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Birth functions in stage structured two-sex models

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Abstract

The most commonly used birth function in two-sex demographic models is the harmonic mean birth function. This function treats all individuals of one sex as identical, i.e., stage specific fecundity is not taken into account. In the analysis presented here, the harmonic mean birth function is developed to incorporate size and sex specific fecundities. This structured birth function is compared with the harmonic mean birth function using both a hypothetical population and data for populations of the limpet *Patella vulgata*. A general expression to calculate the threshold value where the unstructured and the structured birth functions coincide is also provided. Using the structured birth function resulted in changes in population dynamics, growth rate, proportion of males and reproductive output. In conclusion, the choice of birth function is important due to its effects on the deterministic population characteristics, which in turn may have consequences for the managements of endangered or vulnerable species.

Keywords: Two-sex model; Harmonic mean; Birth functions; *Patella vulgata*

1. Introduction

Most demographic models are one-sex models where it is assumed that both sexes have identical vital rates or that the dynamics of the population are determined by only one sex (Caswell, 2001). However, there are many examples of sexual dimorphism in vital rates such as juvenile mortality (Clutton-Brock et al., 1985) and fecundity (Clutton-Brock, 1988), which indicate the need for two-sex models. Male or female dominance may on the other hand be large so that there always are enough individuals of the subordinate sex and thus sexual dimorphism in survival rates will not influence the asymptotic population growth, although it will give rise to skewed sex ratios. There are populations where dominance is weak, i.e., where the abundance of both sexes is important for the reproductive output, e.g., polygamous populations. Several birth functions have been used in population modelling and the harmonic mean function is regarded the least flawed in human demography (Caswell, 2001). The fertility functions derived from the harmonic birth function are fixed clutch sizes times the proportion of males (for female fertility) or females (for male fertility) and the maximum per capita (p.c.) birth rate of the popula-

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tion occur at the 1:1 sex ratio (cf., Caswell, 2001). The harmonic birth function has been applied in several non-human demographic studies (e.g., Lindström and Kokko, 1998; Ranta and Kaitala, 1999; Ranta et al., 1999; Engel et al., 2001) and has further been modified and applied in polygamous systems (Ranta and Kaitala, 1999), where the maximum reproduction of a population occurs at a skewed sex ratio. However, a limitation of the harmonic birth function is that the age or stage structure within each sex is ignored.

Human demographers have developed age structured birth functions and one approach has been to use separate functions for male and female growth. The problem with these models has been that the separate sexes may develop different growth rates leading to extinction of the sex with the lowest growth rate (Martcheva, 1999). There are examples of age or stage structured birth functions that do not have this problem like the discrete Birth Matrix-Mating Rule model (BMMR; Pollak, 1986) and the continuous analogue of that (Martcheva, 1999), which can be applied to monogamous populations.

Many marine organisms and wind pollinated terrestrial plants are polygamous in the sense that they release their gametes (or only male gametes) in the water column or in the air and as a result of mixing of gametes many pairs of parents are possible. Often these organisms also have indeterminate growth and size-dependent fecundity and it can be argued that large individuals with larger fecundity will have a larger clutch size than smaller individuals. However, fertilisation success will also depend on other factors such as the synchrony of the spawning event and the spatial distribution of individuals (Levitan et al., 1992; Yund, 2000). The birth functions mentioned above cannot directly be applied to spawning organism with size-dependent fecundity and in this paper we modify the harmonic birth function, so it can be applied to such organisms. The aim here is to describe a birth function for reproduction in demographically structured two-sex populations, compare this function with the harmonic birth function and illustrate its dynamics when applied in a matrix population model. It is common to include size specific fecundity or fertility in one-sex matrix population models (for examples, see Caswell, 2001). There are also examples of two-sex models where differential fertility between sexes and other stages are taken into account (Heide-Jorgensen et al., 1992). There are other models that include age structured fecundity, but in an implicit way (Pollard, 1997; Hsu Schmitz and Castillo-Chavez, 2000). However, in this paper, we develop and analyse a model that can be adopted to either size, age or sex structured populations, or any combination thereof. We compare it with the harmonic birth function as well as the harmonic function modified for a harem scenario and this has to our knowledge not been done before.

The motivation for this work came from our attempt in developing a demographic model for the limpet *Patella vulgata*. This species is a sequential hermaphrodite, where all individuals are born as neuter, they nearly all mature as males and at an age of about three years they change sex and become females (Ballantine, 1961; Salerna de Mendonca Corte-Real, 1992). This free-spawning and sedentary species has indeterminate growth and size-dependent fecundity, and the modified birth function is expected to capture the main features of the reproduction in *P. vulgata* as well as other size and sex structured organisms.

2. Methods

The basic harmonic birth function is given by Caswell (2001) to be:

$$B(\mathbf{n}) = \frac{2kn_\mathrm{m}n_\mathrm{f}}{n_\mathrm{m}+n_\mathrm{f}} \tag{1}$$

where k is the clutch size and n_m and n_f are the densities of reproductive males and females, respectively. This model assumes monogamy and an equal clutch size of each male and female regardless of its size or other stage category. Both the model in Eq. (1) and the modified function described below has the important assumption that each offspring has one male and one female parent, thus the fertility functions become (cf., Caswell, 2001):

for males:

$$F_\mathrm{m}(\mathbf{n}) = \frac{kn_\mathrm{f}}{n_\mathrm{f}+n_\mathrm{m}} \tag{2}$$

and for females:

$$F_\mathrm{f}(\mathbf{n}) = \frac{kn_\mathrm{m}}{n_\mathrm{f}+n_\mathrm{m}} \tag{3}$$