# Comparing Actual and Random Distributions of Nearest Neighbors

Ronald P. Larkin

*Illinois Natural History Survey, 607 East Peabody Drive, Champaign, Illinois 61820, USA*

Pearson (1991) watched Field Sparrows (*Spizella pusilla*) and White-throated Sparrows (*Zonotrichia albicollis*) feeding on artificial patches of three sizes. He compared the observed distributions of distances between nearest neighbors in small groups with computer-generated expected distributions. Two principal results were given (presented here in reverse order from Pearson's paper). First, both species occurred disproportionately often on portions of the patches near a nearby brush pile. Pearson concluded the birds were attracted to cover. Second, observed distributions of distances between birds differed from Monte Carlo (computer-generated) distributions and differed between the two species for most combinations of group size and patch size. The Monte Carlo method was complete spatial randomness (CSR; Diggle 1983:4), presumably accomplished by generating a pseudorandom *X*-value and *Y*-value for each point. The points were constrained only to be at least 1 cm apart; 1,000 nearest-neighbor distances were generated for each group size in this manner.

Pearson's (1991) conclusions were derived from differences between the spacing of real and Monte Carlo-generated birds, although he stated that spacing behavior "could not be separated from these birds' affinity for cover." The conclusions are valid only to the extent that CSR represents a realistic expectation of the birds' behavior in the absence of social interactions. However, because the birds were attracted to the brush pile, we know that they did not conform to CSR. In the absence of social interactions, one would expect nearest-neighbor distances on average to be less than those predicted by the purely random model, because the birds were bunched at one end.

Fortunately, Pearson's (1991) detailed data allow construction of a more suitable alternative model. Values for *X* are computed pseudorandomly, as in Pearson's study. Values for *Y* are computed by using a weighted pseudorandom number generator (Robertson 1977), based on the known distributions in Pearson's figures 4 and 5. The weighted values cast birds on the plane with a preference for proximity to a "brush pile" at *Y* of zero; for instance, they place 72% of the computer-generated "Field Sparrows" within the closest 5 cm of a small patch when group size is two.

The alternative model (Fig. 1) differs greatly from Pearson's (1991) figure 1. Although the mean may not be a meaningful measure of central tendency in these distributions, the recalculated means are 0.61 to 0.64 those of Pearson's model. They differ by 3 to 14 cm. Although Pearson's interesting conclusions about differences between spacing behaviors of the two species of sparrows may be unaffected, his conclusions about the degree of randomness in their spacing (Pearson 1991:fig. 3) are not supported by his data when a more realistic distribution of birds is used for comparison.

The alternative model for random spacing with a preference for cover (Fig. 1) assumes that the sparrows have no overall preference for certain regions in the *X* direction, that the six "zones" described in Pearson (1991) are an accurate description of the birds' use of space, and that positions in *X* and *Y* are uncorrelated. Pearson did not test these assumptions, nor can they be tested from the published data.

Comparison of the alternative weighted model with observed distributions, though more valid, is probably less powerful than comparison of Pearson's (1991) purely random model. This is because the birds' distribution in the *Y* direction is determined both by a known preference for *Y* of zero and by a suspected minimum or preferred distance between birds. Thus, using the observed *Y* distribution taints the model with an unknown component of social spacing itself.

Monte Carlo methods allow testing for spatial patterning when conventional methods fail (Diggle 1983, Krebs 1989, Manly 1991). The technique of using weighted number generators (Larkin 1982) extends Monte Carlo methods to some situations in which distributions in one or more dimensions are not purely random.
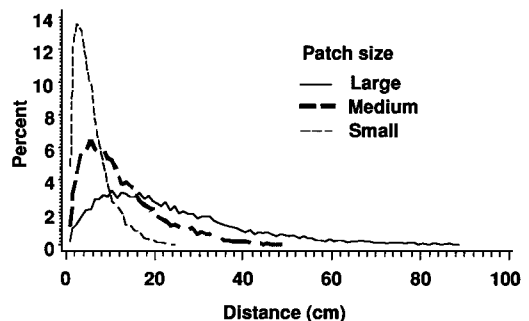


Fig. 1. Distributions of nearest-neighbor distances for group size of four computed by a random-number generator weighted on one axis (see text). Plot is comparable to Pearson's (1991) figure 1. Distances plotted at 1-cm intervals, 10,000 distances computed for each patch size, ordinate is percent (not frequency), and distributions are truncated below 0.03%.

Another alternative approach may hold promise, provided that positions are not correlated among dimensions. Holding one dimension fixed, one shuffles values for the other dimension(s), so that each dimension retains its distribution after the shuffle but the spatial organization, if any, is lost. The relative advantages or disadvantages of this method over the weighted method are not immediately obvious.

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LITERATURE CITED

DIGGLE, P. J. 1983. Statistical analysis of spatial point patterns. Academic Press, New York.

KREBS, C. J. 1989. Ecological methodology. Harper and Row, New York.

LARKIN, R. P. 1982. Spatial distribution of migrating birds and small-scale atmospheric motion. Pages 28–37 *in* Avian navigation (F. Papi and H. G. Walraff, Eds.). Springer, Berlin.

MANLY, B. F. J. 1991. Randomization and Monte Carlo methods in biology. Chapman and Hall, New York.

PEARSON, S. M. 1991. Food patches and the spacing of individual foragers. Auk 108:355–362.

ROBERTSON, S. A. 1977. A BASIC program to randomly generate members of a weighted set. Behav. Methods Res. Instrum. 9:547–548.

# Reply to Larkin

SCOTT M. PEARSON[1]

*Department of Zoology and Institute of Ecology, University of Georgia, Athens, Georgia 30602, USA*

My goal (Pearson 1991) was to examine the spacing of individuals of two sparrow species foraging on food patches of defined areas. I compared the observed spacing within monospecific Field Sparrow (*Spizella pusilla*) and White-throated Sparrow (*Zonotrichia albicollis*) groups to the spacing within groups generated by computer simulation where the individual group members are randomly positioned on the food patch. Larkin (1992) has criticized my use of a completely random model because Field and White-throated sparrows both demonstrated an attraction to a nearby brush pile. He contended that this attraction should be considered in modeling random spacing. For this reason, he suggested that a weighted random model would have been a more appropriate choice for the simulation.

I (Pearson 1991) discussed two forces that may affect spacing in social groups. While the attractive force of social distance keeps a group cohesive, the repulsive force of individual distance maintains minimum distance between group members. By changing the patch size, I attempted to find the distances over which one of these forces predominates. On small patches, spacing may be determined by individual distance that imposes a minimum nearest-neighbor distance. On large patches, social distance may limit nearest-neighbor distance to some maximum value (Fig. 1). However, under the experimental conditions employed, the maximum nearest-neighbor distances were constrained most strongly by the individuals' attraction to protective cover; social distance was confounded with cover dependency. Presumably, the groups did not collapse to the edge of the patch near the brush pile, because the repulsive force of individual distances maintained spacing between individual birds. In the paper, I stated that "Unfortunately, any effect of Emlen's [1952] attractive force within flocks could not be separated from the birds' affinity for cover." Larkin (1992), in his second paragraph, appears to have taken this quote out of context.

The completely random model may be naive, but it provided an easily understood reference point. By using this model as my null expectation, I was able to demonstrate the affinity of the sparrows for the brush pile. Simulating the spacing of birds on a plane requires a two-dimensional model. As Larkin pointed out, the most appropriate null model for testing for the effects of social behavior would be one that simulates the behavior of the birds in the absence of any social influence (attraction to cover is not considered a social influence). I agree that a weighted random model would be more realistic than the completely random model I used. However, as Larkin acknowledged, parameters for this model are difficult to estimate. Using observational data from group sizes greater than one would be inappropriate, because these data likely contain both cover and social influences.

[1] Present address: Environmental Sciences Division, Oak Ridge National Laboratory, P.O. Box 2008, Oak Ridge, Tennessee 37831, USA.