

A spatially explicit model for an Allee effect: Why wolves recolonize so slowly in Greater Yellowstone

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Abstract

A reduced probability of finding mates at low densities is a frequently hypothesized mechanism for a component Allee effect. At low densities dispersers are less likely to find mates and establish new breeding units. However, many mathematical models for an Allee effect do not make a distinction between breeding group establishment and subsequent population growth. Our objective is to derive a spatially explicit mathematical model, where dispersers have a reduced probability of finding mates at low densities, and parameterize the model for wolf recolonization in the Greater Yellowstone Ecosystem (GYE). In this model, only the probability of establishing new breeding units is influenced by the reduced probability of finding mates at low densities. We analytically and numerically solve the model to determine the effect of a decreased probability in finding mates at low densities on population spread rate and density. Our results suggest that a reduced probability of finding mates at low densities may slow recolonization rate.

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1. Introduction

Biological invasion theory predicts that populations with high reproductive rates and long distance dispersal will spread quickly (Fisher, 1937). In the Greater Yellowstone Ecosystem (GYE, MT and WY, USA) the reintroduced gray wolf population (*Canis lupus*) increased by 65% percent between 1996 and 1997 (Smith, 1998). Wolves can also disperse distances greater than 800 km (Ballard et al., 1983; Fritts, 1983; Boyd and Pletscher, 1999). Yet wolves do not recolonize as quickly as biological invasion theory predicts. Assuming logistic population growth and a Gaussian distribution of dispersal distances, the Fisher (1937) model predicts a recolonization rate of 93.9 km/year

(see Appendix A) by wolves to the GYE. The observed GYE recolonization rate between 1997 and 2002 is an order of magnitude lower, only 9.78 km/year (Table 3). This slower than predicted spread suggests a possible Allee effect (Lewis and Kareiva, 1993; Kot et al., 1996; Veit and Lewis, 1996; Wang et al., 2002). A reduced probability of finding mates at low densities is a frequently hypothesized mechanism that can cause an Allee effect (Boukal and Berec, 2002; Bessa-Gomes et al., 2004; and references therein). Our objective is to determine the effect of a reduced probability of finding mates at low densities on the spread rate of a sexually reproducing, invading, population.

Recent work defines a *component* Allee effect as a positive relationship between a component of individual fitness and population density or number (Stephens et al., 1999; Boukal and Berec, 2002) and a *demographic* Allee effect as a positive relationship between total fitness and population density or number (Stephens et al., 1999). Many mechanisms have been identified that may give rise to an Allee effect in a component of fitness (Dennis, 1989;

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Courchamp et al., 1999; Stephens and Sutherland, 1999; Møller and Legendre, 2001). In canids, Allee effects may arise when hunting is cooperative, as shown for African wild dog *Lycaon pictus* (see Courchamp et al., 2000). However, this is unlikely for wolves if small packs are able to secure more prey per capita than large packs (Schmidt and Mech, 1997, but see Vucetich et al., 2004). Several studies report the mortality of wolves that disperse long distances to regions of low wolf density (Nowak, 1983; Licht and Fritts, 1994; Mech et al., 1995; Boyd-Heger, 1997). We suggest the most likely source of an Allee effect in wolves is a reduced probability of finding mates at low densities during the dispersal phase.

Excellent reviews of approaches used to model Allee effects are found in Boukal and Berec (2002) and Taylor and Hastings (2005). Many studies have investigated the effect of a reduced probability of finding mates at low densities on population dynamics (Engen et al., 2003; Bessa-Gomes et al., 2004; Berec and Boukal, 2004; and numerous others) and some have investigated the effect of a reduced probability of finding mates at low densities on population spread rate (e.g. Wang et al., 2002; Veit and Lewis, 1996). We model a reduced probability of finding mates at low densities as influencing only the component of fitness associated with the probability of establishing new breeding units. Our model derivation assumes a component Allee effect and our analysis determines how this assumed component Allee effect influences recolonization rate. We model population growth as two separate processes: (1) establishment of new breeding units and (2) net annual change in breeding group size/density through immigration, emigration, births and deaths. Even when broken into these two separate processes, decreased success in finding a mate at low densities should still be considered a component Allee effect, since a positive relationship exists between mate density and the probability of finding a mate. This distinction between establishment and subsequent growth yields a biologically realistic model which can be parameterized and validated with empirical data.

To model pair formation it is necessary to understand how organisms search for mates. Because little is known regarding where wolves or other mammals search for mates with respect to the beginning and end of their dispersal paths, we consider the extreme possibilities (searching for the mates at the very beginning and very end). We determine the spread rates predicted by the extreme searching strategies and use these as the upper and lower estimates for the predicted spread rate. The model is validated by comparing the predicted range of spread rates for the parameterized model to an empirical estimate of the recolonization rate for wolves in the GYE.

2. Model derivation

We model local population density $N(x)$ as the sum of the density of individuals in new packs and the density of

existing packs after reproduction,

$$\underbrace{N_{t+1}(x)}_{\text{local density in year } t+1} = \underbrace{f(N_t(x))}_{\text{local density after reproduction by existing breeding units}} + \underbrace{D_t(x)}_{\text{local density from formation of new breeding units}} \quad (1)$$

where t indicates the year, locations in space are denoted as x . In Eq. (1), $N_{t+1}(x)$ is the sum of the density due to reproduction by existing breeding units and the density due to the formation of new breeding units. The distinction between new and existing breeding units is that new breeding units were formed less than 1 year ago (see Tables 1 and 2 for definitions and units of all variables and parameters).

Our model derivation makes several simplifying assumptions:

- (A1) Space is homogeneous on the scale for which the model is parameterized.
- (A2) There is a critical density N_c , below which the population grows geometrically (at rate r) and no dispersers are produced. Once local density has reached N_c it never drops below that level.
- (A3) When local density exceeds N_c , dispersers are produced at density $G_t(y)$ with a 1:1 sex ratio, where y denotes locations in space prior to dispersal. The distribution of dispersal distances is denoted by the probability density function k which is unbiased in either direction (symmetric) and identical for male and female dispersers.
- (A4) Only dispersers can form pairs (new breeding units), and the establishment of new breeding units depends on the density of dispersers, the distance at which dispersers can detect each other ϕ and the probability that dispersers that encounter will pair, ψ .
- (A5) Only dispersers that form pairs can reproduce. Failure to find a mate is assumed to result in mortality before the next breeding season. Therefore, a reduced probability of finding mates at low density impacts individual fitness (i.e. component Allee effect, Stephens et al., 1999).

We derive two sub-models for D_t where dispersers search for mates and form pairs: (1) prior to dispersal and (2) following dispersal.

Table 1
Table of variables

Variable	Definition	Units
x	Location in space after dispersal	km
y	Location in space prior to dispersal	km
t	Time	years
N_t	Density	wolves/km
D_t	Density of individuals in new packs	wolves/km
x_t	Spatial extent of the disperser producing population	km

Table 2
Table of parameters

Parameter	Definition	Estimate	Units
N_c	Critical threshold density that must be exceeded for disperser production	0.25 ^a	Wolves per km
γ	Density of dispersers produced when pack density exceeds N_c	0.09 ^a	Wolves per km
α	Laplace coefficient	0.02	Per km
r	Geometric growth rate for packs > 1 year old	1.33	Unitless
σ	The number of wolves in newly formed breeding units at the end of the first year	5.64	Wolves per pair
ϕ	The radius at which one disperser can detect another	20.7 ^b , 39.2 ^b	km
ψ	The probability that given two dispersers of the opposite sex meet, they form a pair	1 ^b	Unitless
T_D	Average territory diameter	26.4	km

^aThis estimate of N_c equates to 6.6 wolves per territory or 0.012 wolves per km². Furthermore, $\gamma = 0.02$ equates to 0.53 dispersers per territory or 0.00097 dispersers per km².

^bFrom the data we estimate $\psi\phi$. For simplicity we fix $\psi = 1$. To ensure that the proportion of dispersers that find mates is 0.47 for the first four years following reintroduction ϕ is different for the pair formation prior ($\phi = 20.7$) and pair formation following dispersal ($\phi = 39.2$) models.

2.1. Pair formation prior to dispersal

Let $G_t(y)$ denote the density of dispersers produced at y as a function of local density. We assume an equal sex ratio at any point in space such that the density of a single sex of disperser produced at y is $H_t(y) = G_t(y)/2$. For a female located at y , the expected number of male dispersers she can detect (and vice versa) is denoted by $I_t(y)$ and is given by the formula

$$I_t(y) = \frac{1}{2} \int_{y-\phi}^{y+\phi} G_t(\xi) d\xi, \tag{2}$$

where ϕ is the detection distance in km. We approximate I_t by the mid-point rule such that $I_t \approx \phi G_t$. Using the Law of Mass Action, the density of opposite sex encounters is $E_t(y) = H_t(y)I_t(y) \approx \phi G_t^2(y)/2$. Dispersers that encounter each other will pair with probability ψ , such that the density of pairs is $\psi E_t = \psi \phi G_t^2(y)/2$. Since the density of pairs is a monotonically increasing function of disperser density, $G_t(y)$, a component Allee effect exists between the density of dispersers and the component of fitness associated with the formation of pairs. Dispersal of pairs occurs via a redistribution kernel $k(x - y)$ yielding J_t , the density of pairs after dispersal,

$$\begin{aligned} J_t(x) &= \int_{\Omega_t} \psi E_t(y) k(x - y) dy, \\ &= \psi \frac{\phi}{2} \int_{\Omega_t} G_t^2(y) k(x - y) dy, \end{aligned} \tag{3}$$

where Ω_t is the region over which the density of pairs formed prior to dispersal is non-zero and x is an individual's final location after dispersal. Therefore, the density of individuals in new packs, D_t , when pair formation occurs prior to dispersal is

$$\begin{aligned} D_t(x) &= \sigma J_t(x), \\ &= \sigma \psi \frac{\phi}{2} \int_{\Omega_t} G_t^2(y) k(x - y) dy, \end{aligned} \tag{4}$$

where σ is the number of wolves in a newly formed pack when the pack is 1 year old.

2.2. Pair formation following dispersal

We derive an alternative sub-model for D_t where dispersers disperse first and then pair. The density of either sex of dispersers after dispersal, but prior to pair formation, is

$$H_t(x) = \frac{1}{2} \int_{\Omega_t} G_t(y) k(x - y) dy. \tag{5}$$

In this case, the number of male dispersers $I_t(x)$ that can be detected by a female disperser located at x is

$$\begin{aligned} I_t(x) &= \frac{1}{2} \int_{x-\phi}^{x+\phi} \int_{\Omega_t} G_t(y) k(\xi - y) dy d\xi, \\ &\approx \phi \int_{\Omega_t} G_t(y) k(x - y) dy. \end{aligned} \tag{6}$$

The density of encounters is $E_t = H_t I_t$. Opposite sex encounters result in pair formation with probability ψ ; hence, the density of pairs is

$$\begin{aligned} J_t(x) &= \psi E_t(x) = \psi H_t(x) I_t(x), \\ &= \psi \frac{\phi}{2} \left(\int_{\Omega_t} G_t(y) k(x - y) dy \right)^2. \end{aligned} \tag{7}$$

Again, note the positive relationship between disperser density $G_t(y)k(x - y)$ and the density of pairs $J_t(x)$ which implies a component Allee effect as it did for the pair formation prior to dispersal model. Given Eq. (7), the density of individuals in newly formed packs is

$$\begin{aligned} D_t(x) &= \sigma J_t(x) \\ &= \sigma \psi \frac{\phi}{2} \left(\int_{\Omega_t} G_t(y) k(x - y) dy \right)^2. \end{aligned} \tag{8}$$

2.3. General model

We substitute these forms of D_t into Eq. (1) to understand the population level consequences of the component Allee effect via density dependent pair formation. The general model for pair formation prior to dispersal is

$$N_{t+1}(x) = f(N_t(x)) + \sigma\psi \frac{\phi}{2} \int_{\Omega_t} G_t^2(y)k(x-y) dy, \quad (9)$$

and the general model for pair formation following dispersal model is

$$N_{t+1}(x) = f(N_t(x)) + \sigma\psi \frac{\phi}{2} \left(\int_{\Omega_t} G_t(y) k(x-y) dy \right)^2. \quad (10)$$

The differences between Eqs. (9) and (10) are a result of dispersal occurring prior to the application of the Law of Mass Action in the pair formation prior to dispersal sub-model (Eqs. (2)–(3)) and after dispersal in the pair formation following dispersal sub-model (Eqs. (5)–(7)).

2.4. Functional forms

We specify the functional forms of $f(N_t)$, G_t and $k(x-y)$ that we will use for our analysis. We define disperser production G_t as a piecewise function where a density of γ dispersers/km is produced when local population density exceeds a critical threshold density N_c . Formally,

$$G_t(y) = \begin{cases} \gamma & \text{if } N_t(y) \geq N_c, \\ 0 & \text{otherwise.} \end{cases} \quad (11)$$

Given this definition of $G_t(y)$, the region Ω_t over which dispersers are produced is the region over which $N_t(y)$ exceeds N_c . We use a geometric population growth function,

$$f(N_t(x)) = rN_t(x) \quad \text{for } f(N_t(x)) \leq N_e, \quad (12)$$

where N_e is a critical threshold below which population growth is geometric with a reproduction ratio $r > 1$. For simplicity we let $N_e = N_c$. We assume that once local density exceeds the critical threshold N_c it will always remain above the N_c threshold. We do not define a form of the growth function for $f(N_t) > N_e$ as disperser production is constant for $N_t \geq N_c$.

For our analysis we chose the dispersal kernel $k(x-y)$ to be a Laplace kernel,

$$k(x-y) = \frac{\alpha}{2} \exp(-\alpha|x-y|) dy. \quad (13)$$

It was not possible to choose a dispersal kernel based on fit to the data, since we do not have data on wolf dispersal distances in the GYE. We choose the Laplace kernel for $k(x-y)$ since it can be understood mechanistically as arising from a one-dimensional random walk where wolves ‘settle’ out from the population at a constant rate to start

new packs (Neubert et al., 1995). Substituting the functional forms of $f(N_t)$, G_t and $k(x-y)$ into the equation for pair formation prior to dispersal (Eq. (9)) yields

$$N_{t+1}(x) = rN_t(x) + \sigma\psi\phi\gamma^2 \frac{\alpha}{4} \int_{\Omega_t} \exp(-\alpha|x-y|) dy, \quad (14)$$

and into the equation for pair formation following dispersal (Eq. (10)) yields

$$N_{t+1}(x) = rN_t(x) + \sigma\psi\phi\gamma^2 \frac{\alpha}{8} \int_{\Omega_t} \exp(-2\alpha|x-y|) dy. \quad (15)$$

2.5. Parameter estimation: GYE wolves

We estimate model parameters from demographic, dispersal and pair formation data from the GYE wolf population. Wolves were released into YNP following a period of confinement in reacclimation pens. We omit data from the first year after packs were released from reacclimation pens as forced confinement influenced the probability that wolves would disperse upon release (Fritts et al., 2001).

Disperser production and critical population size (γ and N_c) are estimated using data on pack sizes and the number of dispersers produced as provided in annual reports for the YNP Wolf Project² (Phillips and Smith, 1997; Smith, 1998; Smith et al., 1999, 2000, 2001; Smith and Guernsey, 2002; Smith et al., 2003) and Rocky Mountain Wolf Recovery³ (US Fish and Wildlife Service et al., 2000, 2001, 2002, 2003). However, these progress reports do not record when no wolves dispersed from a pack. To correct for this, we augmented the disperser production data by adding observations of no dispersers in the cases where all pack members were accounted for through mortality or survival in the pack. To convert pack sizes and number of dispersers produced to densities, we divided these values by the mean territory diameter ($T_D = 2\sqrt{A_T/\pi}$, where $A_T = 545.6 \text{ km}^2$, Carroll et al., 2003 is the mean pack territory area). We used a maximum likelihood fit of Eq. (11) to the density data to estimate the parameters γ and N_c .

Smith et al. (2000) report the mean dispersal distance for GYE wolves from 1995 to 1999 as $\bar{u} = 76.7 \text{ km}$. We equate the mean dispersal distance $\bar{u} = 76.7 \text{ km}$ (Smith et al., 2000) with the mean of the two-dimensional dispersal kernel with constant settling rate (Eq. (20), see Appendix A).

As $\psi\phi$ always occurs as a product in our models (Eqs. (14) and (15)) it is not necessary to estimate the values of ψ and ϕ separately. During the first four years of recolonization to the GYE the proportion of dispersers that found mates was 0.47 (Smith et al., 2000). We estimate the product $\psi\phi$ so that for each model (Eqs. (14) and (15))

²Available on-line at <http://www.nps.gov/yell/nature/animals/wolf/wolfup.html>.

³Available online at <http://westerngraywolf.fws.gov/annualreports.htm>.

the proportion of dispersers that find mates in the first four years is 0.47 (see Appendix A). Hence, only the density of new breeding units formed varies between the two models (Fig. 3).

We estimate σ using data on wolf pack sizes in the GYE for the first three years following the formation of a new pack (Appendix B). The parameter σ is the number of wolves in a newly formed pack when the pack is 1 year old (where a pack is defined as 1 year old on the first April after pair formation). We calculate σ as the mean number of individuals in newly formed packs at the first April following pair formation. To find the reproductive ratio r we divided the total density of wolves at time $t + 1$ by the total density of wolves at time t . We performed this calculation for $t = 1$ and 2 and estimated r as the mean of the results. Since r is the reproductive ratio of packs at low densities which were established for at least 1 year, we included only packs that are 1–3 years old with a density of less than or equal to N_c . We excluded packs that were influenced by human intervention (other than legal control actions).

2.6. Model validation: finding the observed rate of spread

We calculate the spread rate for the model (Eqs. (14) and (15)) in the next section. We validate the model by comparing the predicted spread rate (Eq. (18)) to the observed rate of recolonization by wolves to the GYE. We used maps of wolf territory locations from YNP Wolf Project annual reports from 1997 to 2002 to estimate the empirical rate of wolf recolonization in the GYE (km/year). We determine the area occupied by disperser producing packs at the start of each year by estimating the 100% minimum convex polygon (MCP) of all territories above the critical threshold for disperser production using the animal movements extension (Hooge and Eichenlaub, 1996) in ArcView 3.2 (see Fig. 2A). For simplicity, the area encompassed by the 100% MCP is assumed circular, with a radius x_t equal to the extent of the disperser producing population at time t . The linear spread rate c (km/year) is the slope of the linear regression of x_t versus time. To be consistent, the linear regression does not include the range radius of the population in 1996 as this is less than 1 year after wolves were released from reacclimation pens.

3. Analysis and results

We analyze a general model (Eq. (16)) of which the models (Eqs. (14) and (15)) are special cases. We analyze the model for two initial conditions. Given initial condition 1 (shown in Fig. 1A and defined in Appendix A), the region in space occupied by the disperser producing population Ω_t is $(-\infty, x_t]$. Evaluating Eqs. (14) and (15) in the region $x > x_t$ yields

$$N_{t+1}(x) = rN_t(x) + A \exp(-w\alpha(x - x_t)), \tag{16}$$

where $w = 1$ for the pair formation prior to dispersal model, $w = 2$ for the pair formation following dispersal model and $A = \sigma\psi\phi\gamma^2/(4w)$. In Appendix A we show that

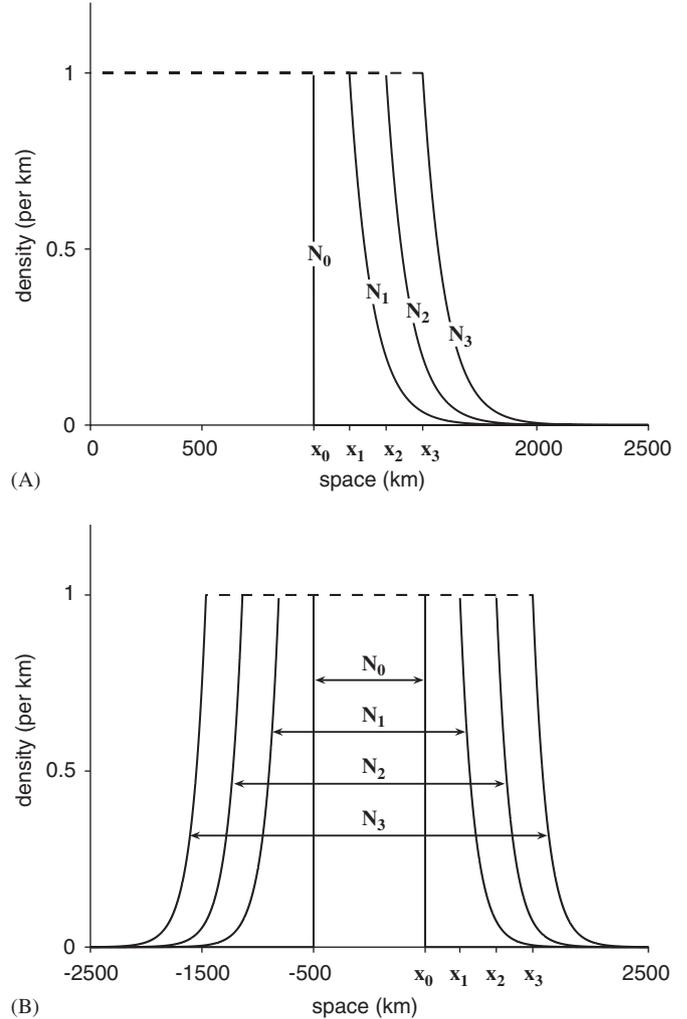


Fig. 1. Two different initial population densities are shown. (A) Initial condition 1 labelled as N_0 where initially a population has invaded the left side of the domain. Formally, initial condition 1 is defined as $N_0(x) \geq N_c$ for $-\infty < x < x_0$ and $N_0(x) = 0$ otherwise. Example solutions to Eq. (14) show the population spreading to the right. The parameters are: $\alpha = 0.01$, $r = 1$, $A = 25$, $N_c = 1$. The extent of the disperser producing population is $x_0 = 1001$, $x_1 = 1161$, $x_2 = 1342$, $x_3 = 1523$. (B) Initial condition 2 labelled as N_0 where initially a population has invaded the center of the domain. Formally, initial condition 2 is $N_0(x) \geq N_c$ for $-x_0 \leq x \leq x_0$ and $N_0(x) = 0$, otherwise. Example solutions to Eq. (15) show the population spreading in both directions. The parameters are: $\alpha = 0.04$, $r = 1.135$, $A = 12.5$, $N_c = 1$. The extent of the disperser producing population is: $x_0 = 500$, $x_1 = 811$, $x_2 = 1137$, $x_3 = 1464$. In both (A) and (B) the dotted line indicates that our analysis focuses on modeling the population dynamics at low densities.

for initial condition 1, Eq. (16) can be solved such that

$$N_{t+1}(x) = \exp(-w\alpha(x - x_0)) \left(r + \frac{A}{N_c} \right)^t \quad \text{for } x > x_{t+1}. \tag{17}$$

Eq. (17) is graphically depicted in Fig. 1A. For initial condition 2, numerical solutions to Eq. (16) ($w = 2$) are shown in Fig. 1B. For both initial conditions the spread rate for the spatially explicit Allee effect model (Eq. (16))

Table 3
The predictions of two models compared to the observed spread rate for wolves recolonizing the GYE

Model	Spread rate (km/year)
Pair formation prior to dispersal	41.11
Pair formation following dispersal	20.00
Observed spread rate (95% CI upper limit)	12.05
Observed spread rate	9.78
Observed spread rate (95% CI lower limit)	7.51

has the same form,

$$c = \frac{1}{w\alpha} \log\left(r + \frac{A}{N_c}\right) \quad (18)$$

(see Appendix A). When parameterized Eq. (18) predicts a spread rate of 41.11 km/year for the pair formation prior to dispersal model and 20.00 km/year for the pair formation following dispersal model (Tables 2 and 3). To estimate the actual rate that wolves introduced to YNP have recolonized the GYE we calculated the area occupied by wolf packs of density larger than N_c from 1997 to 2002 (Fig. 2A). The area occupied by wolf packs of density greater than N_c increased from 6542 km² in 1997 to a maximum of 29,093 km² in 2002. Assuming an approximately circular area, we calculated range radii of packs with density exceeding the critical threshold as 45.631 km in 1997 increasing to 96.230 km in 2002. The linear regression of radii versus time was significant, radii = 25.02 + 9.78 × (years since reintroduction), $F_{1,4} = 142.62$, $p = 0.0003$, $R^2 = 0.97$ (Fig. 2B). The slope of the linear regression (9.78 km/year) is the mean spread rate, with SE(c) = 3.43, resulting in a 95% confidence interval of 7.51–12.05 km/year (Table 3).

4. Discussion

Our results provide a link between a mechanism that can cause a component Allee effect and population spread rate. To understand population level dynamics at the leading edge of the invasion front, we derive a component Allee effect model (Eqs. (14) and (15)) with biologically meaningful parameters that describes population density when the probability of finding a mate decreases with decreasing density of potential mates. We show that for GYE wolves a reduced probability of finding mates at low densities slows the predicted rate of recolonization.

The component Allee effect model predicts a spread rate of between 20.00 and 41.11 km/year, which is slower than the spread rate predicted by the Fisher model (see Appendix A). An integrodifference model with a Laplace dispersal kernel but no component Allee effect would predict a spread rate faster than the Fisher model, since the spread rate of an integrodifference equation with a Laplace dispersal kernel is faster than an integrodifference model with the equivalent Gaussian dispersal kernel (Kot et al.,

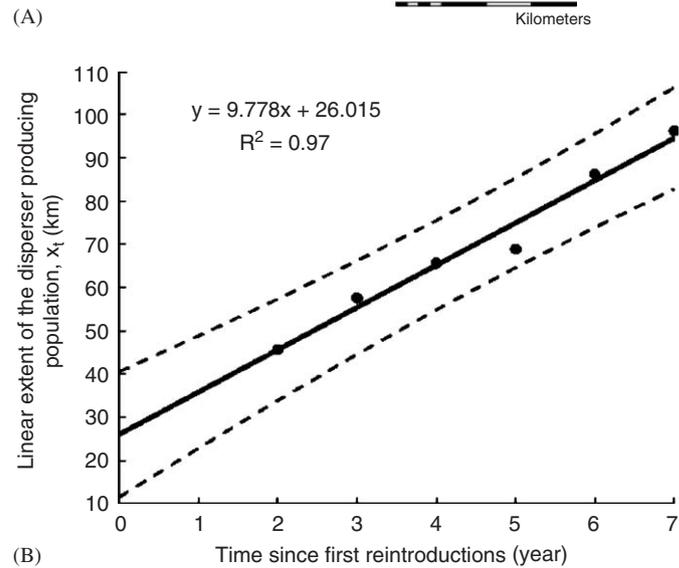
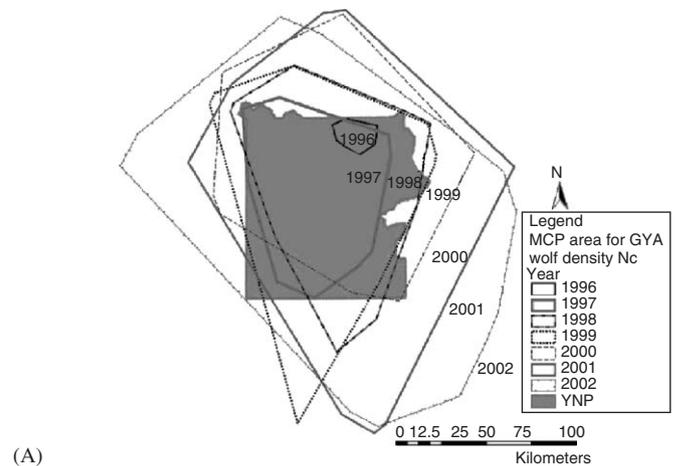


Fig. 2. Wolf recolonization to the GYE. (A) For each year, the area occupied by all wolf packs of density N_c or greater is calculated as a minimum convex polygon (MCP). The Yellowstone National Park shape file was provided by Spatial Analysis Center at Yellowstone National Park. (B) The MCP area recolonized is assumed circular with radius equal to x_i the linear extent of recolonization by packs with density N_c or greater (dots). The population spread rate is equal to the slope of the linear regression. The 95% confidence interval for the linear regression are shown as dotted lines.

1996). Fisher’s model and integrodifference models for biological invasions typically assume all dispersers are equally likely to reproduce. For a sexually reproducing population where individuals must search to find mates (such as wolves) this implies that the probability of finding a mate is independent of mate density. Therefore, we conclude that a reduced probability of finding mates at low densities slows the population spread rate for GYE wolves.

Furthermore, the spread rate for the spatially explicit Allee effect model (Eq. (18)) is an increasing function of the ratio A/N_c . The constant A can be interpreted as a measure of the density of new packs formed in a single time interval (see second term on the right of Eq. (16)). It is the dimensionless ratio of this density measure A to the dispersal density threshold N_c (above which wolves disperse) that appears in the spread rate formulation

(Eq. (18)). To understand the effect of behavioral components on population spread, the constant A can be broken down into its component parameters $A = \sigma\psi\phi\gamma^2/(4w)$. Hence A , as well as the corresponding spread rate (Eq. (18)), is an increasing function of size of newly formed pack (σ), likelihood of pair formation (ψ), radius of detection for a mate (ϕ) and density of dispersers produced (γ). The parameter A is reduced when pair formation is post-dispersal ($w = 2$), rather than pre-dispersal ($w = 1$). In this way, the spread rate with Allee effect is connected explicitly to the behavioral components that give rise to the Allee effect.

Table 3 shows that when pair formation occurs prior to dispersal the population spreads more quickly than if pair formation occurs after dispersal. This is because the different pair formation strategies give rise to different densities of new breeding units or pairs. Fig. 3 compares the density of pairs for the pair formation prior to dispersal (Eq. (3)) and pair formation following dispersal (Eq. (7)) strategies. In both cases the proportion of dispersers that find mates is the same, however, the locations of the pairs are influenced by the pair formation strategy. Furthermore, Eq. (18) also provides a useful rule of thumb: if all individuals search for mates at the beginning of their dispersal path the population will spread twice as quickly when compared to a population where all individuals search for mates at the end of their dispersal path. This rule of thumb holds for GYE wolves and all populations where A/N_c is much greater than r (see Eq. (18)).

However, while the component Allee effect models slow the predicted spread rate, the predicted spread rate is still faster than the observed recolonization rate of wolves to the GYE (Table 3). We believe the main mechanism for the

higher model-based estimate of spread rate compared to the empirical spread rate arises because of differences in wolf population dynamics between source (inside YNP) and sink (outside YNP) areas. Our models were parameterized with population data for wolves in the first seven years following reintroduction when a large proportion of the wolves inhabited a protected area. Over time the population spread further into non-protected areas. We expect that r is an overestimate of the geometric growth rate outside YNP. Hence, by Eq. (18) the overestimate in r will produce an overestimate in c as the population spreads outside YNP. Regardless, the reasonable match between model and empirical estimates supports the important role of Allee effects in pair formation in dispersing wolves.

While we have shown that a reduced probability of finding mates at low densities may slow spread rate, separating the two processes that lead to population growth (breeding unit establishment and subsequent growth following the establishment of breeding groups) may result in different model outcomes (e.g. unconditional extinction, unconditional survival or extinction–survival scenarios, Boukal and Berec, 2002) which may, in turn, suggest different strategies to best control the abundance of target species (Taylor et al., 2004). While Eq. (18) precisely describes the relationship between model parameters and spread rate, it is only valid when the population is spreading (e.g. spread rate is greater than zero). In this paper, we have not determined the full range of model outcomes which we leave for future work. Another area of future work is to derive a similar model for pair formation where there is sex-biased dispersal which occurs in large mammals and birds (Pusey, 1987).

Our study provides several meaningful results: (1) the derivation of a spatially explicit model for a reduced probability of finding mates at low densities, (2) a reduced probability of finding mates at low densities may slow invasion rates and (3) a formula for the population spread rate that is a function of demographic, dispersal and pair formation parameters (Eq. (18)). While other studies have investigated Allee effects caused by a reduced probability of finding mates at low densities (see Introduction), the utility of our work is in the additional realism garnered from separating breeding group establishment and population size/density changes following establishment through immigration, emigration, births and deaths.

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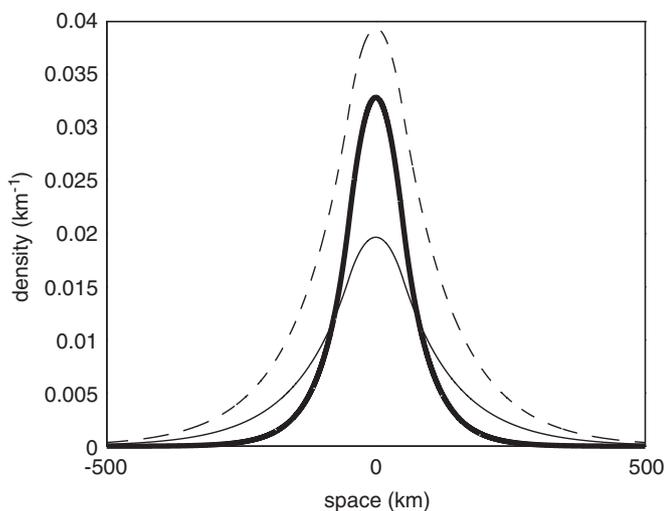


Fig. 3. Given an initial distribution of dispersers (*dashed*) we calculate the density of successful dispersers for (1) pair formation prior to dispersal (*fine line*, Eq. (3)) and (2) pair formation following dispersal (*bold line*, Eq. (7)). In the figure, the proportion of total dispersers that are successful (ρ) is the same for both pair formation strategies. Parameter values are: $\alpha = 0.01$, $\phi = 20$ (pair formation prior), $\phi = 84.83$ (pair formation following dispersal), $\psi = 1$, $\gamma = 0.1$ and $x_t = 50$.

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Appendix A

A.1. Fisher model

Fisher model is

$$\frac{\partial N}{\partial t} = rN \left(1 - \frac{N}{K}\right) + D \frac{\partial^2 N}{\partial x^2} \tag{19}$$

(Fisher, 1937). The diffusion coefficient D is calculated as $D = \bar{u}^2/\pi$ (Shigesada and Kawasaki, 1997) where \bar{u} is the mean dispersal distance ($\bar{u} = 76.7$, Smith et al., 2000). The reproductive rate r is calculated as the slope of a linear regression of $N_{t+1} - N_t$ versus N_t , where N_t is the density of wolves in YNP at time t . We assume the area of YNP is 10,000 km² and calculate the density of wolves in YNP from 1996 to 2002. The spread rate is calculated as $c = \sqrt{rD}$, $r = 1.18$, $D = 1872$ km²/year.

A.2. Parameter estimation

A.2.1. Estimating α from two-dimensional dispersal data

The Laplace kernel (Eq. (13)) can be understood mechanistically as arising from a one-dimensional random walk with diffusion coefficient D where wolves ‘settle’ out from the population at a constant rate a to start new packs (Neubert et al., 1995). When the wolves are given enough time to settle, the distribution of settled wolves is given by Eq. (13) with $\alpha = \sqrt{a/D}$. Alternatively a two-dimensional random walk with constant settling rate yields

$$k(\mathbf{x} - \mathbf{y}) = \frac{\alpha^2}{\pi} K_0(\alpha|\mathbf{x} - \mathbf{y}|), \tag{20}$$

where K_0 is a zeroth order modified Bessel function and \mathbf{x} and \mathbf{y} are the two-dimensional locations in space before and after dispersal (Broadbent and Kendall, 1953). The marginal distribution of this radially symmetric dispersal kernel is the Laplace kernel (Eq. (13)). Lewis et al. (2006) show that, for an advancing ‘planar’ invasion front, a one-dimensional model incorporating the marginal distribution of the two-dimensional dispersal kernel is the appropriate model. We equate the mean of Eq. (20) with the reported mean dispersal distance for wolves in the GYE (Smith et al., 2000) such that $\bar{u} = \pi/(2\alpha)$. Therefore, we calculate the Laplace coefficient as $\alpha = \pi/(2\bar{u})$ where $\bar{u} = 76.7$.

A.2.2. Calculating the proportion of dispersers that find mates

We calculate ρ , the proportion of dispersers that find a mate in the first τ years, for both the pair formation prior to and following dispersal models (Eqs. (14) and (15)). We calculate the total number of successful dispersers in any year as twice the integral of J_t over the entire region, where J_t is given by Eqs. (3) and (7). The total number of dispersers produced in any year for both models is the

integral of $G_t(y)$ evaluated on the interval Ω_t . Therefore, ρ the proportion of dispersers that successfully find mates after τ years for our models is

$$\rho = \frac{\sum_{t=1}^{\tau} 2 \int_{-\infty}^{\infty} J_t(x) dx}{\sum_{t=1}^{\tau} \int_{\Omega_t} G_t(y) dy}. \tag{21}$$

For the pair formation prior to dispersal model J_t is given by Eq. (3) such that $\psi\phi$ is given by the equation

$$\psi\phi = \frac{\rho \sum_{t=1}^{\tau} \int_{\Omega_t} G_t(y) dy}{\sum_{t=1}^{\tau} \int_{-\infty}^{\infty} \int_{\Omega_t} G_t^2(y) k(x - y) dy dx}. \tag{22}$$

Substituting G_t (Eq. (11)) and $k(x - y)$ (Eq. (13)) into Eq. (22) we calculate $\psi\phi$ for the pair formation prior to dispersal model as

$$\begin{aligned} \psi\phi &= \frac{\rho \sum_{t=1}^{\tau} \int_{-x_t}^{x_t} \gamma dy}{\sum_{t=1}^{\tau} \int_{-\infty}^{\infty} \int_{-x_t}^{x_t} (\alpha\gamma^2/2) \exp(-\alpha|x - y|) dy dx}, \\ &= \frac{4\rho}{\gamma}. \end{aligned} \tag{23}$$

For the pair formation following dispersal model, where J_t is given by Eq. (7),

$$\psi\phi = \frac{\rho \sum_{t=1}^{\tau} \int_{\Omega_t} G_t(y) dy}{\sum_{t=1}^{\tau} \int_{-\infty}^{\infty} \left(\int_{\Omega_t} G_t(y) k(x - y) dy \right)^2 dx}. \tag{24}$$

Substituting G_t (Eq. (11)) and $k(x - y)$ (Eq. (13)), $\psi\phi$ for the pair formation after dispersal model yields

$$\begin{aligned} \psi\phi &= \frac{\rho \sum_{t=1}^{\tau} \int_{-x_t}^{x_t} \gamma dy}{\sum_{t=1}^{\tau} \int_{-\infty}^{\infty} \left(\int_{-x_t}^{x_t} (\alpha\gamma/2) \exp(-\alpha|x - y|) dy \right)^2 dx} \\ &= \frac{16\alpha\rho \sum_{t=1}^4 x_t}{\gamma \sum_{t=1}^4 \exp(-2\alpha x_t) (3 + 2\alpha x_t + \exp(2\alpha x_t) (4\alpha x_t - 3))}. \end{aligned} \tag{25}$$

A.3. Model analysis: initial condition 1

We find N_{t+1} and the population spread rate c for Eqs. (14) and (15) for two different initial conditions. Initial condition 1 (Fig. 1A) is defined as

$$\begin{aligned} N_0(x) &\geq N_c \quad \text{for } -\infty < x \leq x_0, \\ &= 0 \quad \text{otherwise.} \end{aligned} \tag{26}$$

Given initial condition 1, the region in space occupied by the disperser producing population Ω_t is $(-\infty, x_t]$. Evaluating Eqs. (14) and (15) in the region $x > x_t$ yields

$$N_t(x) = rN_{t-1}(x) + A \exp(-w\alpha(x - x_{t-1})), \tag{27}$$

where w and A are: $w = 1$, $A = \sigma\psi\phi\gamma^2/4$ (pair formation prior to dispersal, Eq. (14)) and $w = 2$, $A = \sigma\psi\phi\gamma^2/8$ (pair formation following dispersal, Eq. (15)). We suppose that solutions for Eq. (27) have a slope of $\exp(-w\alpha x)$ for $x > x_t$ such that

$$N_t(x) = B_t \exp(-w\alpha x) \quad \text{for } x > x_t. \tag{28}$$

Substituting Eq. (28) into Eq. (27) yields

$$N_{t+1}(x) = rB_t \exp(-w\alpha x) + A \exp(w\alpha x_t) \exp(-w\alpha x) = B_{t+1} \exp(-w\alpha x),$$

where

$$B_{t+1}(x) = rB_t + A \exp(-w\alpha x_t) \quad \text{for } x > x_t. \quad (29)$$

Therefore, we show that if N_t has a slope of $\exp(-w\alpha x)$, N_{t+1} also has a slope of $\exp(-w\alpha x)$. We look for solutions in the region $x > x_0$ by solving Eq. (27) for $t = 1$, where $N_0(x)$ is described by initial condition 1,

$$N_1(x) = A \exp(w\alpha x_0) \exp(-w\alpha x) \quad \text{for } x_0 < x. \quad (30)$$

Therefore, $B_1 = A \exp(w\alpha x_0)$ and N_t and N_{t+1} have a slope of $\exp(-w\alpha x)$ for all t .

Solutions to Eq. (27) have an exponential slope for $x > x_t$ where $A > 0$ such that

$$N_t(x) = B_t \exp(-w\alpha x) \quad \text{for } x > x_t. \quad (31)$$

The point at which the population starts the exponential drop is x_t where

$$N_t(x_t) = N_c. \quad (32)$$

We calculate x_t from Eqs. (31) and (32) to yield

$$\exp(w\alpha x_t) = \frac{B_t}{N_c}. \quad (33)$$

We can substitute Eqs. (31) and (33) into Eq. (27) to find the relationship between B_{t+1} and B_t such that

$$B_{t+1} = B_t \left(r + \frac{A}{N_c} \right) = B_1 \left(r + \frac{A}{N_c} \right)^t, \quad (34)$$

where $B_1 = A \exp(w\alpha x_0)$. Substituting Eq. (34) into Eq. (31), N_t is given by the equation

$$N_t(x) = \exp(-w\alpha(x - x_0)) \left(r + \frac{A}{N_c} \right)^{t-1} \quad \text{for } x > x_t. \quad (35)$$

Eq. (35) is graphically depicted in Fig. 1A. The extent of the disperser producing population is

$$x_{t+1} = \frac{1}{w\alpha} \log \left(\exp(\alpha x_0) \frac{A}{N_c} \left(r + \frac{A}{N_c} \right)^{t-1} \right), \quad (36)$$

and we find the rate of population spread is given explicitly in terms of the model parameters as

$$c = x_{t+1} - x_t = \frac{1}{w\alpha} \log \left(r + \frac{A}{N_c} \right). \quad (37)$$

A.4. Model analysis: initial condition 2

We show that the spread rate for Eqs. (14) and (15) is the same for both initial conditions. Initial condition 2 (Fig. 1)

is defined as

$$N_0(x) \geq N_c \quad \text{for } -x_0 \leq x \leq x_0 \\ = 0 \quad \text{otherwise.} \quad (38)$$

For this initial condition it is not possible to provide a general model for different values of w .

A.4.1. Pair formation prior to dispersal

Evaluating Eq. (14) where the limits of integration are dictated by initial condition 2 gives $\Omega_t = [-x_t, x_t]$. Therefore, Eq. (9) where $x > x_t$ yields

$$N_{t+1}(x) = rN_t(x) + 2A \exp(-\alpha x) \sinh(\alpha x_t), \quad (39)$$

where $A = \sigma\psi\phi\gamma^2/4$. We consider solutions to Eq. (39) of the form $N_t(x) = B_t \exp(-\alpha x)$ for $x > x_t$. Substituting N_t into Eq. (39), the relationship between B_{t+1} and B_t is

$$B_{t+1} = rB_t + 2A \sinh(\alpha x_t). \quad (40)$$

We evaluate B_1 as

$$B_1 = 2A \sinh(\alpha x_0), \quad x > x_0, \quad (41)$$

and therefore show that $N_t = B_t \exp(-\alpha x)$ for all t where $x > x_t$. We use Eq. (33) ($w = 1$) to calculate the extent of the disperser producing population,

$$\exp(\alpha x_{t+1}) = r \frac{B_t}{N_c} + \frac{2A}{N_c} \sinh(\alpha x_t). \quad (42)$$

We substitute $B_t = N_c \exp(\alpha x_t)$ from Eq. (33) to yield

$$x_{t+1} = \frac{1}{\alpha} \log \left(r \exp(\alpha x_t) + \frac{2A}{N_c} \sinh(\alpha x_t) \right). \quad (43)$$

Eq. (43) can be evaluated through cobwebbing (as shown in Fig. 10 in Kot et al., 1996). The cobwebbing diagram for Eq. (43) is shown in Fig. 4. The spread rate for this model, $c = x_{t+1} - x_t$, is the vertical distance between the dashed line and the 1:1 line. Note that the spread rate for Eq. (43) becomes constant as $t \rightarrow \infty$. The spread rate, $c = x_{t+1} - x_t$, becomes constant as $x_t \rightarrow \infty$:

$$c = \lim_{x_t \rightarrow \infty} \frac{1}{\alpha} \log \left(r \exp(\alpha x_t) + \frac{2A}{N_c} \left(\frac{\exp(\alpha x_t) - \exp(-\alpha x_t)}{2} \right) \right) - x_t. \quad (44)$$

Since $\exp(-\alpha x_t) \rightarrow 0$ as $x_t \rightarrow \infty$,

$$c = \lim_{x_t \rightarrow \infty} \frac{1}{\alpha} \log \left(\exp(\alpha x_t) \left(r + \frac{A}{N_c} \right) \right) - x_t \\ = \lim_{x_t \rightarrow \infty} \frac{1}{\alpha} \log \left(r + \frac{\sigma\psi\phi\gamma^2}{4N_c} \right). \quad (45)$$

Therefore, Eq. (45) yields the same result as Eq. (18) and the spread rate for Eq. (14) is the same for either initial condition.

A.4.2. Pair formation following dispersal

For initial condition 2, we evaluate Eq. (15) as

$$N_{t+1}(x) = rN_t(x) + 2A(\exp(-2\alpha x)(\cosh(2\alpha x_t) - 1)), \quad (46)$$

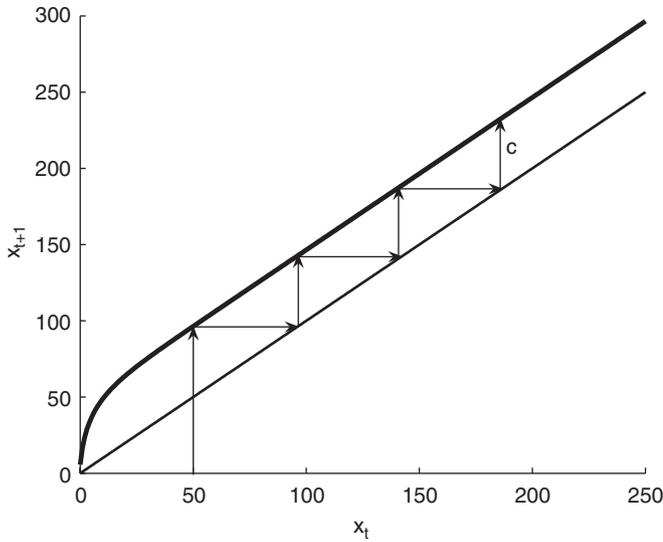


Fig. 4. Finding the extent of the disperser producing population via cobwebbing. Eq. (43) (dark line) predicts the spatial extent of the disperser producing population x_{t+1} as a function of x_t for initial condition 2. The 1:1 line is shown as a light line. The values on the x -axis that correspond to the location of the vertical axis correspond to $x_t, x_{t+1}, x_{t+2}, x_{t+3}$. The vertical distance between the dashed line and the 1:1 line is the spread rate for a given value of x_t . This figure shows a constant spread rate as x_t tends towards infinity. The parameter values used to generate this figure are: $r = 1.33, \alpha = 0.05, A = 1.1, N_c = 0.247$.

for $x < x_t$ where $A = \sigma\psi\phi\gamma^2/8$. We let $N_t = B_t \exp(-2\alpha x)$ and substitute N_t into Eq. (46). Therefore, B_{t+1} as a function of B_t is

$$B_{t+1} = rB_t + 2A(\cosh(2\alpha x_t) - 1). \quad (47)$$

We evaluate B_1 as

$$B_1 = 2A(\cosh(2\alpha x_0) - 1) \quad \text{where } x > x_0, \quad (48)$$

and therefore we show that $N_t = B_t \exp(-2\alpha x)$ holds for all t where $x > x_t$.

We use Eq. (33) (where $w = 2$) to find x_{t+1} for Eq. (47),

$$\exp(2\alpha x_{t+1}) = r \frac{B_t}{N_c} + \frac{2A}{N_c} (\cosh(2\alpha x_t) - 1). \quad (49)$$

We substitute $B_t = N_c \exp(2\alpha x_t)$ from Eq. (33) into Eq. (49) and calculate the extent of the disperser producing population, x_{t+1} , as

$$x_{t+1} = \frac{1}{2\alpha} \log \left(r \exp(2\alpha x_t) + \frac{2A}{N_c} (\cosh(2\alpha x_t) - 1) \right). \quad (50)$$

Eq. (50) can be evaluated by cobwebbing (see Fig. 4). The spread rate, $c = x_{t+1} - x_t$, becomes constant as $x_t \rightarrow \infty$, therefore the asymptotic spread rate is

$$c = \lim_{x_t \rightarrow \infty} \frac{1}{2\alpha} \log \left(r \exp(2\alpha x_t) + \frac{2A}{N_c} \left(\frac{\exp(2\alpha x_t) + \exp(-2\alpha x_t)}{2} - 1 \right) \right) - x_t. \quad (51)$$

Since $\exp(-2\alpha x_t) \rightarrow 0$ and $\exp(2\alpha x_t) \gg A/N_c$ as $x_t \rightarrow \infty$,

$$c = \lim_{x_t \rightarrow \infty} \frac{1}{2\alpha} \log \left(\exp(2\alpha x_t) \left(r + \frac{A}{N_c} \right) \right) - x_t \quad (52)$$

$$= \lim_{x_t \rightarrow \infty} \frac{1}{2\alpha} \log \left(r + \frac{\sigma\psi\phi\gamma^2}{8N_c} \right), \quad (53)$$

where Eq. (52) yields the same results as Eq. (18) and therefore the population spread rate for Eq. (15) does not depend on the initial condition.

Appendix B. Supplementary data

Supplementary data associated with this article can be found in the online version at 10.1016/j.tpb.2006.06.009

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