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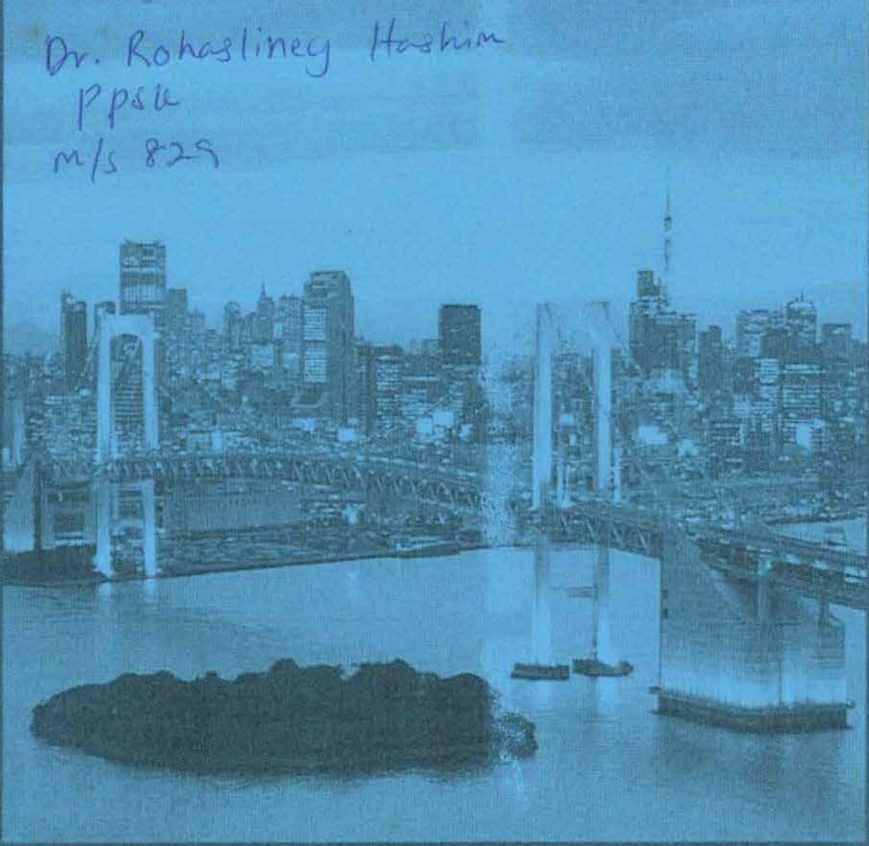

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Species spreading due to environmental hostility, dispersal adaptation and Allee effects

Sanjeeva Balasuriya

Abstract—A phenomenological model for species spreading which incorporates the Allee effect, a species' maximum attainable growth rate, collective dispersal rate and dispersal adaptability is presented. This builds on a well-established reaction-diffusion model for spatial spreading of invading organisms. The model is phrased in terms of the "hostility" (which quantifies the Allee threshold in relation to environmental sustainability) and dispersal adaptability (which measures how a species is able to adapt its migratory response to environmental conditions). The species' invading/retreating speed and the sharpness of the invading boundary are explicitly characterised in terms of the fundamental parameters, and analysed in detail.

Keywords—Allee effect, dispersal, migration speed, diffusion, invasion

I. INTRODUCTION

THE speed and the structure of population dispersal is an important area of study, in particular in the protection of native fauna and flora from invasive species. Factors influencing this include the species' range, density-dependence in its growth, dispersal rate, dependence of the dispersal rate on environmental conditions and density, habitat variation, and collective behaviour. Many types of mathematical models have been used to understand the ecology of spatial spreading, including partial differential equations [1]–[7], discrete models [4], [8], integro-differential equations [9], and neural nets [10]. Different models offer successes in different situations.

One factor influencing population spreading is whether the population is growing at a sufficient rate. The standard measure of this is the per capita growth rate (pgr), which is the rate of increase of the population per individual. The pgr is density-dependent in many relevant situations. The most common density-dependence expresses pgr as a linear decreasing function of the density, modelling the fact that an environment has limited resources. This simple pgr curve does not take into account an important phenomenon postulated by Warder Allee [11], in which the pgr curve increases at small densities [11]–[14]. Among many explanations for this phenomenon are the inability to find mates successfully, diminished anti-predator vigilance and reduction of genetic diversity [13]. If the pgr is actually negative at small densities, this is called the strong Allee effect, which has been demonstrated in gypsy moths [15], bighorn sheep [16], African wild dogs [17] and annual plants [18], [19]. The weak Allee effect (the pgr does not become negative) has been exhibited in flour beetles [11], the California channel island fox [20] and smooth cordgrass [21].

Assuming that a population is increasing sufficiently, its spatial spreading is measured by a dispersal rate. This relates to how individuals move around: their typical range, the shape of the probability distribution of the range, the speed at which they move, etc. The density profile of the population as a whole moves according to how *all* the individuals move. For plants, the spatial probability distribution of the progeny of a plant and the frequency of seeds (and seasonality) contribute to the dispersal rate. Commonly used models for dispersal are neural-net simulations which populate a spatial grid based on a probabilistic dispersal [10], [21], or diffusion equations which incorporate the randomised individual motions into a deterministic model for the collective density [1]–[3], [5], [6], [22].

In this article, an extension to a well-established model [3], [4] which includes both Allee dynamics and diffusive spread is examined. The goal is to determine the spreading rate and the shape of the density profile, in terms of parameters fundamental to the species and the environment. As a first step, this is done in terms of the species' maximum attainable per capita growth rate, natural dispersal rate, and the *hostility* (a newly defined parameter which incorporates the Allee threshold and the environmental carrying capacity). As a second step, the fact that a species will change its dispersal rate depending on environmental conditions is considered, as suggested by Fretwell in his ideal free distribution hypothesis [23]. This can be incorporated in different ways, most of them mathematically difficult: density-dependent diffusion [6], [7], [22], [24], [25], discrete resource-dependent dispersal models [8], [9], and a host of habitat selection models (see the introduction of [26] for a review). Here, a simpler implementation of Fretwell's hypothesis through the definition of a new parameter, the species' *dispersal adaptability*, is formulated. This measures a species' ability to change its dispersal rate depending on resources and intra-species competition. The dependence of the spreading rate and density profile on these fundamental parameters is examined in detail, and ecological implications discussed.

II. PER CAPITA GROWTH RATE

The model for the pgr, ignoring dispersal, is first presented. The important parameters which are used in the model are summarised in Table I, for quick reference. If u is the population density (population per unit habitat length) of a species, the pgr in the presence of Allee effects could be modelled by [4], [14]

$$\mathrm{pgr} = L\left(1 - \frac{u}{K}\right)\left(\frac{u}{\alpha} - 1\right), \qquad (1)$$

is used, in which L is a positive normalizing constant, K is the carrying capacity, and α is the Allee threshold. While K needs to be non-negative to be ecologically meaningful, it is first argued that α needs to be less than K. Firstly, $\alpha = K$ is not a legitimate choice, since pgr is negative even for any $u < K$, any population below the carrying capacity will decay to zero (see Figure 1(a)). Secondly, $\alpha > K$ would result in Figure 1(b), in which α would be a stable equilibrium, while K would be unstable. The population density would therefore approach a value *greater* than the environmental carrying capacity K. Thus, $\alpha < K$.

The normalizing factor L in (1) modifies the height of the curve, and can be chosen in many ways (see [5] for a discussion). Following Lewis and Kareiva [5], it shall be chosen to relate to a parameter of potential ecological significance: the species' maximum attainable per capita growth rate r. Elementary calculus reveals that the maximum value is seen to occur at $u = (\alpha + K)/2$, and hence

$$L = \frac{4\,K\,\alpha}{(K-\alpha)^2}\,r\,. \qquad (2)$$

By replacing L with the above, the pgr can be expressed by

$$\begin{aligned} \mathrm{pgr} &= \frac{4\,K\,\alpha}{(K-\alpha)^2}\,r\left(1-\frac{u}{K}\right)\left(\frac{u}{\alpha}-1\right) \\ &= \frac{4\,r}{(K-\alpha)^2}\,(K-u)\,(u-\alpha)\,, \end{aligned} \qquad (3)$$

The graph of the pgr in (3) is shown in Figure 2. There are two qualitatively different possibilities for α which model ecological situations: $-K < \alpha \leq 0$ and $0 < \alpha < K$. As a special case of the former, suppose $\alpha = 0$, meaning that the organism does not encounter negative pgr. This is the weak Allee effect, whose graph is shown in Figure 2(a). This same qualitative increase in pgr at small densities occurs if $-K < \alpha < 0$, whose graph can be obtained by shifting the zero at $u = 0$ in Figure 2(a) to the left by the appropriate amount. As long as $-K < \alpha$, the peak of the graph occurs at positive u, leaving a region at small densities in which pgr initially increases with u. (If $\alpha \leq -K$, pgr is strictly decreasing for positive u, and hence qualitatively similar to standard logistic growth.) Weak Allee effects have been shown to exist in nature in both animals [11], [20] and plants [10], [21]. The strong Allee effect relates to $0 < \alpha < K$, and is shown in Figure 2(b). The strong Allee effect has been exhibited in animals [15]–[17], and in plants [18], [19].

The *environmental hostility* parameter h is now defined by

$$h = \frac{\alpha}{K}\,. \qquad (4)$$

For a particular species, the carrying capacity K is highly susceptible to the environment, for example through habitat destruction or resource depletion. The Allee threshold α is less influenced by environmental conditions. Thus, if a given species is considered in different environments, those which are most conducive to the species' survival have a higher K value, and therefore an h closer to zero. In contrast, in harsh environments with limited resources, K will be small, and in the worst case will approach α, meaning that h will be close to one. Thus, h represents the hostility of the environment in relation to the species, with h nearing 1 implying an environment highly hostile to the species, in which growth can occur only in a tiny density range $\alpha < u < K$. Since $-K < \alpha < K$, h satisfies $-1 < h < 1$, with $-1 < h \leq 0$ representing the weak Allee effect. If $h = 0$, the environment is friendly enough so that no negative growth occurs, with more negative h implying that the species has a better growth rate at small densities.

III. SPATIAL DISPERSAL

Let Φ be the natural dispersal rate constant; species which have greater speeds of motion, or which typically move over longer distances, have a larger value of Φ. For animal species,

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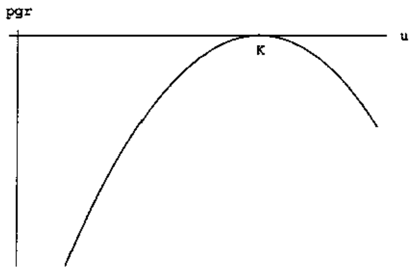
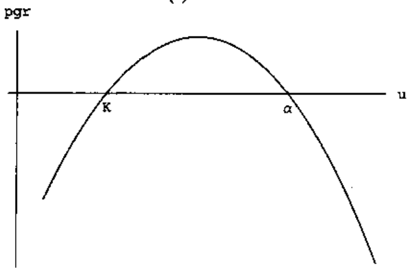
TABLE I
LIST OF PARAMETERS AND VARIABLES USED IN THIS ARTICLE.

Quantity	Name	Dimensions
α	Allee threshold	Individuals
c	Spreading rate	Length/Time
h	Environmental hostility, $h = \alpha/K$	Dimensionless
K	Carrying capacity	Individuals
n	Dispersal adaptability	Dimensionless
Φ	Natural dispersal rate	Length^2 / Time
r	Maximum per capita growth rate	Time^{-1}
u	Population density	Individuals/Length



(a) $\alpha = K$



(b) $\alpha > K$

Fig. 1. Ecologically meaningless choices for pgr: (a) $\alpha = K$, and (b) $\alpha > K$.