



## Critical patch-size for two-sex populations

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### ARTICLE INFO

#### Keywords:

Two-sex model

Critical patch size

Reaction-diffusion equations

Habitat loss

### ABSTRACT

As environments become increasingly degraded, mainly due to human activities, species are often subject to isolated habitats surrounded by unfavorable regions. Since the pioneering work by Skellam [25] mathematical models have provided useful insights into the population persistence in such cases. Most of these models, however, neglect the sex structure of populations and the differences between males and females. In this work we investigate, through a reaction-diffusion system, the dynamics of a sex-structured population in a single semipermeable patch. The critical patch size for persistence is determined from implicit relationships between model parameters. The effects of the various growth and movement parameters are also investigated.

### 1. Introduction

Population dynamics studies usually assume that a species is characterized by a single sex-class of individuals, usually females. This approach is surely appropriate for hermaphrodite species and in systems where population dynamics is determined by a single limiting sex [24]. However, as in many species males and females have quite distinct demographic parameters and no sex dominates population dynamics, these unstructured models become unrealistic and models that take into account the dynamics of both sexes are needed [4].

Males and females can show, for instance, quite distinct dispersal abilities, which can have a great impact on their spatial distributions. To cite a few examples, dispersal of *C. carcharias* (white shark) is sex-biased with philopatric (non-roving) females and roving males [21]; at local scale, dispersal in the common vole *M. arvalis* is strongly male-biased [10]. It has been suggested as a general result that in mammals males usually disperse more frequently than females, while in birds females are the most dispersive sex [11]. In human-altered environments sex-biased dispersal is thought to expose populations to an even greater risk of extinction [6]. Individuals that used to disperse to other sites in the landscape may not find suitable areas, resulting in increased loss of the most dispersive gender. As a consequence, sex-biased dispersal may lead to biased sex-ratios in the natal population, leaving a higher number of individuals unpaired.

Despite the increasing number of empirical studies on sex-related effects, very few mathematical studies have analyzed the dynamics of sex-structured populations in space. Miller et al. [20] derived an explicit expression for the speed of invasion of a two-sex integrodifference

model. The effect of sex-biased dispersal on the spreading speed was then studied. Reaction-diffusion equations have also been used to study the dynamics of sex-structured populations in space [1,14]. Jin et al. [14] modeled populations with short reproductive seasons in patches of limited sizes through a periodic impulsive reaction-diffusion system with Dirichlet boundary conditions, and identified conditions for population persistence.

Increasing degradation of natural areas frequently subject populations to habitats of limited size surrounded by unfavorable regions. Since the pioneering work by Skellam [25], reaction-diffusion equations have become one of the most important mathematical tools in the study of population persistence in such situations. Skellam posed the “minimal size problem” of how large a patch must be to support a population. For a single population with hostile boundaries, diffusion constant  $d$  and intrinsic growth rate  $r$ , the critical size of a one-dimensional patch is  $l_c = \pi\sqrt{d/r}$ .

In this study we examine the minimal size problem for sex-structured populations. We model population dynamics through a reaction-diffusion system with reproduction given by the standard harmonic mean mating function [16,19]. We study the problem of species persistence in a finite domain with semipermeable boundaries and show how standard techniques in the analysis of monotone parabolic partial differential equations can be used to find an implicit relation that determines the critical patch size. In the limit of completely hostile boundary conditions, this critical patch size can be expressed explicitly in terms of model parameters. Moreover, we study how distinct males' and females' traits affect the critical patch size.

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2. The model

Growth in two-sex models is a process that involves pair formation and the production of new offspring by females. The number of couples for certain local female ( $f$ ) and male ( $m$ ) populations is given by the mating (or birth) function  $\mathfrak{B}(m, f)$ . Several forms for  $\mathfrak{B}$  have been proposed [12,20]. This function is usually required to follow some desired properties [3,12]: it needs to be a positive, non-decreasing function for all  $m, f \neq 0$ , as well as homogeneous, that is,  $\mathfrak{B}(am, af) = a\mathfrak{B}(m, f)$  for all  $a \neq 0$ . The harmonic mean function

$$\mathfrak{B}(m, f) = \frac{2mf}{m + f} \tag{1}$$

follows all these properties and is free from the difficulties other functions present [15]. The geometric mean  $\mathfrak{B}(m, f) = \sqrt{mf}$  and minimum function  $\mathfrak{B}(m, f) = \min(m, f)$  are other common mating functions. The harmonic mean mating function is often considered the least objectionable mating function [16]. Also, Miller and Inouye [19] verified in a laboratory experiment that the harmonic mean mating function best describes the growth of the bean beetle (*Callosobruchus maculatus*) at low densities.

$\mathfrak{B}$  can be easily modified to account for polygamous systems, in which males or females can mate with more than one partner. If  $h$  represents the number of females with which each male mates, also known as the “harem” size, the number of “harems” formed is given by  $\mathfrak{B}(m, f/h)$  [24]. The number of paired females is then given by  $h\mathfrak{B}(m, f/h)$ . Polygynous, monogamous and polyandrous mating systems can be accommodated by setting  $h > 1$ ,  $h = 1$  or  $h < 1$ , respectively.

Now we assume that individuals of both sexes move and reproduce in a single one-dimensional habitat of size  $l$ . The local number of reproducing females for given male ( $m$ ) and female ( $f$ ) densities is assumed to be given by the harmonic mean mating function, Eq. (1). Different mating systems are accommodated by properly introducing the harem size ( $h$ ) into the model, as described above. We also assume that male and female diffusivities,  $d_m$  and  $d_f$  respectively, are distinct in general. Denoting time as  $t \geq 0$  and spatial positions by  $x \in [-l/2, l/2]$ , we write the reaction-diffusion system of equations for male and female populations as:

$$\frac{\partial m}{\partial t} = d_m \frac{\partial^2 m}{\partial x^2} + c g \frac{2mf}{m + f/h} - \mu_m m \tag{2}$$

$$\frac{\partial f}{\partial t} = d_f \frac{\partial^2 f}{\partial x^2} + (1 - c)g \frac{2mf}{m + f/h} - \mu_f f, \tag{3}$$

where  $c \in [0, 1]$  is the fraction of males at birth and  $g$  is the rate of production of new offsprings per paired female, while  $\mu_m$  and  $\mu_f$  are the male and female mortality rates, respectively.

At patch boundaries we impose semipermeable boundary conditions [5,27]. We initially write these conditions in the form given by Van Kirk and Lewis [27]:

$$\frac{\partial m}{\partial x}(\pm l/2) = \mp c_m m(\pm l/2) \tag{4}$$

$$\frac{\partial f}{\partial x}(\pm l/2) = \mp c_f f(\pm l/2), \tag{5}$$

where parameters  $c_{m, f} \geq 0$  represent the enticement of individuals to leave the patch. For  $c_m = 0$  ( $c_f = 0$ ) no males (females) leave the patch and we get no-flux conditions. In the limit  $c_{m, f} \rightarrow \infty$ , individuals leave the patch and never return.

We introduce the new scaled quantities:

$$M = m, \quad F = \frac{f}{h}, \quad T = gt, \quad X = \sqrt{\frac{g}{d_m}} x, \quad \tilde{\mu}_{m,f} = \frac{\mu_{m,f}}{g},$$

$$D = \frac{d_f}{d_m}, \quad L = \sqrt{\frac{g}{d_m}} l,$$

and rewrite the equations as:

$$\frac{\partial M}{\partial T} = \frac{\partial^2 M}{\partial X^2} + c \frac{2MF}{M + F} - \tilde{\mu}_m M \tag{6}$$

$$\frac{\partial F}{\partial T} = D \frac{\partial^2 F}{\partial X^2} + (1 - c) \frac{2MF}{M + F} - \tilde{\mu}_f F. \tag{7}$$

In this new scaling we can define the boundary permeability of males and females as

$$\alpha_{m,f} = \frac{c_{m,f} \sqrt{\frac{d_m}{g}}}{\left(1 + c_{m,f} \sqrt{\frac{d_m}{g}}\right)}.$$

Boundary conditions then read:

$$(1 - \alpha_m) \frac{\partial M}{\partial X}(\pm L/2) = \mp \alpha_m M(\pm L/2) \tag{8}$$

$$(1 - \alpha_f) \frac{\partial F}{\partial X}(\pm L/2) = \mp \alpha_f F(\pm L/2). \tag{9}$$

Parameters  $\alpha_{m, f} \in [0, 1]$  control boundary permeability and can represent both individual movement decisions [27] and the quality of the exterior region [17]. In the limit  $\alpha_{m,f} = 0$  no individuals are lost through the boundaries and we get no-flux conditions. Yet when  $\alpha_{m,f} = 1$  we get hostile boundary conditions. In this case, every individual that hits a boundary leaves the patch and never returns.

The Eqs. (6)–(7) form a system of nonlinear partial differential equations that is homogeneous, in the sense that if  $(M(X, T), F(X, T))$  is a solution to the system, then  $(sM(X, T), sF(X, T))$ , with  $s$  a given constant, is a solution as well. Note also that there is no saturating mechanism in our mating function and therefore solutions either decrease to zero or grow to infinity asymptotically. Accordingly, our model is appropriate to investigate the growth of small populations and specifically the critical size problem.

3. Results

Our goal is to derive persistence conditions for our sex-structured model, i.e. conditions for which the population can grow. Persistence conditions for problems without Allee effects are typically derived from the linear stability of the trivial zero steady state solution [2]. When we try to linearize Eqs. (6)–(7) around the (0, 0) state, though, we obtain an indeterminacy in the sex-ratio of populations,  $M/F = 0/0$ , which leads to the mating function being undefined. In what follows below, we obtain conditions for species persistence instead by finding particular exponential solutions for this system and determining conditions for the growth of these solutions. Using results from maximum principles for parabolic partial differential equations, we then show that these conditions imply persistence of the population for a general class of initial conditions.

3.1. Particular solutions

We seek solutions of the form:

$$M(X, T) = M_0 e^{\lambda T} V(X) \tag{10}$$

$$F(X, T) = F_0 e^{\lambda T} V(X), \tag{11}$$

where  $M_0$  and  $F_0$  are given positive constants. As population densities are always positive, we consider only real values of  $\lambda$ , and  $V(X) \geq 0$ . Substituting these expressions into Eqs. (6) and (7),  $V(X)$  must satisfy

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