Demography, dispersal, and invasion speed: a comparative study

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1 Introduction

Organisms are born, mature, reproduce, and eventually die. While doing so, they move from place to place. The rates at which they move and develop determine their distribution and abundance, and the study of distribution and abundance requires theory that can incorporate these rates into a model of population dynamics.

Changes in abundance are described by demographic models, which describe the life cycle and the vital rates (a collective term for the rates of birth, development, mortality, reproduction, etc.) that govern transitions from stage to stage within the life cycle (e.g., Tuljapurkar and Caswell 1997, Caswell 2001). The fundamental conclusion of demographic theory is the potential, shared by all living organisms, for exponential population growth; the most basic tool for demographic data analysis is the recipe, shared by all demographic models, for computing this potential growth rate (denoted by $\lambda$ in discrete time or $r = \log \lambda$ in continuous time).

Changes in distribution are described by coupling demographic models to models for the dispersal of individuals in space. One of the most fundamental conclusions of such models is the potential for spatial expansion of a population in the form of an invasion wave, and the rate of advance of such a wave — the invasion wave speed — can be calculated from such models.

The power of such analyses has recently increased due to the development of integrodifference equations as models for population growth and spread (refs.) Integrodifference equations have advantages over other models because . . .

Neubert and Caswell (2000) showed how to combine integrodifference equation models for dispersal with stage-classified matrix population models for demography, and to compute invasion wave speeds from the resulting models. These analytical methods are summarized in Section ??.

Neubert and Caswell (2000) included a couple of examples of wave speed analysis, pieced together from previously published results on demography and dispersal. Much more extensive studies exist, however, and here we have gathered results from the best of these. Our goal is to provide the first comparative study, across a range of plant and animal taxa, of wavespeed and its determinants. We will examine patterns of wavespeed across taxa, variation among populations within species, the results of perturbation analyses, the results of alternative descriptions of dispersal, and the importance of long-distance dispersal.

2 The Model

This section closely follows Neubert and Caswell (2000), who describe the formulation of structured IDE models for population growth and spread in detail.

To see how IDE models work, it is best to start with a simple life history in which all individuals are identical, so that the population can be described by its abundance $n$. Such a life history can be modeled with a scalar integrodifference equation (Kot et al. 1996). The model is composed of two parts. The first is a difference equation that describes population growth at each spatial location:

$$n(y, t + 1) = b[n(y, t), y] n(y, t),$$

(1)

where $n(y, t)$ is the population density at location $y$ and time $t$, and $b[\cdot]$ is the per-capita population growth rate, which may depend on both density and location. The second part is an integral
operator which accounts for the movement of individuals. We define \( k(x, y) \) to be the probability density function for the location \( x \) to which an individual at \( y \) disperses. To find the population density at \( x \) at time \( t + 1 \) we sum the contributions from all locations \( y \) to obtain:

\[
n(x, t + 1) = \int_{-\infty}^{\infty} k(x, y) b[n(y, t), y] n(y, t) \, dy.
\] (2)

The probability density function \( k \) is variously known as the “redistribution kernel” or “dispersal kernel”. In plant population biology, where the dispersing individuals are often seeds, the kernel is called the “seed shadow”.

Individuals are not, of course, identical; they differ in age, size, developmental stage, or other factors. To account for the stage structure of the population, we must expand model (1) to a system of \( m \) difference equations (one equation for each of the \( m \) stages). Designating \( n_i \) as the population density in the \( i \)th stage and \( b_{ij} \) as the per capita production of stage \( i \) individuals at time \( t + 1 \) by stage \( j \) individuals at time \( t \) we have

\[
n_i(y, t + 1) = \sum_{j=1}^{m} b_{ij} \left( n_1(y, t), \ldots, n_m(y, t), y \right) n_j(y, t),
\] (3)

for \( i = 1, \ldots, m \). In matrix notation (3) becomes

\[
n(y, t + 1) = B_n(y)n(y, t)
\] (4)

where \( B_n(y) \) is the density-dependent population projection matrix at location \( y \).

To allow for stage-specific dispersal, we must specify a dispersal kernel for each of the \( m^2 \) possible transitions between stages. We define \( k_{ij}(x, y) \) to be the probability that an individual making the transition from stage \( j \) to stage \( i \) moves from location \( y \) to location \( x \). If there is no dispersal during a given transition the associated kernel is the Dirac delta function \( \delta(x - y) \) (Bracewell 1978); a function which (very roughly speaking) is zero if \( x \neq y \), is infinite when \( x = y \), and integrates to 1. (I.e. with probability one such an individual stays where it is.)

The stage structured analog of (2) is then given by

\[
n_i(x, t + 1) = \int_{-\infty}^{\infty} \sum_{j=1}^{m} k_{ij}(x, y) b_{ij} \left( n_1(y, t), \ldots, n_m(y, t), y \right) n_j(y, t) \, dy,
\] (5)

for \( i = 1, \ldots, m \). Just as (3) is simplified by (4), if we create a matrix \( K(x, y) \) from the kernels \( k_{ij} \) the complex notation of (5) is greatly simplified:

\[
n(x, t + 1) = \int_{-\infty}^{\infty} \left[ K(x, y) \circ B_n(y) \right] n(y, t) \, dy.
\] (6)

The symbol “\( \circ \)” stands for the Hadamard product (Horn and Johnson 1985), wherein multiplication is computed element by element. (So the element in the \( i^{th} \) row and \( j^{th} \) column of \( K(x, y) \circ B_n(y) \) is \( k_{ij}(x, y)b_{ij}(y) \)).
Figure 1: The life cycle graph of nodding thistle (Carduus nutans) after Shea and Kelly (1998). Stages: (1) seeds in the seed bank, (2) small plants, (3) medium plants, (4) large plants. Dashed lines represent transitions during which dispersal occurs.

2.1 Simplifying Assumptions

We now adopt two major simplifying assumptions. First, we assume that the environment is spatially homogeneous, which implies that the vital rates depend only on local population density and not explicitly on spatial location. (I.e. $B_n(y) = B_n$.) Next, we assume that dispersal to the left is as likely as dispersal to the right. Along with the assumption of spatial homogeneity, this implies that dispersal from $x$ to $y$ depends only on the distance between the two points. As a result, the dispersal kernels are symmetric and depend only on the single variable $|x - y|$. With this extra assumption, equation (6) becomes:

$$n(x, t + 1) = \int_{-\infty}^{\infty} \left[ K(|x - y|) \circ B_n \right] n(y, t) \, dy.$$  

(7)

These assumptions, and others we discuss later, are required for much of the analysis of invasion speed that follows below. We emphasize, however, that model (6) can be used to describe more complicated, heterogeneous situations, and to study them by numerical simulation.

2.2 An Example

As a simple example, consider a model for the monocarpic perennial thistle Carduus nutans, an introduced Eurasian weed of major economic importance in pasture systems. Shea and Kelly (1998) developed a matrix population model for $C. nutans$ in which they divided the population into four classes: seeds ($n_1$), small adults ($n_2$), medium adults ($n_3$), and large adults ($n_4$). The life cycle graph is illustrated in Fig. [?]

Assume that germination rates decrease with local adult population density, and that the other vital rates are density-independent. The demographic part of this model is

$$B_n = \begin{pmatrix} 0.038 & 8.250 & 179.413 & 503.143 \\ 0.185g(N) & 1.091g(N) & 22.180g(N) & 62.185g(N) \\ 0.000 & 0.009 & 0.000 & 0.000 \\ 0.000 & 0.006 & 0.022 & 0.000 \end{pmatrix},$$  

(8)

where

$$g(N) = \left(1 + \sum_{i=2}^{4} n_i(x)\right)^{-1}.$$  

(9)

To describe dispersal we need to decide which stages disperse and pick a dispersal kernel to describe their movement. For $C. nutans$, the dispersing stage is seeds. Those seeds either germinate
and become adults of various sizes in the next year, or remain in a seed bank (Fig. [?]). We fit a Laplace distribution,
\[ k(x) = \frac{1}{2\alpha} \exp\left(-\frac{|x|}{\alpha}\right), \tag{10} \]
to measurements of the distances that *C. nutans* seeds dispersed (ref). The dispersal kernel matrix is then
\[
K = \begin{pmatrix}
\delta(x) & k(x) & k(x) & k(x) \\
k(x) & \delta(x) & k(x) & k(x) \\
k(x) & k(x) & \delta(x) & \delta(x) \\
k(x) & k(x) & \delta(x) & \delta(x)
\end{pmatrix}.	ag{11}
\]

The upper right quadrant contains the dispersal kernel \(k(x)\); the other entries, corresponding to stages that do not disperse, contain the delta function \(\delta(x)\) described above.

In Fig. [?], we show the result of iterating this model forward from an initially small population concentrated at the origin. As the invasion develops, the speed with which it proceeds converges to a constant value (Fig. [?], inset). This is the invasion speed that we want to calculate from the matrices \(B_n\) and \(K\).

### 2.3 Travelling Waves

The solution in Fig. 2.2 appears to be a travelling wave; i.e., a solution that maintains a fixed shape in space while moving at a constant speed. Integrodifference models can have such solutions. Weinberger (1978, 1982), Lui (1982a, 1982b, 1983) and Kot (1992, Kot et al. 1996) have studied the mathematical properties of scalar travelling waves; Lui (1989a) and Neubert and Caswell (2000) have described the travelling wave solutions of structured models.

Travelling wave solutions exist under the following conditions:

1. The matrix \(B_n\) is positive, or nonnegative and primitive (Caswell 1989) for all \(n \geq 0\). In practice most population projection matrices have this property.

2. Let \(A = B_0\) (i.e. \(B_n\) evaluated at \(n = 0\)). This matrix represents the set of vital rates at low population densities. We will require the largest eigenvalue \(\lambda\) of \(A\) to be larger than one. With this assumption we are guaranteed that the population will grow when small.

3. Increased population density has a negative effect on the organism’s vital rates:
\[
B_n n \leq A n \text{ for all } n \geq 0, \tag{12}
\]
where the inequalities are evaluated elementwise. A sufficient condition for (12) to hold is that all of the elements of \(B_n\) are nonincreasing functions of the elements of \(n\).

4. Every kernel \(k_{ij}(x)\) has a moment generating function
\[
m_{ij}(s) \equiv \int_{-\infty}^{\infty} k_{ij}(x) e^{sx} dx. \tag{13}
\]
That is, they have exponentially bounded tails. Models with dispersal kernels that do not satisfy this requirement can produce accelerating invasion waves, rather than waves that move at a constant speed. (Mollison 1972, Kot et al. 1996).

There are a number of statistics that characterize the travelling wave. They include:
Figure 2: Simulated invasion dynamics of *C. nutans*. Model (7), with the demographic matrix (8) and the dispersal matrix (11), was iterated fifty times from an initial distribution of plants concentrated at the origin. Seeds (solid line) and small adults (dashed line) are shown. Larger plants (not shown) have similar distributions but much lower densities. For this simulation, $\alpha = 1.7958$ m.

2.3.1 The Invasion Wave Speed: $c^*$

When these conditions hold, model (7) has infinitely many traveling wave solutions. Each of these waves moves at a speed greater than or equal to a minimum speed $c^*$. The initial conditions determine which wave a population initially concentrated in a finite region of space will never spread faster than $c^*$ and asymptotically will spread at a rate of exactly $c^*$. The invasion wave speed $c^*$ thus gives the asymptotic invasion speed, for a large and important class of population growth models and dispersal kernels, and for initial conditions corresponding to biologically reasonable invasion scenarios.

Lui (1989a) and Neubert and Caswell (2000) showed that

$$c^* = \min_{0 < s < \delta} \left[ \frac{1}{s} \ln \rho_1(s) \right].$$

Equation (14) is complicated; we beg the reader’s patience as we explain its components.
The function \( \rho_1(s) \) is the largest eigenvalue of the matrix

\[
H(s) = A \circ M(s).
\]

(15)

The elements of the matrix function \( M(s) \) are the moment generating functions of the elements of the matrix \( K(x) \). (I.e. they are given by equation (13).

Returning to our thistle example, the demographic matrix at low population density is given by

\[
A = \begin{pmatrix}
0.038 & 8.250 & 179.413 & 503.143 \\
0.185 & 1.091 & 22.180 & 62.185 \\
0.000 & 0.009 & 0.000 & 0.000 \\
0.000 & 0.006 & 0.022 & 0.000
\end{pmatrix},
\]

(16)

and the matrix of moment generating functions is

\[
M(s) = \begin{pmatrix}
1 & m(s) & m(s) & m(s) \\
1 & m(s) & m(s) & m(s) \\
1 & 1 & 1 & 1 \\
1 & 1 & 1 & 1
\end{pmatrix},
\]

(17)

where

\[
m(s) = \frac{1}{1 - \alpha^2 s^2}.
\]

(18)

(The moment generating function of a delta function is the constant 1, and the moment generating function of the Laplace distribution (10) is \( \frac{1}{1 - \alpha^2 s^2} \)).

The minimization in equation (14) is taken over the interval \((0, \hat{s})\). The upper limit \( \hat{s} \) is imposed because, in general, the moment generating function of a kernel only exists for some finite interval around \( s = 0 \). We therefore assume that there exists some \( \hat{s} \) such that all of the elements of \( M(s) \) exist for all \( 0 \leq s < \hat{s} \). In the thistle example, \( \hat{s} = 1/\alpha \).

Using formula (14) we computed the invasion wave speed for our exemplar thistle population as \( c^* = 3.1933 \) m yr\(^{-1}\). Numerical simulations of the model also produce this speed (Fig. [?], inset).

### 2.3.2 The Wave Shape: \( s^* \)

We will use the symbol \( s^* \) for the value of \( s \) in formula (14) that corresponds to the minimum speed, \( c^* \). The parameter \( s^* \) has an important biological meaning. Far in front of an invasion wave advancing to the right, and asymptotically in time, the population density of every stage is approximately proportional to \( e^{-s^*x} \). Thus the population wavefront is exponential in space and \( s^* \) is the rate of decay of the wavefront. The larger \( s^* \), the steeper the front. Alternatively, \( \log 2/s^* \) gives the length over which the density declines by half. For our thistle example, \( s^* = 0.38 \) m\(^{-1}\), with a half-length of 1.8m. Theses results match our numerical simulations.

### 2.3.3 Local Population Growth Rate: \( \rho^* \)

Another descriptive statistic,

\[
\rho^* \equiv \rho_1(s^*),
\]

(19)
Figure 3: Simulated invasion front for *C. nutans*. Model (7), with the demographic matrix (8) and the dispersal matrix (11), was iterated 100 times from an initial distribution of plants concentrated at the origin. For this simulation, $\alpha = 1.7958$ m. The slope of the invasion front plotted on a logarithmic scale matches the prediction, $s^* = 0.38$ m$^{-1}$.

describes the rate of local population growth. Imagine an observer standing far in front of the travelling wave at a fixed location $x$. If that observer were to track the local population density over time, he would see it increase at the rate $\rho^*$. By rearranging equation (14), we find

$$\rho^* = e^{s^*c^*}.$$  

Thus, *ceterus paribus*, steeper, faster waves produce larger rates of local population growth. In the thistle example, $\rho^* = 3.37$ yr$^{-1}$.

### 2.3.4 The Stable Wavefront Stage Distribution: $w^*$.

Accompanying $\rho^*$, the dominant eigenvalue of $H(s^*)$, is $w^*$, the associated right eigenvector. When scaled so that $\sum_i w_i^* = 1$, this eigenvector gives the fraction of the population in each of the stages in the invasion wavefront. For thistle,

$$w^* = \begin{bmatrix} 0.8437 \\ 0.1556 \\ 0.0004 \\ 0.0003 \end{bmatrix}.$$  

### 3 Comparative wavespeed data

*these are just notes; this needs to be expanded –HC*

A study of invasion speed requires two kinds of data:

1. Demographic data sufficient to parameterize a stage-classified population projection matrix. Ideally, the vital rates should be measured under low-density conditions (corresponding to the leading edge of the invasion wave).

2. Dispersal data sufficient to estimate a set of stage-specific dispersal kernels.
These data can be obtained in many different ways, with differing degrees of approximation. The first steps in a demographic analysis are to decompose the life cycle into demographically relevant stages and to choose a projection interval (Caswell 2001). Stages are chosen to capture the aspects of the individual (age, size, condition, etc.) that are relevant to that individual’s demographic fate. The projection interval is chosen to reflect the time scale on which the demographic processes occur. Both choices are subject to compromise based on the kinds of measurements that are feasible to make. Dispersal adds one more consideration to the choices. Now, stages should be chosen to capture the aspects of the individual relevant to both demographic fate and dispersal, and the projection interval should reflect not only the time scale of the life cycle, but also the timing of dispersal.

For this study, we have collected a large number of data sets that include both demography and dispersal. Some of these were collected intentionally to study invasion processes; others were assembled for that purpose after the fact. Table xxx lists the species and populations that we used. 

This table needs to be constructed; not sure yet what should go in it. Maybe it should appear at the beginning of the Appendix. HC

The data include trees and shrubs (xx data sets on xx species), herbaceous perennial plants (xx data sets on xx species), annual plants (xx data sets on xx species), birds (xx data sets on xx species), mammals (xx data sets on xx species), and insects (xx data sets on xx species). As the last item should make clear, this collection is not a random sample of species, but reflects the kinds of organisms for which demographic and dispersal data are most routinely collected.

Some of the multiple data sets on a single species represent populations studied under different environmental conditions (plots, years, weather conditions). These provide valuable information on variability of wavespeed and related statistics within a single taxon. Others represent different estimation procedures applied to the same data set. These serve as a kind of sensitivity analysis showing how results depend on choices in data analysis.

Appendix A describes, for each species, the life cycle and projection matrix, the dispersal biology and the way in which the dispersal kernels were measured. The analyses reported here are only a fraction of what can be extracted from these data, and are not intended to completely describe any of the studies.

In the next section, we begin by examining patterns in $c^*$ and $s^*$, as they vary across taxa and in relation to other population parameters. In a following section, we turn our focus to the dispersal kernel, and examine the effects of different estimation methods and the consequences of multiple dispersal mechanisms. Then we will explore prospective and retrospective perturbation analysis, to see how wavespeed changes in response to changes in both demography and dispersal.

4 Comparisons of wave speed

This section reports on comparisons of wave speed $c^*$ among taxa.

We begin (Section ??) with comparisons of broad taxonomic groups. In some cases, we are able to compare the calculated wave speed $c^*$ with observed rates of spread; we report those comparisons in Section ?? . In Section ?? we look for correlations between $c^*$ and other life history and dispersal variables; these correlations reveal some of the general determinants of wave speed. Finally, in Section ?? we look at contrasts among populations or data sets within selected taxa.
4.1 Inter-taxon contrasts

The 141 case studies were separated into six groups; herbs, shrubs, trees, insects, birds and mammals (Table 4.1). Herbs included annuals, monocarpic perennials and polycarpic perennials. The insect group comprised only one beetle species /txtitCephaloleia fenestrata. In general, herbs (mean 1.41 m.yr\(^{-1}\)) and shrubs (mean 0.97 m.yr\(^{-1}\)) had slower estimated wave speeds than trees (mean 3.46 m.yr\(^{-1}\)). The predicted wave speeds \(c^*\) of herbs and shrubs ranged between 0.04 and 8.79 m.yr\(^{-1}\); white trillium had the slowest speed and spear thistle the fastest. The estimated speeds for trees reached up to 13 m.yr\(^{-1}\), for one of the long-leaved pine cases. The speed for the beetle ranged between 24 and 52 m.yr\(^{-1}\).

The estimated wave speeds for birds and mammals (vertebrates) were three to four orders of magnitude higher than those for plants, and ranged from 700 to more than 80,000 m.yr\(^{-1}\). The Starling colonizing the USA had the fastest wave speed and the Red Kite expanding its range in Wales (Britain) had the slowest. The majority of the estimated vertebrate wave speeds were below 10,000 m.yr\(^{-1}\).

\(\lambda\) was always, by necessity, greater than 1 and the mean value across all cases was 1.35. Most cases had \(\lambda\) less than 2, but eight had higher values and yellow rattle, when hay cut, had the highest \(\lambda\) at 8.02. \(R_0\), the lifetime reproductive output of the average individual, varied hugely within the plants but vertebrates had more limited maxima; reflecting the very high seed production of some plant species.

Because most (ALL?) dispersal kernels were leptokurtic, the 50 and 99.5 percentiles of the dispersal data for each case study were used as descriptors of dispersal distances (note that these percentiles were from the non-marginalized kernels). The 99.5 percentile was used as a descriptor of the tail of the dispersal kernel, while the 50 percentile describes the main part of the dispersal kernel. Both percentiles were three to four orders of magnitude higher for vertebrates than plants. Trees dispersed further than herbs and shrubs.
4.2 Comparison of estimated and observed wave speeds

Observed spread velocities were known for only 10 species of plants (59 cases), but for all the vertebrate cases; three mammals (four cases), and 15 birds (20 cases). These observed speeds varied greatly among the six groups (Table 4.1). Herbs (mean 4.8 m yr$^{-1}$) had the lowest speeds, and shrubs and trees (mean 85.4 m yr$^{-1}$) were an order of magnitude faster. The observed velocities for mammals fell within the range of birds. Both groups had speeds up to three orders of magnitude higher than in plants. Generally the estimated wave speeds for the plants were lower than the observed ones (Fig RoballCvsobs, Fig RobselCvsobs, C vs observed speeds from all and selected data). This may reflect the fact that dispersal kernels were often measured at much smaller scales than those at which the observed speeds were measured and so dispersal was under-estimated. Estimates for the two yellow rattle cases were close to the observed, probably because dispersal and spread velocities were both measured at the same scale.

Estimated wave speeds among birds and mammals were much closer to the observed, probably because dispersal and spread were measured at the same, large, scales. Observed velocities for vertebrates ranged from 500 to nearly 100,000 m yr$^{-1}$. The observed speeds for the Starling colonizing the USA (91,600 m yr$^{-1}$) and the Cattle Egret colonizing South- and North America (106,000 m yr$^{-1}$) were by far the highest. On the European continent the highest velocity was recorded for the Collared Dove expanding its range from the southeast into the northwest (43,700 m yr$^{-1}$). The estimated wave speeds fitted quite well to the observed velocities of expansion (Figure 4.1), but in general they were slightly higher.

4.3 Correlates of wave speed

4.3.1 Rationale for analyses

The data set of 141 case studies represents 37 species. Where a species was represented in multiple case studies most of these used the same dispersal kernel (matched with different demographic matrices) or the same demographic matrix (matched with different dispersal kernels). Three species (yellow rattle, buzzard and sparrowhawk) each had two case studies with different demographic matrices and dispersal kernels. Therefore, the 141 case studies all differed in some of the variables used to estimate wave speeds, but they were not truly independent. To achieve rigor in comparisons,
Figure 5: INSERT Fig RobselCvsobs, C vs observed speeds from selected data
we compared correlations among variables using the whole data set (141 cases) with correlations using an extremely conservative 'selected' data set comprising completely independent cases. Apart from the three species with multiple independent cases, the selected data set contained only one case for each species. Two selection criteria were applied. The selected case had the demographic matrix giving the highest $\lambda$ for a species, which may best reflect the low density conditions at the wave front. Where multiple cases used this demographic matrix, the selected case had the dispersal kernel which was considered to best approximate the real dispersal function. The selected data set comprised 40 case studies and all 37 species.

Vertebrates (birds and mammals) had very different dispersal capabilities than the plants and insect and therefore much higher estimated wave speeds (Table 4.1). We therefore analyzed correlations among variables both for all species together and separately for vertebrates and plants (the latter included the beetle). Thus correlations were analyzed in six data sets; whole, whole-plants, whole-vertebrates, selected, selected-plants and selected-vertebrates. Data were logged for all correlation and regression analyses.

4.3.2 Correlations among important variables

$c^*$ was negatively correlated with $s^*$ in all data sets (Table 4.2, Figure RoballCvsS C vs S from all data, Figure RobselCvsS C vs S from selected data). The relationship was particularly strong when plant and vertebrate data were combined ($r > -0.9$), but was somewhat weaker in the separate vertebrate and plant data sets. Thus cases with a higher wave speed $c^*$ had a shallower slope to the wave front. BLAH ABOUT WHAT THIS MEANS.

Unsurprisingly, in all data sets the population growth rate at the wave front $\rho$ was highly correlated with $\lambda$, with $r$ values of about 0.9 or higher. The lifetime reproductive output $R_0$ was only correlated with $\lambda$ for the vertebrates. The lack of a correlation in plants probably reflects the wide variety of life history types found in this group compared to the great uniformity in types among the vertebrates.

The 50 and 99.5 percentiles of the dispersal distances were correlated. This relationship was extremely strong when vertebrate and plant data sets were combined, due to the large differences in dispersal between these two groups. Separating the groups weakened the relationship, especially
Table 2: Table 4.2 Correlations among particular variables (log values), for the six data sets

<table>
<thead>
<tr>
<th>Data set</th>
<th>$c^<em>$ vs $s^</em>$</th>
<th>$\rho$ vs $\lambda$</th>
<th>$R_0$ vs $\lambda$</th>
<th>99.5 vs 50 percentile</th>
</tr>
</thead>
<tbody>
<tr>
<td>whole</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$r$</td>
<td>-0.934</td>
<td>0.91</td>
<td>-0.009</td>
<td>0.965</td>
</tr>
<tr>
<td>$n$</td>
<td>140</td>
<td>140</td>
<td>103</td>
<td>105</td>
</tr>
<tr>
<td>$p$</td>
<td>***</td>
<td>***</td>
<td>ns</td>
<td>***</td>
</tr>
<tr>
<td>whole-plants</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>$r$</td>
<td>-0.623</td>
<td>0.89</td>
<td>-0.017</td>
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<td>116</td>
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<td>***</td>
<td>***</td>
<td>ns</td>
<td>***</td>
</tr>
<tr>
<td>whole-vertebrates</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$r$</td>
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<td>0.994</td>
<td>0.856</td>
<td>0.779</td>
</tr>
<tr>
<td>$n$</td>
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<td>24</td>
<td>24</td>
<td>24</td>
</tr>
<tr>
<td>$p$</td>
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<td>***</td>
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<td>selected</td>
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<tr>
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<td>37</td>
</tr>
<tr>
<td>$p$</td>
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<td>***</td>
</tr>
<tr>
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<tr>
<td>$r$</td>
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<td>18</td>
</tr>
<tr>
<td>$p$</td>
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<td>***</td>
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<td></td>
<td></td>
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</tr>
<tr>
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<td>19</td>
</tr>
<tr>
<td>$p$</td>
<td>***</td>
<td>***</td>
<td>***</td>
<td>***</td>
</tr>
</tbody>
</table>

Figure 7: INSERT Fig RobsellCvsS, C vs S from selected data
Table 3: Table 4.3 Linear regression of \( c^* \) against dispersal and demographic variables

<table>
<thead>
<tr>
<th></th>
<th>significant single regressions ((P &lt; 0.05))</th>
<th>multiple regression</th>
<th>( n )</th>
<th>partial ( R^2 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>All</td>
<td>99.5% dispersal ( R_0 )</td>
<td>99.5% dispersal ( \lambda )</td>
<td>99</td>
<td>0.866</td>
</tr>
<tr>
<td></td>
<td>50% dispersal ( \rho )</td>
<td></td>
<td></td>
<td>0.058</td>
</tr>
<tr>
<td>All plants</td>
<td>99.5% dispersal ( R_0 )</td>
<td>99.5% dispersal ( \lambda )</td>
<td>75</td>
<td>0.221</td>
</tr>
<tr>
<td></td>
<td>( \rho )</td>
<td></td>
<td></td>
<td>0.235</td>
</tr>
<tr>
<td></td>
<td>50% dispersal ( \rho )</td>
<td></td>
<td></td>
<td>0.077</td>
</tr>
<tr>
<td>All vertebrates</td>
<td>99.5% dispersal ( R_0 )</td>
<td>99.5% dispersal ( R_0 )</td>
<td>24</td>
<td>0.884</td>
</tr>
<tr>
<td></td>
<td>( \rho )</td>
<td></td>
<td></td>
<td>0.050</td>
</tr>
<tr>
<td>Selected</td>
<td>99.5% dispersal ( R_0 )</td>
<td>99.5% dispersal ( \lambda )</td>
<td>35</td>
<td>0.884</td>
</tr>
<tr>
<td></td>
<td>50% dispersal ( \rho )</td>
<td></td>
<td></td>
<td>0.050</td>
</tr>
<tr>
<td>Selected plants</td>
<td>( \lambda )</td>
<td>( \lambda )</td>
<td>16</td>
<td>0.388</td>
</tr>
<tr>
<td></td>
<td>( \rho )</td>
<td>( \rho )</td>
<td></td>
<td>0.336</td>
</tr>
<tr>
<td>Selected vertebrates</td>
<td>99.5% dispersal ( \rho )</td>
<td>99.5% dispersal ( \rho )</td>
<td>19</td>
<td>0.434</td>
</tr>
</tbody>
</table>

for the vertebrates. The lack of a perfect correlation is a consequence of the leptokurtosis of the dispersal kernels. (DO WE EXPECT \( R=1 \) FOR A NORMAL DISTRIBUTION?) Thus the 50 and 99.5 percentiles describe different aspects of the dispersal data.

### 4.3.3 Correlates of \( c^* \)

The ability of \( \lambda \), \( R_0 \), \( \rho \) and the 50 and 99.5 percentiles to explain variation in \( c^* \) among case studies was investigated using linear regression. The first three variables describe aspects of demography while the last two describe the dispersal kernel. First \( c^* \) was regressed onto each variable separately. While certain of these variables were strongly correlated we included all in stepwise regressions of \( c^* \). When variables are correlated, stepwise regression will select the variable which explains most variation, and which is thus the most important predictor of \( c^* \).

All six data sets produced very similar regression patterns. The 99.5 dispersal percentile was consistently significant in the single regressions (except the selected-plants data set, see below), while \( \lambda \), \( R_0 \), \( \rho \) and the 50 percentile were important in some data sets (Table 4.3). In the stepwise regressions, the 99.5 dispersal percentile explained a great amount of variation in \( c^* \) (\( \geq 86\% \)) for data sets combining vertebrate and plant data (Fig RoballCvsD995, C vs D995 from all data, Fig RobsellCvsD995, C vs D995 from selected data). \( \lambda \) explained a small amount of additional variation (5-6\%) (Fig RoballCvs\( \lambda \), C vs lambda from all data, Fig RobsellCvs\( \lambda \), C vs lambda from selected data). Therefore, the dispersal kernel was far more important than the demographic matrix in determining variation in \( c^* \) among cases. Furthermore, the tail of the dispersal kernel,
described by the 99.5 percentile, was more important in predicting $c^*$ than the median dispersal distance.

When the vertebrate and plant data sets were separated stepwise regression gave a model which explained a high percentage of variation in $c^*$ (53 - 77%). The 99.5 percentile remained an important predictor for all but one data set, but demography was now roughly equally important (Table 4.3). This reflects the huge difference in dispersal between the vertebrates and plants. Among more similar taxa both dispersal and demography are equally important in predicting $c^*$. The important demographic variable for the vertebrate data sets was not $\lambda$, but $R_0$. Among plants both $\lambda$ and $R_0$ were important predictors of $c^*$. (DISCUSS WHY FECUNDITY PREDICTS C* BETTER THAN OR AS WELL AS STRAIGHT POPULATION GROWTH RATE). Surprisingly, dispersal was not a significant predictor in the selected-plants data set. This was caused by outliers from the common heather and bell heather case studies (Fig RobsellCvsD995, C vs D995 from selected data). In both, $c^*$ was much higher than might be expected from the 99.5 dispersal percentile. This is probably because the 99.5 dispersal percentile (1 m for common heather, 1.6 m for bell heather) was a poor descriptor of the tail of the extremely leptokurtic dispersal kernels which extended to
Figure 10: INSERT Fig RoballCvs lam, C vs lambda from all data

Figure 11: INSERT Fig RobsellCvs lam, C vs lambda from selected data
Table 4: Table 4.4 Linear regression of $s^*$ against dispersal and demographic variables

<table>
<thead>
<tr>
<th></th>
<th>significant single regressions ($P &lt; 0.05$)</th>
<th>multiple regression</th>
<th>n</th>
<th>partial $R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>All</td>
<td>99.5% dispersal $R_0$</td>
<td>99.5% dispersal $R_0$</td>
<td>99</td>
<td>0.970</td>
</tr>
<tr>
<td></td>
<td>50% dispersal $\rho$</td>
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<td></td>
<td>0.002</td>
</tr>
<tr>
<td>All plants</td>
<td>99.5% dispersal $R_0$</td>
<td>99.5% dispersal</td>
<td>75</td>
<td>0.778</td>
</tr>
<tr>
<td></td>
<td>50% dispersal $\rho$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>All vertebrates</td>
<td>99.5% dispersal $R_0$</td>
<td>99.5% dispersal $\lambda$</td>
<td>24</td>
<td>0.906</td>
</tr>
<tr>
<td></td>
<td>50% dispersal $\rho$</td>
<td></td>
<td></td>
<td>0.055</td>
</tr>
<tr>
<td>Selected</td>
<td>99.5% dispersal $R_0$</td>
<td>99.5% dispersal</td>
<td>35</td>
<td>0.970</td>
</tr>
<tr>
<td></td>
<td>50% dispersal $\rho$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Selected plants</td>
<td>99.5% dispersal $R_0$</td>
<td>99.5% dispersal</td>
<td>16</td>
<td>0.576</td>
</tr>
<tr>
<td></td>
<td>50% dispersal</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Selected vertebrates</td>
<td>99.5% dispersal $R_0$</td>
<td>99.5% dispersal $R_0$</td>
<td>19</td>
<td>0.915</td>
</tr>
<tr>
<td></td>
<td>50% dispersal</td>
<td></td>
<td></td>
<td>0.047</td>
</tr>
</tbody>
</table>

80 m. When these cases were excluded from the data set the 99.5 percentile ($R^2 = 0.41$) and $\lambda$ ($R^2 = 0.29$) were significant the stepwise regression.

4.3.4 Correlates of $s^*$

Variation in $s^*$ was investigated using the same approach as used for $c^*$. $s^*$ was regressed onto $\lambda$, $R_0$, $\rho$ and the 50 and 99.5 percentiles using both single and stepwise regression. Again, we found a high degree of consistency in results among the six data sets. In the single regressions the 50 and 99.5 dispersal percentiles were important in all data sets, while $R_0$ and $\rho$ were occasionally important. $\lambda$ was never significant.

In the stepwise regressions, the 99.5 dispersal percentile explained a large amount of variation in $s^*$ in all data sets (58-97%) (Fig RobsallSvsD995, S vs D995 from all data, Fig RobsellSvsD995, S vs D995 from selected data). Other, demographic, variables were rarely important and only explained a small amount of variation (¡ 5%). Therefore, variation in $s^*$ was almost solely related to variation in the dispersal kernel, contrasting with $c^*$, for which demography and dispersal were equally important. BLAH ABOUT WHY THIS IS SO.
Figure 12: INSERT Fig RobsallSvsD995, S vs D995 from all data

Figure 13: INSERT Fig RobsellSvsD995, S vs D995 from selected data
5 Exploring the dispersal kernel

Estimates of wavespeed and other aspects of invasion depend on the dispersal kernel or, more accurately, on an estimate of the dispersal kernel. Estimating dispersal kernels is an important problem with its own large literature (e.g., refs.). As with most estimation problems, there is usually a multiplicity of methods to decoricate a feline. Thus the results of any specific study will be influenced by the choice of data and methods of estimation. Here we want to explore some studies in which we can compare results using different approaches.

Five species provide the opportunity to investigate the effects of contrasting approaches to kernel estimation. These included one monocarpic perennial (nodding thistle, *Carduus*), two shrubs (scotchbroom and gorse, *Cytisus* and *Ulex*), one tree (long-leaf pine *Pinus* and one beetle (a rolled leaf hispine, *Cephaloleia*).

Fourteen species provide contrasting sets of field data on dispersal (whether differences in our data set are due to reality or to field methodology is indicated in parentheses following the name of each species). The plants span a range of life forms, including one annual, yellow rattle (*Rhinanthus*) (reality); one monocarpic perennial, nodding thistle *Carduus* (methodology); two long-lived polycarpic perennials, a Mexican member of the prayer plant family (*Calathea ovandensis*) (reality) and large-flowered trillium (*Trillium*) (reality); two shrubs, dwarf gorse *Ulex* (reality) and scotchbroom *Cytisus* (both reality and methodology); and three trees, red maple (*Acer*) (reality), long-leaf pine (*Pinus*) (methodology), and red oak (*Quercus*) (reality). The animals include four birds, Gosshawk (*Accipiter nisus*) (reality: spatial and stage-specific); Buzzard (*Buteo*) (reality); Pied flycatcher (*Ficedula*) (reality); and House sparrow (*Passer*) (reality).

5.1 Parametric and nonparametric estimators

We begin by considering the choice between parametric and nonparametric estimates of the dispersal kernel.

Say something in general about the choices involved here. The advantage of a parametric formulation is that it extrapolates beyond the observed data to provide an estimate of dispersal probability over the entire support of the function chosen to describe the kernel. The disadvantage is that it extrapolates beyond the observed data ....

5.1.1 Fitting parametric functions

Is there anything general we want to say here; perhaps just list some of the functions that have been used, and cite descriptions of methods (moments, maximum likelihood, Bayesian) that have been used to estimate them.

5.1.2 The empirical estimate of the moment generating function

Explain briefly how this works, how to deal with 1-d and 2-d data, translating histograms into kernels, resampling from histograms.

5.1.3 Examples

Describe some examples where wave speed is estimated from different data or from the same data analyzed in different ways, showing the extent of the differences in $c^*$. 22
Conclusion probably ends up being that if different estimators give kernels that differ in their tails, the effect on $c^*$ is likely to be large (relate back to the importance of the tails of the kernel in the previous section, and ahead to the LTRE section).

5.2 Compound kernels and multiple dispersal mechanisms

Almost any dispersal process is more complex on close examination than it appears at first sight. Assumptions about basic dispersal processes (e.g., diffusion and advection) can be elaborated to arrive at parametric kernels (Neubert et al. 1995). More detailed aerodynamic considerations can be used to generate kernels for wind-dispersed seeds (Nathan et al. 2002). One particularly interesting case occurs when two (or more) different mechanisms combine to bring about dispersal. This leads to a compound dispersal kernel that must be constructed from the individual mechanisms. Neubert and Caswell (2000), for example, constructed very simple compound kernels to explore a hypothetical mixture of seed dispersal by falling off the plant and by floating for teasel, and a not-so-hypothetical mixture of dispersal by different, and differently mobile, ant species in Calathea ovandensis.

Here we explore several cases where seeds are dispersed by a mixture of ballistic and ant dispersal.

\textbf{this description needs to be made more specific, including actual description of the kernel construction and tabulation of the results} – HC Our data includes several examples that investigate the relative contributions of biotic and abiotic dispersal to wave speed. In particular, the effects of ants as seed dispersal agents was investigated for two leguminous shrubs (one highly invasive) and two forest understory herbs (one tropical and one temperate).

The two shrubs, scotchbroom (Cytisus) and dwarf gorse (Ulex), have seeds that are ballistically dispersed first and then they are picked up by ants. The ballastic dispersal is accomplished through a particular “behavior” of the seed pod when it opens. The ant dispersal occurs because the seeds bear an oily appendage that serves as an attractant and reward for ants. The dispersal kernel for each process was estimated independently by experimental work. The two dispersal kernels were then combined into a composite by a convolution (see the section on dispersal kernel). The effects of ants on dispersal was determined by comparing the wave speed from the model that included ballistic dispersal alone to the wave speed from the model that included the composite kernel. For the invasive scotchbroom (Cytisus), ants increased the wave speed 1.4 fold and for the non-invasive dwarf gorse (Ulex), ants increased the wave speed 2.8 fold. These analyses indicate that ants are important to the spread of the population. However, for one of these plants, scotchbroom, a different kind of approach to the same question gave a different answer. This second analysis of the effects of ants was done because there was an additional kind data: the observed distribution of seedlings that had arisen in the field from the combination of both dispersal processes occurring together naturally. The wave speed calculated from this estimation of the combined dispersal process was not generally higher than that calculated for the ballistic process and this analysis leads to the conclusion that ants are not important to the spread of the population.

The two forest herbs depend upon ants for dispersal, producing an oily appendage on seeds to attract and feed the ants, without any other mechanism for dispersal. These studies address the question of the importance of ants in a different way than the shrub studies. The core of these analyses was empirical data on the distances that seedlings were displaced under two contrasting conditions: strong interaction with ants and weak interaction with ants. In the temperate forest
herb, the large flowered trillium \((Trillium)\), there was a natural experiment. One year was very rainy and there were very few ants. In another year of much better weather, there were lots of ants. There was a 2-fold higher wave speed with abundant ants than in the absence of ants. In the tropical forest herb, the Mexican member of the prayer plant family, \((Calathea ovandensis)\), there was an experimental manipulation of the reward; the oily appendage was stripped from seeds or left intact. There was a 2-fold higher wave speed with intact ant rewards than in the absence of the reward, holding demography constant. For this species, one additional comparison was possible because empirical data also was available on the demographic fates of the seeds with and without rewards. Wave speed calculated for the combined effects of ant rewards on the dispersal kernel and on the demography indicated a 3-fold increase due to strong interactions with ants. In summary, these examples illustrate the potential of the model to reveal interesting effects of a variety of dispersal vectors on population spread.

6 Prospective perturbation analysis

Invasion wave speed depends on demography and dispersal. Changes in either the demographic rates or in the distribution of dispersal distances thus produce changes in the wavespeed, and perturbation analysis explores these changes. Prospective perturbation analysis (Caswell 2000) calculates the partial derivative of \(c^*\) to a parameter, holding all other parameters constant. This partial derivative is called the sensitivity of \(c^*\). The corresponding quantity giving the proportional derivative of \(c^*\) to a proportional change in the parameter is called the elasticity of \(c^*\). Retrospective perturbation analysis (Caswell 2000) decomposes an observed difference in \(c^*\) into contributions from the demographic and dispersal parameters. We begin with results for sensitivity and elasticity analysis, and address retrospective analyses later, in Section ??.

6.1 Sensitivity and elasticity of \(c^*\)

Demographic analysis has been greatly extended by the use of the sensitivity and elasticity (i.e. \(\lambda\) to changes in the vital rates (Caswell 1978, 2001). In this section, we present formulae for the sensitivity and elasticity of \(c^*\), the asymptotic invasion wave speed, to changes in the entries of the matrix \(A\) and to changes in the dispersal parameters. In the context of the models we examine, the parameter changes represent changes in the life history. But there are other, equally compelling reasons for a sensitivity analysis of this sort. For example, errors in estimating the parameters result in errors in \(c^*\). The most important errors will be those in the parameters to which \(c^*\) is most sensitive. Information on the sensitivity of \(c^*\) to changes in the parameters can thus be used to design sampling procedures that maximize the precision of the estimates of the most critical parameters. Sensitivity analyses of invasion wave speeds may also be valuable in the evaluation of management strategies for the control of invasive species (c.f. Sharov and Liebhold 1998).

Neubert and Caswell (2000) derived formulae for the sensitivity of \(c^*\) to changes in the demographic parameters \(a_{ij}\):

\[
\frac{\partial c^*}{\partial a_{ij}} = \frac{m_{ij}}{s^* \rho_1} \frac{\partial \rho_1}{\partial h_{ij}}.
\]
and the elasticity of $c^*$ to changes in the demographic parameters

$$\frac{a_{ij} \partial c^*}{c^* \partial a_{ij}} = \frac{1}{\ln \rho_1} \left[ \frac{h_{ij} \partial \rho_1}{\rho_1 \partial h_{ij}} \right]. \quad (23)$$

The quantities $m_{ij}$, $\rho_1$, $h_{ij}$ and their derivatives are all functions of $s$; in equations (22) and (23) they are all evaluated at $s = s^*$.

Neubert and Caswell (2000) also calculated the sensitivities and elasticities of $c^*$ to changes in the dispersal parameters. Suppose that the kernel $k_{ij}$ depends upon a parameter $\alpha_{ij}$. The sensitivity of $c^*$ to $\alpha_{ij}$ is

$$\frac{\partial c^*}{\partial \alpha_{ij}} = a_{ij} s^* \frac{m_{ij} \partial \rho_1}{\rho_1 \partial h_{ij}}, \quad (24)$$

and the elasticity is

$$\frac{\alpha_{ij} \partial c^*}{c^* \partial \alpha_{ij}} = a_{ij} \alpha_{ij} s^* \frac{m_{ij} \partial \rho_1}{\rho_1 \ln \rho_1 \partial \alpha_{ij} \partial h_{ij}}. \quad (25)$$

where again $m_{ij}$, $\rho_1$, $h_{ij}$ and their derivatives are evaluated at $s = s^*$. (This corrects a typographical error in equation (29) of Neubert and Caswell (2000).)

In each of these four formulae we use the well-known eigenvalue sensitivity formula to evaluate

$$\frac{\partial \rho_1}{\partial h_{ij}} = \frac{v_i w_j}{\langle v, w \rangle}. \quad (26)$$

Here $w$ and $v$ are the right and left eigenvectors of $H(s^*)$ corresponding to $\rho_1(s^*)$ and $\langle \cdot \rangle$ denotes the scalar product (Caswell 1978).

The sensitivity of $c^*$ to changes in dispersal requires the derivatives of the moment generating function of the dispersal distribution. The nature of these derivatives depends on the nature of the dispersal kernel. A parametric function will contain one or more parameters that can be interpreted as describing a “typical” dispersal scale (the mean, the median, or some other index of location). Differentiating $m_{ij}(s)$ in (??xx) with respect to these parameters characterizes the response of wavespeed to changes in this characteristic dispersal scale. When the nonparametric empirical moment-generating function is used, each observed dispersal distance can be treated as a parameter (one of the order statistics of the distribution; Caswell et al. 2002).

It is intuitively obvious that increases in any of the $a_{ij}$ will increase both $\lambda$ and $c^*$. The surprising finding of Neubert and Caswell (2000) was that the sensitivities and elasticities of $c^*$ to the $a_{ij}$ are very highly correlated with the corresponding sensitivities or elasticities of $\lambda$. That is, if changes in $a_{ij}$ produce large changes in $\lambda$, then they are very likely to produce large changes in $c^*$.

6.2 Results: sensitivity and elasticity of wave speed

6.3 Perturbation analysis of $c^*$ and $\lambda$

6.3.1 Variation in structure of $c$ elasticity vs $\lambda$ elasticity

We investigated the relative sensitivities of wavespeed and population growth rate to demographic transitions, within species under different conditions. To summarize and be able to compare across matrices, we started by calculating three sums with respect to the elasticity of population growth
rate, $\lambda$: a sum over fecundity entries, a sum over stasis transitions and a sum over growth transitions. We further calculated the same kinds of sums for the elasticity of wavespeed, $c$. The relative importance of particular demographic transitions for $\lambda$ varies among populations (as measured by elasticities). It is often the case that as $\lambda$ increases, transitions involving early life history stages increase in elasticity. This pattern is seen in our examples ($Acer rubrum$, $Cytisus scoparius$, $Pinus palustris$, $Quercus rubra$). For plants but not animals, we found that elasticity of $c^*$ to fecundity and growth transitions were higher than elasticity of $\lambda$, while elasticity of $c^*$ to stasis transitions were lower. We propose that this difference is due to differences in which stages disperse. In plants the young disperse and rapid growth leads to earlier production of the dispersing propagules; stasis may aid in population growth while contributing little to population expansion. In contrast, the adults are the dispersing stage for animals, thus stasis of adult stages may contribute just as much to population expansion across space as it does to in situ population growth. For several plant species with multiple demographic matrices ($Acer rubrum$, $Cytisus scoparius$, $Pinus palustris$, $Quercus rubra$), the discrepancy between growth and fecundity elasticities to $\lambda$ and growth and fecundity elasticities to $c^*$ increases as the $\lambda$ of demographic matrices increases (see figure JHRLelas).

7 Contrasting demographic and dispersal data

I am not sure about where these comparisons will eventually go, so I’m putting them in their own little section for now –HC

Seventeen species provide contrasting sets of demographic data (the type of contrast is indicated in parentheses after each species name). Plant examples include one annual, yellow rattle ($Rhinanthus$) (habitat: haycut or not); two monocarpic perennials, nodding thistle ($Cirsium$) (Habitat: wet vs dry) and spear thistle ($Cirsium$) (Habitat: grazing light or heavy); two long-lived polycarpic perennials a Mexican member of the prayer plant family ($C. ovandensis$) (experimental: seed fates for seeds dispersed by ants vs seed fates for undispersed seeds) and the large flowered trillium ($Trillium$) (spatial); two invasive shrubs, shoebutton Ardisia ($Ardisia$) (pooled, and population at the front of the invasion), and scotchbroom ($Cytisus$) (temporal, spatial); one non-invasive shrub ($Ulex$) (habitat: mixed vs solo); and three trees, red maple ($Acer$) (pooled and spatial), long-leaf pine ($Pinus$) (Habitat), red oak ($Quercus$) (pooled and spatial). Animal examples include five birds, Goshawk ($Accipiter genitilis$) (spatial), Sparrow hawk ($Accipiter nissus$) (spatial), Buzzard ($Buteo$) (spatial), Pied flycatcher ($Ficedula$) (spatial), and House sparrow ($Passer$) (spatial), and one mammal the muskrat ($Ondatra$) (temporal: contrast in hunting).

7.1 Interaction effects: crossing demography with kernels

For some species, we have multiple demographic matrices and multiple kernels. In these cases what is the relative effect of the kernel in one demographic condition vs in the other condition?

We have a set of figures that illustrate these comparisons. Since we have more than one dispersal case per each demographic matrix, we can examine how changing the kernel affects wave speed for each matrix and then compare the magnitude of the effect across the range of matrices. A common feature we have seen in all these figures is that as $\lambda$ increases, the relative effect of the kernel also increases.
Table 5: The species for which factors are crossed and it is possible to examine interaction effects on wave speed.

<table>
<thead>
<tr>
<th>Species</th>
<th>matrices</th>
<th>dispersal data</th>
<th>kernel estimates</th>
<th>cases</th>
</tr>
</thead>
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<td>Carduus</td>
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<td></td>
<td>4</td>
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<td>Trillium</td>
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<td>2</td>
<td></td>
<td>4</td>
</tr>
<tr>
<td>Cytisus</td>
<td>8</td>
<td>2</td>
<td>4</td>
<td>32</td>
</tr>
<tr>
<td>Ulex</td>
<td>2</td>
<td>3</td>
<td>3</td>
<td>6</td>
</tr>
<tr>
<td>Pinus</td>
<td>13</td>
<td>2</td>
<td>2</td>
<td>39</td>
</tr>
<tr>
<td>Ficedula</td>
<td>2</td>
<td>2</td>
<td></td>
<td>4</td>
</tr>
<tr>
<td>Passer</td>
<td>2</td>
<td>2</td>
<td></td>
<td>4</td>
</tr>
</tbody>
</table>
7.2 Density?
The relationship between density, $\lambda$ and wave speed is of general interest because wave speeds are thought to be governed by low-density demography when population growth is not limited by intra-specific competition. We therefore expect that demographic matrices from populations at low densities near the front of an invasion yield greater wave speeds. There are three relevant examples in our data set, two invasive plants and one invasive bird species. In all cases, wave speeds and $\lambda$’s from populations close to the leading edge of an invasion front were uniformly higher than those of more established populations (Ardisia elliptica, Cytisus scoparius) or within native ranges (Sternus vulgarus).

Density may or may not be correlated with population growth rate, since many features of the life history contribute to variation in population growth. Among the species for which we have data, only longleaf pine (Pinus palustris) provided the opportunity for us to examine the effects of density while holding several other factors constant. Population growth rates were higher for low density stands; however, the differences were not great. For red maple and red oak (Acer rubrum, Quercus rubra), there was no relationship between stand density and $\lambda$, or stand density and wave speeds. We probably did not find a strong effect of density on $\lambda$ and wave speeds for these species because their demographic matrices are parameterized from long-established populations where stand density is influenced by environmental conditions.

8 Retrospective perturbation analysis

8.1 LTRE analyses of wave speed

Many of the studies reviewed here (give the numbers) have observations on two or more populations, experiencing different environmental conditions. Those conditions have effects on the wavespeed, which can be characterized by differences in wavespeed between, or variances in wavespeed among, populations. In the demographic context, such studies have been called life table response experiments (LTREs; Caswell 1989a, 1996a,b, other refs), treating both experiment and life table in a broad sense. Caswell et al. (2002) extended the idea further, to comparisons between “treatments” (any kind of comparative observation, whether it involves manipulation or not) in which the response variable is a “life table” including both the demographic rates and dispersal distributions.

A LTRE has two complementary goals. The first is to synthesize all the diverse stage-specific effects of the treatments into a single biologically relevant index. Population growth rate $\lambda$ serves this purpose in demographic studies; the wave speed $c^*$ does so in studies involving both demography and dispersal. The second goal is to decompose the differences in the index into contributions from the treatment effects on each of the stage-specific rates. Experience with such analyses has conclusively refuted the naive expectation that the biggest effects on the vital rates makes the biggest contribution to the effects on $\lambda$ or $c^*$ (Caswell 2001, Caswell et al. 2002). Instead, the most important contributions typically come from small effects on parameters to which $\lambda$ or $c^*$ is very sensitive.

8.2 LTRE designs

In analogy with standard analysis of variance theory, the decomposition analysis can be divided into fixed, random, and regression designs (Caswell 1996a, 2001), of which we will consider only
the first two here.

**Fixed designs** In a fixed design, the specific treatment conditions observed are of interest. Suppose that there are \(N\) treatments, yielding demographic matrices \(A_1, \ldots, A_N\) and dispersal distributions characterized by parameter vectors \(\alpha_1, \ldots, \alpha_N\). These data yield wave speeds \(c_1^*, \ldots, c_N^*\).

Choose a reference condition relative to which the performance of other treatments is to be measured; denote this treatment by \(r\). This might be the mean, or a control treatment, or some other particularly interesting baseline condition. Then, to first order, the wave speed in any treatment \(h\) can be approximated as

\[
c_h^* \approx c_r^* + \sum_{i,j} \left( a_{ij}^{(h)} - a_{ij}^{(r)} \right) \frac{\partial c^*}{\partial a_{ij}} + \sum_k \left( \alpha_k^{(h)} - \alpha_k^{(r)} \right) \frac{\partial c^*}{\partial \alpha_k} \tag{27}
\]

where the derivatives are evaluated at the mean of \(\bar{A}_h\) and \(\bar{A}_r\) and of \(\bar{\alpha}_h\) and \(\bar{\alpha}_r\). The terms in the first summation are the contributions of differences in the demographic parameters to differences in \(c^*\). The terms in the second summation are the contributions of differences in the dispersal parameters to differences in \(c^*\).

**Random designs** In a random design the treatment conditions are (or, more likely, are treated as) a random sample of conditions; what is of interest is not the results of specific treatments, but the variability among treatments (Brault and Caswell 1993). The variance among treatments is given, to first order, by

\[
V(c^*) \approx \sum_{ij,kl} \frac{\partial c^*}{\partial a_{ij}} \frac{\partial c^*}{\partial a_{kl}} \text{Cov}(a_{ij}, a_{kl})
+ \sum_{m,n} \frac{\partial c^*}{\partial \alpha_m} \frac{\partial c^*}{\partial \alpha_n} \text{Cov}(\alpha_m, \alpha_n)
+ \sum_{i,j,m} \frac{\partial c^*}{\partial a_{ij}} \frac{\partial c^*}{\partial \alpha_m} \text{Cov}(a_{ij}, \alpha_m) \tag{28}
\]

The terms in the first summation are contributions, to \(V(c^*)\), from the covariances among the demographic parameters; those in the second summation are the contributions from the covariances among the dispersal parameters; those in the third are the contributions from the covariances between the demographic and dispersal parameters. All the derivatives are evaluated at the mean \(\bar{A}\) of the dispersal parameters and the mean \(\bar{\alpha}\) of the dispersal parameters.
8.3 Examples

8.3.1 Fixed designs

8.3.2 Random designs

9 The importance of long-distance dispersal

10 Discussion

11 Appendix 1. Species descriptions

11.1 Temperate deciduous trees

The demographic transitions and seed dispersal distances of the six temperate forest tree species studied were estimated from long-term studies of tree populations in the Southern Appalachians (Clark et al. 1998, Beckage et al. 2000, Wyckoff and Clark 2000, HilleRisLambers et al. in prep). The data was collected from secondary forests (approximately 90 years old) at the Coweeta Hydrologic Laboratory, in Western North Carolina. Species include *Acer pensylvanicum*, *Acer rubrum*, *Betula spp.*, *Fraxinus americana*, *Liriodendron tulipifera* and *Quercus rubra*.

Because fecundity, growth and survival transitions of the six tree species considered here are estimated in the same manner, we summarize data collection and parameter estimation here. All data were collected from five 80 by 80 meter vegetation plots established in 1993. Trees in these plots are tagged and identified, and were recensused for growth and mortality in 1995, 1996, and 1998. One hundred seed traps in plots were emptied multiple times a year to estimate fecundity (from 1991 to 1998). Seed bank densities were estimated from soil cores removed annually from 1995 until 1999. Finally, tagged seedlings in 100 1 m by 1 m seedling quadrats (paired with seed traps) were visited annually (in 1996, 1997, 1998, and 1999) to determine seed germination, first year seedling survival and second year seedling survival.

A Lefkovitch matrix \( A \) was constructed for each species, with a projection interval of one year (see Figure? for an example life-cycle graph of *Acer pensylvanicum*). The number of stages (see Table 3.?1) depends on whether a species has a persistent seed bank, and the maximum size class (determined by the largest tree of that species recorded in North Carolina). Stages include a seed bank stage (stage 0 -when applicable), a first year seedling stage, a \( j \), first year seedling stage, a (non-reproductive) sapling stage (defined as trees between 1 cm and 5 cm in diameter), and several adult tree stages, each adult stage encompassing 10 cm diameter range in size (e.g. 5-15 cm dbh, 15-25 cm dbh, etc).

11.1.1 Fecundity transitions

For seed banking species, the first row of our transition matrix is the seed bank. Individuals in the seed bank are produced by each adult class \( j \), and depends on size-specific seed production (\( ss \) in units of seeds per basal area), the size of the contributing trees (\( d_i \), the midpoint of the diameter size class \( j \), and the proportion of those seeds entering the seed bank (\( p_b \));

Equation here (1)

Because seed production likely saturates with size, we assumed that seed production of trees larger than the maximum size observed at our research sites (Table 3.?1) is constant. Fecundity
(ss) was parameterized from a seed dispersal model fit to seed density data collected from seed traps in the mapped stands (for details, see Clark et. al 1998, Clark et. al 1999). The proportion of dispersed seeds entering the seed bank \( (p_b) \) was estimated from a model relating seed survival in the soil to annual seed rain inputs (HilleRisLambers et al. in prep).

The first or second row (depending on whether species have seed banks) of our transition matrix represents first year seedlings. For species without a persistent seed bank, seed production \( (ss) \) is scaled by the proportion of seeds that germinate and enter the first year seedling class \( (p_g) \) and diameter of the contributing size class \( (d_i) \);

\[
\text{Equation here (2)}
\]

Germination \( (p_g) \) was determined by dividing first year seedling densities by seed densities (in adjacent seed traps and in seed banks from adjacent soil cores) from the previous year.

For seed banking species, first year seedling production is determined by seed production \( (ss) \), seed viability \( (v) \), the diameter of the contributing size class \( (d_j) \), and the proportion of seeds that do not enter the seed bank but survive to become first year seedlings \( (p_g) \);

\[
\text{Equation here (3)}
\]

For seed banking species, the probability of germination was estimated by dividing first year seedling densities in seedling quadrats by available seed densities; both from previous years seed measured in seed traps but not entering the seed bank (scaled by seed viability \( v \)) and from seeds in the seed bank (scaled by seed mortality \( m \)). Annual mortality of seeds in the soil \( (m) \) was determined from a model relating annual seed rain inputs to seed bank densities through negative exponential decay (HilleRisLambers, Clark and Lavine in prep). Seed viability \( (v) \) was estimated from data collected by the National Tree Seed Testing laboratory.

11.1.2 Survival transitions (S)

Survival of seeds in the soil was estimated from a model relating seed bank densities to annual soil seed inputs (HilleRisLambers, Clark and Lavine in prep). The loss of seed viability in the soil was assumed to be constant, yielding an estimate of annual seed mortality \( m \). Seed survival (the first element of the diagonal for seed banking species) is therefore;

\[
A_{00} = 1 - m
\]

(29)

All first year seedlings (that do not die) enter into the first year seedling class, thus annual survival of first year seedlings \( (A_{11}) \) was set at 0. Survival of first year seedlings \( (A_{22}) \) was estimated from tagged individual in 100 1 m2 seedling quadrats, censused from 1997 to 1999. Sapling survival \( (A_{33}) \) was also estimated from tagged individuals in the 5 80 by 80 meter plots, censused from 1993 to 1998.

In spite of our spatially and temporally extensive data set, (6 years of data from 32,000 m²), there was simply not enough data to determine size-specific survival of adult tree classes. Instead we based survival transitions for adult size classes on an overall survival rate (determined from survival probabilities of all 5 cm trees in our 80 by 80 meter plots), the size distribution of the trees at our plots (as described by parameters \( a \) and \( b \) of a Weibull distribution), and the covariance between growth rates and tree size;

Missing equation here (5)
11.1.3 Growth transitions (G)

Growth transitions (the subdiagonal of the matrix) were estimated in the following manner. The germination of seeds from the seed bank (the first element of the second row for seed banking species $A_{10}$) is $p_g$ (see equation 2). All first year seedlings become $\dot{z}$ first year seedlings, this transition ($A_{21}$) is therefore determined by the survival of first year seedlings from one year to the next (estimated from recensused individuals). Growth of $\dot{z}$ first year seedlings into the sapling class ($A_{32}$) was estimated by dividing the density of saplings by the density of $\dot{z}$ first year seedlings. Finally, the growth of adult trees from one size class to the next was estimated from the covariance between growth and size, integrating over the current size distribution (as described by parameters $a$ and $b$ of a Weibull distribution).

Missing equation here (6)

11.2 Striped maple *Acer pennsylvanicum*

Striped maple (*Acer pennsylvanicum*, family Aceraceae) is an understory tree found primarily in northeastern deciduous forests. It is a small tree (maximum height about 15 meters Burns and Honkala 1990), and never a major component of temperate forests. Striped maple is slow-growing and shade-tolerant. Its southern range limit is in the Southern Appalachians, where it is found (primarily at higher elevations) together with other species common in New England, e.g. sugar maple, american ash, sweet birch and basswood. The species is temporally dioecious, in that it switches sex from year to year. Smaller individuals are more often male than female, and trees that produce seeds one year generally do not the next. Striped maple produces winged fruits in pairs (called samaras) that are primarily dispersed by wind. There are reports of some seeds being dispersed long distances over the snow in the winter.

11.3 Red maple *Acer rubrum*

Red maple (*Acer rubrum*, family Aceraceae) is one of the most wide-ranging tree species found in eastern North America. It ranges from Central Florida to southern Newfoundland, the Coastal plain of the Eastern Seaboard west into Texas and Minnesota. It is a medium sized tree, generally 27 meters in height and 75 cm in diameter (Burns and Honkala 1990). It is found in a wide variety of soil and forest types. Although it is ubiquitously common in temperate forests, it was not a significant component of pre-settlement forests, and its recent abundance is generally thought to be the result of disturbance (Abrams 1998). Red maple is sometimes considered an early-successional tree species, as it tends to quickly colonize abandoned agricultural fields. This is consistent with its early reproductive maturation and association with disturbance. However, this species is also found as a component of late-successional forests. Like striped maple, this species is dioecious and can switch sex from year to year, although this occurs with much lower frequency than for striped maple. Seed crops are usually high, and seeds are wind-dispersed samaras just like striped maple seeds. Unlike most temperate deciduous trees, seeds are dispersed in the spring, and either germinate immediately or remain viable in a persistent seed bank (Marquis 1975, Peroni 1995, HilleRisLambers et. al in prep). Because *Acer rubrum* is abundant in our plots, we also estimate wave speeds from plot-specific estimates of dispersal and juvenile growth and survival.
11.4 Birch *Betula allegheniensis* and *lenta*  
Both yellow and black (*B. allegheniensis* and *B. lenta*, family *Betulaceae*) birch reach their southern-most distribution in the Southern Appalachians, black birch occurs as far north as Maine, yellow birch reaches Newfoundland. Both species are medium-sized, but can be over a meter in size. However, yellow birch is restricted to upper elevations in the Southern Appalachians, and tends to be found in moister sites. Both species are considered mid-successional - they have small seeds, high seed production and are shade-intolerant as seedlings. Both species also have a persistent seed bank (Marquis 1975, HilleRisLambers et. al in prep), and require mineral soil for successful seedling establishment. Both species are monoeocious, and produce winged nutlets throughout the fall that are wind-dispersed, sometimes great distances over the snow. Because we do not differentiate yellow and black birch at early life-history stages, and because they have very similar life-histories, we constructed a common matrix for these two species.

11.5 White ash *Fraxinus Americana*  
White ash (*Fraxinus americana*, family *Oleaceae*) is a common, but usually not dominant, medium-sized tree of eastern forests from North Florida to Nova Scotia. Although often considered early-successional, it is not always common in abandoned agricultural fields because it requires moist, fertile sites for growth. White ash is dioecious, and produces a large crop of wind-dispersed seeds every two to three years. Seeds have long samaras which allow them to be dispersed over long distances.

11.6 Tulip tree *Liriodendron tulipifera*  
Tulip tree (*Liriodendron tulipifera*, family *Magnoliaceae*), is a common component of southeastern forests. It ranges from central Florida into Michigan, generally growing on moist fertile sites. It is one of the tallest (up to 60 meters in height) and largest (2.5 meters diameter) eastern trees. This tree is considered mid-successional, because although it is often found in old-growth forests (e.g. Joyce Kilmer in North Carolina), its seedlings and saplings need light to successfully establish. Tulip tree maintains a persistent seed bank, and seeds remain viable in the soil for up to 5 years (Clark and Boyce 1964, HilleRisLambers et. al in prep) before germinating. Tulip poplar is monoeocious, and produces large numbers of wind dispersed seeds with samaras. Seeds can be dispersed long distances by wind.

11.7 Northern red oak *Quercus rubra*  
Red oak (*Quercus rubra*, family *Fagaceae*) is common in most eastern deciduous forests, ranging from southern Alabama to Nova Scotia. It (and other oaks) have replaced the American Chestnut (*Castanea dentata* removed from the eastern forests as a result of the chestnut blight) as the most abundant tree species in eastern forests. Red oak is considered mid- to late successional, because although seeds do not require light for germination and seedlings are shade-tolerant, saplings and trees are relative fast growing. Seeds (large acorns) are produced in large crops every two to five years. Seeds are eaten and cached by a number of rodent and birds (e.g. squirrels, blue-jays), and eaten by many other animal species (deer, insects). Seeds are dispersed short distances when they drop from trees, and individual acorns can be further dispersed over very long distances if cached
by mammals or jays (Carter-Johnson and Webb 1989). Because Quercus rubra is abundant in our plots, we also estimate wave speeds from plot-specific estimates of dispersal and juvenile growth and survival.

Table here: Species and species traits incorporated in Lefkovitch matrices to calculate invasion speeds.

11.8 Carduus nutans nodding thistle

Carduus nutans is a Eurasian species of major economic importance in pasture systems. It has spread to N. and S. America, Australia and New Zealand. C. nutans is a monocarpic perennial. Plants overwinter either as seed or as rosettes. Flowering is vernalization, age and size dependent (Popay and Medd 1990). C. nutans is 20-200 cm tall with spiny winged stems. Flowering of C. nutans is completed by late June, and flowering heads are solitary, 1.5-4.5 cm in diameter, and usually nodding. Plants produce a large number of seeds per individual. Plants die after reproduction. Seeds are estimated to survive for up to 20 years in the soil. No vegetative reproduction has been reported.

Shea and Kelly (1998) developed stage-structured matrix models for C. nutans in New Zealand, using data from 8000 individuals, which were mapped at two sites (one wet: Midland and one dry: Argyll) on the South Island. Plants were classified as seed (in the seed bank for ≤ 1 year), small, medium and large plants. The life cycle diagram is shown in Fig x; transitions are annual (a yearly projection interval).

Only reproductive transitions (seed production) are involved in dispersal. Seeds are usually wind dispersed, but the pappus detaches easily (possibly as a function of age, climate and physical impact, Delahunty 1962), and seeds rarely move more than a few meters from the parent plant (Kelly et al. 1988). However, seed can also be dispersed by water, animals, and as a contaminant of agricultural seed. We focus in this case study on wind dispersal only, so our results are a conservative estimate of true spread rates. Dispersal kernels for this species in New Zealand were derived from two data sets. The first data set (Delahunty 1962) collected seeds for 7 days in sticky traps at right angles to a strip of thistles along the border of a paddock. Eight rows of collecting tins (2 inches in diameter) were set up at 1, 2, 4, 8, 16, 32 and 64 feet (see fig x in dispersal data set-up.ppt). The exponential shape parameter was estimated from data, using max likelihood methods, and used to generate an exponential moment generating function. The second data set (McCallum 198?) collected seeds in contiguous bins (up to 2m) in the direction of the prevailing wind on either side of 4 isolated plants. Data at equal distances on either side of the target plant were lumped (so we have seed number at distance, not displacement) (see fig xx in dispersal data set-up.ppt). These data were collected along a transect in a 2-D world, so need to be marginalized to be useful in a 1-D model. Data were converted to densities and used to derive an empirical moment generating function: a histogram of seed densities. From this a pdf was calculated and used in a Monte Carlo randomization to create many (10^5) seed displacements. These 2-dimensional displacements were converted to distances along a single dimension (assuming symmetrical dispersal) to create the mgf. We investigated all four combinations of the two matrix models, and the two dispersal data moment generating functions.
11.9 *Cytisus scoparius* Scotch broom

*Cytisus scoparius* is a large shrub in the legume family. It is native to Europe and the British Isles and has been introduced into North America, South America, Australia, and New Zealand, where it is considered a noxious invasive species (Hosking et al 1996, Bossard 2000, Paynter et al 1998). *C. scoparius* has no form of clonal growth and is entirely dependent on seed set for reproduction. The population dynamics and dispersal of *C. scoparius* were studied in Washington State, USA, where the plant invades both urban old fields and relatively undisturbed glacial outwash prairies (Parker 2000, Parker and Reichard 1997). Demographic parameters were estimated at the edges of expanding invasive patches.

The Lefkovitch matrix for *C. scoparius* was constructed using a combination of life history and size criteria. The matrix has 7 stages: seeds, seedlings (first year), juveniles, and four size classes of adults (see Parker 2000 for details). Seeds include both newborns and dormant seeds; thus fecundities are calculated as the number of seeds produced next year by a plant in a given stage this year. The projection interval was one year, with a census performed at the end of the dry season, after all seeds had fully matured.

*C. scoparius* has ballistic dispersal, in which fruits dry and dehisce with an explosive action, sending seeds away from the plant. Propagules, which include eliasomes (lipid-rich bodies attached to the seeds), are then secondarily dispersed by ants. Dispersal was quantified in two ways (Parker 1996). Ballistic dispersal was measured around an isolated adult plant by putting out a 1m x 8m strip of plastic divided into .5m sections using Tanglefoot. We calculated the moment-generating function for ballistic dispersal using the famous histogram approach, collapsing to 1D using simulation. Ant dispersal was measured by putting out groups of seeds in an area without *C. scoparius* and mapping seedlings after germination. The combined effect of ballistic dispersal plus ants was measured by cutting down mature, dispersing adult plants and setting them out into the same area using rebar and cable ties. Seedlings were mapped after germination. We calculated wave speeds for ant dispersal and ballistic + ant dispersal using a simple empirical moment generating function, collapsed to 1D by besselizing. In addition to the empirical estimates of ballistic + ant dispersal, we calculated an analytical measure of the total dispersal by taking the Hadamard product of the matrices of moment generating functions for ballistic dispersal and ant dispersal. We present a comparison between *C. scoparius* invasion in urban old-fields (slowest-growing population) and in outwash prairies (fastest-growing population), using four estimates of dispersal: 1) ballistic dispersal only, 2) ant dispersal only, 3) ballistic and ant dispersal measured empirically, and 4) ballistic and ant dispersal measured separately and combined in a composite moment generating function.

11.10 *Ardisia elliptica*

*Ardisia elliptica* (Myrsinaceae) is an invasive tropical, shade-loving, understory shrub, native to SE Asia. It is known to be invasive in Hawaii, S. Florida, Okinawa and Jamaica. The data in the present study are from a study site in subtropical hardwood forest on a limestone substrate the Everglades National Park, S. Florida (Hole-in-the-Donut and Palma Vista Hammock). The history and locale of introduction of *A. elliptica* in the Park is known. The population is currently expanding outward from a dense mono-specific stand. Seeds are borne singly in fleshy fruits, which are attractive to vertebrates, especially catbirds and raccoons.

Six life history stages were used to characterize the population for a Lefkovich matrix model of population dynamics: seeds, seedlings, juveniles, pre-reproductives, small adults and large adults.
(Figure ardisia1). The time step was one year, December to December. Matrix entries come from censusing marked individuals in plots (Koop in prep). All individuals of non-seedling stages were marked. Seedlings were marked in smaller subplots. Fecundity estimates came from counting branches, which is a good predictor of fruit production. Germination was estimated from experimental seed bags in field (Koop in prep). Demographic data utilized here are mostly from the first transition year, however mortality of non-seed stages was estimated from pooled observations over three years.

(Figure ardisia1). Structure of the matrix model for *Ardisia elliptica*. Each nonzero entry in the matrix is indicated with a dot. Transitions at which dispersal occurs are additionally marked by a square around the dot.

To estimate a dispersal kernel, all individuals in an 85 x 60m grid were mapped to the nearest 1 m. Each square meter was considered a "seedling trap" and each reproductive adult was considered a potential source of seedlings. The number of branches is correlated with seed production and was used as a plant size estimator. Seedling dispersal is assumed to represent seed dispersal well, since seeds germinate readily. Only seedlings arising from bird or gravity dispersed seeds (ie only those NOT found in "raccoon piles"), were included in the estimation of the kernel. The most likely parent plant of each seedling was determined by fitting the distribution of seedlings was to a bivariate Gaussian kernel by the methods of Clark et al. (1999); the estimate of the distance parameter, $\alpha$ (Clark, 1999, equation 5b), was 17.44 m. In all, 16,213 seedlings and 655 reproductive plants were mapped and included in the analysis.

Two analyses of wave speed were carried out. Both analyses used the moment-generating function for the marginalized bivariate Gaussian kernel as estimated from the seedling trap grid. The analyses differed in that one used the pooled demographic data six populations, while the other used the demographic data from a single population, the one nearest to invasion front (Palma Vista Hammock).

11.11 *Cephaloleia fenestrata*

*Cephaloleia fenestrata* (Hispinae) is a host specific herbivorous beetle that lives and feeds on *Pleiochorya pruinosa* (Marantaceae), a large (up to 2.5 m) understory herbaceous monocot of tropical wet forests of Central America. It feeds mostly on young, tender rolled leaves that are borne from the central meristem of the patchily occurring hosts. A mark-recapture study of the metapopulation dynamics of the beetle was carried out in lowland, evergreen tropical wet forest at La Selva Biological Station, Costa Rica (Johnson in prep). Host plants at this site are usually in the flood plain of the river (Figure beetle1), in a fairly linear arrangement along the river. The adult beetles disperse from plant to plant and the movement is one-dimensional rather than two-dimensional in nature.

(Map of host plant patches).

(Figure beetle1). Host plant patches along the Saripiqui River.

Four life history stages were used to characterize the population for a Lefkovitch matrix model of population dynamics: eggs, larvae, pupae, adults (Figure beetle2). The time step for the model is 25 d (14.6 intervals per year). Matrix entries come from several kinds of data. First, all life stages found on plants at each of 14 censuses were counted; numbers of each stage were averaged over the 14 censuses to give an average stage-distribution. Stage duration data also came from
lab studies of eggs and pupa. Adult survival came from mark-recapture studies of 1,100 uniquely marked individuals during 1 year, within and among plants. Growth transitions were estimated from survival and stage duration, assuming a population growth rate of 1 (Caswell 2001). Fecundity estimates are from a colonization experiment (Johnson in prep).

To estimate the dispersal kernel, the distance beetles moved between censuses was determined from the x-y coordinates of the particular plant in which each beetle was found at each census during the mark-recapture study. (Check with Johnson on how distances were estimated when beetles were not captured at all censuses).

Three analyses of wave speed were carried out. The first analysis is the one that best captures the biology, but we present the other two for comparative purposes. The first analysis used the empirical moment-generating function for 1-d distances. The second used the empirical moment-generating function that marginalized the distances (equivalent to taking the x-coordinate of the radial distance) and assumed the observed distances were 2-d radial in nature. The third analysis used a parametric form of a probability density function for 1-d distances, specifically the La Place moment generating function (Neubert and Caswell 2001), in which the parameter, α was parameterized from the mean of the observed distances.

11.12 *Calathea micans*

*Calathea micans* (Marantaceae) is a polycarpic perennial ant-dispersed tropical forest herb of small stature (¡15 cm tall), commonly found from Peru to Mexico. The data in the present study are from a lowland, evergreen tropical wet forest at La Selva Biological Station, Costa Rica. Two kinds of flowers are produced: chasmogamous (CH) flowers on longer, erect stalks (¡ 10 cm) that open and require insect pollination to set fruit and cleistogamous (CL) flowers on short stalks (3 cm), borne at the base of plants that set fruit without opening (from selfing). This evergreen plant reproduces in both the wet and the dry season (LeCorff 1993). Seeds from both kinds of flowers bear oily arils and are dispersed by ants (LeCorff 1996).

Five life history stages were used to characterize the population for a Lefkovitch matrix model of population dynamics: CH seedlings (seedlings arising from seeds produced by chasmogamous flowers), CL seedlings (seedlings arising from seeds produced by chasmogamous flowers), juvenile vegetative plants, reproductive plants-with-new-shoots and reproductive plants-without-new-shoots. These stages were chosen because they have distinct fates/reproductive behavior (LeCorff 1993). The time step for the model is 6 mos (2 intervals per year). Since the demography varies seasonally, two matrices were characterized: one containing the transitions from Mar-Oct (the wet season) and one containing the transitions from Oct-Mar (the dry season). Transitions were estimated from data derived from marking and following fates of plants (N=600) in study plots from Oct 1990 - Mar 1991 and from Mar 1991 - Oct 1991 in a natural population, the Cordia Plantation site. Growth, survival and seedling recruitment were recorded as well as data on reproduction by plants.
with and without new shoots (J. LeCorff and C. Horvitz, unpublished). The seasonal matrices were combined into a single megamatrix model (Pascarella and Horvitz 1998, Tuljapurkar, Horvitz and Pascarella, in prep). This system is described by a 10×10 matrix, five life history stages and two habitat states. The habitat states cycle repeatedly, dry-wet-dry-wet, etc (Figure micans1). The growth rate from the megamatrix is for a 6 mo interval; squaring it gives the annual growth rate. This model is equivalent to the periodic model of Caswell and Trevisan (1994).

The original estimate of annual growth rate was slightly less than 1. Several parameters were altered from field observations to get an annual increase ¿1 in the population, to simulate low density conditions.

Figure micans1. Structure of the matrix model for it Calathea micans. Each nonzero entry in the matrix is indicated with a dot. Transitions at which dispersal occurs are additionally marked by a square around the dot.

To estimate dispersal kernels of CH and of CL seedlings, individual seeds were color-coded (distinguishing CL from CH) and placed in “depots,” allowing ants to redistribute the seeds. Five months later, seedlings were surveyed in circular plots around the depots. Since seed coats (bearing the intact color-coding) stay attached to seedlings, dispersal distances of each of the two kinds seedlings were easy to measure. There is no long-term seed dormancy; seeds germinate within 4-5 months. Radial distances and angles were recorded for each seedling (LeCorff, 1996).

One analysis of wave speed was carried out. We used the empirical moment-generating function that marginalized the distances (equivalent to taking the x-coordinate of the radial distance) and assumed the observed distances were 2-d radial in nature.

11.13 Calathea ovandensis

*Calathea ovandensis* (Marantaceae) is a polycarpic perennial ant-dispersed tropical forest herb of small stature (<40 cm tall), found only in southern Mexico and Guatemala. The data in the present study are from a lowland, seasonal forest at Laguna Encantada, San Andres Tuxtla, Los Tuxtlas region of Veracruz, Mexico. This plant is deciduous in the dry season, losing all above-ground tissue. Germination and new growth begins in the early rainy season, and reproduction peaks in the late wet season. Seeds bear oily arils and are dispersed by ants. There are two kinds of seed dormancy. Seeds are produced near the end of the rainy season; they are obligately dormant through at least one dry season, germinating after about 9 mos at the beginning of the next rainy season. Subsequently, enforced dormancy occurs and not all seeds germinate in the first year. In shady, cool conditions and in non-”el Nino” years, many seeds remain dormant, but viable for several years (Horvitz and Schemske 1994, 1995).

Nine life history stages were used to characterize the population for a Lefkovitch matrix model of population dynamics: new-seeds-on-plants, old-seeds-in-soil, seedlings, juveniles, pre-reproductives, and four size classes of reproductives, small, medium, large and extra-large, based on leaf area (Figure ovandensis1). This is one more stage than was previously used to model population dynamics of this species; the dispersal model requires separation of new seeds from dormant seeds. Matrix entries come from marking and following fates of plants and counting seed production in natural populations in four plots over five years. Seed dormancy and germination parameters came from several field experiments. The demographic transitions chosen for this analysis were based on the data of a plot-year combination (site 2, 1982-1983) that had high population growth rate, relatively
high germination and low long-term dormancy. The effects of ant-dispersal on demography were introduced by lowering the survival of seeds, in accord with the results of an experiment (Horvitz and Schemske 1994, 1995).

(Figure ovandensis1. Structure of the matrix model for Calathea ovandensis. Each nonzero entry in the matrix is indicated with a dot. Transitions at which dispersal occurs are additionally marked by a square around the dot.)

To estimate the effects of ants on the dispersal kernel, individual seeds were randomly assigned to treatments (ARIL-INTACT and ARIL-EXCISED), color-coded and placed in "depots," allowing ants to redistribute the seeds. One, two and three yrs later, seedlings were surveyed in circular plots around the depots. Since seed coats (bearing the intact color-coding) stay attached to seedlings, dispersal distances of each of the two kinds seedlings were easy to measure. Radial distances were recorded for each seedling (Horvitz and Schemske 1994).

Three analyses of wave speed were carried out. All three used the empirical moment-generating function that marginalized the distances (equivalent to taking the x-coordinate of the radial distance) and assumed the observed distances were 2-d radial in nature. The first analysis estimated the dispersal kernel for seeds dispersed by ants (ARIL-INTACT). The second analysis estimated the dispersal kernel for seeds not attractive to ants (ARIL-EXCISED). The third analysis also used the dispersal kernel for seeds not attractive to ants (ARIL-EXCISED), but it differed from the first two by using a demographic matrix in which the transitions representing the fates of seeds were lower, in accord with experimental data.

11.14 *Trillium grandiflorum*

*Trillium grandiflorum* (Liliaceae) is a self-incompatible, polycarpic perennial herb that occurs in the understory of deciduous woods throughout northeastern North America. Plants are non-clonal, single-stemmed, arising from a tuber-like rhizome and can be readily classified into three developmental stages distinguished by leaf number and flower production. Seedling emergence requires two years. In the first year after dispersal, the seed germinates, produces roots, but no above ground parts. In the second year, the seed produces a cotyledon, but no true leaves. In subsequent years, these non-reproductive plants produce a single leaf. A minimum size threshold must be met for one-leaf plants to transition to non-reproductive three-leaf plants or for non-reproductive three-leaf plants to transition to the flowering three-leaf stage (Hanzawa and Kalisz, 1993). Plants may also become dormant, producing no above ground structures in one or more years before reappearing above ground. Flowering T. grandiflorum is a preferred food of white-tailed deer.

To quantify individual fecundity and the transitions among stages, all plants in the study area were permanently tagged and their location mapped (see Fig 1, Kalisz, et al, 2001). Between 1990 and 1994, each plant was scored for leaf number, leaf area, and number of seeds produced. Some plants failed to re-appear in the population in the following year or years, but emerged in a subsequent census. These missing plants were assigned to a dormant stage. Some plants had all leaves and flowers consumed by deer. These plants were assigned to separate stage (eaten). To quantify the probability of germination, in each of two years we constructed 20 experimental seed baskets using the techniques of Kalisz (1982). Each basket contained 100 *T. grandiflorum* seeds. Seed germination and seedling emergence were scored each year. These seed basket data were used to determine transitions from the seed to the seedling stages. The seven stages in the
matrix are germinated seeds, seedlings, 1-leaf juveniles, 3-leaf non-reproductives, 3-leaf flowering plants, plants eaten by herbivores and dormant rhizomes. The projection interval is one year. Two populations of T. grandiflorum were used in the model. The MI matrix used data from the same population from which the dispersal data were collected (see below). The PA matrix used data from a demographically similar population in Pennsylvania, however no dormant stage was observed in this population.

Dispersal occurs only in the seed stage (dotted arrow, Figure x.x). Seed release from focal plants and secondary dispersal of seeds by ants was followed using color-coded and radiolabeled maternal sibships of seeds. Post dispersal, the study area was searched for seeds. Locations of all recovered seeds were mapped and dispersal from the maternal parents were calculated (see Kalisz et al, 1999 for a complete description). This protocol was followed for two years, resulting in two, two-dimensional dispersal maps.

11.15 Calluna vulgaris Common Heather

Calluna vulgaris is a perennial, polycarpic dwarf shrub in the Ericaceae. Mature, old (¿25 years) plants are about 2 m in diameter and 0.6 m tall. It is the dominant species of Atlantic heathlands systems with very nutrient-poor acid soils. The species was studied in Dorset, SW England, where it is colonizing abandoned arable farmland areas that were once heathland (dominated by Calluna and Erica cinerea) which were ploughed and used in arable production; now grassed over and being colonised by heathers.

Demographic data were collected from 3 sites over 3 years, by planting seeds and marking plants at different stages (J.M. Bullock, unpublished data). Data were used to develop a Lefkovitch matrix comprising 16 stages: seeds in the soil (both new seeds and those surviving from previous years); seedlings; and 14 size classes of adult (i.e. seed-producing) plants, ranging in size from 0.05 - 2.45 m (Fig. 1). Values were taken by merging data across years and sites. The transition interval is one year, running from April to April.

Calluna has very small seeds (c. 0.4 mm maximum diameter) which are wind-dispersed and are produced in large quantities (up to 3 million seeds per plant). Dispersal was quantified by placing seed traps at measured distances, to a maximum of 80 m, along transects (oriented in compass directions) from an isolated plant (Bullock and Clarke 2000). Dispersal distances were highly leptokurtic, but with a fat tail. Data were converted to densities and used to derive a moment generating function empirically, using the histogram approach. This converted the data to create a histogram of seed densities in contiguous (but not necessarily even-sized) bins. From this a pdf was calculated and used in a Monte Carlo randomization to create many (1 million) seed displacements. These 2-dimensional displacements were converted to distances along a single dimension (i.e. the x-axis, assuming symmetrical dispersal) to create an mgf.

11.16 Erica cinerea Bell heather

Bell heather is a perennial, iteroparous dwarf shrub in the Ericaceae. Mature, old (¿25 years) plants are about 1.5 m in diameter and 0.6 m tall. Erica is a common species of Atlantic heathlands systems with very nutrient-poor acid soils. The species was studied in Dorset, SW England, in the same habitat as Calluna.

Demographic data were collected from 3 sites over 3 years, by planting seeds and marking plants at different stages (J.M. Bullock, unpublished data). Data were used to develop a Lefkovitch matrix
which comprises 11 stages: seeds in the soil (both new seeds and those surviving from previous years); seedlings; and 9 size classes of adult (i.e. seed-producing) plants, ranging in size from 0.05 to 1.92 m (Fig. 2). Values were taken by merging data across years and sites. The transition interval is one year, running from April to April.

*Erica* has very small seeds (c. 0.6 mm maximum diameter) which are wind-dispersed and are produced in large quantities (up to 750,000 seeds per plant). Dispersal was quantified (Bullock and Clarke 2000) and used to obtain a moment generating function in the same way as for *Calluna*.

### 11.17 *Rhinanthus minor* Yellow rattle

Yellow rattle is an annual herb in the Scrophulariaceae. It grows in unfertilized grassland and is hemi-parasitic parasitizing on a range of plant species. It was studied colonizing agriculturally improved grassland in Oxford, UK, where it was introduced as part of a grassland diversification experiment.

Demographic data were collected within two treatments within a grassland management experiment: a haycut treatment and an unmanaged treatment. Data was obtained by planting seeds and following the fate of emerging plants (J.M. Bullock, unpublished data). Data were used to develop a Lefkovitch matrix for each population which comprises 2 stages: seeds in the soil (both new seeds and those surviving from previous years) and adults (Fig. 3). Values were taken by merging data across replicates. The transition interval is one year, running from June to June.

*Rhinanthus* has seeds c. 7 mm diameter with flattened edges (giving a discus-like appearance) which facilitate wind-dispersal (and dispersal by agricultural machinery). Dispersal was quantified in both haycut and unmanaged grasslands (thus linking directly to the two population types of the demographic data) by placing seed traps at measured distances, to a maximum of 25 m, along transects (oriented in compass directions) from isolated groups of 20 plants (J.M. Bullock, unpublished data). Dispersal distances for the haycut treatment were leptokurtic, but with a fat tail, and had a maximum of 19 m. Dispersal was much more truncated for the unmanaged treatment, with a maximum of 1.3 m. Data were converted to densities and used to derive a moment generating function empirically, using the histogram approach.

### 11.18 *Ulex minor* Dwarf gorse

*Ulex minor* is a perennial, polycarpic dwarf shrub in the Fabaceae. Mature, old (¿15 years) plants are about 1-2 m in diameter and 0.5 m tall. *U. minor* is a sub-dominant of Atlantic heathlands systems with very nutrient-poor acid soils. This species was studied in Dorset, SW England, growing as an established sub-dominant of heathland. Demographic data were collected from two environments. In one, mixed the congeneric *U. gallii* was present, in the other, solo, the congeneric was absent. Each environment was represented by two sites and data were collected over 2 years, by planting seeds and marking plants at different stages (J.M. Bullock, unpublished data).

A Lefkovitch matrix was developed, which comprises 16 stages: seeds in the soil (both new seeds and those surviving from previous years); and 15 size classes of adult (i.e. seed-producing) plants, ranging in stem diameter from 2 to 15 mm (Fig. 4). Values for each environment were taken by merging data across years and sites. The transition interval is one year, running from October to October.

*Ulex* seeds (c. 2 mm maximum diameter) are ballistically dispersed from simple pods. Most (80-90%) of these seeds are then picked up and dispersed by ants (attracted by an elaiosome on
the seed). Ballistic dispersal was quantified by placing seed traps at measured distances, to a maximum of 2 m, along transects (oriented in compass directions) from each of 3 isolated plants (J.M. Bullock, unpublished data). The maximum dispersal distance was 0.5 m. These data were converted to densities and used to derive a moment generating function empirically, using the histogram approach. Ant dispersal was measured by placing seeds out in depots and following ants as they removed seeds. Distance and direction of dispersal were measured. The moment generating function was derived empirically using the modified Bessel function. The matrix of moment generating functions for combined ballistic and ant dispersal was derived as the Hadamard product of the matrices of moment generating functions for ballistic and ant dispersal. We examined both the combined ant and ballistic dispersal data, and also dispersal by ants only and by ballistic only. Note that only one set of dispersal data was used across both populations.

11.19  *Cirsium vulgare* Spear thistle

*Cirsium vulgare* is a monocarpic perennial in the Asteraceae. It is a weed of overgrazed fertile grassland in Britian and many other parts of the world. This species was studied as it invaded fertile grazed grassland in Oxfordshire, S. England. Sixteen plots (populations) were set up in an experiment in which sheep grazing intensity was varied. Two were chosen for this study; representing extremes of calculated values of $\lambda$ (excluding any with $1 < \lambda$), and also light grazing (low $\lambda$) and heavy grazing (high $\lambda$). Data were collected over 2 years, by planting seeds and marking plants at different stages (Bullock et al. 1994).

A Lefkovitch matrix was developed which comprises 4 stages: seeds in the soil (both new seeds and those surviving from previous years); and 3 size classes of plants, ranging in diameter from 50–500 mm (Fig. 5). Values for each population were taken by merging data across years. The transition interval is one year, running from June to June. *Cirsium* seeds (c. 4 mm maximum diameter) have plumes and are dispersed by wind. 256 seeds were followed individually as they left the parent plant and the distance noted at which they settled (Klinkhamer and de Jong). Seeds traveling >32 m were censored at that distance. The data are now available only as the number of seeds falling within certain distance ranges (eg 0-0.5m, 0.5-1m, etc), and as a certain number falling beyond 32 m. These were used to estimate an $\alpha$ for the Laplace distribution (Hals method used, this needs to be explained) which was 3.6529 m. This was used to estimate a moment generating function. Note, only one set of dispersal data was used across both populations.

11.20  *Pinus palustris* Long leaf Pine

*Pinus palustris* is a long-lived, polycarpic savanna tree. Longleaf pine historically was the dominant tree in many coastal plain savannas of southeastern North America (Platt 1999). The few remaining old-growth longleaf pine populations (e.g., on the Wade Tract) are uneven-aged/sized and locally patchy in distribution (Platt et al. 1988, Noel et al. 1998, Gilliam and Platt 1999). There is a wide range of variation in density, from local stands of trees with closed canopy to open spaces containing scattered or no trees (Platt et al. 1988, Platt and Rathbun 1993). The open aspect of these savannas results from periodic hurricanes that uproot and snap some trees, opening patches in stands (Platt and Rathbun 1993, Platt et al. 2000), as well as from frequent fires that topkill hardwood trees and shrubs, but not pines. The life history of longleaf pine has often been related to high frequencies of fires originating from lightning strikes (Chapman 1932, Wahlenberg 1946,
Croker and Boyer 1975, Platt et al. 1988, Myers 1990, Platt 1999). Some pre-reproductive stages (e.g., grass stage) survive fires, and trees are resistant to fires as a result of thick, flaky bark.

A life cycle graph was constructed for longleaf pine based on the different Wade Tract studies (Figure x). This life cycle graph is based on sequential annual stages in the first four years, followed by nine stages in which individuals may persist for indefinite periods of time. The life cycle is assumed to begin with release of seeds from a parent tree in the fall of the year. Wind-dispersed seeds germinate within a few days or at most a few weeks after dispersal. Thus, there is no separate seed stage and no seed bank in the life cycle.

Pre-reproductives comprise six classes: four age classes and two stage classes. Seedlings (Stage 1: year 1) have relatively low mortality, but growth and survival is influenced by neighborhood trees and by fires (Grace and Platt 1995a,b). During a pre-grass stage (Stage 2-4: years 2-4) juveniles develop secondary leaves capable of resisting fires, and during this period, they are influenced by surrounding trees and are vulnerable to fires. The grass stage (Stage 5), during which a deep root system is developed and above ground growth is slow (but remains $\leq 1.5m$), lasts an indefinite period, but typically 5-15 yrs (Platt et al. 1988, Rebertus et al. 1993). Trees $\leq 1.5$ m tall, but $\leq 10.0$ cm DBH have rapid height growth (Stage 6) as they enter the tree stages of the life cycle. Trees, all reproductives, comprise seven classes: 10.1 -20.0 (Stage 7), 20.1 - 30.0 (Stage 8),...70.1+ (Stage 13). Growth and mortality of trees are highest in the smallest size classes, and decrease with size, and fecundity increases with size. Longleaf pine has a longevity of several hundred years, with maximum longevity about 500 yrs. Longleaf pine does not exhibit clonal growth (although resprouting can occur in damaged pre-grass stages), and growth is sufficiently slow that trees do not jump size classes.

The demography has been investigated using separate studies of pre-reproductive and reproductive life cycle stages within an old-growth stand. In 1979, about 8,000 trees ($\geq 1.5$ m dbh) were tagged, measured and mapped in a 60 ha. plot in the Wade Tract, Thomas County, Georgia. Trees in the mapped stand have been censused annually for mortality. Growth of trees and recruitment into tree size classes have been measured quadrennially; data from 1979, 1983, and 1987 are used in this analysis (Platt et al. 1988, Platt and Rathbun 1993). Approximately 8,000 longleaf pines are in the data set. Biennial fires have occurred on the Wade Tract. In 1985, the eye of Hurricane Kate crossed the Wade Tract, producing mortality of in tree stages (6-13) of the life cycle (Platt and Rathbun 1993). Separate transition matrices were constructed assuming that stands were or were not affected by the hurricane.

Longleaf pine masts, with wide variation in seed production from year to year (Ashe 1894, Schwarz 1907, Buttrick 1914, Mattoon 1922, Forbes 1930, Wahlenberg 1946, Maki 1952, Boyer 1963, Croker 1973, McLemore 1975, Platt et al. 1988, Hamrick et al. 1993). Periodic abundant and synchronized seed production is interspersed with a number of years of low seed production. A random sample of 400 trees on the Wade Tract was used to estimate cone production by field counts during the fall of each year during a 10-year period (1981 - 1990). Both the proportions of trees of given sizes that produced cones and numbers of cones on trees that produced cones varied over this period (W .J. Platt, unpublished data). In two years, the cone production was much higher for all sizes, especially trees $\geq 60$ cm dbh, and more trees produced cones than in the other eight years. However, counts of seeds per cone indicated no substantial differences among years. Two years were designated as mast years, with the other eight years being designated as non-mast years. These differences in cone production multiplied by seed production per cone were used to develop fecundities for mast and non-mast years. The survival of seeds immigrating onto
local sites also differed in mast/non-mast years. Estimates of immigration were obtained from seed traps, and seedling germination was measured in adjacent plots of similar size. These estimates of survival of immigrating seeds varied from an average of about 10% among plots in the 1987 mast year to \(0.01\%\) in the two subsequent non-mast years (1988, 1989). Thus, size-specific fecundity differences in mast/non-mast years were multiplied by differences in survival of seeds to obtain estimated seedling numbers in Row 1 of the transition matrix.

Demography of pre-reproductive stages has been studied using cohorts of recruits. Survival and growth of tagged grass-stage juveniles dating from a 1978 mast year were measured over time in 10 one ha plots (Platt et al. 1988; Rebertus et al. 1993). Data from this study were used to obtain estimates of transition probabilities associated with grass stages (remaining in that stage or entering height growth). Seedling plots (1000 - each 1m²) were established prior to seed fall in a mast year (1987), the first since 1979. Data from the first five years (1988 -1992) are used in this study. The cohort of seedlings that germinated in the fall of 1987 (germination occurs shortly after dispersal) was followed over time, censused at least annually over the subsequent five years (Grace 1994, Grace and Platt 1995a,b). Seedling growth and survival were studied in relation to position along slopes, adult tree density, and fire (Grace and Platt 1995a,b). These data were used to construct four transition matrices for the seedling/pre-grass stages. Survival at high/low densities of trees and with/without fires (years 2 and 4) was used to generate four transition matrices for the first four stages.

Transition matrices for longleaf pine were generated using a one-year projection interval, the common denominator for measurements of the different elements of each matrix. A total of 16 different transition matrices were generated based on the four dichotomous conditions: hurricane/no hurricane, masting/non-masting, fire/no fire, and high/low tree density. Each matrix was assembled using three selected components of the demography: tree survival and growth (hurricane/no hurricane), the fecundity/seed survival (masting/non-masting), and the pre-grass stage juveniles (fire/no fire; high/low density of trees).

Longleaf pine seeds are wind-dispersed samaras capable of long-distance dispersal. On the Wade Tract seed mass averages 0.1 g (range 0.02 - 0.19g). The large surface area (longleaf pine has the longest wing length of any pine species in North America; McCune 1988) averages 3.2 cm² (range 0.4 - 6.1cm²). The resulting high wing-loading suggests that seeds potentially can travel some distance, especially above the canopy, if wind speeds are substantial and movement is unimpeded (Grace 1994). Mean dispersal distances from tall trees (30-40m) in brisk winds (3.5 - 7m sec⁻¹) have been estimated to be 85 -170m (30m tall) and 115-230m (Grace 1994). Such potentially long dispersal distances suggest an ability to invade new areas (cf. Rejmanek and Richardson 1996 with Platt 1999).

Seed dispersal was studied using seeds collected in mapped traps present on the Wade Tract during the 1987 mast year (Grace 1994). In that year, the cone production of all trees ≥ 1.5m tall within 75 m of all traps was measured by field counts using binoculars. Seeds that were collected from traps during the fall of 1987 were weighed and surface area was measured. Allozyme studies were conducted on seeds collected in traps and on trees within 75m of seed traps. Needle tissue collected from trees were analyzed using laboratory procedures described in Hamrick et al. (1993) and Grace (1994). Female gametophytic tissue and embryonic tissue of 2618 seeds were analyzed using laboratory procedures described in Grace (1994). Ten polymorphic loci common to embryonic, gametophytic, and adult needle tissue were analyzed to determine the multilocus allozyme genotype for each embryo, its associated gametophyte and each adult. Maternity exclusion analyses were
conducted for each seed. Each allele at each locus of the haploid female gametophyte was compared to the two alleles at that locus for each reproductive adult within 75 m of the seed trap from which the seed was collected. Any adult with all 10 loci compatible with those of the gametophyte was considered a possible maternal parent. Results of maternity exclusion analyses indicated that 222 seeds (8.5%) had no possible maternal parent within 75m. A total of 184 seeds (7.0%) had a single possible maternal parent within 75m, and 2212 (84.5%) had multiple possible female parents.

We constructed different dispersal kernels based on the allozyme data analyses. All dispersal kernels were based on the data for seeds with single possible maternal parents within 75m. We assumed that seeds with one possible maternal parent came from trees that were randomly distributed in the population, and the distribution of dispersal distances reflected all maternal trees in the population. For seeds with single maternal parents, the distance from the parent to the seed trap was calculated from map coordinates. These distances were grouped into 15 classes with 5m intervals (0-5, 5-10, 10-15...70-75m). A running average of each point with neighbors on either side was used to construct the dispersal distance curves. The resulting curves were normalized to estimate the proportions of seeds expected at different distances from a parent tree, assuming no long-distance dispersal. To include long-distance dispersal, the 8.5% of seeds with no possible maternal parent within 75m was specified as the amount of the dispersal curve located beyond 75m. Gamma functions with and without specified amounts of long distance dispersal were fit to the data.

Bird species: The bird species used in this paper are all examples of increasing and expanding populations primarily in Europe and North America. Examples include expansion after introduction into a region were it did not lived before (name), recovery after a period of human induced decline (species name) or a natural range expansion without any apparent human interference (species name). For bird all species, data on reproduction, survival and first age of breeding were found in literature (Table 1). Survival, reproduction, age of first breeding parameters used are summarized in Table 1. All species included in the study exhibited a sex ratio of 1:1 unless stated otherwise.

In general birds disperse just prior to their first breeding attempt and show site fidelity to their first nesting site in subsequent seasons (Greenwood 1980, Greenwood ). Dispersal data were collected from either banded or tagged birds. Based on tagged birds one collects data on the exact location of birds and their nests (of origin). For banded birds only recoveries within the breeding season and within their presumed breeding habitat were used for constructing a dispersal kernel. For some species no exact dispersal data were available. In these cases a dispersal kernel was estimated, based on distribution maps of different moments in time and known long distance dispersal events (see Lensink 1997, 1998 for further details on these species). The dispersal kernels used for each species are summarized in Table 1.

In standard demographic analyses, only the female (reproducing) part of the population is considered. However, in some raptor species the females disperse further than the males. In these case the kernel for the males was taken. Since most dispersal is connected to the first year of breeding, the dispersal kernel in the matrices was linked to the first age-class in which breeding occurs. Therefore, (the age of first breeding + 1) defines the dimension of the matrix for each species. Based on maps of different moments in time, the velocity of the expanding population was calculated. This aerial method is described in Van den Bosch et al. (1992) (see also Williamson
1996). The area occupied by a species can be written as:

\[ A_t = \pi (r_t)^2 = \pi (O_m + C(t - m))^2 \]  

where \( r_t \) is the radius at time \( t \), \( C \) the velocity of range expansion and \( O_m \) a correction factor for the initial period of population build up with length \( m \). The square root of the area is the best linear estimate of the time course of the spread of a species. The velocity of range expansion, \( C \), can be calculated from the slope of this line, where the initial time period of first settlement is excluded. If range expansion is not symmetrical, a correction was applied. Some observed wave speeds used in this analysis were previously published (Van den Bosch et al. (1992), Lensink (1997, 1998)) while the rest were calculated from map data (Lensink unpublished).

11.21 Cattle Egret *Bubulcus ibis*

The Cattle Egret is native to Southeast Asia, the Mediterranean and parts of mid and southern Africa (Del Hoyo et al. 1992). Around 1900 the Asian subspecies *B. i. coromodus* spread into Australia and New Zealand. At the same time the nominate *B. i. ibis* spread into South Africa. Around 1930 it also crossed the Atlantic and invaded into South America and later North America. Dispersal data were found in South-African banding reports (Van den Bosch et al. 1992). Observed expansion of this species was 106 km/year for South and North America between 1950 and 1970 (Van den Bosch et al. 1992). The latter invasion is the focus of this study.

In the US, Cattle Egrets start breeding at the latest after three winters or non-breeding seasons (Telfair II 1993). In this analysis, the average age of first reproduction is taken as 2.5 years. Reproduction ranges from 1.0 to 1.45 young/female/year; average 1.225 (Telfair II 1993). Survival figures are known from the US, ranging from 0.57 in the first year and 0.74 after two years (Telfair II 1993). For this study recoveries were taken for birds banded as juveniles and recovered during the breeding season (two month prior to their day and month of banding). The demographic matrix used for Cattle Egret has three ages:

\[
\begin{pmatrix}
0 & 0.435 & 0.907 \\
0.47 & 0 & 0 \\
0 & 0.71 & 0.74 \\
\end{pmatrix}
\]  

11.22 Egyptian Goose *Alopochen aegyptiacus*

The Egyptian Goose is native in tropical and subtropical Africa south of the Sahara (Brown et al. 1982). In the 18th century it was introduced into England, were it was kept as an ornamental species in parks and estates. A small, naturalized population later developed with a stronghold in East-Anglia (Gibbons et al. 1994). On the European continent, naturalized populations developed from the late 1960’s onward: The Hague (1967), Groningen (1980) (both The Netherlands) and Brussels (1980) (Belgium) (Lensink 1998, Lensink and Sage in prep.). The increase and spread of the Dutch Egyptian Goose population has been analyzed by Lensink (1996, 1998). The dispersal distances are measured from yearly distribution maps of individual breeding pairs in successive years (Lensink 1998).

The average time to first breeding is 2.0 years in most Egyptian Geese (i.e. their second spring) (Lensink and Sage in prep.). In the Netherlands, breeding pairs produce 0.95 young/female/year (Lensink 1998). Population modeling of Egyptian Geese in the Netherlands since 1967 estimates
the average survival of 1st year birds as 0.7/year and birds >2 years as 0.85/year (Lensink 1998).
The demographic matrix of the Egyptian Goose has three age classes:

\[
\begin{pmatrix}
0 & 0.808 & 0.808 \\
0.7 & 0 & 0 \\
0 & 0.85 & 0.85 \\
\end{pmatrix}
\] (32)

11.23 Ruddy Duck *Oxyura jamaicensis*

The Ruddy Duck is a native of North America, where it breeds in subtropical, temperate and boreal fresh water habitats (Del Hoyo et al. 1992). In Britain a naturalized population developed due to escapes from a wildfowl research center (Sharrock 1976). There numbers increased steadily and the species colonized the British Isles (Sharrock 1976, Gibbons et al. 1993, Hughes 1998). From the early nineties onwards breeding occurred on the nearby European mainland (Lensink and Van den Berk 1996, Hughes 1998); the origin of these might be British as well as local. The British birds are part of this study.

The average time of first breeding for Ruddy Ducks is 2.0 years (i.e. in their second spring) (Hughes 1998). Breeding females produce on average produce 2.7 young/females/year. Population modeling of the ruddy duck in Britain since 1962 estimates the average survival of 1st year birds as 0.6 and of > 2 older birds at 0.7/year (Hughes 1998). The demographic matrix of the Ruddy Duck has three age classess :

\[
\begin{pmatrix}
0 & 1.873 & 1.873 \\
0.6 & 0 & 0 \\
0 & 0.7 & 0.7 \\
\end{pmatrix}
\] (33)

11.24 Red Kite *Milvus milvus*

The distribution of the Red Kite is restricted to the mainland of Western Europe, with a small, isolated population in Wales (Britain) (Cramp and Simmons 1980). The European populations are mainly migratory, where as the Welsh birds are residents. Due to persecution, the Welsh Red Kite populations were nearly extirpated halfway through the 20th century. After protection and conservation measures a slow but steady recovery started (Davis and Newton 1981), which has been well documented and analyzed (e.g. Newton et al. 1981, 1989, 1994).

The Red Kite breeds on average for the first time at the age of 3.5 years (Newton et al. 1989). The sex ratio is 1.0, whereas breeding pairs produce on average 0.27 young females/year (Newton et al. 1994). Survival in the red kite increases from 0.60 in the first year to 0.94 in the third and later years (Newton et al. 1989). These survival figures lead to an expected lifespan of 55 years. Since maximum life span is about 40 years (Newton 1979), the survival of older birds was estimated as 0.932/year. Dispersal distances are based on recoveries of wing tagged birds (Newton et al. 1989). The demography matrix of the Red Kite has four age classes:

\[
\begin{pmatrix}
0 & 0 & 0.126 & 0.252 \\
0.60 & 0 & 0 & 0 \\
0 & 0.79 & 0 & 0 \\
0 & 0 & 0.932 & 0.932 \\
\end{pmatrix}
\] (34)
11.25 White-tailed Eagle *Haliaetus albicilla*

The White-tailed Eagle breeds in the northern parts of Eurasia with smaller numbers in remote areas at lower latitudes (Cramp and Simmons 1980). This species has been subject to persecution and poisoning for a long time. Due to protection and conservation measures in Eastern Europe a slow but steady recovery started in 1980 (Hauff 1998). The areas of the remaining Polish and German populations joined around 1990 (Hauff 1998). In the following years the White-tailed Eagle spread further west into Northern Germany (Hauff 1998, Willems 1999). The dispersal distance is derived from sightings of color-banded birds (Willems 1999).

White-tailed Eagles are long-lived birds that breed on average for the first time at the age of 5.0 years (Cramp and Simmons 1980). Breeding pairs produce 0.415 young/female/year (Willems 1999). Survival is estimated at 0.5 in the first year and 0.94 for later years (Willems 1999). The demographic matrix for White-tailed Eagles has six age classes:

\[
\begin{pmatrix}
0 & 0 & 0 & 0 & 0.390 & 0.390 \\
0.50 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0.94 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0.94 & 0.94
\end{pmatrix}
\]

(35)

11.26 Marsh Harrier *Circus aeruginosus*

The Marsh Harrier breeds in marshes and along rivers in the northern Hemisphere (Cramp and Simmons 1980, Del Hoyo et al. 1994). In Europe its distribution has long been restricted to the mainland. In the mid 1960s, the first breeding was observed in East-Anglia along the east coast of Britain (Sharrock 1976). The probable source for these birds was a thriving population in The Netherlands across the North Sea. In the following decades this species slowly colonized the coastal and marshy areas in East Anglia and surrounding districts (Gibbons et al. 1993). Isolated breeding populations can occur hundreds of kilometers away from known breeding areas (Gibbons et al. 1993).

Marsh Harriers breed for the first time after 2 winters. The success of first time breeders is low, but increases in later years. Breeding females produce on average 1.076 young/females/year (Underhill-Day 1990). The survival of first year birds is estimated at 0.52, increasing up to 0.73 after 3 years and older (Dijkstra 1995). The demographic matrix for the Marsh Harrier has four age classes:

\[
\begin{pmatrix}
0 & 0.350 & 0.700 & 0.785 \\
0.52 & 0 & 0 & 0 \\
0 & 0.65 & 0 & 0 \\
0 & 0 & 0.65 & 0.73
\end{pmatrix}
\]

(36)

11.27 Goshawk *Accipiter gentilis*

The Goshawk has a Holarctic distribution (Del Hoyo et al. 1994). In Western Europe in the 1950-1960s a sharp decline occurred due to the widespread use of pesticides with organochlorine and other components (Newton 1979). After a ban on these pesticides in the late 1960s, a steady population increase was registered followed a few years later by a steady expansion (Bijlsma 1994).
Despite these positive measures, the species was highly persecuted in Britain, and its increase and expansion there were limited (Marquiss 1993). In the Netherlands, Goshawks have been studied extensively by Bijlsma (1994). The dispersal kernel was derived from recoveries of dead birds within the breeding season (Bijlsma in litt).

On average Goshawks breed for the first time after two winters (Cramp and Simmons 1980). In expanding populations the proportion of first year breeders is relatively high, but is near zero in stable populations (Bijlsma 1994). Dutch pairs produce on average 0.865 young females/year (Bijlsma 1994). In the persecuted British population the average is lower: 0.62 young/females/year (Marquiss and Newton 1982), but in an undisturbed population the output was 0.90 (Anonymous 1990). Survival data are only known for the Netherlands: 0.59 in the first year and 0.71 in later years (Bijlsma 1994). The demographic matrix for Goshawks has three age classes – Dutch Goshawks:

\[
\begin{pmatrix}
0 & 0.614 & 0.614 \\
0.59 & 0 & 0 \\
0 & 0.71 & 0.71 \\
\end{pmatrix}
\] (37)

and for British Goshawks (undisturbed population):

\[
\begin{pmatrix}
0 & 0.639 & 0.639 \\
0.59 & 0 & 0 \\
0 & 0.71 & 0.71 \\
\end{pmatrix}
\] (38)

\subsection{Sparrowhawk Accipiter nisus}

The Sparrowhawk breeds in most parts of Europe and the adjacent parts of Asia (Cramp and Simmons 1980). Like many other raptors, a sharp decline in numbers was noticed in the 1950-1960s due to the widespread use of pesticides with organochlorine and other lethal components (Newton 1979, 1988). A ban on the use of these pesticides resulted in a recovery. Both in Britain and the Netherlands the increasing and expanding populations have been studied extensively (e.g. Newton 1988, Bijlsma 1994). Therefore in the analyses it was possible to present data on a more or less stable population in Scotland (Newton 1976, 1988, 1993), an increasing population in The Netherlands (Bijlsma 1994), and a rapid increasing population in England (Wyllie and Newton 1991).

First time breeding among Sparrowhawks in the Netherlands and Scotland occurs on average after 2.0 years (Newton 1985, Bijlsma 1994). In the fast growing population in England this was calculated at 1.5 years (Wyllie and Newton 1991). Among the populations under study the lowest survival rates were calculated for the Dutch birds; accompanied by the highest reproductive output. The highest survival rates were recorded in England. The lowest reproductive output was found in Scotland (Table 1). Dispersal was derived from recoveries of birds found dead in the breeding season (The Netherlands) and sightings of wing tagged birds (Scotland). Separate demographic matrixes were constructed based on the data from each country: Netherlands (three age classes)

\[
\begin{pmatrix}
0 & 0.867 & 0.867 \\
0.43 & 0 & 0 \\
0 & 0.68 & 0.68 \\
\end{pmatrix}
\] (39)

Scotland (three age classes)

\[
\begin{pmatrix}
0 & 0.662 & 0.662 \\
0.49 & 0 & 0 \\
0 & 0.675 & 0.675 \\
\end{pmatrix}
\] (40)
and England (two age classes)

\[
\begin{pmatrix}
0.254 & 0.766 \\
0.49 & 0.74
\end{pmatrix}
\]  

(41)

11.28 Common Buzzard *Buteo buteo*

The Common Buzzard breeds across Europe and deep into Asia (Cramp and Simmons 1980). In the 19th and 20th century in Western Europe this species was much persecuted, and the distribution was limited to the forested and less inhabited areas in this part of the world. In the 1950-1960s a further decline was caused by the use of pesticides containing organochlorine (Newton 1979). After a ban on these pesticides and a better protection in most parts of Western Europe a recovery was obvious, later followed by colonization into regions where it had not bred for centuries. In most parts of England expansion was negligible (Elliot and Avery 1991) and the distribution was long limited to that documented in the 1970s (Sharrock 1976, Gibbons et al. 1993). Only in recent years have Common Buzzard populations shown rapid expansion into most parts of England (???? 2000). The dispersal estimate was derived from recoveries of birds found dead in the breeding season (Bijlsma 1994, Tubbs 1976).

On average Common Buzzards breed for the first time after 2.0 years (Cramp and Simmons 1980) and this figure is assumed to be valid for increasing populations. In a stable and non-persecuted population in Wales first breeding occurred after 3.5 years (Davies and Davies 1992). In the Netherlands the average reproductive output was 0.685 young/female/year while in England 0.665 young/female/year was recorded (Bijlsma 1994, Tubbs 1976, Picozi and Weir 1976). The following three age class demographic matrixes were used: Netherlands

\[
\begin{pmatrix}
0 & 0.527 & 0.527 \\
0.47 & 0 & 0 \\
0 & 0.77 & 0.77
\end{pmatrix}
\]

(42)

England

\[
\begin{pmatrix}
0 & 0.512 & 0.512 \\
0.47 & 0 & 0 \\
0 & 0.77 & 0.77
\end{pmatrix}
\]

(43)

11.29 Osprey *Pandion halitus*

The Osprey has a cosmopolitan distribution (Del Hoyo et al. 1994). In Europe it has long been confined to the northern and eastern parts of this continent (Cramp and Simmons 1980). In 1970 in northern Scotland a breeding pair was located, probably originating from Scandinavia (Williamson 1975, Sharrock 1976). This pair was the first of a slowly increasing and expanding Scottish population over the next decades (Gibbons et al. 1993). In recent years the first pair has reached England. The species is able to disperse over distances of some hundreds of kilometers.

Breeding in Osprey first occurs on average after 3.0 years. The reproductive output in Scotland was 0.68 young/female/year (British Birds in serie). Survival of this species was studied extensively
in Michigan (USA, Postupalsky 1989). The four age class demographic matrix for Osprey is:

\[
\begin{pmatrix}
0 & 0 & 0.558 & 0.558 \\
0.43 & 0 & 0 & 0 \\
0 & 0.82 & 0 & 0 \\
0 & 0 & 0.82 & 0.82
\end{pmatrix}
\]

(44)

11.30 Peregrine Falcon *Falco peregrines*

The Peregrine Falcon has a cosmopolitan distribution (Del Hoyo et al. 1994) that declined significantly due to the use of organochlorine containing pesticides (Ratcliffe 1970). After the ban on these chemicals, populations increased, with their recovery on the British Isles especially well documented (Ratcliffe 1993a, 1993b). The dispersal kernel was derived from sightings of wing tagged birds (Mearns and Newton 1984).

First breeding in Peregrine Falcons occurs at the average age of 2.0 years (Mearns and Newton 1984), with a reproductive output of 0.57 young/female/year (Mearns and Newton 1988, Ratcliffe 1993a). Survival increases from 0.6 in the first year up to 0.9 in the third year and older (Mearns and Newton 1984). These survival figures lead to an expected life span of 40 years. Since maximum life span is known to be about 25 years (Ratcliffe 1993a), the survival of older birds was adjusted to be 0.88/year. The demographic matrix is of Peregrine Falcons has three age classes:

\[
\begin{pmatrix}
0 & 0.399 & 0.502 \\
0.6 & 0 & 0 \\
0 & 0.7 & 0.88
\end{pmatrix}
\]

(45)

11.31 Collared Dove *Streptopelia decaeocto*

In the 19th century the Collared Dove spread from Persia into Turkey. In the next century it further spread into the Balkan until it reached the Alps in the 1930-1940s. Populations successfully crossed the Alps and colonized Western Europe, reaching The Netherlands and Britain in the 1950s (Hengeveld 1988, Hengeveld and Van den Bosch 1991). The dispersal kernel is derived from recoveries of birds found dead in the breeding season (Van den Bosch et al. 1992).

Birds born in the beginning of the breeding season are able to breed for the first time themselves at the end of the first season; and all breed after one winter. Therefore, the average time of first breeding is 0.9 year (Cramp and Simmons 1985). On average, 1.56 young/female/year in are produced in total (Nowak 1965, Cramp and Simmons 1985). Survival is calculated at 0.52 for the first year, declining to 0.29 in the fourth year and later (Van den Bosch et al. 1992). The demographic matrix is based on half year steps and has 9 ages:

\[
\begin{pmatrix}
0 & 0.096 & 0.936 & 1.154 & 1.154 & 0.889 & 0.889 & 0.78 & 0.78 \\
0.86 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0.60 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0.60 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0.74 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0.74 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0.57 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0.57 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.50 & 0.50
\end{pmatrix}
\]

(46)
11.32 Pied Flycatcher *Ficedula hypoleuca*

The Pied Flycatcher breeds in most parts of West-, North- and Central Europe (Cramp 1994). During the 20th century it slowly spread into the north and west. In the Netherlands the first breeding was confirmed around 1910 (Van IJzendoorn 1950), colonization started about a decade later. In the following decades this species spread over the eastern half of the country. In 1983 the population was estimated at about 15,000 pairs (SOVON 1987). In the second half of the 20th century the species also expanded its range into England (Sharrock 1976, Gibbons et al. 1994). Dispersal data came from an extensive long term banding study in Germany (Winkel, printed in Glutz von Blotzheim 1993). From this source dispersal of first time breeders and older birds are available.

The average time of first breeding of female Pied Flycatchers is 1.5 years (Sternberg 1989, Cramp 1994). Because this species easily breeds in nest boxes, the breeding biology is well studied (overview in Lundberg and Atalato 1992). Dutch studies in 1973-1983 showed an average output of 2.20 young/females/year (Dekhuizen and Schuyl 1996), and an English study in Cumbria of 2.75 young/females/year (Lundberg and Atalato 1992). Survival is calculated at 0.35 in the first year, and on average 0.50 in later years (Glutz von Blotzheim 1993). The demographic matrix of Pied Flycatchers has five age classes:

Netherlands
\[
\begin{pmatrix}
0.386 & 1.285 & 1.140 & 1.016 & 0.661 \\
0.35 & 0 & 0 & 0 & 0 \\
0 & 0.583 & 0 & 0 & 0 \\
0 & 0 & 0.52 & 0 & 0 \\
0 & 0 & 0 & 0.461 & 0.30 \\
\end{pmatrix}
\] (47)

England
\[
\begin{pmatrix}
0.481 & 1.603 & 1.430 & 1.268 & 0.825 \\
0.35 & 0 & 0 & 0 & 0 \\
0 & 0.583 & 0 & 0 & 0 \\
0 & 0 & 0.52 & 0 & 0 \\
0 & 0 & 0 & 0.461 & 0.30 \\
\end{pmatrix}
\] (48)

11.33 Starling *Sturnus vulgaris*

Originally the breeding distribution of the Starling was confined to Europe and the adjacent parts of Asia (Cramp 1994). At the end of the 19th century it was introduced in the United States, Australia and New Zealand (Lever 1987). After some failures the introduction in North America (New York) was successful in 1890-1891 (Wing 1943). The spread over this continent was well documented, and around 1930 the Starling reached the west coast of North America (overview in Hengeveld 1989). Analyses of banded bird recoveries was used to calculate a dispersal kernel (Van den Bosch et al. 1992).

In the 1950-1960s, extensive population studies were carried out in the US and Canada (Kessel 1957, Collins and de Vos 1966). On average Starling breeds at the age of 1.86 years (Collins and de Vos 1966). Most pairs breed twice a year, resulting in a reproductive output of 3.957 young in Guelpen (South Canada) and 3.553 young/females/year (Ithaca, New York) (Kessel 1957, Collins and de Vos 1966). Survival was calculated at 0.49 in the first year, 0.57 in the second and 0.47 in
later years (Collins and de Vos 1966). The three age class demographic matrix becomes:

\[
\begin{pmatrix}
0.2575 & 2.140 & 1.765 \\
0.49 & 0 & 0 \\
0 & 0.57 & 0.47
\end{pmatrix}
\]

(49)

11.34 **House Sparrow* *Passer domesticus**

The House Sparrow is a Eurasian species, originally breeding in the more populated parts of the moderate and subtropical regions (Cramp 1994). Halfway through the 19th century this species was introduced into North-America, and from 1850/1851 onwards a successful colonization started (Wing 1943). In the same period it colonized parts of remote areas in North-Europe, Russia and Siberia. This colonization was mostly due to spread of human settlements in these regions (Summers-Smith 1956). Analyses of banded bird recoveries was used to calculate dispersal (Van den Bosch et al. 1992).

For both continents detailed studies on the breeding biology and survival were available. These are summarized in Summers-Smith (1983) and Van den Bosch et al. (1992). House Sparrows breed for the first time after their first winter. They produce on average 8.25 young/females/year (Europe) and 6.0 young/females/year (USA). During the colonization of the American continent House Sparrows could have multiple nests per year (Barrows 1889), which contrast to single nests in stable populations (Summers-Smith 1983). The following two age class demographic matrices have been used: Europe

\[
\begin{pmatrix}
4.95 & 3.795 \\
0.60 & 0.46
\end{pmatrix}
\]

(50)

US

\[
\begin{pmatrix}
3.6 & 2.04 \\
0.60 & 0.34
\end{pmatrix}
\]

(51)

**Mammal species**

In the general sense of this study mammals do not differ much from the birds in the previous paragraph. The general remarks made there are also valid for the mammals. Relevant life-history parameters are summarized in the Table 1.

11.35 **Coyote* *Canis latrans**

The coyote is confined to North America. In the pre-European times its distribution was centered in the Mid-West of the USA. Thereafter numbers increased and the coyote spread in all directions. At the end of the 20th century its range reached from Northern Canada and Alaska into Southern Mexico (Moore and Parker 1983). The dispersal kernel is based on the telemetry data of male and female coyotes that finished their dispersal (Harrison 1992).

Coyote females do breed not earlier than after their second winter. Under certain conditions first year females may breed also (Green 1994 Windberg 1995). The average age of first breeding used here is 1.9 years. Of adult females only 39-41% produces viable fetuses (Windberg 1995, Dumond and Villard 1999). Litters have on average 6.0 pups with a range from 5 to 7 (Green et al. 1994, Dumond and Villard 1999). Based on telemetry studies the survival of first year coyotes is 0.42 (Windberg 1995). The adult survival rate depends on food supply, hunting pressure and social
factors, ranging from 0.47 up to 0.90 (Davison 1980, Andelt 1985, Crabtree 1988, Gese et al. 1989, Windberg 1995, Chamberlain and Leopold 2000). Here 0.69 is used, as it represents the average population. The three age class demographic matrix of the coyote is:

$$
\begin{pmatrix}
0.050 & 0.828 & 0.828 \\
0.42 & 0 & 0 \\
0 & 0.69 & 0.69 \\
\end{pmatrix}
$$

(52)

11.36 Red Fox *Vulpus vulpus*

Originally the red fox is confined to the Eurasian continent (). In the 19th and 20th century it was introduced in several parts of the world, mainly for hunting purposes. In the Netherlands around 1939 the distribution was restricted to the forested and more natural parts in the east (Broekhuizen et al. 1988). In the next decades it spread westward, despite ongoing hunting pressure. Around 1970 it reached the coastal dunes in the west. From there the red fox spread further north and south.

Data on reproduction, survival and dispersal were obtained from a five year study using telemetry (Mulder 2000) in an coastal area without any hunting. On average foxes have their first litter after 1.5 years, resulting in an average of 1.512 young/females/year. Survival was calculated as 0.45 for the first year and 0.65 for later years. The three age class demographic matrix for the red fox is:

$$
\begin{pmatrix}
0.340 & 0.9828 & 0.9828 \\
0.45 & 0 & 0 \\
0 & 0.65 & 0.65 \\
\end{pmatrix}
$$

(53)

11.37 Muskrat *Ondatra zibethicus*

The muskrat is native to North-America (). In the beginning of the 20th century it was introduced into Europe. The first documented escape took place in the Czech Republic in 1905. These mammals are the ancestors of today’s European population (overview in Hengeveld 1989, Van den Bosch 1990). The increase and spread of muskrats in Europe has two periods. During 1905-1930 the expansion was not hindered by human interference. In the period 1930-1960 in West-Europe an eradication program was in force, to diminish further damage to banks and dikes along rivers and waterways.

Muskrats disperse throughout their lives (Van den Bosch et al. 1992). Reproduction of this mammal was studied extensively in the Netherlands, Germany and Belgium (Doude vanTroostwijk 1976, Becker 1967, Moens 1978, summarized in Van den Bosch et al. 1992). Muskrats have their first litter on average after 0.9 years; early young are able to give birth to their own successors late in their first year. The sex ratio is 0.9m:1.0f and reproductive output is on average 4.70 young/females/year. During 1905-1930 survival was higher than during 1930-1960. For each time
period an age-structured demographic matrix is constructed: 1905-1930 (6 age classes)

\[
\begin{pmatrix}
0 & 0.405 & 2.303 & 1.786 & 1.88 & 0.752 \\
0.98 & 0 & 0 & 0 & 0 & 0 \\
0 & 0.81 & 0 & 0 & 0 & 0 \\
0 & 0 & 0.49 & 0 & 0 & 0 \\
0 & 0 & 0 & 0.38 & 0 & 0 \\
0 & 0 & 0 & 0 & 0.40 & 0.16 \\
\end{pmatrix}
\]  

(54)

1930-1960 (5 age classes)

\[
\begin{pmatrix}
0 & 0.325 & 1.598 & 0.987 & 0.940 \\
0.98 & 0 & 0 & 0 & 0 \\
0 & 0.65 & 0 & 0 & 0 \\
0 & 0 & 0.34 & 0 & 0 \\
0 & 0 & 0 & 0.21 & 0.20 \\
\end{pmatrix}
\]  

(55)