Ecological Applications, 16(2), 2006, pp. 820–828

AVERAGE DISPERSAL SUCCESS: LINKING HOME RANGE, DISPERSAL, AND METAPOPULATION DYNAMICS TO RESERVE DESIGN

William F. Fagan[1,3] and Frithjof Lutscher[2]

[1]*Department of Biology, University of Maryland, College Park, Maryland 20742-4415 USA*
[2]*Department of Mathematics, University of Alberta, Edmonton, Alberta AB T6G 2G1 Canada*

Abstract. Spatially explicit models for populations are often difficult to tackle mathematically and, in addition, require detailed data on individual movement behavior that are not easily obtained. An approximation known as the "average dispersal success" provides a tool for converting complex models, which may include stage structure and a mechanistic description of dispersal, into a simple matrix model. This simpler matrix model has two key advantages. First, it is easier to parameterize from the types of empirical data typically available to conservation biologists, such as survivorship, fecundity, and the fraction of juveniles produced in a study area that also recruit within the study area. Second, it is more amenable to theoretical investigation. Here, we use the average dispersal success approximation to develop estimates of the critical reserve size for systems comprising single patches or simple metapopulations. The quantitative approach can be used for both plants and animals; however, to provide a concrete example of the technique's utility, we focus on a special case pertinent to animals. Specifically, for territorial animals, we can characterize such an estimate of minimum viable habitat area in terms of the number of home ranges that the reserve contains. Consequently, the average dispersal success framework provides a framework through which home range size, natal dispersal distances, and metapopulation dynamics can be linked to reserve design. We briefly illustrate the approach using empirical data for the swift fox (*Vulpes velox*).

Key words: average dispersal success; critical patch size; home range; long-distance dispersal; mark–recapture studies; natal dispersal distance; reserve design; spatially explicit models; swift fox; Vulpes velox.

Introduction

Lack of dispersal data is often a major weakness in conservation programs that use reserves or networks of reserves to protect native species (Doak and Mills 1994, Haig et al. 1998, Halpern and Warner 2003). Long-distance dispersal is a particular problem, and this gap is especially troubling because ecological theory makes it clear that long-distance dispersal is critical to a diversity of ecological processes, including spatial spread (e.g., Neubert et al. 1995, Clark et al. 1999) and metapopulation dynamics (Hanski 1999). In contrast, when dispersal data are available from field studies, they often tend to be "local" in nature. That is, scientists typically know more about the movements and fates of individuals that restrict their activities to areas near active study sites than they do about individuals that travel far from those study sites. This is especially true for research on vertebrate species in which dispersal studies may provide solid movement data relevant to determining home range size (Person and Hirth 1991, Poole 1994, Maehr et al. 2002) or natal dispersal (Gese and Mech 1991, Byrom and Krebs 1999, Sutherland et al. 2000), but the movements and fates of individuals dispersing far from study areas remain largely unknown (Koenig et al. 2000). This issue also manifests itself in vertebrate studies as the "study area size problem": estimates of dispersal parameters change depending upon the size of the study area in which the monitoring was conducted (e.g., Baker et al. 1995, Lahaye et al. 2001). Overall, a striking mismatch exists between the kinds of data that are often required to work with dispersal models and the kinds of data that are typically available from field studies of dispersal.

Recent advances in mathematical ecology offer a novel route out of this dilemma and provide one avenue by which the most readily available types of empirical data on animal movements can be directly incorporated into conservation planning. Lutscher and Lewis (2004) developed the theory necessary for linking local dispersal data to conservation planning in the context of what Van Kirk and Lewis (1997) had termed a population's "average dispersal success." This quantity, which we define formally later in the paper, may be something of a misnomer to some applied ecologists. Rather than distinguishing "successful" dispersers as those that survive emigration to a different population and "unsuccessful" dispersers as those that die en route, the theory underlying average dispersal success actually distinguishes between individuals that disperse locally vs. those that disperse far away. Thus the theory

Manuscript received 13 June 2005; revised August 19 2005; accepted 18 July 2005. Corresponding Editor: J. Van Buskirk.

[3] E-mail: bfagan@glue.umd.edu

distinguishes dispersal events that are, on some scale, philopatric as successful and those that are non-philopatric as unsuccessful (i.e., success is viewed from the perspective of the source population). Spatial scale is also an important consideration in these analyses, because "local" dispersal can be within a particular habitat patch, within a system of patches, or even within a user-defined region of study within some larger landscape.

The application of average dispersal success builds on the concept of "critical habitat size" (Latore et al. 1998; see also Hanski and Ovaskainen 2000), which extends the idea of a population's "critical patch size" (Skellam 1951, Kindvall and Ahlen 1992, Cantrell et al. 2001, Beier et al. 2002, Lockwood et al. 2002, Pereira et al. 2004) by incorporating conditions on the size and productivity of networks of patches and the distance between them. Specifically, for a population in which many individuals disperse, the fraction of individuals that establish locally is an inherently useful quantity for understanding population dynamics and guiding management decisions related to the amount of habitat necessary for population persistence.

In this paper we characterize the linkages between average dispersal success, home range size, and natal dispersal to outline a technique that connects the behavioral ecology of territorial vertebrates with their habitat needs in reserve networks. For clarity, we have broken the paper into seven sections, as follows. We begin by reviewing some recent results from the theoretical literature that allow spatially explicit dispersal to be incorporated within the well-known mathematical framework of matrix demography (Caswell 2001). We next formally define average dispersal success in the context of kernel-based models of dispersal (Neubert et al. 1995). In the third and fourth sections, we discuss average dispersal success as a conservative approximation to results from far more complicated spatially explicit models of dispersal, and we provide a novel demonstration of how home range size and reserve design issues can be linked via average dispersal success. Next we transition from the theoretical foundations of the approach to a concrete example wherein we illustrate the linkages among home range size, reserve design, and average dispersal success in a case study for a relatively little-known vertebrate predator, the swift fox (*Vulpes velox*). Sixth, we present new theoretical results that extend the average dispersal success concept to the case of metapopulations. We conclude with a discussion of the advantages and disadvantages of average dispersal success from both practical and theoretical perspectives and suggest routes for additional research.

MATRIX MODELS AND DISPERSAL

Matrix models have proven to be valuable tools for describing stage-structured populations in discrete time and are increasingly gaining acceptance among empiricists (Caswell 2001). Recently, these models have been extended to include effects of spatial movement of individuals (Neubert and Caswell 2000, Lutscher and Lewis 2004). In the following, we describe two possible approaches, one spatially implicit, the other spatially explicit. For convenience, we limit ourselves to linear matrix models, but it is straightforward to extend the concepts developed to models with density dependence. In matrix models, a population is divided into $s \geq 1$ stages, where the column vector $\mathbf{n} = (n_1, \ldots, n_3)^{\mathsf{T}}$ denotes population densities in the respective stages. (The symbol T denotes the transpose of the vector.) These population densities change in time according to

$$\mathbf{n}(t+1) = \mathbf{B}\mathbf{n}(t). \tag{1}$$

Here the entries of the demographic projection matrix $\mathbf{B} = (b_{ij})$ are the rates at which stage i is produced from stage j. Population growth occurs if the dominant eigenvalue of $\mathbf{B}$ (traditionally called the population multiplier and symbolized as λ) exceeds 1. If $\lambda < 1$, then the population will decline.

To incorporate the effects of spatial movement into a matrix model, we assume that population growth and dispersal occur during separate phases. We assume that the population lives in a (not necessarily connected) habitat unit Ω, which, as previously mentioned, could be a particular patch, system of patches, or user-defined region of study. When studying the critical habitat size necessary to support a population, one typically assumes that Ω is homogeneous and connected, and further assumes, as a "worst case scenario," that there is emigration but no immigration. Later, we will turn to networks of patches of possibly different quality with movement among patches.

As a simple heuristic, spatially implicit approach, we multiply each rate b_{ij} by the probability that an individual of stage i that was produced from stage j will remain inside habitat Ω during dispersal. Denoting these probabilities by p_{ij} and forming the matrix $\mathbf{P} = (p_{ij})$, we obtain the following modified matrix model:

$$\mathbf{n}(t+1) = [\mathbf{P} \circ \mathbf{B}]\mathbf{n}(t) \tag{2}$$

where the symbol $\circ$ stands for the so-called Hadamard product of entrywise matrix multiplication. Again we turn to the dominant eigenvalue of the matrix to understand the population's fate. If the dominant eigenvalue of the matrix $\mathbf{P} \circ \mathbf{B}$ exceeds 1, then the population can persist, i.e., Ω is larger than the critical size for the given population vital rates b_{ij}. In contrast, if the dominant eigenvalue is less than 1, then the population goes extinct, i.e., Ω is smaller than the critical size required for these parameters.

Three questions arise immediately from this simple approach. (1) How do the probabilities p_{ij} depend on the dispersal behavior and on the geometry of the habitat patch? (2) Can the nonspatial model be related to or derived from a spatially explicit model with an underlying mechanistic model of dispersal? (3) How do the predictions of the simple, spatially implicit model compare to those of related explicit movement models?

In the following paragraphs, we will answer these three questions. We start by deriving an appropriate spatially explicit movement model for (1). For simplicity, we consider the case of a single stage first, i.e., $s = 1$. To describe the outcome of dispersal events, we use a dispersal kernel (e.g., Neubert et al. 1995), written $k(x, y)$, that denotes the probability that an individual moves from position y to x during one dispersal phase. Frequently it is assumed that dispersal is a function of distance only, i.e., $k(x, y) = \hat{k}(|x - y|)$, and the example presented later will be of this form. However, it should be noted that the model formulation allows for explicit dependence on the initial and final point, i.e., it can accommodate for edge effects and heterogeneous landscapes (e.g., Van Kirk and Lewis 1997, Morales 2002, Robbins 2004). The number of individuals at time $t + 1$ at location x is obtained by multiplying the number of individuals produced at location y by $k(x, y)$ and integrating over all possible y:

$$n(t+1,x) = \int_\Omega k(x,y)bn(t,y)\,dy. \tag{3}$$

To incorporate stage structure of the population and stage dependence of dispersal, we index the dispersal kernels by both the "from" and "to" stages of the population, writing $k_{ij}(x, y)$ for the dispersal kernel of an individual of stage i produced from an individual of stage j. This general model can handle situations in which, for example, first- and second-year breeders may have different fecundities and/or dispersal proclivities, even though for many species of conservation interest, reproduction and dispersal occur in different life history stages. After summarizing all of these kernels into one matrix $\mathbf{K} = (k_{ij})$, the spatially explicit matrix model is given by the following equation:

$$\mathbf{n}(t+1,x) = \int_\Omega [\mathbf{K}(x,y) \circ \mathbf{B}]\mathbf{n}(t,y)\,dy \tag{4}$$

where $\mathbf{B}$ is the projection matrix from above and $\mathbf{n}$ is again the vector of population stages. Neubert and Caswell (2000) studied the spreading speed of dispersing populations in this stage-structured integro-difference equation. Lutscher and Lewis (2004) analyzed Eq. 4 on bounded domains with respect to stability and bifurcation behavior. Given certain ecologically reasonable conditions on the matrices $\mathbf{B}$ and $\mathbf{K}$, the integral operator defined by the right-hand side of Eq. 4 has a dominant eigenvalue that determines population growth or collapse just as in the simpler matrix case (Eq. 1).

Dispersal Kernels and the Average Dispersal Success

Dispersal kernels can sometimes be derived from mechanistic movement models (Neubert et al. 1995), and they can also be obtained from experiments and mark–recapture studies (Clark et al. 1999, Baguette 2003). One of the simplest mechanisms assumes that individuals perform a random walk with diffusion coefficient D and settle at a constant rate σ. In one spatial dimension, these assumptions lead to the double exponential or Laplace kernel (Broadbent and Kendall 1953):

$$k_1(x,y) = \sqrt{\frac{\sigma}{4D}}\exp\left(-\sqrt{\frac{\sigma}{D}}|x-y|\right). \tag{5}$$

The same process in two space dimensions leads to the kernel (Van Kirk 1995):

$$k_2(x,y) = \frac{\sigma}{2\pi D}K_0\left(\sqrt{\frac{\sigma}{D}}|x-y|\right) \tag{6}$$

where K_0 is the modified Bessel function of the first kind (Gradshteyn and Ryzhik 1980). The two-dimensional kernel is unbounded at $x = y$, and k_1 is the marginal distribution of k_2. More complicated assumptions can include individual behavior at habitat edges (Van Kirk and Lewis 1999) or dispersal in heterogeneous landscapes (Robbins 2004). Yet, quantifying dispersal in patchy landscapes remains a major challenge in ecology, in part because good empirical estimates of long-distance dispersal, which can be critical to characterizing the shape of dispersal kernels, are difficult to obtain.

Here we focus instead on a different dispersal metric, the "average dispersal success" (Van Kirk and Lewis 1997). This metric, which we will derive, has an important advantage in applied settings because it is a much better match to the types of ecological data that are typically available for territorial species. Although it is conceptually based on dispersal kernels, calculation of a population's average dispersal success requires knowledge of localized dispersal instead of the more uncertain long-distance dispersal. Nevertheless, the average dispersal success still captures essential information about a species' dispersal behavior and the geometry of its habitat patch that can inform reserve design issues.

We first define "dispersal success" as the probability that an individual, which starts dispersal at some location inside the habitat, successfully settles inside that habitat. Hence, dispersal success is specific to the starting location. An individual close to a boundary is more likely to leave the habitat than an individual at the center, and would therefore have a lower dispersal success. As a worst case analysis with respect to conservation, individuals lost from the habitat are not taken into account, regardless of whether or not they survive outside that habitat. Incorporating landscape complexities, such as habitat edges, actually would change neither the formulation of the model nor the tools presented in our manuscript.

The average dispersal success is defined as the spatial average of the dispersal success over that habitat. Mathematically, it is given by

$$p = \frac{1}{|\Omega|}\int_\Omega\int_\Omega k(x,y)\,dxdy \tag{7}$$

where $|\Omega|$ denotes the area of Ω. Regardless of the details of a species' dispersal kernel (including any effects that patch size, shape, or other characteristics may have on the kernel), the average dispersal success metric is a nondecreasing function of patch size (Fig. 1). Thus defined, p is exactly the (spatial) average probability that an individual remains within the habitat during dispersal as defined in the previous section. Specific numerical values for average dispersal success obviously depend on the relationship between a species' dispersal behavior (such as average dispersal distance) and the patch characteristics (such as size and shape). Therefore, given a mechanistic movement model, the expression in Eq. 7 provides a mathematical answer to our first question. For each kernel $k_{ij}(x, y)$ we form the average dispersal success p_{ij} (which ranges from 0 to 1) and collect these quantities in the matrix $\mathbf{P} = (p_{ij})$.

The Average Dispersal Success Approximation

We now use the average dispersal success to approximate the spatially explicit model (Eq. 4) by a much simpler model, which nonetheless captures all the necessary information. We first introduce the vector of spatial averages of the different population stages:

$$\bar{\mathbf{n}}(t) = \frac{1}{|\Omega|}\int_{\Omega} \mathbf{n}(t, x)\, dx. \tag{8}$$

Averaging both sides of Eq. 4, expanding in Taylor series, and neglecting terms of higher order, we find that over time $\bar{\mathbf{n}}$ changes approximately as

$$\bar{\mathbf{n}}(t + 1) = [\mathbf{P} \circ \mathbf{B}]\bar{\mathbf{n}}(t). \tag{9}$$

Details of the derivation are given in Lutscher and Lewis (2004). Note that Eq. 9 is exactly the matrix model (Eq. 2), which is the original nonspatial model (Eq. 1) modified to include loss due to emigration. All of the population dynamic parameters are given in the matrix $\mathbf{B}$, whereas the dispersal- and habitat-related details are captured by $\mathbf{P}$. This result provides the answer to question (2). We have derived the heuristic model (Eq. 2) as the first term in a Taylor series of the model (Eq. 4), in which the dispersal kernels k_{ij} might come from a mechanistic description of movement. This derivation puts Eq. 2 on firm ground mechanistically and mathematically and, in addition, reduces the spatially explicit model (Eq. 4) to a modified matrix model, to which all the well-developed tools of that modeling framework apply.

We now turn to question (3) and explore how the persistence conditions (i.e., critical habitat size predictions) of the spatially explicit model (Eq. 4) and the simplified model (Eqs. 2 and 9) compare. Suppose that, in the absence of any spatial considerations, the population modeled by Eq. 1 grows, i.e., $\lambda(\mathbf{B}) > 1$. The same growing population in a bounded habitat will suffer emigration loss as described by Eqs. 2, 4, and 9. In a small habitat, an individual has a small probability of staying during dispersal; therefore, the entries of $\mathbf{P}$ for the dispersing stages are small and the dominant eigenvalue of $\mathbf{P} \circ \mathbf{B}$ is small. As the habitat becomes larger, the average dispersal success increases, and as the entries of $\mathbf{P}$ increase, the dominant eigenvalue of $\mathbf{P} \circ \mathbf{B}$ increases (Lutscher and Lewis 2004). As the habitat becomes infinitely large, the average dispersal success approaches 1 and the dominant eigenvalue of $\mathbf{P} \circ \mathbf{B}$ approaches the dominant eigenvalue of $\mathbf{B}$. Hence, there is a unique critical habitat size above which the population can persist and below which emigration losses will override local productivity, leading to extinction. Under the assumption of symmetric dispersal, we demonstrate in Appendix A that if a population can persist according to the approximation (Eq. 9), then it can also persist according to the full, spatially explicit model (Eq. 4). Hence, the critical habitat size for the simplified model will never be smaller than that for the full spatially explicit model. The question of how much the critical domain size is overestimated by the simpler model depends on other model parameters and is currently under investigation. Numerical comparisons can be found in VanKirk and Lewis (1997) and Lutscher and Lewis (2004).

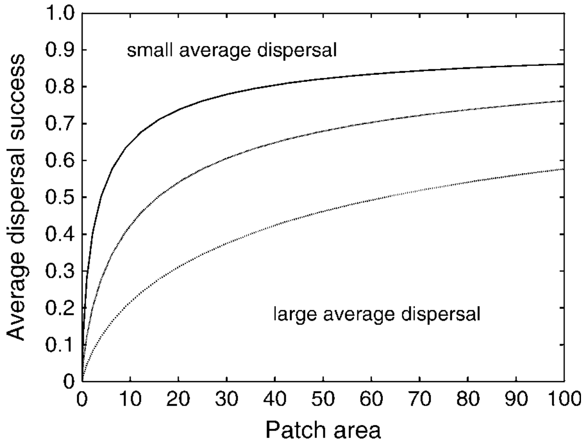

Fig. 1. Average dispersal success (Eq. 7) in relation to patch area, using the two-dimensional kernel (Eq. 6); average dispersal success is computed numerically. Average dispersal distances have been rescaled to one (top curve), two (middle curve), and four (bottom curve) spatial units. Results in one spatial dimension are qualitatively comparable.

Linking Home Range Size to Reserve Design via Average Dispersal Success

The critical habitat size condition $\lambda(\mathbf{P} \circ \mathbf{B}) > 1$ gives lower thresholds for the values p_{ij} that guarantee persistence of the population, independent of the detailed movement behavior. This critical habitat size can be estimated either using empirical data or by making some assumptions about how individuals move. For example, the functional relationship between the average dispersal success and patch size could be obtained empirically by measuring a species' average dispersal success over a range of differently sized patches. Such data are probably available for many species for which researchers are already attuned to the effects that the size of a study area or habitat patch has on estimates of dispersal distances (e.g., Baker et al. 1995, Koenig et al. 2000, Lahaye et al. 2001). If we have reason to assume a certain functional form (e.g., because we have a mechanistic model for dispersal), we can use the field data to fit the parameters of the theoretical model directly. Otherwise, we can characterize the dependence of a species' average dispersal success on patch length by fitting a single, monotonically increasing curve to the data using standard techniques.

On the other hand, if we lack such data, we can also estimate the critical habitat size for the population if we make certain assumptions about individual movement. Suppose individuals disperse by random walk with constant settling probability as previously described. The average dispersal success of the one-dimensional Laplace kernel (Eq. 5) on the patch $\Omega = [0, L]$ is given by

$$p = 1 - \sqrt{\frac{D}{\sigma}}\frac{1}{L}\left(1 - e^{-\sqrt{\sigma/D}L}\right) \tag{10}$$

where $\sqrt{D/\sigma}$ is the average dispersal distance. There is no similar explicit formula for the two-dimensional case (Eq. 6). In Fig. 1, we plot the average dispersal success for a square patch $\Omega = [0, L] \times [0, L]$ of area L^2. For population persistence, the average dispersal success must exceed a certain threshold, and because the average dispersal success is an increasing function of the habitat size, we can define this threshold in terms of a critical size $L > L^*$. (We refer to patch "size" to indicate the length in the one-dimensional case and the length of one side of the square patch in the two-dimensional case.) If we now rewrite patch size as a multiple of the average home range size of the species (H), yielding $L = \beta H$, then the condition for persistence becomes $\beta > L^*/H$. Therefore, the minimum number of home ranges necessary to ensure population persistence in the face of emigration losses is given by β^*, the smallest integer that exceeds L^*/H.

APPLYING AVERAGE DISPERSAL SUCCESS TO EARLY-STAGE PLANNING FOR SWIFT FOX

As an example of how these theoretical results could be applied to a real species, we consider a population with two only stages, juveniles and adults, denoted by n_J and n_A, respectively, and parameterize it for the swift fox (*V. velox*), a relatively little-known, small-bodied canid of the North American Plains (Schauster et al. 2002, Harrison 2003, Kamler et al. 2003). The nonspatial matrix model is given by

$$\begin{pmatrix} n_J \\ n_A \end{pmatrix}_{t+1} = \begin{pmatrix} a & b \\ c & d \end{pmatrix}\begin{pmatrix} n_J \\ n_A \end{pmatrix}_t. \tag{11}$$

Pooling data on survivorship and reproduction across studies, we estimate the stage-specific demographic parameters for swift foxes (*V. velox*) as follows. Survival of juveniles as juveniles is $a = 0.0$ (i.e., juveniles reach adulthood their first year; Schauster et al. 2002, Harrison 2003). Production of juveniles by adults is $b = 0.7$ (we obtain this estimate assuming that 60% of females breed, with an average litter size of 2.4, and a 1:1 sex ratio; Schauster et al. 2002). Survival of juveniles and maturation to adults is $c = 0.5$ (a lower bound from Kamler et al. [2003]), and survival of adults is $d = 0.85$ (Schauster et al. 2002, Harrison 2003, Kamler et al. 2003). The dominant eigenvalue of the matrix in Eq. 11 with these parameters is $\lambda = 1.15$, which exceeds 1, so that the population can persist in a nonspatial setting. The sensitivity matrix is given by

$$\begin{pmatrix} 0.2 & 0.34 \\ 0.48 & 0.79 \end{pmatrix} \tag{12}$$

so that we expect the population to be most vulnerable to losses in the adult stage and the juvenile to adult transition. The average dispersal success matrix **P** consists of four entries characterizing the movement and consequent loss of adults (p_A), juveniles that remain juveniles (p_{JJ}), juveniles that mature to adults (p_{JA}), and new offspring produced (p_J). The average dispersal success approximation for the critical habitat size is then given by the dominant eigenvalue of the following matrix:

$$\left[\begin{pmatrix} p_{JJ} & p_J \\ p_{JA} & p_A \end{pmatrix} \circ \begin{pmatrix} a & b \\ c & d \end{pmatrix}\right]. \tag{13}$$

We assume that juveniles stay with their parents until they become adults and have to emigrate to find their own territory. This implies an absence of dispersal-related loss within the juvenile stages, and we have $p_J = p_{JJ} = 1$. In Fig. 2A, we plot the conditions on p_A and p_{JA}, under which this population can persist. We see that persistence of swift fox populations is possible only in areas where both juvenile and adult dispersal success are sufficiently large (Fig. 2A). For example, p_A can be as low as 0.77 if all juveniles recruit locally, whereas p_{JA} can be as low as 0.45 if no adults emigrate.

Next we relate these thresholds to critical habitat size by supposing that maturing juveniles and adults disperse by random walk with constant settling rate, as described previously. The results are plotted in Fig. 2B for the one-dimensional case and in Fig. 2C for the two-dimensional case. The critical habitat size ranges from just slightly larger than the average juvenile dispersal distance (when adults do not disperse) to more than five times that distance (if adults exhibit the same dispersal outcomes as juveniles) (Fig. 2B). In the more realistic two-dimensional case, the critical L^* is again slightly larger than the average juvenile dispersal distance if adults do not disperse. If adults disperse 50% of the juvenile dispersal distance, then the critical L^* is about five times as high as the average juvenile dispersal distance, whereas if adults disperse the same as juveniles, it is almost eight times as high (Fig. 2C). From Schauster et al. (2002), we take the estimate of 12 km average dispersal distance for both juveniles and adults, if they disperse. In the one-dimensional case, this

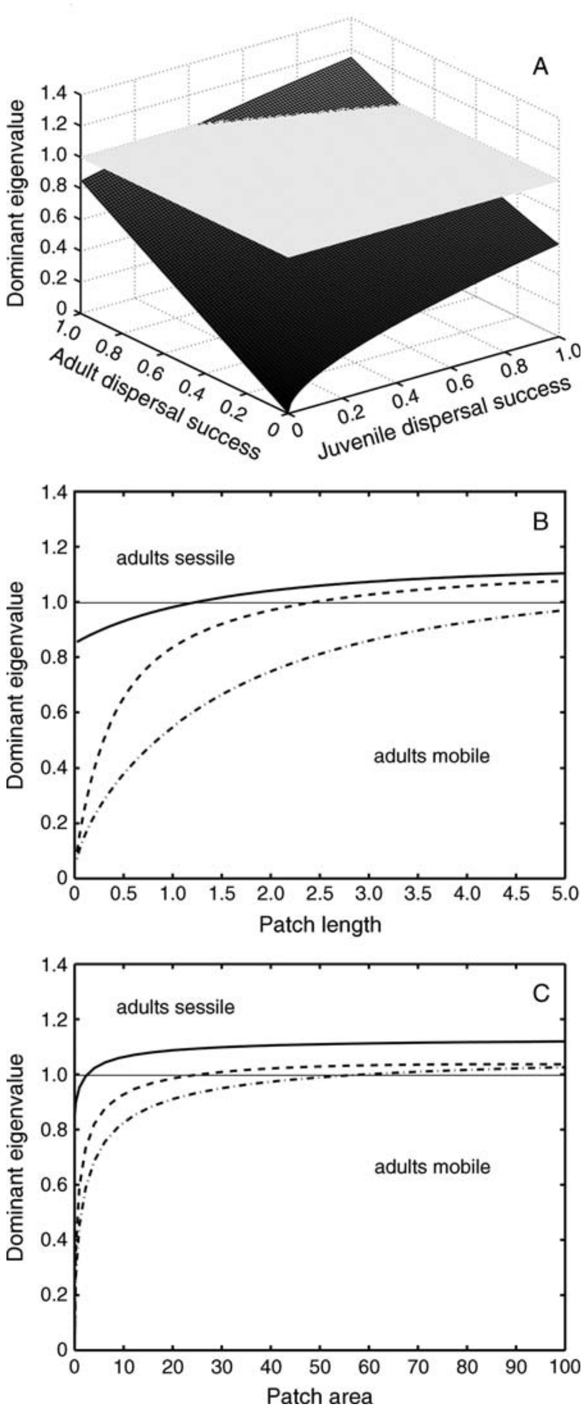

FIG. 2. Dependence of swift fox population persistence on average dispersal success; parameters are as in Eq. 11. (A) The dominant eigenvalue as a function of the two average dispersal success parameters. When the eigenvalue is greater than 1.0 (i.e., above the light gray plane), then the population can survive; if it is $<$1.0, the population will go extinct. (B) The dominant eigenvalue as a function of patch length, assuming dispersal according to the Laplace kernel (Eq. 5) in a one-dimensional habitat. The unit length is taken to be the average dispersal distance (rescaled) of juveniles. The solid line assumes that adults do not move, i.e., $p_A = 1$. If adults move, then the critical patch size increases. The dashed line shows the result when the average dispersal distance of adults is 20% of that of the juveniles; the dash-dot line corresponds to the case when adults have the same average dispersal distance as the juveniles. (C) Similar to (B), but assuming dispersal in two dimensions (patch area, rescaled) according to the kernel (Eq. 6). The patch is taken to be $\Omega = [0, L] \times [0, L]$ with area L^2. The dashed line now represents adult dispersal at half of the juvenile dispersal distance.

←

estimate results in a critical length of the habitat of $\sim$17 km in case adults do not disperse, and $>$60 km if adults disperse at the same rate as juveniles. In two space dimensions, the length of the side of a square habitat would have to be 19 km (area 361 km^2) and 96 km (9216 km^2), respectively. In Appendix B, we outline some aspects of sensitivity analysis for this model; here, we simply report some numerical results. Varying the average dispersal distance for juveniles by 10% while assuming that adults do not disperse changes the outcome by 11% in one dimension and 12% in two dimensions, respectively. For comparison, the study area of Schauster et al. (2002) is 1040 km^2. Home range size varied between day and night, male and female, and season in Schauster et al. (2002), with a low of $>$2 km^2 and a high of $>$10 km^2. In a different landscape, Kamler et al. (2003) found average home range sizes of just over 10 km^2. Hence, in the two-dimensional case without adult movement, one would need between 36 and almost 200 home ranges to sustain a population.

A word of caution may be in order here. Schauster et al. (2002) present data only on distances moved and the range, but not the distribution, of distances. Before we can apply the mechanistic kernel, we would want to compare the theoretical and empirical distribution of dispersal distances. Also, Schauster et al. (2002) classify short-distance moves as "relocation" rather than dispersal and explicitly exclude those from the calculations. Including these moves into the calculation for the average distance seems to be more consistent with the assumptions of the mechanistic movement model here and would produce a smaller critical habitat size. One can incorporate a probability of dispersal α into the model in Eq. 3 (and similarly Eq. 4) by choosing the dispersal kernel as $k(x, y) = \alpha\kappa(x, y) + (1 - \alpha)\delta(x - y)$, where κ describes the actual dispersal events and the δ function indicates that individuals are not moving. The average dispersal success p is given in terms of the average dispersal success p_κ of κ as $p = \alpha p_\kappa + (1 - \alpha)$. Whereas the average dispersal success approximation is analogous for these models, certain mathematical subtleties prevent us from proving the analogous statements for the spatially explicit model (see Lutscher and Lewis 2004).

AVERAGE DISPERSAL SUCCESS WITHIN A METAPOPULATION

So far, we have concentrated on a single patch, but the theory behind average dispersal success is equally applicable in more complex landscapes. Here we show

how the concept can be extended to a metapopulation. For simplicity, we illustrate this issue for an unstructured (i.e., single-stage) population in a habitat with only two disjoint patches, Ω_1 and Ω_2 (which may be of different size, shape, and/or quality). The integrodifference equation now reads

$$n(t+1,x) = \int_{\Omega_1 \cup \Omega_2} k(x,y)b(y)n(t,y)\,dy \qquad (14)$$

where the reproduction term b(y) may depend on location. We could, as before, average the density over the two patches and use the average dispersal success to obtain an approximation for the critical habitat size. In this case, the average dispersal success gives the average probability that an individual stays anywhere in the two patches combined (see Fig. 3). However, this approach will not allow us to incorporate different habitat quality in the two patches. To deal with issues of different patch qualities, we form the average of the population density over each of the two patches separately (denoted $\bar{n}_1$ and $\bar{n}_2$, respectively). We assume that production is homogeneous in each of the patches and denote it by $b_{1,2}$ on $\Omega_{1,2}$, respectively. Next, we form the average dispersal success from patch j into patch i as

$$p_{ij} = \frac{1}{|\Omega_i|}\int_{\Omega_i}\int_{\Omega_j} k(x,y)\,dydx \qquad (15)$$

which reduces to Eq. 7 when $i = j$. For $i \neq j$, the expression denotes the average probability that an individual from patch j successfully settles in patch i. Note that such data on interpatch movement can be obtained empirically if individuals are marked differently depending on their source patch, and both target patches are monitored for dispersers. Hence, p_{ij} takes into account the area of the respective patches as well as the distance between them. The average dispersal success approximation leads to the following equation:

$$\begin{bmatrix} \bar{n}_1(t+1) \\ \bar{n}_2(t+1) \end{bmatrix} = \begin{pmatrix} p_{11}b_1 & p_{1,2}b_2 \\ p_{21}b_1 & p_{22}b_2 \end{pmatrix} \begin{bmatrix} \bar{n}_1(t) \\ \bar{n}_2(t) \end{bmatrix}. \qquad (16)$$

The matrix in Eq. 16 contains the parameters for reproduction (b_j) and the average dispersal success from Eq. 15 (p_{ij}). (Note again, that subscripts now denote patch number and not stage.) If the dominant eigenvalue of the matrix in Eq. 16 is greater than 1, the metapopulation of the two patches combined can grow, whereas if the eigenvalue is less than 1, the metapopulation will decline. Suppose, for example, that each of the two patches alone is too small to sustain a population. By the average dispersal success approximation, this is the case if $p_{11}b_1 < 1$ and $p_{22}b_2 < 1$. According to Eq. 16, the population on the two patches combined can survive if

$$p_{12}b_1p_{21}b_2 > (1 - p_{11}b_1)(1 - p_{22}b_2). \qquad (17)$$

This condition, which can also be derived directly from matrix population theory (Caswell 2001), has a straightforward interpretation. The combined gain from reproduction and cross-migration between patches, which is given by the expression on the left-hand side, must exceed the loss from the network, which is given by the expression on the right-hand side.

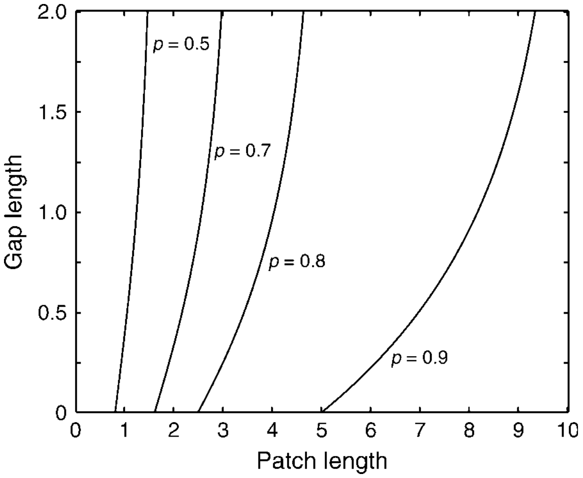

FIG. 3. Contour plot showing different levels of the average dispersal success (p) of the Laplace kernel for a one-dimensional habitat consisting of two patches of equal length and depending on the length of the gap between the patches. Rescaled length variables are unitless.

DISCUSSION

Recasting theoretical models with dispersal in terms of the average dispersal success is advantageous for two major reasons. First, and perhaps more important to field ecologists, the average dispersal success is useful because it is directly connected to the kinds of empirical data routinely available from field studies involving demographic and/or mark–recapture techniques. The fraction of dispersing individuals that remain *inside* a well-monitored patch (or patch network or demarcated study area) is far easier to obtain from field studies than anything involving movement *outside* that patch (or network or demarcated study area). For example, if researchers "simply" mark juveniles living inside a patch, and then monitor that patch to identify which juveniles successfully disperse from their natal range to obtain a home range in the same patch, they can calculate the average dispersal success for the patch. Researchers could, of course, use the fraction of dispersing individuals directly in patch models, but having dispersal kernels as a mechanistic basis of the average dispersal success framework is a key advantage in those cases in which there is reason to suspect that dispersal will be similar in different (but unstudied) patches or landscapes. However, even though average dispersal success offers some distinct advantages because of its close match to the types of dispersal data typically available from field studies, the approach could still fail to provide useful information if the amount of dispersal data available is insufficient to accurately characterize the fraction of individuals that settle locally.

For marking–monitoring programs that cover multiple patches, the average dispersal success framework for analyzing dispersal becomes increasingly advantageous because, in combination with patchwise demographic data, it allows for estimates of metapopulation growth or decline. Consequently, the average dispersal success framework could prove especially helpful in field systems where little is known about the details of dispersal through matrix habitat, but where successful movements among patches are actively monitored. Extensions of the average dispersal success framework may also be relevant to planning for marine protected areas where issues of juvenile dispersal are of critical importance (e.g., Dugan and Davis 1993, Sanchirico and Wilen 2001, Lockwood et al. 2002). This is because a key goal in marine reserve theory is to balance local recruitment success and leakage of recruits across the reserve boundary to augment fisheries in the surrounding waters.

The second major advantage, perhaps of more interest to theoreticians, is that the average dispersal success allows complex, spatially explicit models to be reduced in complexity, often to a substantial degree. For example, the average dispersal success provides a means of reducing complex, difficult-to-analyze models, such as the integro-difference equation system in Eq. 4, to the projection-matrix framework of structured population models, which are well-understood and well-developed theoretically (Caswell 2001) and which are also widely used by empiricists. Average dispersal success is quantitatively appealing because it can be derived analytically for a variety of mathematical dispersal kernels whose origins in behavioral ecology are understood (Stamps et al. 1987, Neubert et al. 1995, Lutscher and Lewis 2004). For other types of dispersal behavior, carefully developed simulation models (e.g., Gustafson and Gardner 1996) could also be used to estimate the average dispersal success for patches or networks of patches. As a theoretical tool, the average dispersal success actually has even broader utility. For example, it can be used to study approximate conditions for stability of nonzero steady states (Lutscher and Lewis 2004) and even periodic orbits in host–parasitoid systems (Cobbold et al. 2005). A major theoretical challenge is to characterize the mathematical relationship between landscape-scale statistics (e.g., percentage of habitat, patch size, fragmentation) and average dispersal success for a species living in and moving through that landscape. Clearly, this theoretical challenge is linked to the broader need for theoretical study of dispersal in heterogeneous landscapes. An additional theoretical challenge would be to use empirical average dispersal success from a patch network in an inverse problem to characterize the species' dispersal kernel.

Because the relevant data are frequently available, estimates of a species' home range size often enter into reserve planning exercises and habitat management analyses (e.g., Locke 1996, Wielgus 2002). For example, many studies of vertebrate dispersal quantify dispersal distances in terms of the number of home ranges traversed by a dispersing individual (e.g., Greenwood et al. 1979, Stamps et al. 1987, Newton and Wyllie 1991, Matthysen et al. 1995). Likewise, researchers who adopt a minimum viable population framework for reserve design may quantify habitat needs for the reserve in terms of multiples of home range size (Wielgus 2002, Haight et al. 2004). The average dispersal success framework provides a way to synthesize data pertinent to territory structure, demography, and natal dispersal into structured population modeling, a mathematical technique that is broadly used in ecology and conservation biology.

Continued development of the average dispersal success framework, from both empirical and theoretical perspectives, will help to link key aspects of a species' social and dispersal behavior with its metapopulation dynamics. In particular, a meta-analysis of empirical data that quantifies how average dispersal success depends upon habitat size for a diversity of species in different landscapes would be quite instructive to theoretical models dealing with critical habitat size. Likewise, theoretical investigations of how different types of individual movement behaviors in heterogeneous landscapes translate into kernel-type representations of dispersal outcomes would help to answer the overarching question of when we can rely on generalized approximations to describe dispersal and when we must focus on the specific details of particular species × landscape combinations.

ACKNOWLEDGMENTS

W. F. Fagan is indebted to M. Lewis and the Departments of Mathematics and Biology at the University of Alberta for facilitating his visit to Canada. A. Stephens made key contributions through a literature search. F. Lutscher gratefully acknowledges funding through the Pacific Institute for the Mathematical Sciences, and is thankful for inspiring discussions with M. Lewis. We thank three anonymous reviewers for their suggestions.

LITERATURE CITED

Baguette, M. 2003. Long distance dispersal and landscape occupancy in a metapopulation of the cranberry fritillary butterfly. Ecography **26**:153–160.

Baker, M., N. Nur, and G. R. Geupel. 1995. Correcting biased estimates of dispersal and survival due to limited study area: theory and an application using Wrentits. Condor **97**:663–674.

Beier, P., M. Van Drielen, and B. O. Kankam. 2002. Avifaunal collapse in West African forest fragments. Conservation Biology **16**:1097–1111.

Broadbent, S. R., and D. G. Kendall. 1953. The random walk of Trichostrongylus retortaeformis. Biometrica **9**:460–466.

Byrom, A. E., and C. J. Krebs. 1999. Natal dispersal of juvenile arctic ground squirrels in the boreal forest. Canadian Journal of Zoology **77**:1048–1059.

Cantrell, S., C. Cosner, and W. F. Fagan. 2001. How predator incursions affect critical patch size: the role of the functional response. American Naturalist **158**:368–375.

Caswell, H. 2001. Matrix population models. Sinauer Associates, Sunderland, Massachusetts, USA.

Clark, J. S., M. Silman, and R. Kern. 1999. Seed dispersal near and far: patterns across temperate and tropical forests. Ecology **80**:1475–1494.

Cobbold, C., M. A. Lewis, J. Roland, and F. Lutscher. 2005. How habitat structure governs host–parasitoid dynamics of the forest tent caterpillar. Theoretical Population Biology **67**: 109–125.

Doak, D. F., and L. S. Mills. 1994. A useful role for theory in conservation. Ecology **75**:615–626.

Dugan, J. E., and G. E. Davis. 1993. Applications of marine refugia to coastal fisheries management. Canadian Journal of Fisheries and Aquatic Sciences **50**:2029–2042.

Gese, E. M., and L. D. Mech. 1991. Dispersal of wolves (Canis lupus) in northeastern Minnesota, 1969–1989. Canadian Journal of Zoology **69**:2946–2955.

Greenwood, P. J., P. H. Harvey, and C. M. Perrins. 1979. The role of dispersal in the great tit (Parus major): the causes, consequences, and heritability of natal dispersal. Journal of Animal Ecology **48**:123–142.

Gradshteyn, I. S., and I. M. Ryzhik. 1980. Table of integrals, series and products. Academic Press, New York, New York, USA.

Gustafson, E. J., and R. H. Gardner. 1996. The effect of landscape heterogeneity on the probability of patch colonization. Ecology **77**:94–107.

Haig, S. M., D. W. Mehlman, and L. W. Oring. 1998. Avian movements and wetland connectivity in landscape conservation. Conservation Biology **12**:749–758.

Haight, R. G., B. Cypher, P. A. Kelly, S. Phillips, K. Ralls, and H. P. Possingham. 2004. Optimizing reserve expansion for disjunct populations of San Joaquin kit fox. Biological Conservation **117**:61–72.

Halpern, B. S., and R. R. Warner. 2003. Matching marine reserve design to reserve objectives. Proceedings of the Royal Society of London Series B, Biological Sciences **270**:1871–1878.

Hanski, I. 1999. Metapopulation ecology. Oxford University Press, Oxford, UK.

Hanski, I., and O. Ovaskainen. 2000. The metapopulation capacity of a fragmented landscape. Nature **404**:755–758.

Harrison, R. L. 2003. Swift fox demography, movements, denning, and diet in New Mexico. Southwestern Naturalist **48**:261–273.

Kamler, J. F., W. B. Ballard, E. B. Fish, P. R. Lemons, K. Mote, and C. C. Perchellet. 2003. Habitat use, home ranges, and survival of swift foxes in a fragmented landscape: conservation implications. Journal of Mammalogy **84**:989–995.

Kindvall, O., and I. Ahlen. 1992. Geometrical factors and metapopulation dynamics of the bush cricket, Metrioptera bicolor philippi (Orthoptera, Tettigoniidae). Conservation Biology **6**:520–529.

Koenig, W. D., P. N. Hooge, M. T. Stanback, and J. Haydock. 2000. Natal dispersal in the cooperatively breeding Acorn Woodpecker. Condor **102**:492–502.

Lahaye, W. S., R. J. Gutierrez, and J. R. Dunk. 2001. Natal dispersal of the Spotted Owl in Southern California: dispersal profile of an insular population. Condor **103**:691–700.

Latore, J., P. Gould, and A. M. Mortimer. 1998. Spatial dynamics and critical patch size of annual plant populations. Journal of Theoretical Biology **190**:277–285.

Locke, H. 1996. Yellowstone to Yukon. Wildlife Conservation **99**:24–32.

Lockwood, D. R., A. Hastings, and L. W. Botsford. 2002. The effects of dispersal patterns on marine reserves: Does the tail wag the dog? Theoretical Population Biology **61**: 297–309.

Lutscher, F., and M. A. Lewis. 2004. Spatially-explicit matrix models. Journal of Mathematical Biology **48**:293–324.

Maehr, D. S., E. D. Land, D. B. Shindle, O. L. Bass, and T. S. Hoctor. 2002. Florida panther dispersal and conservation. Biological Conservation **106**:187–197.

Matthysen, E., F. Adriaensen, and A. A. Dhondt. 1995. Dispersal distances of nuthatches, Sitta europaea, in a highly fragmented forest habitat. Oikos **72**:375–381.

Morales, J. M. 2002. Behavior at habitat boundaries can produce leptokurtic movement distributions. American Naturalist **160**:531–538.

Neubert, M. G., and H. Caswell. 2000. Demography and dispersal: calculation and sensitivity analysis of invasion speeds for structured populations. Ecology **81**:1613–1628.

Neubert, M. G., M. Kot, and M. A. Lewis. 1995. Dispersal and pattern formation in a discrete-time predator–prey model. Theoretical Population Biology **48**:7–43.

Newton, I., and I. Wyllie. 1991. Demography of an increasing population of sparrowhawks. Journal of Animal Ecology **60**: 749–766.

Pereira, H. M., G. C. Daily, and J. Roughgarden. 2004. A framework for assessing the relative vulnerability of species to land-use change. Ecological Applications. **14**:730–742.

Person, D. K., and D. H. Hirth. 1991. Home range and habitat use of coyotes in a farm region of Vermont. Journal of Wildlife Management **55**:433–441.

Poole, K. G. 1994. Characteristics of an unharvested lynx population during a snowshoe hare decline. Journal of Wildlife Management **58**:608–618.

Robbins, T. 2004. Seed dispersal and biological invasion: a mathematical analysis. Dissertation. University of Utah, Salt Lake City, Utah, USA.

Sanchirico, J. N., and J. E. Wilen. 2001. A bioeconomic model of marine reserve creation. Journal of Environmental Economics and Management **42**:257–276.

Schauster, E. R., E. M. Gese, and A. M. Kitchen. 2002. Population ecology of swift foxes (Vulpes velox) in southeastern Colorado. Canadian Journal of Zoology **80**:307–319.

Skellam, J. G. 1951. Random dispersal in theoretical populations. Biometrika **38**:196–218.

Stamps, J. A., M. Buechner, and V. V. Krishnan. 1987. The effects of edge permeability and habitat geometry on emigration from habitat patches. American Naturalist **129**: 533–552.

Sutherland, G. D., A. S. Harestad, K. Price, and K. P. Lertzman. 2000. Scaling of natal dispersal distances in terrestrial birds and mammals. Conservation Ecolog **4**(1): 16. ⟨http://www.consecol.org/vol4/iss1/art16⟩

Van Kirk, R. W., and M. A. Lewis. 1997. Integrodifference models for persistence in fragmented habitats. Bulletin of Mathematical Biology **59**:101–137.

Van Kirk, R. W., and M. A. Lewis. 1999. Edge permeability and population persistence in isolated habitat patches. Natural Resources Modeling **12**:37–64.

Wielgus, R. B. 2002. Minimum viable population and reserve sizes for naturally regulated grizzly bears in British Columbia. Biological Conservation **106**:381–388.

APPENDIX A

Comparison of critical patch sizes from the implicit and explicit models (*Ecological Archives* A016-033-A1).

APPENDIX B

Sensitivity analysis of critical habitat size (*Ecological Archives* A016-033-A2).