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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.

Keywords: Allee effect; Integrodifference equation; Wolf recolonization; Pair formation; Spread rate; Component Allee effect

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,

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

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