

## MANAGING PLANT POPULATION SPREAD: PREDICTION AND ANALYSIS USING A SIMPLE MODEL

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**Abstract.** Models can be used to direct the management of population spread for the control of invasives or to encourage species of conservation value. Analytical models are attractive because of their theoretical basis and limited data requirements, but there is concern that their simplicity may limit their practical utility. We address the applied use of simple models in a study of a declining annual herb, *Rhinanthus minor*. We parameterized a population-spread model using field data on demography and dispersal for four management systems: grazed only (GR), hay-cut once (H1), hay-cut twice (H2), and hay-cut with autumn grazing (HG). Within a replicated experiment we measured spread rates of introduced *R. minor* populations over eight years. The modeled and measured spread rates were very similar in terms of both patterns of management effects and absolute values, so that in both cases  $HG > H2, H1 > GR$ . The treatments affected both dispersal and demography (establishment and survival) and so we used decomposition approaches to analyze the major causes of differences in population spread. Increased dispersal under hay-cutting was more important than demographic changes and accounted for ~70% of the differences in spread rate between the hay-cut and grazed-only treatments. Furthermore, management effects on the tail of the dispersal curve were by far the most critical in governing spread. This study suggests that simple models can be used to inform practical conservation management, and we demonstrate straightforward uses of our model to predict the impacts of different management strategies. While simple models can give accurate projections, we emphasize that they must be parameterized with high-quality data gathered at the appropriate spatial scale.

**Key words:** conservation ecology; demography; habitat management; human-aided dispersal; management impact on dispersal; matrix model; *Rhinanthus minor*; wave-speed model.

### INTRODUCTION

Land managers often require accurate guidance on how to manage the spread of populations (Shigesada and Kawasaki 1997, Bullock et al. 2002). The objective can be the control of invasions by nonnatives or genetically modified crops (Buckley et al. 2005, Kirchner et al. 2006), or the facilitation of colonization, as in reintroductions or planning for climate change (Higgins et al. 2003). Because observations and experiments investigating spread are expensive and long-term, models are critical for timely planning of strategies. Analytical models that are generic and simplified should be preferable to complex simulations because they represent only key processes and so are relatively easy to parameterize and use. For the practical manager however, concerns must arise about the accuracy of such simple models. In order to address these issues, we tested

the accuracy of an analytical model of population spread for a declining grassland herb, *Rhinanthus minor*.

Skellam (1951) characterized population spread in a straightforward model as a product of diffusion (dispersal) and population growth. While simple models have been successful in some instances (Shigesada and Kawasaki 1997), spread modeling has advanced greatly over recent years. The aim of these models has been to represent the spread process accurately, to allow assessment of the key constraints on spread (e.g., sensitivity analyses), and to predict future spread, especially as the outcome of changed management or other interventions. As is seen generally in applied ecology, complex simulation models are popular because they can include a large number of processes—such as explicit representation of space or movement of individuals—whose form and interactions can be designed around the particular study system (Grimm and Railsback 2005). However, simpler analytical models allow a more generic approach in that they have few parameters, their mathematical formulation means they can be used readily and generally (compared to the complex and specific coding of simulation models), they

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provide straightforward analytical solutions, and sensitivity analyses have a solid theoretical basis (Grimm and Railsback 2005, Clark and Gelfand 2006). Their simplifying assumptions are clearly formulated, which allows identification of the key factors and a structure for investigating the causes of model failure.

Analytical wave-speed models have developed since Skellam (1951) to address certain assumptions. Diffusion has been replaced by more realistic dispersal formulations that allow for leptokurtic kernels (Kot et al. 1996) or even empirical dispersal data (Clark et al. 2001). Neubert and Caswell (2000) replaced the simplified demography of these models using matrix models to represent structured populations. Many simplifying assumptions remain, such as no spatial or temporal variation, but these wave-speed models are becoming a common currency for analyzing population spread (Buckley et al. 2005, Jacquemyn et al. 2005, Le Corff and Horvitz 2005, Garnier and Lecomte 2006). It is important to ask, therefore, whether the outputs of wave-speed models are accurate in comparison with measured rates of spread. This is especially important for applied ecologists, where prediction of spread rates and their responses to management is the primary aim of modeling. In this paper we assess the utility of Neubert and Caswell's (2000) model in analyzing and predicting the impact of management on the spread of a declining meadow herb. We derive accurate measures of population spread using a field experiment and show that this simple model is able to replicate the subtle effects of management on spread rates. We then use the model to analyze the key factors driving change in spread rates and to suggest strategies for the conservation of this herb.

## MATERIALS AND METHODS

### *Rhinanthus spread experiment*

We studied yellow rattle, *Rhinanthus minor* (Scrophulariaceae), a hemi-parasitic annual herb with a wide host range, which grows in grassland habitats on soils of low to moderate fertility (Westbury 2004). It is native throughout Europe and introduced in parts of North America and is of conservation importance because it has suffered large population losses in its native range (Preston et al. 2002). It is being widely reintroduced across Europe because it plays a keystone role in meadow diversity (Bullock and Pywell 2005). *Rhinanthus* germinates in spring, requiring winter chilling to break dormancy, and produces seed in midsummer (Coulson et al. 2001). The large, disc-shaped seeds are dispersed short distances by wind but much farther by farm machinery (Bullock et al. 2003).

Population spread was measured in an experiment in Oxfordshire, England (15°37' N, 1°10' W), on a grass-dominated permanent pasture that had no previous populations of *Rhinanthus* (Coulson et al. 2001). The aim was to study how best to introduce *Rhinanthus* to new sites or those from which it has gone extinct in order

to increase the number of populations within its range. Four standard grassland management systems were applied as experimental treatments, beginning in 1996: (1) autumn grazed, GR; (2) hay-cut in June, H1; (3) hay-cut in June and September, H2; and (4) hay-cut in June and grazed in autumn, HG. Autumn grazing took place through October at about 40 sheep/ha. Hay-cutting to a height of 10 cm took place in late June and mid-September using a tractor-mounted drum mower. Treatments were assigned randomly to four plots 20 × 10 m (separated by 1-m guard rows) in five blocks (separated by 10-m guard rows). In October 1995 *Rhinanthus* was seeded into each plot along a single band across the 10-m width of the plot. This was done with a tractor-mounted slot-seeder that sprayed a 15-cm-wide band of nonpersistent herbicide to kill the vegetation, and then sowed the seed into a slit cut in the ground along the center of the sprayed band (Coulson et al. 2001). The band was parallel to the plot edge but was located at random, 2–18 m along its length.

### *Population spread*

The spread of *Rhinanthus* from the sown bands was measured in mid-June (during flowering) from 1996 through 2004 by laying three 1-m-wide transects along the length of each plot crossing the sown band at random positions. Transects were re-randomized each year. The presence or absence of *Rhinanthus* was noted for 0.5-m sections of the transect originating at the sown band and continuing to the plot edge in both directions.

The transect data indicated that *Rhinanthus* spread from the sown bands over the years. A straightforward indicator of the extent of spread was the distance of the farthest occupied transect section from the sown band. A degree of patchiness in *Rhinanthus* presence meant that this furthest distance varied among the three transects, but this measure generally suggested a colonization front, which extended each year (Fig. 1). In most plots this front reached the plot edge before 2004 and so rate of spread was calculated using the data on the farthest occupied section until the year in which the plot edge was reached (the solid symbols in Fig. 1). The transects measured spread in both directions from the sown band. We did not detect a directional bias in spread, so we merged data for both directions and curtailed the data set at the year in which the farther plot edge was reached. The rate of spread was calculated from these data on a per plot basis as the slope of a linear regression of distance of the farthest occupied section for each of the three transects on year; the assumption of a linear relationship was supported by graphical examination of the data (e.g., Fig. 1) and high  $r^2$  values for the regressions, which ranged over 0.38–0.89 (mean = 0.67).

### *Rhinanthus demography and dispersal*

*Rhinanthus* demography was measured in all treatments in three of the five blocks, a total of 12 plots.

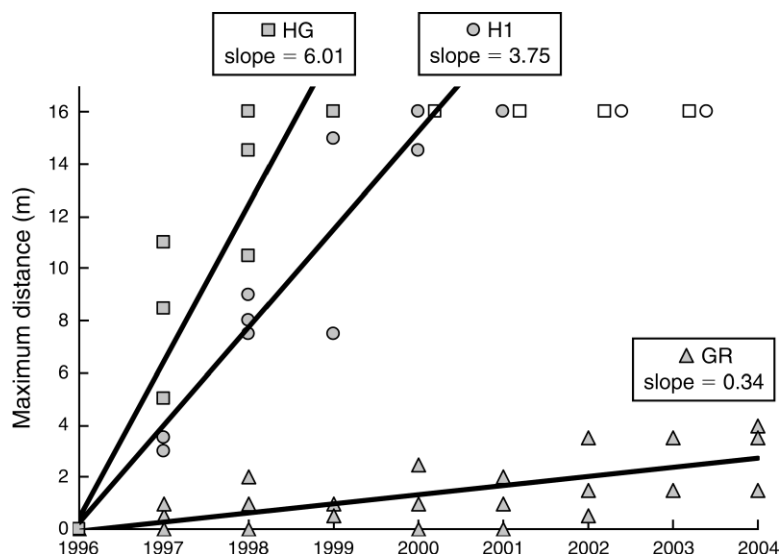


FIG. 1. Spread of yellow rattle, *Rhinanthus minor* (Scrophulariaceae), a hemi-parasitic annual herb, from the sown band (at 0 m) measured in 0.5-m sections along three transects laid perpendicular to the sown band (see *Methods: Population spread*). Here we plot the farthest distance colonized along each transect in each year (the transect positions were randomized each year) for example plots in three management treatments (GR = grazed only, H1 = hay-cut once, HG = hay-cut and grazed). Rate of spread was calculated as the slope of a linear regression of this farthest distance against year (for GR,  $r^2 = 0.49$ ; for H1,  $r^2 = 0.89$ ; and for HG,  $r^2 = 0.88$ ). In some cases *Rhinanthus* reached the plot edge before 2004. In these cases the regression included only those years before the plot edge was reached, indicated by the solid symbols (open symbols indicate data for subsequent years).

Following the requirement of the Neubert and Caswell (2000) model demography was analyzed in low-density conditions. In each plot eight permanent  $50 \times 30$  cm quadrats were laid out along a transect parallel to, but as far as possible from, the sown band of *Rhinanthus*. In October 1999 individual *Rhinanthus* seeds were sown into each quadrat in five rows 10 cm apart and at 2.5-cm intervals along each row, forming a grid of  $5 \times 11$  seeds and totalling 440 seeds in each plot. From January 2000 and subsequently at two-week intervals each point on the grid was searched for *Rhinanthus* plants. At the same time a parallel unsown grid offset by 5 cm from the sown rows was searched to detect any background germination of *Rhinanthus* from unsown seeds. Seedlings were followed until they died or flowered (in May 2000) and produced seed (in June 2000). All seeding plants were bagged as seed capsules formed and the total numbers of capsules and ripe seeds were counted.

Survival of ungerminated seed in the soil was measured by burying eight mesh bags containing 30 seeds in each of the 12 plots in early November 1999. In November 2000 the intact seeds in each bag were counted and their viability tested using the tetrazolium method (Bullock 2006).

Our measurement of dispersal is reported in Bullock et al. (2003). This was done in four grassland habitats all within a few hundreds of meters of the *Rhinanthus* spread experiment: unmanaged, sheep grazed, hay-cut in late June, and hay-cut in late July. Shortly before seed maturation and hay-cut, groups of *Rhinanthus* plants were transplanted into fields with no existing *Rhinan-*

*thus*. Seed traps were set up along 25-m transects in four directions (northeast, northwest, southeast, southwest) in an array design with increasing trap numbers at farther distances in order to maintain sampling effort. Two replicates were done for each treatment. Here, we consider only the June hay-cut and unmanaged data sets because they correspond to the treatments in the spread experiment. The dispersal data from the June hay-cut and unmanaged habitats were very different (Fig. 2), with wind dispersal in the latter resulting in very limited dispersal: a median displacement of  $\pm 0.09$  m, a maximum of 1.4 m, and a short tail (kurtosis = 5.4). In the hay-cut habitat the distances were much greater (median  $\pm 0.7$  m, maximum 21 m) and the tail more significant (kurtosis = 24.5) as a result of dispersal by the rotating blades of the hay-cutting machinery.

#### Spread modeling

Neubert and Caswell (2000) introduced an analytical approach to modeling population spread that combines matrix models describing population growth for a structured population with integro-difference equations describing dispersal. Neubert and Caswell (2000), Caswell et al. (2003), and Lewis et al. (2006) give the mathematics of this approach and practical guidance on its application, and so we give a summary here.

The approach describes how population density  $\mathbf{n}$  at each location  $x$  evolves from time  $t$  to  $t + 1$ :

$$\mathbf{n}(x, t + 1) = \int_{-\infty}^{\infty} [\mathbf{K}(x - y) \circ \mathbf{B}_n] \mathbf{n}(y, t) dy. \quad (1)$$

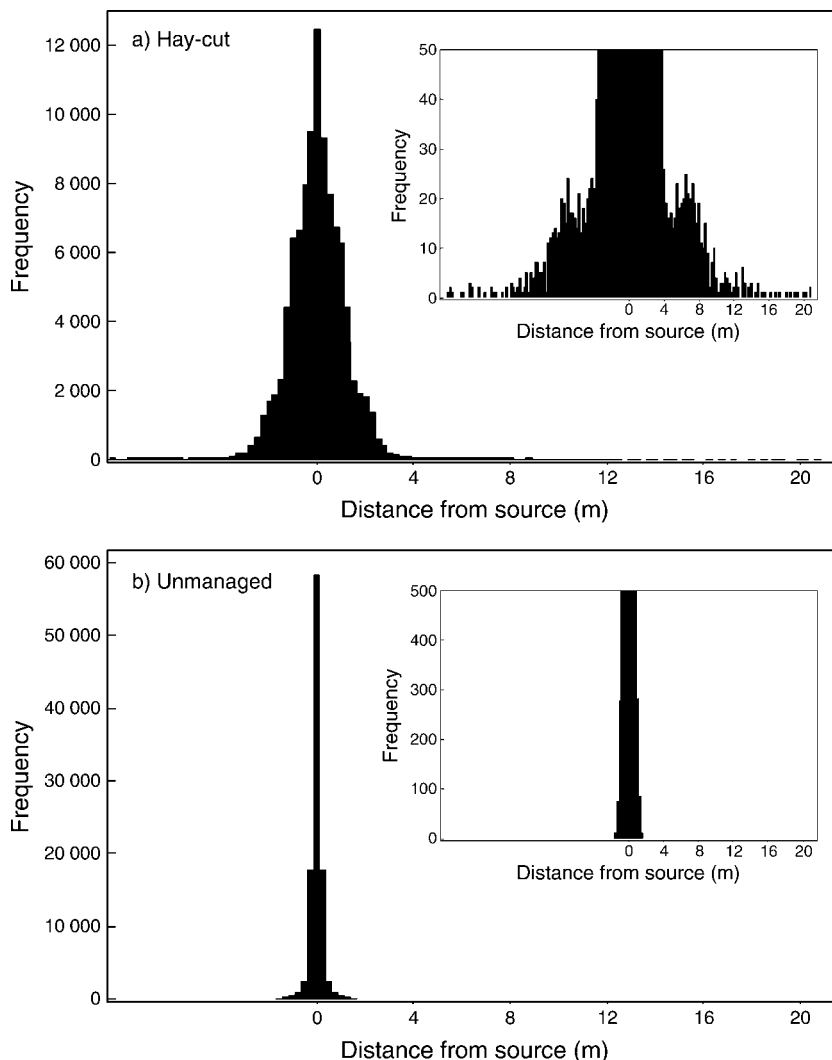


FIG. 2. Dispersal kernels for *Rhinanthus* in (a) hay-cut and (b) unmanaged grasslands, with insets showing details of the tails. Data are from Bullock et al. (2003). Seeds were trapped at set distances from the source, and measured densities were extrapolated over "bins" that extended halfway between adjacent traps. The plotted data are  $10^5$  samples of displacements in one dimension taken from the resulting probability density distributions. Dispersal was similar in all directions for the unmanaged habitat, and the plotted kernel is from an average of all directions and of two replicates. In the hay-cut habitat the vast majority of seeds were dispersed in the direction of the hay-cut and so the kernel represents only the hay-cut direction, averaged across two replicates. Note the different y-axis scales.

$\mathbf{B}_n$  is a stage-structured population projection matrix that describes density-dependent population growth at location  $y$ , and  $\mathbf{K}(x - y)$  is a matrix of dispersal kernels that describe the set of probabilities of the relocation from  $y$  to  $x$  of individuals undergoing each demographic transition;  $\circ$  is the Hadamard product (element-wise multiplication). Thus, over a time step the population grows at each location  $y$  and individuals are dispersed. The population at location  $x$  is given by integrating this process over all locations  $y$ . Neubert and Caswell (2000) showed that under this model a population forms a wave of constant shape that advances at constant speed, and this asymptotic wave speed,  $c^*$ , can be derived analytically. The approach allows differences in dispers-

al ability among stages and realistically complex dispersal kernels, but there are some simplifying assumptions such as no temporal variation or Allee effects. In particular, the environment is treated as spatially homogeneous so that demography does not vary and dispersal from  $x$  to  $y$  depends only on their distance apart.

The approach describes spread of a population into unoccupied space, so the density-dependent matrix  $\mathbf{B}_n$  is substituted in Eq. 1 by  $\mathbf{A}$  ( $=\mathbf{B}_0$ ) which summarizes demography at low density. An assumption is that the dominant eigenvalue of  $\mathbf{A}$ ,  $\lambda$ , is greater than 1, which indicates the population will grow when small. Each transition in  $\mathbf{A}$  is associated with a dispersal kernel. For

dispersing stages, the kernel must be bounded exponentially so that it can be described in terms of a moment-generating function. If this is not the case, as when a kernel is fat tailed, this will result in an accelerating rate of spread and no asymptotic solution. In many cases the dispersal kernel cannot be summarized straightforwardly by an exponentially bounded function (e.g., the Laplace), as is the case for the *Rhinanthus* data (Bullock et al. 2003). For such cases, Lewis et al. (2006) describe methods for calculating a moment-generating function directly from dispersal data. Where (as in our case; see below) the data are  $N$  displacements  $r_1, \dots, r_N$  in one dimension, the moment-generating function is

$$m_{ij}(s) = \frac{1}{N} \sum_i \exp(sr_i). \tag{2}$$

The parameter  $s$  describes the shape of the advancing wave and is found using Eq. 4 (see below).  $\mathbf{M}(s)$  is a matrix of the same dimensions as  $\mathbf{A}$  that comprises the moment-generating function for each transition  $m_{ij}(s)$  in which seed dispersal takes place (for nondispersing transitions,  $m_{ij}(s) = 1$ ). A new matrix  $\mathbf{H}$  is created by element-wise multiplication:

$$\mathbf{H}(s) = \mathbf{A} \odot \mathbf{M}(s) \tag{3}$$

and the dominant eigenvalue of  $\mathbf{H}$  is  $\rho$ . Neubert and Caswell (2000) show that the asymptotic rate of spread of a population,  $c^*$ , is given by

$$c^* = \min \left\{ \left( \frac{1}{s} \right) \ln[\rho(s)] \right\}. \tag{4}$$

Demographic data from each plot describing seedling establishment (EST), plant survival to flowering (FL), seed production (PR), and seed survival between years (SS) were used to create 12 plot-specific (3 replicates  $\times$  4 treatments) population matrices. *Rhinanthus* is strictly annual so the matrix comprised transitions from June to June of two stages: seeds in the soil and adult plants. The matrices were calculated as follows:

$$\mathbf{A} = \begin{bmatrix} (1 - \text{EST})\text{SS} & \text{PR}(1 - \text{EST})\text{SS} \\ \text{EST} \times \text{FL} & \text{PR} \times \text{EST} \times \text{FL} \end{bmatrix}. \tag{5}$$

We assumed that seeds were dispersed during transitions from adult plant to seed bank and from adult to adult. That is, we considered only primary dispersal of seeds leaving the adult plant. Secondary dispersal of these seeds or of seeds in the soil seed bank was assumed to be minimal—a conclusion partly supported by the fact that Bullock et al. (2003) found no evidence for seed dispersal of *Rhinanthus* in the dung or on the fleece of sheep.

Population matrices for treatments H1, H2, and HG in the spread experiment were linked to the dispersal kernels for the late-June hay-cut habitat. The most appropriate kernel for the GR population matrices was from the unmanaged dispersal environment because GR

was grazed only in October and so the vegetation was tall and resembled the unmanaged state during seed dispersal. In order to retain the richness and complexity of the dispersal data we derived the moment-generating function of each dispersal kernel using the empirical approach developed by Caswell et al. (2003) following Clark et al. (2001) and described in detail in Lewis et al. (2006). The seed-trap data were used to generate dispersal kernels by assuming the density recorded at a distance was an accurate estimate of the density in a bin extending halfway between the previous and subsequent trapping distances. A sample of  $10^5$  ( $N$ ) distances taken from the kernel was used to generate a one-dimensional distribution of displacements (Fig. 2) that were applied to Eq. 2 to generate  $\mathbf{M}$ .

RESULTS

*Demographic differences*

ANOVA with Tukey pairwise comparisons showed that seedling emergence differed among the management treatments ( $F_{3,6} = 64, P < 0.001$ ) in the order hay-cut in June and grazed in autumn (HG) > hay-cut twice, in June and September (H2) > hay-cut in June (H1), grazed in autumn (GR) (Fig. 3a). We corrected for background seedling emergence in each plot by subtracting the number of seedlings in the unsown grid from those in the sown grid. The survival of seedlings to adulthood and seed production also differed among treatments ( $F_{3,6} = 31, P < 0.001$ ), but with a subtle difference in pattern such that HG > H2, H1 > GR (Fig. 3b). Seed number per plant ( $F_{3,6} = 4.6$ ) and proportional survival of ungerminated seed ( $F_{3,6} = 0.9$ ) did not differ among treatments and had values of  $60.1 \pm 3.2$  (mean  $\pm$  SE) and  $0.043 \pm 0.006$ , respectively. These demographic variables were combined according to Eq. 5 to create a stage projection matrix for each management type in each replicate block. Using average values across replicate blocks, the created stage projection matrices were:

Grazed only, GR	Hay-cut once, H1
$\begin{bmatrix} 0.035 & 2.7 \\ 0.014 & 1.09 \end{bmatrix}$	$\begin{bmatrix} 0.049 & 2.78 \\ 0.029 & 1.64 \end{bmatrix}$
Hay-cut twice, H2	Hay-cut and grazed, HG
$\begin{bmatrix} 0.044 & 2.92 \\ 0.053 & 3.57 \end{bmatrix}$	$\begin{bmatrix} 0.019 & 0.918 \\ 0.166 & 8.1 \end{bmatrix}$

The projected population growth rates  $\lambda$  differed significantly among the treatments ( $F_{3,6} = 15, P < 0.01$ ) with the pattern HG > H2 > H1,GR (Fig. 3c).

*Modeled and observed population spread*

Measured spread rates also differed among the treatments ( $F_{3,12} = 96, P < 0.001$ ) such that HG > H2, H1 > GR (Fig. 4). Spread rates were modeled using the three population matrices (excepting a GR replicate which had  $\lambda = 0.98$ ; spread rate modeling requires  $\lambda > 1$ ,

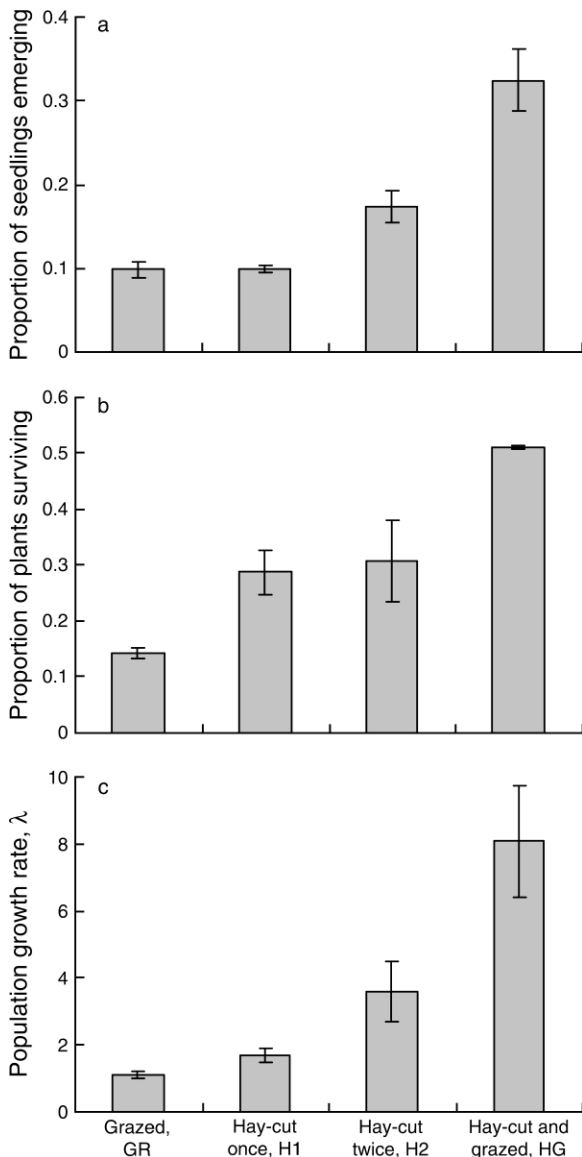


FIG. 3. *Rhinanthus* demographic variables that differed significantly among treatments: (a) emergence of seedlings from the 440 seeds planted per 20 × 10 m plot; (b) survival of seedlings until seed production; (c) projected population growth rate, λ. Values are means ± SE across three blocks.

see *Methods: Spread modeling*, above) for each treatment, combined with the appropriate dispersal kernel (i.e., unmanaged for GR, June hay-cut for H1, H2, and HG) (Fig. 4). This gives three values for each treatment, but is not true replication. Nevertheless, for illustration we also analyzed these values that suggested differences among the treatments ( $F_{3,5} = 34, P < 0.001$ ). The modeled spread rates,  $c^*$ , showed the same responses to the treatments as the measured rates and the values themselves were similar with no systematic differences (Fig. 4), as illustrated by no significant modeled-vs.-measured effect ( $F_{1,23} = 1.7, P > 0.05$ ) in a two-way

ANOVA incorporating treatment ( $F_{3,23} = 110, P < 0.001$ ) and an interaction term ( $F_{3,23} = 1.6, P > 0.05$ ). Overall, the means of the modeled and measured spread rates within treatments differed by less than 0.8 m/yr, which was less than the smallest differences between treatments. The only substantial difference was for GR where the modeled rate was notably lower than the empirical value.

*Life-table response experiments*

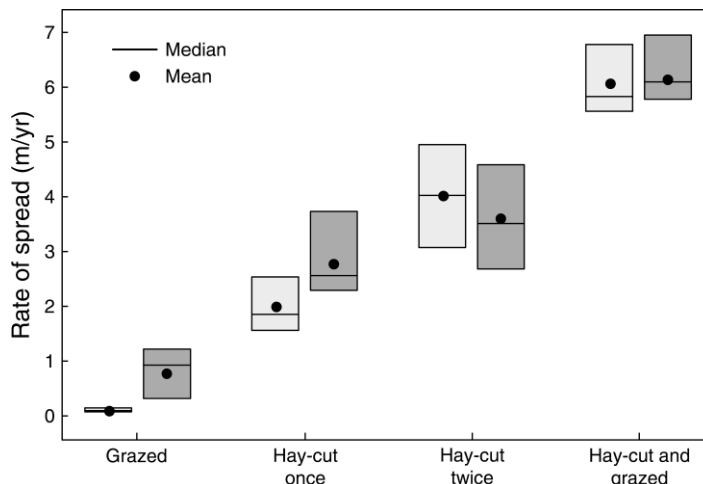
The contrasting management regimes led to differences in demographic variables and the dispersal kernel. It is interesting to ask which of these differences had the most substantial impact on the modeled (and by extrapolation, the actual) spread rates. Caswell et al. (2003) expanded the life-table response experiment (LTRE) approach and showed that the difference in the modeled spread rates of two populations 1 and 2 can be divided into demographic and dispersal contributions using

$$c^{*(2)} - c^{*(1)} \approx \sum_{ij} \{ a_{ij}^{(2)} - a_{ij}^{(1)} \} \frac{\partial c^*}{\partial a_{ij}} \Big|_{(A_1 + A_2)/2} + \sum_{[h]} \{ r_{[h]}^{(2)} - r_{[h]}^{(1)} \} \frac{\partial c^*}{\partial r_{[h]}} \Big|_{(r_1 + r_2)/2} \quad (6)$$

The contribution of differences between the population matrices A is determined by multiplying the sensitivity  $\partial c^*/\partial a_{ij}$  of  $c^*$  to each (i, j) entry by the population difference ( $a_{ij}^{(2)} - a_{ij}^{(1)}$ ) in that entry. A similar approach is used for dispersal contributions whereby the  $10^5$  dispersal distances are described in terms of order statistics and arranged so that the first is the minimum distance and the last the maximum. So  $(r_{[h]}^{(2)} - r_{[h]}^{(1)})$  is the population difference in the hth-order statistic of the dispersal distances and  $\partial c^*/\partial r_{[h]}$  is the sensitivity of  $c^*$  to this statistic. In our analyses we found the approximation accurate to within 6%.

To do this, we averaged the population matrices for each treatment (i.e., the stage projection matrices displayed in *Demographic differences*, above), which gave  $c^*$  values of 0.11, 2.09, 4.17, and 6.15 m/yr for GR, H1, H2, and HG, respectively. Treatments H1, H2, and HG had the same dispersal kernel and so LTRE analysis of  $c^*$  was confined to the demographic differences. Each of the three pairwise comparisons showed that >95% of the difference in  $c^*$  was due to differences in the adult plant–adult plant transition. The GR treatment differed from all the others in terms of both demography and dispersal, and comparisons with treatments H1, H2, and HG showed very similar patterns with differences in the population matrices causing 28%, 31%, and 29%, respectively of  $c^*$  differences. Looking in more detail at these contributions, again the adult–adult transition accounted for >95% of the demographic contribution to differences in  $c^*$  (Fig. 5b). The long-distance dispersers accounted for the vast majority of the dispersal contributions to differences in  $c^*$  (Fig. 5a: the same pattern was seen in the other two treatment comparisons

FIG. 4. Observed rates of spread (dark gray boxes) of *Rhinanthus* from the four treatments in the field experiment, compared with those derived using the Neubert and Caswell (2000) model (pale gray boxes) using measured demographic and dispersal data. The boxes show the range of values.



[not shown]): in the treatment GR vs. HG comparison the upper 1% of distances accounted for 88% of the dispersal contribution.

## DISCUSSION

### *Accuracy of the model*

The use of simple population models for conservation planning has been criticized (Lindenmayer et al. 2003, Sutherland 2006), but as Clark and Gelfand (2006) point out, where simple models work they should be used. Despite the simplifying assumptions of the wave-speed model, in this study it projected rates of spread similar to those measured in the field. This suggests that, at least in this case, the model captured the essential aspects of population spread and that the measured demography and dispersal were accurate representations of these processes in the field. Importantly, the data we used to calculate observed spread rates were independent of the demography and dispersal data used to parameterize the models and so we were able to avoid the problem of circularity in model testing (Turchin 2003). Certain of the simplifying assumptions have been explored in wave-speed models, such as spatial heterogeneity (Shigesada and Kawasaki 2002), temporal stochasticity (Neubert et al. 2000), and Allee effects (Wang et al. 2002), and, unsurprisingly, these tend to slow the projected rate of spread. Apart from greater model simplicity, the attraction of excluding these extra processes is that fewer data are required and this can mean huge savings in costs and time in the field.

We did see a discrepancy for the grazed treatment, with a modeled  $c^*$  (0.13 m/yr) being lower than the observed speed (0.81 m/yr). It is unlikely that the model simplicity is a problem here and we suggest the most likely possibility is that our dispersal kernel from unmanaged grassland was inaccurate because autumn grazing resulted in dispersal of a few seeds by sheep. This is likely to be rare (Coulson et al. 2001, Bullock et al. 2003), but if, for example, we assume a random 0.5%

of seeds travel an extra 10 m by secondary dispersal on sheep then the wave speed becomes 0.68 m/yr.

Modeled and observed spread rates sometimes show a good match (Caswell et al. 2003). Where they do not (Clark 1998, Neubert and Caswell 2000, Neubert and Parker 2004), the problem sometimes seems to lie with the data rather than the model. The issue may be that dispersal is not measured at the appropriate scale; measuring dispersal within a field or a forest stand may not be appropriate for modeling spread over continents. Indeed the vectors of dispersal may change at different scales (Bullock et al. 2006). For example, *Rhinanthus* can be dispersed among fields by attachment to farm machinery (Strykstra et al. 1997), which suggests we would need quantification of this process to model colonization over farmed landscapes. However, the models can be used with confidence to plan management of spread at the field scale.

### *Why use models?*

In this study we were able to measure rates of spread. If that can be done, it is reasonable to ask why one should go to the trouble of modeling. As this study shows, observations of spread take many years, while the dispersal study took place over a few weeks and the demographic measures needed one year. Stage projection matrices can be parameterized by following plants of a range of stages over a single year, and this provides sufficient data for even long-lived perennials (e.g., Stokes et al. 2004). The use of models has other benefits, which we expand upon in the following paragraphs.

Much conservation planning is concerned with demographic analysis and enhancing critical vital rates (Menges 2000). For the declining herb studied here, management effects on dispersal were more than twice as important as those on demography. Indeed, much of this dispersal effect was governed by the small proportion of seeds in the tail of the dispersal kernel (see also Caswell et al. 2003). Generally, this suggests management impacts on dispersal should be part of conserva-

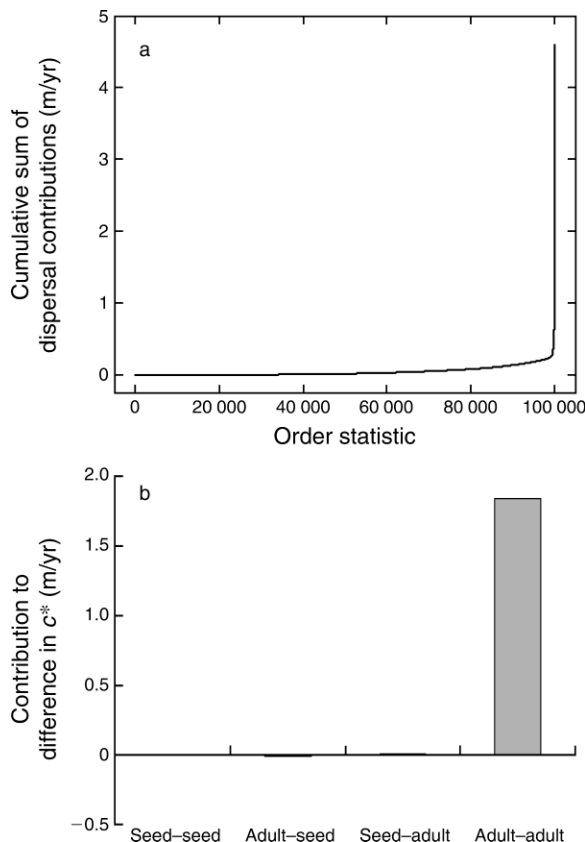


FIG. 5. The difference in modeled spread rates,  $c^*$  (the asymptotic wave-speed), between the treatments GR (grazed in autumn) and HG (hay-cut and grazed), analyzed in relation to contributions of both demographic and dispersal differences (Eq. 6). (a) Dispersal kernels are compared in terms of order statistics, which are arranged such that the first is the minimum distance and the last is the maximum. The contribution to the difference in  $c^*$  of the difference between GR and HG in each order statistic is plotted. The cumulative sums of the contributions are shown to illustrate the low contribution of the lower order (shorter distance) statistics. (b) The importance of demographic differences is presented in terms of the contributions of the differences between GR and HG in each of the four matrix transitions (see Eq. 5). The seed-seed contribution is near zero.

tion planning, and specifically it shows how hay-cutting followed by autumn grazing may be the ideal management for *Rhynanthus* and, potentially, other species typical of hay meadows. Hay-cutting disperses seeds long distances and combines with the late grazing to increase both seedling establishment and survival, which enhance the most important transition in the life cycle. The late-June cut date coincides with the time of seed ripening in *Rhynanthus*, and so it is interesting to ask how a different cut date might affect population spread. Bullock et al. (2003) showed that a later cut date, in late July, decreases dispersal distances (median =  $\pm 0.14$  m, maximum = 2.8 m) as many seeds fall before the hay-cut. If we make the reasonable assumption that demography is unchanged, the wave speed for a late July hay-cut falls

to 0.96 m/yr compared with 6.15 m/yr (using the average HG matrix). In contrast, an earlier hay-cut is likely to affect fecundity rather than the dispersal kernel, because plants are killed before all seed is ripe but the ripe seeds are dispersed by the hay-cutting. If we assume, based on casual observations, that an early June hay-cut reduces fecundity by between two thirds and one half, then wave speed is less seriously affected and decreases to 3.43–4.47 m/yr.

Management effects on demography are, of course, also important. In one of the grazed-only replicates the modeled population growth rate was  $< 1$ , indicating a declining population. As described above, this wave-speed modeling approach cannot be used when  $\lambda < 1$ . This makes biological sense; declining populations will not spread in the long term. When faced with a population that is declining in numbers, a manager clearly needs to implement measures that increase population growth as a priority. A focus on enhancing dispersal in such cases will be ineffective and could be damaging. This reinforces the argument that environmental effects on both demography and dispersal must be considered as a whole when planning population management (Bullock et al. 2002).

Models also allow one to focus experimental effort on the key aspects of the life cycle. Here, the importance of good quality dispersal data is reinforced. While human-aided dispersal is widely acknowledged as critical in the spatial dynamics of many plants and animals (Buchan and Padilla 1999, Bullock et al. 2006), it is rarely quantified. Because of the many ways by which humans disperse other species we are still far from the generic understanding and prediction offered by mechanistic models developed for other vectors such as seed dispersal by wind (Kuparinen 2006). However, the range of methods now available for quantifying dispersal (Nathan 2005, Bullock et al. 2006) should enable researchers to study and model the effects of humans on the dispersal and spread of species.

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