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.

I thank David Enstrom and David Swofford for comments on a previous draft of the manuscript.

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Reply to Larkin

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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.

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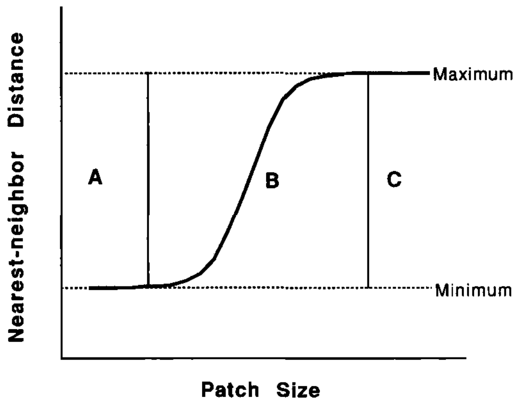

Fig. 1. Effect of food patch size on nearest-neighbor distance is constrained by individual distance and social distance. In region A, minimum nearest-neighbor distance limited by individual distance. In region C, maximum nearest-neighbor distance set by social distance. A balance between these two forces is likely in region B.

However, measuring distance to cover for single birds (group size = 1) on the foraging patch would allow some estimation of the distribution of birds along the axis perpendicular to the brush pile (Larkin's Y-axis) in the absence of social interaction. This measure of cover dependency could then be incorporated into a weighted random model.

Larkin (1992) simulated interbird distances using a weighted random model with data I presented (Pearson 1991). He found that means of these distributions were about 60% of the means from my completely random model. His model simulates cover dependency, which concentrates the birds near the brush pile. The completely random model I used placed birds anywhere on the food patch. Because the weighted random model is constrained in this one dimension, its interbird distances were on average shorter than those of the completely random model.

Larkin's (1992) figure 1 is not directly comparable with my figure 1 (Pearson 1991). I plotted the distributions of the mean nearest-neighbor distances calculated for each group (see Methods of Pearson 1991: 356). Larkin's plot includes the distribution of nearest-neighbor distances for all individuals, not the group means that I used in my calculations. This difference means that Larkin's distribution contains more extreme values (i.e. a longer tail) than mine.

The most important question is whether the completely random model is a grossly inappropriate null model that leads to erroneous conclusions about the influence of individual distance on sparrow spacing. In my opinion, using simulated distances from a weighted random model would find that more of the Field and White-throated sparrow groups had mean nearest-neighbor distances greater than those of simulated groups. This is because simulated groups from weighted random models have smaller nearest-neighbor distances than those from completely random models. In figure 2 of Pearson (1991), lines lying on the isopleth (where the observed percentiles are equal to the simulated percentiles) would be moved to the left, above the isopleth (where observed are greater than simulated), if percentiles from weighted random models had been used. By using the completely random model, I may have underestimated the number of groups that had spacing greater than random, thereby underestimating the role of individual distance relative to patch size.

How important is our estimate of random spacing? In some theoretical endeavors, using the most appropriate random model is critical. In the context of Pearson (1991), "random" is a point along a continuum of mean nearest-neighbor distances. Its exact position depends on the random model being used. I used random spacing as a point of reference with which to compare my observed data. In that paper, I concluded that the repulsion of individual distance is the primary social force influencing these sparrow groups. I also discussed how this force interacts with cover preference in both sparrow species. While Larkin (1992) raised an important point about choosing the most realistic null model, I do not feel that the completely random model compromises the general understanding of forces that influence the spacing of birds in foraging groups as presented in Pearson (1991).

B. D. Watts offered some helpful comments on a previous draft of this reply.

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