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MODELING VERTEBRATE DISPERSAL DISTANCES: ALTERNATIVES TO THE GEOMETRIC DISTRIBUTION¹

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Abstract. The geometric probability distribution is a common way by which to model frequency distributions of vertebrate dispersal distances. This model has two weaknesses: (1) it requires that the probability of stopping, p , is constant across the range of habitat units, and (2) it provides no mechanism for modeling the maximum dispersal distance. The weaknesses of this model are discussed and a family of alternative models, which allows the stopping probability to change and which takes into account the maximum dispersal distance (dispersal scale) is presented. The new models in their simplest form reduce to the geometric probability distribution model. The new models are applied to five sets of published field dispersal data to determine the general properties of their fit as compared to the geometric and to assess their potential as better models of dispersal patterns.

Key words: dispersal; geometric distribution; mathematical modeling; modeling vertebrate dispersal; vertebrate natal dispersal.

INTRODUCTION

The pattern of natal dispersal in vertebrate animals is an important factor affecting the genetic and demographic processes within and between populations. Theories regarding the ultimate advantages and proximal mechanisms of natal dispersal are plentiful (e.g., Gaines and McClenaghan 1980, Shields 1982, Waser and Jones 1983, Waser 1985). However, the evaluation of these theories has been slow, in part because empirical and statistical models of field dispersal data often do not provide enough flexibility to account for the complexity of the underlying dispersal process (Buechner 1987). This limitation has led recent authors (e.g., Waser 1985, Buechner 1987) to modify and reinterpret one of the simplest and most commonly used theoretical distributions of dispersal distance, the geometric distribution, in order to make its fit to field distribution data more meaningful biologically. However, the recent modifications to the geometric model do not relieve it of two important limitations: (1) the requirement that stopping probabilities be homogeneous throughout the dispersal (as we discuss later, “stopping” may be interpreted as settling and/or dying depending on the research question), and (2) its inability to model the maximum dispersal distance (dispersal scale). Here we present a family of models that

retains the simplicity of the geometric but that overcomes these limitations. The new models are offered as alternatives among suitable statistically acceptable models (which include the geometric). To demonstrate their utility, we apply them to several sets of published dispersal data. We discuss the heuristic advantage of these models in light of this treatment.

THE GEOMETRIC MODEL AND ITS ASSUMPTIONS

The geometric distribution assumes a constant probability of “success” (i.e., stopping), denoted by p , in each of a series of trials. In dispersal studies p generally represents the probability that an animal will stop at some habitat unit (home range or territory). Let $f(x)$ be that fraction of the population that stops at habitat unit x , where x is an integer with $x = 0$ for the home habitat. $f(x)$ is given by

$$f(x) = p(1 - p)^x, \quad (1)$$

which is the density function of the geometric distribution. The expected value and variance of x are $(1 - p)/p$ and $(1 - p)/p^2$, respectively. (The mean of $1/p$ given by Buechner [1987] is incorrect for the case of the home habitat corresponding to $x = 0$.)

It is generally argued that the assumption of a constant stopping probability (p) is valid when mortality rates associated with different habitat units are relatively constant (Stamps et al. 1987) or when habitat quality is homogeneous (Buechner 1987). However, that assumption, which seems antithetical to much of

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the field data on vertebrate dispersal, has been questioned by Buechner (1987), who examined its relationship to a large number of field studies. Dispersing animals may suffer higher rates of mortality with increasing distance from the natal site (Shields 1982, Buechner 1987). This may be attributed to a number of factors, including physiological stress related to decreasing familiarity with the landscape. The geometric model offers no way in which to model such changes. Also, natal dispersal patterns for many species of small mammals show a preference for settlement near the natal site, and high degrees of home range overlap between mothers and offspring (e.g., Rongstad 1965, McCarley 1966, Michener and Michener 1977). This suggests that there may be some change in habitat quality with increasing distance from the natal site. Greenwood et al. (1979) suggested that this was the case for Great Tits (*Parus major*). If habitat quality changes with distance from the point of origin of dispersal, then it is important to understand how stopping probabilities relate to that change. Although the geometric distribution with its constant p may accommodate some of these features, in some cases it may be too restrictive and possibly preclude the consideration of such relationships.

The assumption of constant p also prevents the modeling of the influences of social interactions and simple physiological constraints. Several of the various hypotheses put forth to explain small-mammal dispersal (see review by Gaines and McClenaghan 1980) suggest that differences in social interactions between the natal site and outlying areas influence the dispersal process. Field studies of dispersal in small mammals reinforce this notion by showing that the distance of juvenile dispersal is affected by a complex interaction of factors including the presence of adults, the age of the disperser, and the time of year (e.g., Michener and Michener 1977). The geometric assumption of constant p implies that these important social factors are constant across all dispersal zones including the natal site. This assumption seems overly restrictive given the complexity of natal philopatry among vertebrates (Waser and Jones 1983), and the likelihood that social interactions will be much different at the natal site than at sites several habitat units away from the natal site.

A second weakness of the geometric model is its inability to incorporate the concept of maximum dispersal distance, which we call the dispersal scale. The importance of emigration as a factor that affects variation between populations is widely recognized (e.g., Futuyma 1979, Lidicker and Caldwell 1982), but rarely studied, because many researchers tend to view their study populations as isolated entities and because estimating dispersal scale in the field is often difficult. For example, Greenwood et al. (1979) noted the importance of immigrants as breeders in their Great Tit population but made no comment about the possible importance of the emigrants from their population as

breeders in adjacent populations. Models that include parameters that estimate maximum dispersal distance will be helpful in this regard, particularly when they are analyzed in conjunction with careful measurements of the physical limitations of a local population.

ALTERNATIVE MODELS

We envision animals dispersing over a series of habitat units (e.g., home ranges, territories) labeled by $x = 0, 1, 2, \dots, D$, where $x = 0$ denotes the natal or starting site and D is the maximum number of units over which the animals disperse (maximum dispersal distance). The probability that an animal stops at habitat unit $x = 0, 1, 2, \dots, D$ is some function $p(x)$ of x . The probability $p(0)$ that an animal does not leave the natal site is denoted by p_o . By definition, $p(D) = 1$. The three models that we will consider thus constrain the dispersal between $x = 0$ and $x = D$. The density function $f(x)$ of x is the product of the probability of stopping at x and the probability of continuing through previous habitat units:

$$f(x) = p(x)[1 - p(0)][1 - p(1)] \dots [1 - p(x - 1)]. \quad (2)$$

or

$$f(x) = p(x) \prod_{i=1}^x [1 - p(x - i)]. \quad (3)$$

$f(x)$ is the fraction of the dispersing population that has reached habitat x and stopped there; so $\sum_{x=0}^D f(x) =$

1. For the simplest case, where $p(x) = p_o = \text{constant}$, this model reduces to the geometric model:

$$f(x) = p_o(1 - p_o)^x. \quad (4)$$

The density function $f(x)$ of dispersal distances is thus determined by the form of the probability function $p(x)$.

The probability function $p(x)$ that best reproduces the observed field data $f_{\text{obs}}(x)$ will reflect both the environmental and social factors that affect dispersal, and the type of data collected (e.g., mortality, settling, etc.). It should be compared with theoretical interpretations of probability functions, such as those of Waser (1985) and Buechner (1987). For example, Waser (1985) interpreted p (his t) as the probability that an individual territory is available to the disperser. Buechner (1987) interpreted p as the probability of stopping at habitat unit x . Buechner let p include the probability of settling (s) and the probability of dying (m) at x .

The simplest method of connecting $p(0) = p_o$ and $p(D) = 1$ is to allow $p(x)$ to increase linearly with x :

$$p_1(x) = p_o + (1 - p_o)(x/D) \quad (5)$$

(Fig. 1). Because $dp_1(x)/dx$ is non-zero, this model may be applicable to situations in which environmental or social factors that affect stopping probability begin to

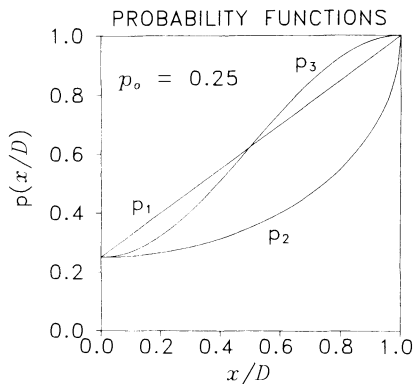


FIG. 1. Three relationships of the probability of stopping, p , and distance moved: $p_1(x) = p_o + (1 - p_o)(x/D)$; $p_2(x) = 1 - (1 - p_o)[1 - (x/D)^2]^n$, elliptical; $p_3(x) = 1 - (1 - p_o)\{1 + \cos[\pi(x/D)]\}^2$, sine function.

vary immediately upon leaving the natal site. The density function $f_1(x)$ derived from $p_1(x)$ is given for a range of values of p_o and D (Fig. 2). Note that although only the ratio x/D appears in Eq. 5 for $p_1(x)$ (and in Eqs. 6 and 7, below), the shapes of the density functions depend on both p_o and D because x is a discrete variable.

The assumption that $p_1(x)$ varies linearly with x may not be adequate (e.g., factors that affect stopping probability may change slowly near the home site). It might be expected that in some cases $p(x)$ would not vary significantly near the natal site. We will incorporate this into the remaining models in the form of an assumption that $dp(x)/dx = 0$ at $x = 0$. For simplicity the models were chosen by taking two extreme values of $dp(x)/dx$ at $x = D$: $dp(x)/dx = \infty$ and $dp(x)/dx = 0$.

For an infinite value of $dp(x)/dx$ at $x = D$, we consider the elliptic form

$$p_2(x) = 1 - (1 - p_o)[1 - (x/D)^2]^n. \quad (6)$$

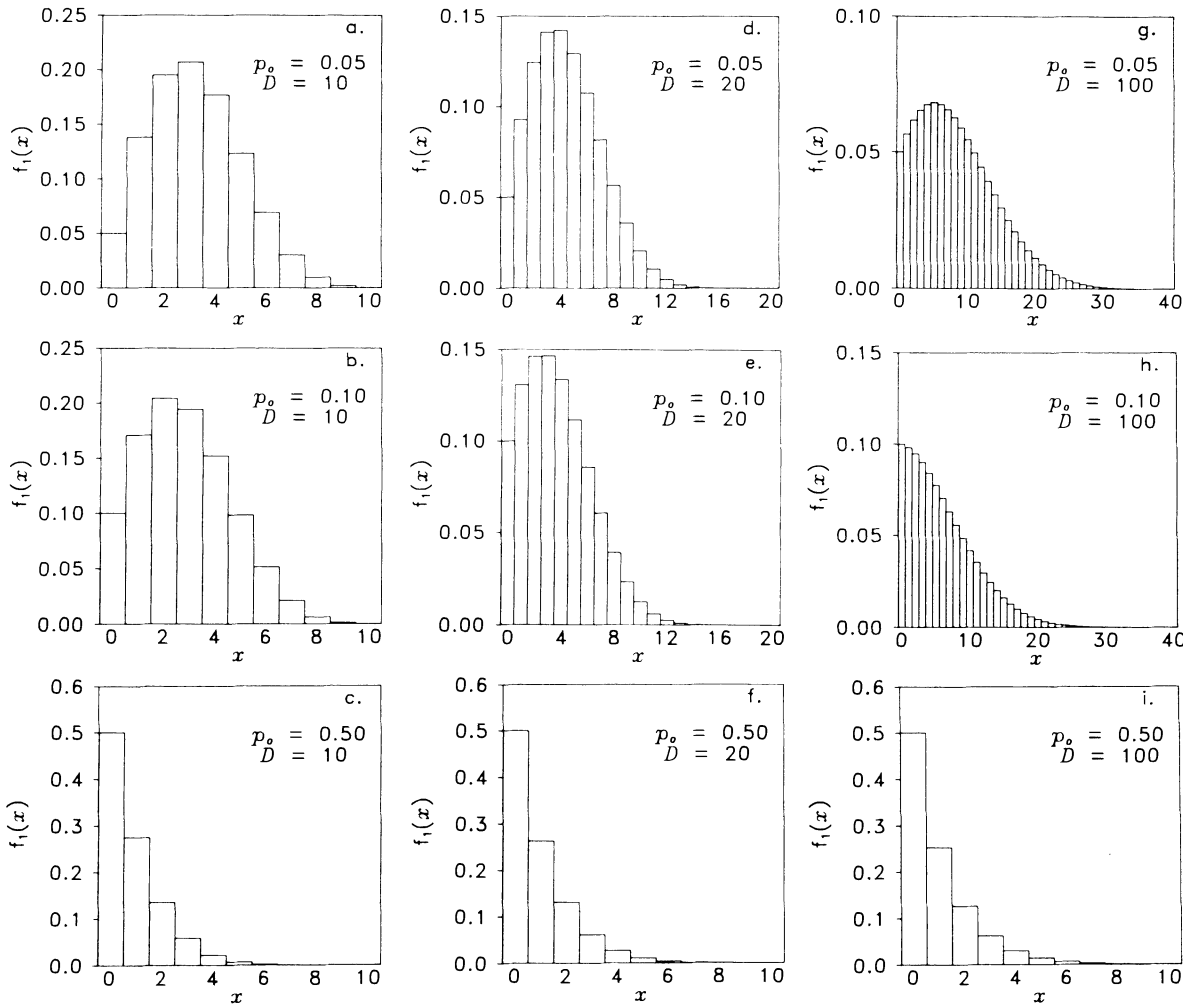


FIG. 2. Density functions for dispersal distance, using $p_1(x)$ (see Eq. 5) for a range of p_o and D .

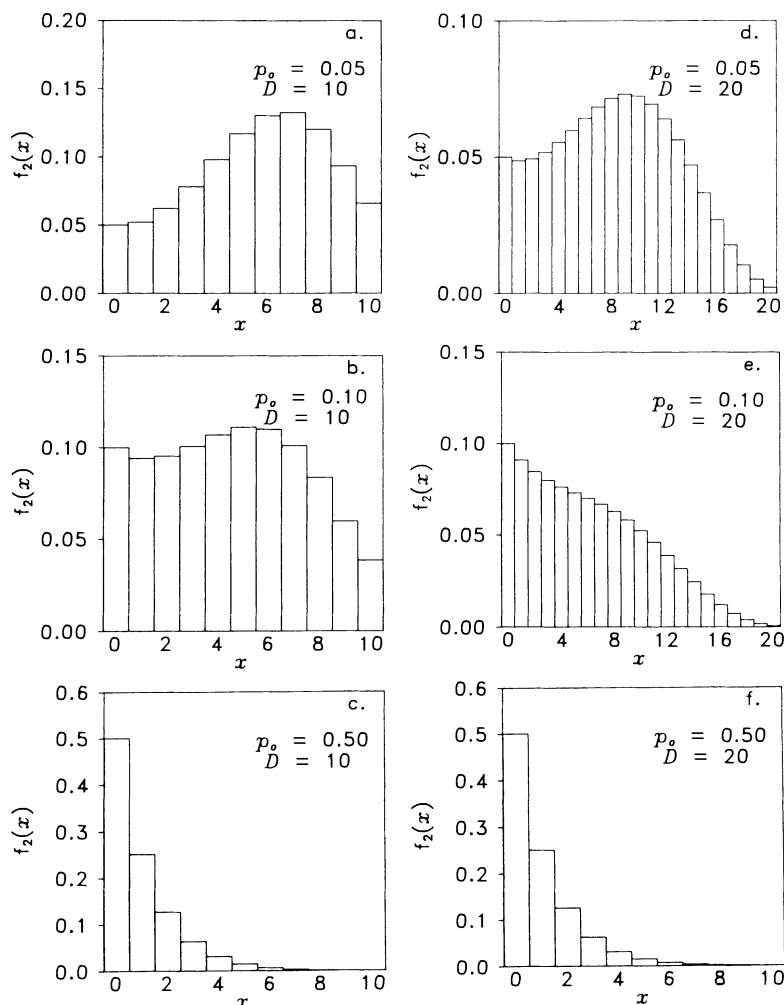


FIG. 3. Density functions for dispersal distance, using $p_2(x)$ (see Eq. 6) for a range of p_o and D .

Fig. 1 shows that $p_2(x)$ varies slowly until, near $x = D$, $p_2(x)$ increases sharply. This may be thought of as a “hard wall” that limits the dispersal abruptly, and might be exemplified by an island where environmental and social factors affecting dispersal vary slowly within the island but change rapidly at the island’s edge.

For the extreme where $dp(x)/dx = 0$ at $x = D$, we use the functional form of a sinusoid,

$$p_3(x) = 1 - (1 - p_o)\{1 + \cos[\pi(x/D)]\}/2 \quad (7)$$

In contrast to the elliptical $p_2(x)$, the probability function $p_3(x)$ begins to increase immediately after the natal site $x = 0$ (Fig. 1). However, the rate of increase of $p_3(x)$ is more gentle than that of $p_2(x)$, occurring over a wider range of x . In the latter half of the dispersal the slope dp/dx actually decreases. This lessening of the rate of increase of $p_3(x)$ may be thought of as a “soft wall” that limits dispersal. This model is included primarily for mathematical completeness, although it

may find application in cases where several competing factors strongly influence the dispersal. For example, for animals moving between two suitable habitat patches across an unfavorable area, the curve might reflect settling probability over the two patches (the ends of the curve) and strong mortality probability in the intervening area (middle of the curve). Such a partitioned p has been suggested by Buechner (1987). Density functions $f_2(x)$ and $f_3(x)$ are presented for a range of values of p_o and D in Figs. 3 and 4, respectively. Hereafter we refer to the models derived from $p_1(x)$, $p_2(x)$, and $p_3(x)$ as p_1 , p_2 , and p_3 , respectively.

As with the geometric distribution, the selection of p_o influences the shapes of the density functions $f(x)$ of our models (Figs. 2–4). In addition, the parameter D influences the new models. Small p_o ($p_o = .05$ and $.10$) tends to reduce the skewness, whereas large p_o ($p_o = .50$) increases it. The importance of the form of the probability functions $p(x)$ in determining the shapes of the density functions is also influenced by the value of p_o .

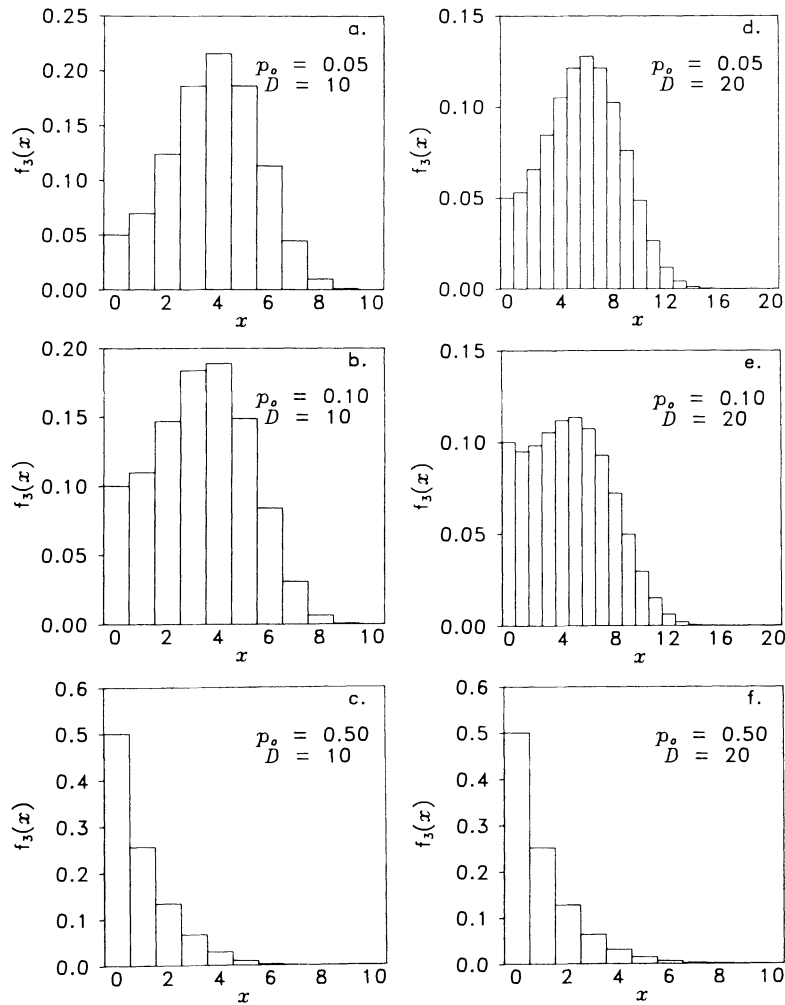


FIG. 4. Density functions for dispersal distance, using $p_3(x)$ (see Eq. 7) for a range of values of p_o and D .

For high p_o , our models produce quite similar density functions regardless of the form of $p(x)$ (compare Figs. 2c, f, i; 3c, f; 4c, f; see also Females in Table 1B, and our discussion). In this case, the dispersal is nearly complete within a few units of the natal site, so the density functions $f_2(x)$ and $f_3(x)$ become similar to the geometric distribution. The choice to be made is thus between the geometric distribution (constant p) and the linear probability function $p_1(x)$ (with p increasing immediately upon leaving the natal site). At lower p_o (.05, .10), the dispersal may occur over a larger range of x , and so the density functions are more sensitive to the form of $p(x)$. Note also that some $f(x)$ are more sensitive to a change in p_o than are others. For example, a doubling of p_o may or may not have a dramatic effect on the shape of the density function (compare Figs. 3d,e and 4d,e).

When the probability of stopping does not increase rapidly until near the end ($x = D$) of the dispersal (a "hard wall," as in Eq. 6 for p_2), the mean dispersal

distance increases. This is expected since lower stopping probabilities close to the natal site imply that animals move farther from that site before stopping. On the other hand, the linear variation of p_1 with x (Eq. 5) means that the probability of stopping begins to increase immediately upon leaving the natal site. As a result, the mean dispersal distance decreases, compared with the probability functions p_2 and p_3 with the same value of D . To clarify the relationship among these distributions, we include a discussion of their mathematical characteristics in the Appendix.

COMPARISON WITH FIELD DATA AND DISCUSSION

In order to determine the utility of the new models and to compare their behavior to that of the geometric model, we analyzed several sets of frequency distribution data from five vertebrate dispersal studies (Table 1). Our specific purposes were (1) to determine if the new models would provide statistically acceptable fits to a wide array of field data and thus offer an ac-

TABLE 1. Fit of observed data to models p_1 , p_2 , and p_3 and to the geometric distribution. A boldface entry indicates that the value was the largest value of D tested. The “***” indicates a frequency distribution significantly different from the observed ($P < .01$).

Parameter	Data	p_1	p_2	p_3	Geometric
A. Great Tit (<i>Parus major</i>), Greenwood et al. 1979					
1. Males					
p_o	0.103	0.106	0.136	0.136	0.149
D	20	50	21	44	...
Mean x	5.093	4.834	5.005	4.989	5.711
Median x	4.0	4.0	4.0	4.0	4.0
Var x	21.49	14.49	17.94	18.06	38.33
d_{\max}	...	0.045	0.035	0.033	0.046
2. Females					
p_o	0.029	0.031	0.071	0.068	0.100
D	26	50	22	45	...
Mean x	7.635	7.159	7.478	7.532	9.000
Median x	7.0	7.0	7.0	7.0	6.0
Var x	31.19	18.69	25.01	25.19	90.00
d_{\max}	...	0.060	0.044	0.041	0.094
B. Prairie Deermice (<i>Peromyscus maniculatus</i>), Dice and Howard 1951					
1. Males					
p_o	0.431	0.322	0.335	0.331	0.336
D	11	40	40	40	...
Mean x	2.323	1.854	1.968	1.949	1.976
Median x	1.0	1.0	1.0	1.0	1.0
Var x	11.94	4.261	5.671	5.161	5.882
d_{\max}	...	0.109	0.096	0.101	0.095
2. Females					
p_o	0.693	0.651	0.651	0.651	0.651
D	12	40	40	40	...
Mean x	0.813	0.526	0.536	0.535	0.536
Median x	0.0	0.0	0.0	0.0	0.0
Var x	4.916	0.771	0.822	0.814	0.824
d_{\max}	...	0.043	0.042	0.042	0.042
C. Red Fox (<i>Vulpes vulpes</i>), Storm et al. 1976					
1. Males					
p_o	0.346	0.325	0.343	0.342	0.34
D	9	20	8	16	...
Mean x	1.735	1.678	1.694	1.694	1.865
Median x	1.0	1.0	1.0	1.0	1.0
Var x	3.902	3.195	3.351	3.389	5.345
d_{\max}	...	0.022	0.024	0.023	0.028
2. Females					
p_o	0.779	0.715	0.717	0.717	0.717
D	7	20	20	20	...
Mean x	0.530	0.388	0.394	0.392	0.395
Median x	0.0	0.0	0.0	0.0	0.0
Var x	1.576	0.512	0.548	0.538	0.551
d_{\max}	...	0.065	0.062	0.063	0.062
D. Scrub Jay (<i>Aphelocoma coerulescens</i>), Woofenden and Fitzpatrick 1978					
1. Males					
p_o	0.340	0.372	0.411	0.389	0.448
D	3	3	2	3	...
Mean x	0.950	0.946	0.889	0.934	1.23
Median x	1.0	1.0	1.0	1.0	1.0
Var x	0.748	0.797	0.699	0.793	2.75
d_{\max}	...	0.033	0.071	0.050	0.108
2. Females					
p_o	0.000	0.076	0.142	0.110	0.245
D	4	4	3	4	...
Mean x	2.000	1.929	1.996	1.906	3.082
Median x	2.0	2.0	2.0	2.0	2.0
Var x	1.131	1.083	1.176	1.064	12.58
d_{\max}	...	0.076	0.142	0.110	0.245***

TABLE 1. Continued.

Parameter	Data	p_1	p_2	p_3	Geometric
E. White-crowned Sparrows (<i>Zonotrichia leucophrys</i>), Baker and Mewaldt 1978					
1. Males					
p_o	0.170	0.206	0.228	0.222	0.250
D	10	17	7	12	...
Mean x	2.460	2.416	2.441	2.384	3.000
Median x	2.0	2.0	2.0	2.0	2.0
Var x	5.008	4.428	4.316	4.041	12.00
d_{\max}	...	0.036	0.058	0.052	0.080
2. Females					
p_o	0.151	0.152	0.180	0.179	0.237
D	10	21	8	16	...
Mean x	3.009	3.088	3.027	3.046	3.219
Median x	2.0	3.0	3.0	3.0	2.0
Var x	5.575	6.126	5.593	5.970	13.58
d_{\max}	...	0.030	0.030	0.028	0.088

ceptable alternative to the geometric, and (2) to determine if the models offered greater modeling precision than the geometric. To investigate modeling precision, we focused on a common observation in vertebrate dispersal studies: one sex often disperses farther than the other (e.g., Woolfenden and Fitzpatrick 1978, Greenwood et al. 1979). We asked whether there were situations where different $p(x)$ functions seemed appropriate for different sexes.

Frequency distributions of dispersal distance constituted the raw data. In some cases these data were obtained from appendix tables in the cited papers. In other cases where the actual frequencies were not published, data were estimated by overlaying a grid on published figures.

To determine the optimal values of p_o and D to be used in the probability functions, we searched a range of these values. This search was centered on the observed values of p_o ($=F_{\text{obs}}(0)$, defined below) and the maximum dispersal distance. For thoroughness we searched up to 25 236 combinations of p_o and D for each data set. (This straightforward procedure required only a few minutes of computer time. In practice, researchers will likely have some preliminary estimate of the variation in p_o and D values. This will reduce the number of combinations required.) Comparisons to the data were made using the Kolmogorov-Smirnov test of goodness of fit (Sokal and Rohlf 1981) using relative frequency distributions. To employ the Kolmogorov-Smirnov (K-S) test, we first formed the cumulative distributions $F(x) = \sum_{i=0}^x f(i)$ for both the theoretical and observed density functions. For each value of p_o and D tested, we determined the value of $d_{\max} = \max [|F(x) - F_{\text{obs}}(x)|]$, where $F_{\text{obs}}(x)$ is the cumulative distribution derived from the field data. The best fit to the field data was obtained for the combination of p_o and D that produced the minimum value of d_{\max} . For each of our three best fitting distribution functions and

the geometric distribution, we calculated the mean, median, and variance of the dispersal distance x for comparison with the data. Although our models do not allow simple closed-form expressions for the mean and variance, the usual summations for the mean expected value $E(x) = \sum_{x=0}^D x[f(x)]$ and variance $\text{Var} = \sum_{x=0}^D [x - E(x)]^2 f(x)$ are easily calculated on a case-by-case basis.

The analysis of the observed data (Table 1) shows that functions other than the geometric may appropriately be employed to model dispersal distance distributions. One practical implication of these results is that the relaxation of certain restrictive assumptions need not prevent the concise modeling of field-dispersal distribution data. In most cases several models meet the Kolmogorov-Smirnov criteria as statistical fits of the data. Which then is most appropriate?

As our analysis shows (Table 1), the question really is how one can choose among alternative acceptable models. Such decisions must be made based on both the statistical applicability of a particular distribution and the nature of the ecological process being considered. From a purely statistical point of view, the "best" choice might be the one that implies the lowest Type I error rate (alpha) as indicated by a lower observed d_{\max} when using the K-S test. In a substantial number of cases shown here, our models provide a lower alpha (Table 1). However, when choosing a posteriori from an array of acceptable models, a choice based solely on the level of alpha may not incorporate the most information. Known (or suspected) biological factors that affect the dispersal (discussed above) should also be considered. These factors are reflected in the internal characteristics of the density function, such as the mean, median, and variance.

Such a situation is evident when the dispersal of Great Tits (Greenwood et al. 1979; Table 1A) is modeled. All four of the models presented yield low d_{\max}

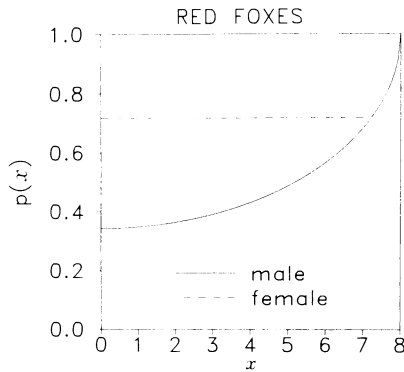


FIG. 5. Functions of stopping probability [$p(x)$] and dispersal distance (x) for male and female red foxes (*Vulpes vulpes*). The elliptical function $p_2(x)$ and the geometric $p(x) = p_o$ are presented for males and females, respectively.

values when compared to the observed data and thus cannot be statistically rejected as suitable models. The choice of an appropriate model then will depend on the relationship of the various characteristics of the candidate models to the research hypothesis. For example, Greenwood et al. (1979) focused their study on the relationship between dispersal distance and various life history and age structure characteristics in Great Tit populations. Models such as the geometric and p_1 and p_3 that either do not consider the scale of the dispersal or that model that scale badly (compare the observed D with that predicted by p_1 and p_3) would be less favorable models in these distance-related comparisons. Likewise, models that present inappropriate (too high or too low) starting probability values (e.g., the geometric in this case), or that misrepresent the variance in dispersal distance (e.g., p_1 and the geometric in this case) might be less acceptable if comparisons of dispersal distributions are to be made between sexes or years (e.g., Greenwood et al. 1979). For these reasons, p_2 appears to be relatively more acceptable as a model for Great Tit dispersal for both males and females.

The analysis of the Great Tit data demonstrates the importance of the way in which the stopping probability $p(x)$ is interpreted. Greenwood et al. (1979) found no relationship between dispersal distance and mortality in male and female Great Tits. However, they did find a positive relationship between reproductive output of females and dispersal distance. Thus the increase in p near the end of the dispersal may reflect more the factors related to habitat choice or mate selection than those related to mortality.

It is important to note that the new models will not necessarily fit better than the geometric model simply because they have an additional parameter. This concern, which is likely a result of the rigorous training in regression analysis that most ecologists receive, is valid only if one is seeking one more term in a general series expansion for $p(x)$. For example, if we were seeking

the constants p_o and C in the expression $p(x) = p_o + Cx$, we would always obtain a better fit to the data compared to the geometric model $p(x) = p_o$. The new parameter D that we introduce is only a scale parameter and does not determine the shape of $p(x)$. (Note that D appears only in the denominator of x/D in Eqs. 5, 6, and 7.) This point is demonstrated clearly by our analysis of the dispersal of prairie deer mice (*Peromyscus maniculatus*; Dice and Howard 1951; Table 1B). For both males and females the geometrical model is preferred. The high values of p_o for males result in similar distributions for all probability functions. The addition of the parameter D does not improve the fit over the geometric. Our models are advanced as alternatives to, and not replacements for, the geometric.

For two of the five sets of field data intersexual differences in dispersal are more precisely modeled by one of the new models. Table 1C, for red foxes (*Vulpes vulpes*; Storm et al. 1976), shows that the geometric model is the better fitting model for females primarily because of the extremely large p_o values for that sex. For the male red foxes, the value of p_o is less than half of that of the females, and thus the influence of the form of $p(x)$ on the density functions is felt. Because the elliptical function p_2 best models the maximum dispersal distance, and also adequately represents the other internal characteristics of the distribution, we prefer it to the other models for red fox males.

Table 1D shows the analysis of the dispersal pattern of Scrub Jays (*Aphelocoma coerulescens*; Woolfenden and Fitzpatrick 1978). Male distance distribution data show an acceptable fit to the geometric, whereas the female data do not (on the basis of d_{\max}). However, when the probability of stopping is allowed to change with the distance from the natal site, as in our models, better fitting distributions become available. The linear p_1 model provides the best fit to both the male and female data based on the significantly lower values of d_{\max} . For these short-range dispersals ($D = 3$ or 4),

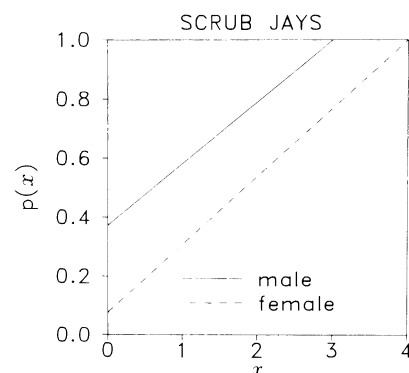


FIG. 6. Functions of stopping probability [$p(x)$] and dispersal distance (x) for male and female Scrub Jays (*Aphelocoma coerulescens*). The linear function $p_1(x)$ with slope $= (1 - p_o)/D$ is presented for both sexes.

models in which $p(x)$ varies slowly or not at all near the natal site are poor representations of the field data.

To what extent do the preferred models refine existing ideas or offer new ones regarding intersexual differences in dispersal in red foxes and Scrub Jays? In their extensive field study of red foxes, Storm et al. (1976) suggested that physiological factors are one of the most important influences of dispersal timing and distance in that species. Moreover, they suggested that because of the longer average dispersal of males and the tendency of males to move large distances on the first night of the dispersal (e.g., up to 9.7 km), such factors more profoundly affect male than female dispersal. The different shapes of the male and female $p(x)$ curves for the red fox (Fig. 5) can substantiate this idea if p can be found to be related in some way to the physiological condition of the males but not to the females. Storm et al. (1976) noted that such an investigation would be beneficial to the understanding of dispersal in the red fox. But the analysis presented here suggests other questions regarding this dispersal pattern that are not directly addressed by Storm et al. (1976). For example, what constrains the dispersal scale (which is similar for both sexes) in red foxes? Perhaps males, who disperse earlier than females (Storm et al. 1976) impose some limitation on female dispersal through social interactions of some kind.

Woolfenden and Fitzpatrick (1978) noted that natal site sex ratios of helpers (subadults that remain at the nest to assist in the rearing of siblings) are often skewed in favor of males in group-nesting birds. For Scrub Jays they hypothesized that this was the result of higher dispersal-related mortality in females. However, the linear $p(x)$ curves for male and female Scrub Jays (Fig. 6) indicate otherwise. The similarity of the slopes of these curves, although not tested statistically, shows that if $p(x)$ is interpreted as a mortality probability, the males suffer the same rate of increase of mortality with distance as do females. Furthermore, the mortality rate is the same for both sexes at the same distance from the dispersal endpoint $x = D$. This suggests that the unbalanced sex ratio at the natal site may be more the result of social interactions at the nest leading to more female dispersal than the result of actual mortality during dispersal. This reasoning illustrates the utility of a probability function $p(x)$ having two independent variables; the slope of the linear $p_1(x)$ is $(1 - p_0)/D$.

Table 1E, for male and female White-crowned Sparrows, shows an inconclusive result. Although the elliptical model p_2 seems preferable for the females, the situation for the males is less clear. Models p_2 and p_3 straddle the observed maximum dispersal distance, and other features of the distributions do not offer an obvious choice.

The models presented here provide a simple and more flexible way to fit dispersal distance data. They incorporate the concept of a maximum dispersal distance through the quantity D , and allow factors affect-

ing the dispersal to be included through the functional form of the probability function $p(x)$. These factors, such as physiological limits, sex differences, and the variation of habitat quality with dispersal distance, characterize the interaction between the animal and its environment, and so determine the nature of the dispersal. Because of their ability to assign a non-uniform or non-linear stopping probability, these models may include more information concerning the nature of dispersal, and thus permit a better understanding of the ecological and evolutionary characteristics of the dispersal pattern.

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APPENDIX

In this brief appendix, we examine some of the mathematical features of our models in order to provide some insight into the results summarized in Table 1. We use the following probability functions with our model:

$$p_1(x) = p_o + (1 - p_o)(x/D), \quad (\text{A.1})$$

$$p_2(x) = 1 - (1 - p_o)[1 - (x/D)^2]^{1/2}, \quad (\text{A.2})$$

and

$$p_3(x) = 1 - (1 - p_o)\{1 + \cos[\pi(x/D)]\}^{1/2}. \quad (\text{A.3})$$

First note that when the value of D becomes large (compared with any of the distances x actually encountered in the dispersal data), these functions all approach the form of the geometric model, $p(x) = p_o = \text{constant}$.

Performing a Taylor series expansion of these functions

about $x = 0$, and keeping only the first non-constant term, gives

$$p_1(x) = p_o + (1 - p_o)(x/D) \quad (\text{exactly}), \quad (\text{A.4})$$

$$p_2(x) = p_o + [(1 - p_o)(x/D)^2]/2 + \dots, \quad (\text{A.5})$$

$$p_3(x) = p_o + (1 - p_o)(\pi/2)^2(x/D)^2 + \dots \quad (\text{A.6})$$

Notice that the first two terms of p_2 and p_3 may be identical if the value of the maximum dispersal distance D used in p_2 (denoted D_2) and the value of D used in p_3 (denoted D_3) are related by $D_3 = (\pi/2)D_2 = 2.2D_2$. This resemblance may also be seen in Fig. 1 by expanding the size of the p_3 -curve by a factor of 2. As a consequence of this resemblance, the probability functions p_2 and p_3 that best fit the data often have the same value of p_o and a value of D_3 that is twice D_2 (see Table 1). In this way, the resulting density function $f_3(x)$ may "shadow" $f_2(x)$, so some care must be taken in interpreting the results when this occurs. In the sets of results summarized in Table 1, the "shadowing" probability function p_3 usually has a maximum dispersal distance D_3 that is much larger than that observed for the field data.