986).

Migratory birds present a more complex situation. Juveniles leave their natal sites, migrate for the winter, and return to breed the following year. Instead of arbitrarily setting a "dispersed" distance criterion, one might consider philopatry as a juvenile might view it. In particular, one should consider the juvenile's experience. For example, if a juvenile is exposed only to a small area around its nest before migration, then it is reasonable to consider return to the natal site as philopatry. However, if a juvenile is exposed to a larger area, then subsequently returns within that exposure area, is it philopatric? If not, has the individual dispersed before migration?

Morton (1992) argues that White-crowned Sparrow (*Zonotrichia leucophrys*) fledglings typically complete dispersal before migration. There is a small but growing body of evidence that juveniles of migratory species visit a variety of potential breeding areas before migrating, and that this exposure can influence return in subsequent years (Berndt and Winkel 1979, van Balen 1979, Adams and Brewer 1981, Holland et al. 1982, Oring and Lank 1986, Morton et al. 1991, Reed and Oring 1992). This might be a common occurrence for migratory species. If wandering individuals are considered philopatric, the definition of philopatry is expanded to include return to any site to which an individual was exposed as a juvenile. Treating dispersal as a continuum avoids the problem of discriminating philopatric from non-philopatric dispersal in the presence of post-fledging experience.

COMPARING DISPERSAL DISTRIBUTIONS

Dispersal distances can be compared using nonparametric tests, such as Kruskal-Wallis or Mann-Whitney tests (e.g., Pärt 1990). These tests are generally useful for comparing median dispersal distances where the underlying distribution is unknown (Siegel and Castellan 1988). The Z-test can be used for comparing mean dispersal distances between two groups of individuals with dispersal distances from the same family of distributions (e.g., both are Poisson). This test can be used for comparing means from non-normal distributions because means are normally distributed (central limit theorem, Ott 1977). Note that the goal here is to compare relative dispersal distances, not to determine the "dispersing" and "non-dispersing" sexes.

The general form of this test is widely known, but typically applied only to normal distributions. Assuming the variances of the two samples are equal, the

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Z-test for normal distributions is

$$Z_n = \frac{\bar{X} - \bar{Y}}{\sqrt{\left(\frac{1}{m} + \frac{1}{n}\right) s^2}},$$

where \bar{X} is mean dispersal distance for m individuals in group one (e.g., males), \bar{Y} is mean dispersal distance for n individuals in the second group, and the denominator is the square root of the pooled variance (Ott 1977).

However, dispersal distributions typically are not normal, and arguments are made for individuals exhibiting different distributions, such as geometric (e.g., Waser 1985). Below I present Z-tests for two common dispersal distributions, geometric and Poisson. Dispersal distances are often reported as number of individuals moving a unit of distance (e.g., 0–100 m, 101–200 m, etc., or number of territories). Distances for these tests will be number of units moved.

The probability density function for the geometric distribution can be depicted as $p(1-p)^x$, where $x = 0, 1, 2, \dots$ units moved, and p is the probability of moving the mean dispersal distance (Appendix). For two samples from geometric distributions,

$$Z_g = \frac{\bar{X} - \bar{Y}}{\sqrt{\left(\frac{1}{m} + \frac{1}{n}\right) \left(\frac{1-p}{p^2}\right)}}.$$

\bar{X} is the mean number of units (i.e., blocks of distance, territories, etc.) moved by m individuals in group one, \bar{Y} is the mean number of units moved by n individuals in group two, and the denominator is the square root of the pooled variance (Appendix). The probability of observing a Z score at least as extreme as that calculated, then, can be found on the same Z table as used for normally distributed data (e.g., Ott 1977).

For two samples from Poisson distributions,

$$Z_p = \frac{\bar{X} - \bar{Y}}{\sqrt{\left(\frac{1}{m} + \frac{1}{n}\right) \left(\frac{\sum X_i + \sum Y_j}{m+n}\right)}}.$$

Again, the denominator is the square root of the pooled variance (Appendix).

The Z-test can be used for comparing means of any known distribution, but means should be taken from distributions of approximately 30 or more individuals (Ott 1977). To determine whether or not observed distributions fit an expected distribution, they can be compared using a G-test (Sokal and Rohlf 1981) or a χ^2 test, or simulated (Caley 1991). However, when the number of distance units individuals moved is small, test power will be low (Cohen 1988, Caley 1991). When the null hypothesis is not rejected, i.e., test results do not give strong reason to reject the null distribution, test power should be calculated (Cohen 1988). If power is unacceptably low (i.e., β is high), it is incorrect to assume the null (expected) distribution is correct. In this case, either compare data to another known distribution, or use a nonparametric test.

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APPENDIX

GEOMETRIC DISTRIBUTION

Given that animals move a certain number of blocks (N) before settling to breed (here blocks can equal the width of a territory, an arbitrary distance such as 100 m, etc.), the mean distance moved is $E(N) = 1/p$, where p is the probability of settling (Larsen and Marx 1986). Variance in the number of blocks moved is $\text{Var}(N) = (1 - p)/p^2$. When comparing the mean dispersal distances between two groups with individual dispersal distances X_1, X_2, \dots, X_m and Y_1, Y_2, \dots, Y_n distrib-

uted geometrically, the null hypothesis is $H_0: p_1 = p_2$. The Z -test is $Z_g = \bar{X} - \bar{Y} / \sqrt{\text{Var}(\bar{X} - \bar{Y})}$. The pooled variance is

$$\text{Var}(\bar{X} - \bar{Y}) = \frac{1}{m} \frac{1 - p_1}{p_1^2} + \frac{1}{n} \frac{1 - p_2}{p_2^2},$$

and under H_0 , $p_1 = p_2$, so A1 becomes

$$\text{Var}(\bar{X} - \bar{Y}) = \left(\frac{1}{m} + \frac{1}{n} \right) \left(\frac{1 - \hat{p}}{\hat{p}^2} \right).$$

The square root of this value is the denominator in the calculation of Z_g in text, with \hat{p} an estimator of p . The maximum-likelihood of $\hat{p}_i = 1/(1 + \bar{X}_i) = m/(m + \Sigma X_i)$ (cf. Larsen and Marx 1986, when x can equal 0; see text); for the pooled sample, $\hat{p}_1 + \hat{p}_2$ can be calculated as

$$\hat{p} = \frac{m + n}{m + n + \Sigma X_i + \Sigma Y_j}.$$

Note that ΣX_i = the total number of units traveled by the individuals in group one.

POISSON DISTRIBUTION

When comparing the mean dispersal distances between two groups with individual dispersal distances X_1, X_2, \dots, X_m and Y_1, Y_2, \dots, Y_n Poisson distributed, the null hypothesis is $H_0: \lambda_1 = \lambda_2$. Pooled variance, $\text{Var}(\bar{X} - \bar{Y})$, is $(1/m)\lambda_1 + (1/n)\lambda_2$; under H_0 , the pooled variance is $(1/m + 1/n)\lambda$. For the Poisson distribution, the maximum-likelihood estimator of λ is \bar{X} (Larsen and Marx 1986). Given $\bar{X} = \Sigma X_i$, substituting into the pooled variance equation, and taking the square root, gives the denominator for the calculation of Z_p in text.

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SOCIAL TUTORING OF ADULT MALE WHITE-CROWNED SPARROWS¹

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Key words: White-crowned Sparrow; *Zonotrichia leucophrys*; social tutoring; song learning; song dialects.

Song learning in White-crowned Sparrows (*Zonotrichia leucophrys*) has been studied extensively (for reviews see Kroodsma 1981, Baker and Cunningham 1985). The focus of attention usually has been restrict-

ed to juveniles during the first few months of life. These studies have included tape-tutoring and social tutoring of males and females in the laboratory and observations of singing behavior during territorial interactions between yearlings and adults (Cunningham and Baker 1983, Petrinovich and Baptista 1984, Baptista and Petrinovich 1984, Baptista and Morton 1988, DeWolfe et al. 1989).

In contrast to studies on young birds, song modification in older adults—those in their second breeding season or later—has received little attention. Observations of adult songs have been mostly anecdotal or ancillary to studies on juvenile song development and apparently no systematic treatment of the subject is

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