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The mechanistic basis of discrete-time population models: The role of resource partitioning and spatial aggregation

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ABSTRACT

The purpose of this paper is to present a unified view to understand mechanistic basis of various discrete-time population models from the viewpoints of resource partitioning and spatial aggregation of individuals. A first-principles derivation is presented of a new population model which incorporates both scramble and contest competition using a site-based framework in which individuals are distributed over discrete resource sites. The derived model has parameters relating to the way of resource partitioning and the degree of spatial aggregation of individuals, respectively. The model becomes various population models in various limits in these parameters. This model thus provides a unified view to understand how various population models are interrelated. The dependence of the stability of the model on the parameters is also examined.

1. Introduction

Discrete-time population models $a_{t+1} = f(a_t)$, where a_t is the population size in generation t, have received much attention for the complex dynamics they can produce (e.g., May, 1976). In most cases, these models have been introduced as top-down, phenomenological models, but in principle, they must result from local interactions between individuals making up the population. It is important to reveal relationship between population dynamics and interactions between individuals (Hassell and May, 1985), and deriving population models from first principles is an effective way to do so. First-principles derivations of discrete-time population models can be broadly classified into continuous-time approaches (e.g., Gurney, 1998; Wells et al., 1998; Thieme, 2003; Geritz and Kisdi, 2004; Eskola and Geritz, 2007; Eskola and Parvinen, 2007, 2009) and discrete-time approaches. Main examples of the discrete-time approaches are derivations using site-based frameworks (Sumpter and Broomhead, 2001; Johansson and Sumpter, 2003; Brännström and Sumpter, 2005b; Anazawa, 2009), which are extensions of a method used by Royama (1992). There are also studies extending the site-based frameworks (Brännström and Sumpter, 2005a, 2006), along with studies by individual-based simulations (e.g., Johst et al., 2008). Extending the work by Brännström and Sumpter (2005b) and Anazawa (2009), this paper provides a first-principles derivation of a new discrete-time population model, which yields a unified view to understand relationships between various population models.

As is well known, there are two contrasting types of competition between individuals: scramble and contest competition (Nicholson, 1954; Hassell, 1975). In scramble competition, resource is assumed to be partitioned evenly between individuals. On the other hand, in contest competition, resource is monopolized by a few competitively superior individuals. Brännström and Sumpter (2005b) derived various population models for either scramble or contest competition by making simple assumptions for these types of competition, and combining them with spatial distribution of individuals. Anazawa (2009) extended their work and derived similar population models by considering resource partitioning explicitly, and furthermore derived population models exhibiting the Allee effect. While actual competitive interactions are considered to incorporate both scramble and contest competition in some cases, there is no derivation of population models incorporating the two types of competition in site-based frameworks, except for one case in Brännström and Sumpter (2005b), which was provided no mechanistic basis at individual level.

This paper provides a first-principles derivation of a new population model for a competition type intermediate between scramble and contest from the consideration of resource partitioning and spatial distribution of individuals. The derived model has two parameters relating to the type of competition and the degree of spatial aggregation of individuals, respectively, and it becomes various population models in various limits in the parameters. The derived model hence provides a unified view to understand relationships between various population models. The dependence of the stability of the model on the parameters is also examined.

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2. Derivation of population models

2.1. Basic framework

As the basic framework in which population models are derived, a site-based framework used in Anazawa (2009) is assumed, which is described in the following. Consider a habitat consisting of n resource sites or patches over which a_t individuals of single species are distributed in generation t. Not moving to the other sites, each individual is assumed to compete for resource with the other individuals in the same site. The individuals that obtain a sufficient amount of resource reproduce, and the others fail to reproduce. All the individuals die after the reproductive season. Offspring emerging from the sites disperse, and are distributed over the resource sites again. They form a population in the next generation.

In this situation, the expected number of individuals in generation $t+1$ is written as

$$a_{t+1} = n \sum_{k=1}^{\infty} p_k(a_t)\,\phi(k). \tag{1}$$

Here, $\phi(k)$, which is referred to as the interaction function, denotes the expected number of offspring emerging from a site containing k individuals. This function relates with local competition between the individuals in a site. On the other hand, $p_k(a_t)$ denotes the probability of finding k individuals in a given site, and is a function of population size a_t. When individuals are distributed completely at random, p_k is given by the following Poisson distribution in the limit as $n \to \infty$ with a_t/n fixed:

$$p_k(a_t) = \frac{1}{k!}\left(\frac{a_t}{n}\right)^k \mathrm{e}^{-a_t/n}. \tag{2}$$

In this paper, we assume p_k to be the following negative binomial distribution in order to examine the effect of aggregation of individuals on population dynamics:

$$p_k(a_t) = \frac{\Gamma(k+\lambda)}{\Gamma(\lambda)\Gamma(k+1)}\left(\frac{a_t}{\lambda n}\right)^k \left(1+\frac{a_t}{\lambda n}\right)^{-k-\lambda}. \tag{3}$$

Here, λ is a positive parameter, where $1/\lambda$ can be interpreted as the degree of aggregation. This distribution includes the Poisson distribution (Eq. (2)) as a special case in the limit as $\lambda \to \infty$.

Table 1 presents the population models that are studied in this paper. Among them, the models for scramble and contest types were derived in Brännström and Sumpter (2005b) and in Anazawa (2009). Extending Anazawa (2009), assuming a way of resource partitioning for a competition type intermediate between scramble and contest, this paper derives a new population model Eq. (7), which includes the other models as special cases.

2.2. Resource partitioning between individuals

In this subsection, a definition of resource partitioning is given for the competition type intermediate between scramble and contest, and a new interaction function (Eq. (6)) is derived from this. First, as in Anazawa (2009), each individual is assumed to have a minimum sufficient resource requirement s to reproduce; if an individual obtains the amount s of resource, it reproduces, and if not, it fails to reproduce. For simplicity, if obtaining the amount s, individuals are assumed not to consume more than that.

Now, we consider resource partitioning in a site which includes k individuals and an amount R of resource. In Anazawa (2009), the ways of resource partitioning for scramble and contest competition were defined as follows. For scramble competition, the resource R is partitioned evenly among the individuals, and for contest competition, it is partitioned in the order of competitive ability

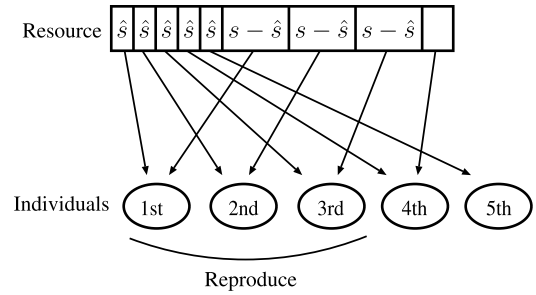

Fig. 1. Illustration of the way of resource partitioning in a site for intermediate competition. At first, each individual equally takes an amount $\hat{s}$ of resource, and then tries to take an amount $s-\hat{s}$ from the remaining resource in the order of competitive ability. Only the individuals that are able to obtain a total of the amount s can reproduce.

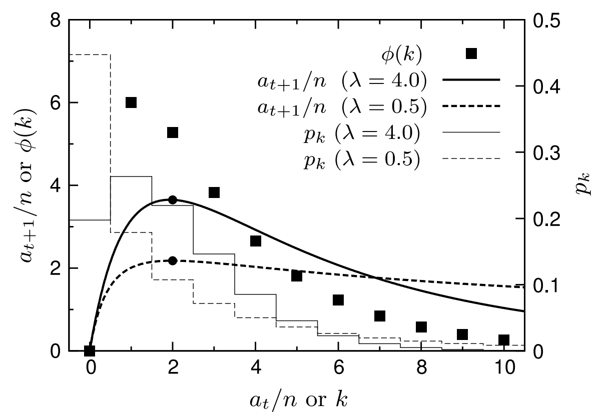

Fig. 2. Illustration of the relationship between Eqs. (6) and (7) in the case of $c = 0.2$, $\beta = 0.4$ and $b = 6$. Here, a_{t+1}/n is obtained by averaging $\phi(k)$ over all the sites following the distribution p_k, which is also described for $a_t/n = 2$. Reproduction curves a_{t+1}/n come to show milder variation with decreasing λ, since the variance of k in a site becomes larger.

of the individuals. After the resource partitioning, only the individuals that obtain the amount s reproduce. Combining the above two ways of partitioning, a way of partitioning intermediate between scramble and contest is defined as follows. First, an amount $\hat{s}$ ($<s$) is evenly given to all the individuals in the site, and then the remaining resource is partitioned in the order of competitive ability (see Fig. 1). In the latter half step, each individual tries to take an amount $s-\hat{s}$ so as to obtain a total of the amount s. We refer to the competition type corresponding to the resource partitioning above as ‘intermediate competition’.

Next, we consider derivation of an interaction function for intermediate competition. We assume that the amount R of resource in a site is not a constant, but takes various values following a probability density distribution $q(R)$. Since, in a site with k individuals, $R - s'k < (s-s')m$ must be satisfied so that the m-th individual in the order of competitive ability obtains the amount s and reproduce, the interaction function is written as

$$\phi(k) = \sum_{m=1}^{k} b' \,\mathrm{Prob}[R - \hat{s}k < (s-\hat{s})m], \tag{4}$$

where b' is a positive parameter representing the expected number of offspring reproduced by an individual which actually reproduces. Now, we consider the case in which $q(R)$ is given by the following exponential distribution with expectation $\bar{R}$:

$$\exp(-R/\bar{R})/\bar{R}. \tag{5}$$

This is a distribution that is obtained by partitioning an amount $n\bar{R}$ of resource among the n sites randomly, and taking the limit