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# NULL MODELS AND DISPERSAL DISTRIBUTIONS: A COMMENT ON AN ARTICLE BY CALEY

In a recent article Caley (1991) outlined a null model for dispersal distributions against which he suggested empirical data should be compared. He first presented Waser's geometric model (Waser 1985), which can be derived as follows: Dispersing individuals move in a straight line from the natal site and settle in the first unoccupied site they encounter. If unoccupied sites occur independently at random with probability $t$ as a result of turnover within the habitat, then the distribution of dispersal distances will follow a geometric distribution in which the probability of settling at distance $i$ is given by

$$p(i) = t(1 - t)^i \quad \text{for } i = 0, 1, 2, 3, \ldots \tag{1}$$

Note that distance traveled in this model is measured in terms of the mean size of the home range and that the natal site is designated site 0. In this model individual dispersal behavior is deterministic, in the sense that individuals settle with probability 1 at the first unoccupied site they encounter. Thus, if we know the distribution of occupied and unoccupied sites and the direction in which an individual is dispersing, then we know exactly how far the individual will travel. Caley suggests that when this model is applied, a null model should also be fitted in order to determine which provides the best description of the data. The null model suggested by Caley is the exponential distribution for which the probability density function is

$$f(x) = \beta e^{-\beta x} \quad \text{for } x \geq 0\,. \tag{2}$$

This distribution is derived by assuming that the probability that an individual will settle in the next short interval, $\Delta x$, is approximately $\beta \Delta x$, which is independent of the distance traveled, $x$. It is also assumed that individual dispersal distances are statistically independent. Note that in this model it is the stochasticity in individual behavior in a homogeneous environment that generates the observed distribution of dispersal distances. In contrast, the geometric model assumes individual behavior is deterministic (see above) and that stochasticity in the environment (i.e., the presence of occupied and unoccupied sites) generates the dispersal distribution.

The main problem with Caley's approach is that the geometric distribution and the appropriate discrete form of the exponential distribution are, in fact, identical.

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To see this, note that in order to form a discrete distribution from the exponential distribution we integrate over each home range

$$\begin{aligned} p(i) &= \int_i^{i+1} \beta e^{-\beta x} dx \quad \text{for } i = 0, 1, 2, \ldots \\ &= e^{-\beta i}(1 - e^{-\beta}) . \end{aligned} \tag{3}$$

Now $p(0) = 1 - e^{-\beta}$, which is $t$ in the geometric model. Substituting for $t = 1 - e^{-\beta}$ in equation (1) gives equation (2), demonstrating the equivalence of the two distributions. This equivalence arises because in both models the probability of an individual's settling is independent of the distance traveled (i.e., the distance-specific rate of settling is a constant). Given this equivalence, it is difficult to see how Caley obtains the results presented in his figure 1, in which the two distributions appear very different. What it appears Caley has done is to equate the mean of the geometric distribution to the mean of the continuous exponential distribution in order to obtain the value of $\beta$ for the exponential model, giving $\beta = t/(1 - t)$. Using this procedure, I have been able to obtain Caley's figure 1*A* and *B*, but not *C*, which appears to be incorrectly drawn. What Caley should have done is to solve $t = 1 - e^{-\beta}$ for $\beta$, giving $\beta = -\ln(1 - t)$: when this expression is used, the probability distributions are identical.

In order to obtain parameter estimates, Caley equates the observed mean dispersal distance to the mean of the theoretical distribution being fitted. A far better approach would be to use maximum likelihood estimation methods (Cox and Oakes 1984); these allow explicit tests of exponentiality (Cox and Oakes 1984, p. 43) and departures from exponentiality to be characterized. In an earlier article, a colleague and I (Rees and Long 1993) give a biological example that allows for discreteness in the data and truncation.

Caley (1991, p. 524) states that "if both a null model and a deterministic model can predict the shape of the same empirical distribution of dispersal distances, the underlying processes of dispersal cannot be safely attributed to the process described by the deterministic model." This statement implicitly assumes that we may infer individual behavior patterns from population-level data. The fact that the geometric model and Caley's null model generate identical patterns at the population level should caution us against interpreting population-level patterns in terms of the behavior of individuals without information on individual behavior.

In the models presented above, all dispersing individuals are assumed to be identical. When this is true we may infer how the probability of an individual's settling varies with distance traveled (though not the underlying behavioral mechanism; see above). In a heterogeneous population this is no longer true (Vaupel et al. 1979; Rees and Long 1993). Consider a population composed of two types of individual. Type 1 individuals occur with probability $p$, and each type disperses according to an exponential distribution but with different $\beta$'s: then any individual will have a constant probability of settling independent of the distance traveled. However, if we looked at the population as a whole, ignoring between-individual differences, then the probability of settling would no longer be independent of

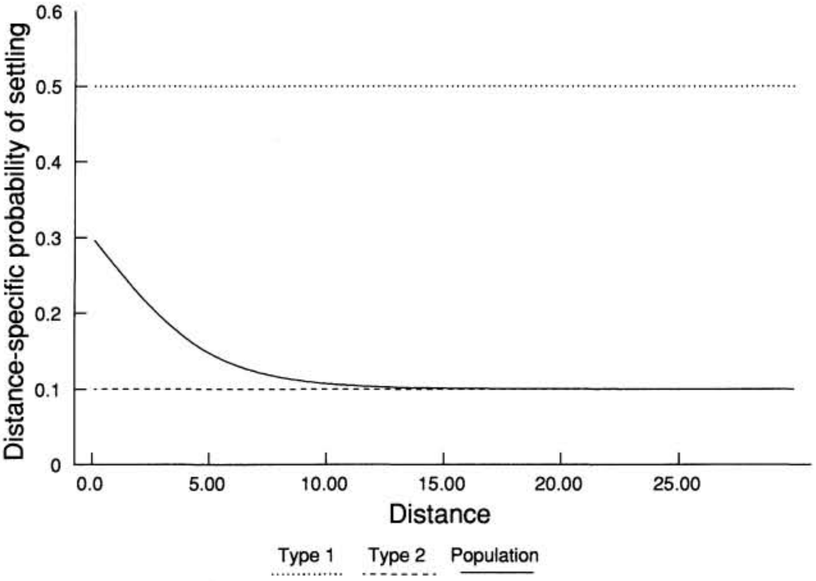

FIG. 1.—Distance-specific rate of settling as a function of the distance traveled for individuals of types 1 and 2, each of which disperse according to an exponential distribution, and for a population initially composed of equal proportions of each type. Parameter values: $\beta_1 = 0.5$, $\beta_2 = 0.1$, $p = .5$.

the distance traveled. The population-level distance-specific rate of settling, $h(x)$, is

$$h(x) = \frac{p\beta_1 e^{-\beta_1 x} + (1 - p)\beta_2 e^{-\beta_2 x}}{pe^{-\beta_1 x} + (1 - p)e^{-\beta_2 x}}, \tag{4}$$

where $\beta_1$ and $\beta_2$ define the exponential dispersal distributions for individuals of types 1 and 2, respectively. Note that if $p = 1$ then $h(x) = \beta_1$, whereas if $p = 0$ then $h(x) = \beta_2$. So, if there is no between-individual variability then the probability of settling is independent of the distance traveled. The initial rate of settling is $h(0) = p\beta_1 + (1 + p)\beta_2$, whereas as $x \to \infty$, $h(x) \to \beta_1$ if $\beta_1 < \beta_2$, or $h(x) \to \beta_2$ if $\beta_1 > \beta_2$. Thus, initially the distance-specific settling rate is simply the average of the two types present in the population. However, at greater dispersal distances the population becomes dominated by those individuals with the lower $\beta$. This means that the population-level distance-specific settling rate declines with increasing distance even though at the individual level it is constant (see fig. 1). Thus, we cannot infer how the probability of an individual's settling varies with distance traveled, let alone the underlying behavioral mechanisms. To quote Pielou (1977, p. 123): "It must be concluded that the fitting of theoretical frequency distributions to observational data can never by itself suffice to 'explain' the pattern of a natural population."

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