



Extended Lotka–Volterra equations incorporating population heterogeneity: Derivation and analysis of the predator–prey case



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ABSTRACT

Extended logistic and competitive Lotka–Volterra equations were developed by Eizi Kuno to understand the implications of population heterogeneity (especially spatial) for population growth. Population heterogeneity, defined as the presence of individuals in some patches of population and not others, is the resulting expression of a number of processes, including dispersal, habitat heterogeneity and searching behaviour. Kuno's models allow the effect of population heterogeneity (thus defined) on a population at equilibrium to be accounted for without using multi-patch models. This paper demonstrates this for the first time using numerical simulations and presents a more complete mathematical derivation of his models. An extension of Kuno's equations to model predator–prey scenarios with heterogeneity in the prey population is also developed. Analysis of this predator–prey case shows that a patchy distribution of prey facilitates their stable coexistence with predators. This paper has broad implications for ecological modelling because it shows how the effects of a number of population processes, including dispersal, are reflected in the density of populations at equilibrium. Therefore, by adjusting the equilibrium solutions of models, the effects of a number of processes are captured without representing the processes themselves in an explicit way.

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1. Introduction

Crowding is a biological process that has been shown to effect competitive processes such as the coexistence and exclusion of multiple interacting species (Kuno, 1988). At a basic level, crowding refers to the way in which some areas of habitat contain more individuals than others. As such, crowding is synonymous with the form of population heterogeneity called spatial heterogeneity, which arises as the result of a number of processes including dispersal, resource availability and genetics (Clobert et al., 2009; Pickett and Cadenasso, 1995). As such, a measure of crowding can be regarded as a surrogate measure of these processes, since it captures their results. Intra-specific mean crowding, as defined by Lloyd and expressed by the notation m^* , is the average number

of animals per other animal of the same species per patch (Lloyd, 1967), and is given by the formula

$$m^* = \frac{\sum_{q=1}^Q (N_q - 1)N_q}{\sum_{q=1}^Q N_q}, \quad (1)$$

where N_q is the number of individuals in the q th patch of habitat. A simple linear model derived by Iwao,

$$m^* = a + bm, \quad (2)$$

describes the relationship between m^* and the mean number of individuals (m) per patch of habitat (Iwao, 1968; Lloyd, 1967). Though often referred to as a linear regression, (2) can equally be viewed as a linear functional relationship (Waters et al., 2014).²

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² The interpretation of the parameters a and b may differ depending on whether (2) is viewed as a function or a statistical model. In particular, the value and interpretation of the parameter a requires further research. Waters et al. (2014) have

Table 1
Values of a and b for animals with different spatial distributions (Iwao, 1968; Kuno, 1988).

Distributional assumptions	b	a
Uniformly distributed individuals	1	-1
Distribution of individuals is regular (underdispersed) but not uniform	0-1	-1
Poisson distributed individuals	1	0
Poisson distributed clusters of individuals	1	>0
Contagiously (negative binomially) distributed individuals	>1	0
Contagiously distributed clusters of individuals	>1	>0

This has informed the incorporation of Iwao’s model into linear differential equation models (Iwao, 1968; Waters, 2012). A unique feature of Iwao’s linear model is that its intercept (a) and slope (b) parameters have been demonstrated to take on particular values when individuals are distributed according to the uniform, Poisson and negative binomial distributions (see Table 1) (Iwao, 1968; Kuno, 1988). Kuno developed a framework of generalised competitive equations using the parameters a and b of Iwao’s linear relationship as constants accounting for the effect of spatial heterogeneity on population dynamics, and showed that patchy spatial distributions are required for the competitive coexistence of two species (Kuno, 1988). This work has been cited rarely despite its potentially broad application (19 citations in 26 years, according to a Google Scholar search on 23 July 2014). A feature of Kuno’s paper is that it does not show how its equations were derived, and gives the impression that some incorrect algebraic substitutions were utilised (for example, substituting the total number of individuals N for the mean number of individuals with little explanation). There are also some typographical errors in the paper. Here, a more detailed mathematical treatment of Kuno’s work is provided. The ecological assumptions, implications and limitations of Kuno’s work are clarified, and his basic idea is extended beyond the competitive scenario to predator–prey scenarios. As a result, Kuno’s novel piece of work, which has thus far been undervalued, is promoted.

2. Derivation of the basic model

2.1. Background

The logistic model is one of the most influential models in mathematical biology and is featured in most introductory textbooks as an improvement on the exponential model for describing the growth of populations (Allman and Rhodes, 2004; Murray, 2002; Zill and Wright, 2009). As commonly formulated, however, the logistic growth model behaves unrealistically in many situations. The logistic model describing the growth of a population of N individuals is most commonly formulated as

$$\dot{N} = rN \left(1 - \frac{N}{K} \right), \tag{3}$$

where \dot{N} is the derivative of population size with respect to time, r is the intrinsic reproductive rate of the population and K is the carrying capacity (Gabriel et al., 2005; Kuno, 1988, 1991b). Carrying capacity is interpreted as the maximum population size that can be supported by the environment (Zill and Wright, 2009). This formulation of the logistic model produces biologically unrealistic results in many situations. The most notably unrealistic property of (3) is that the population increases indefinitely when the

suggested that values of $a > 0$ are poorly supported, but this is only the beginning of a conversation and the matter cannot be considered closed. For this reason, we continue to use generally accepted interpretations of a and b in this manuscript, until this situation is resolved.

reproductive rate is negative, which occurs when the initial value is greater than K (Levin’s paradox) (Gabriel et al., 2005; Kuno, 1991b; Mallet, 2012). A further example of the limitations of this formulation is that it assumes homogeneous mixing – that is, that all individuals have the same number of mates. This is equivalent to assuming that individuals are uniformly distributed in their environment (Kuno, 1988). It is possible to deal with the first problem, Levin’s paradox, by using Verhulst’s older form of the logistic equation (Gabriel et al., 2005; Kuno, 1991b),

$$\dot{N} = rN - hN^2, \tag{4}$$

where h is a positive constant expressing intrinsic limitations on population growth (Gabriel et al., 2005). Verhulst’s form of the logistic growth model is preferred by Kuno (1991a), and is used as the basis of his modelling to resolve the unrealistic assumption of an homogeneously distributed population.

A patch is a subdivision of a population that can be defined either based on size or area. Patches defined based on area are simply divisions of a population’s habitat along geographical lines. A drawback of this approach is that it is essentially a geographically-rather than a biologically-meaningful definition of a patch: an area in an animal’s territory with no animals in it is just as much a patch as an area with three mating pairs or a single individual. An alternative approach is to define patches based on size, that is the number of individuals comprising a biologically-meaningful unit. For example, one study defined a patch as a location where the number of individuals exceeded the average by one standard deviation (Stabeno et al., 1996). Another study used the number of trees per stand to describe the patch structure of forests (Woodbridge and Detrich, 1994). Iwao expressed the same idea in distinguishing clump size and clump area (Iwao, 1972). Under this approach, a discrete group of individuals interacting in a biologically significant way amongst themselves but not with other groups of individuals comprises a patch. This effective biological independence arises when between-patch processes such as dispersal have equilibrated, such that the state of the system is almost perfectly described only by within-patch processes such as reproduction. The assumptions of a patchy habitat defined on the basis of patch size rather than patch area, and the dominant influence of within-patch rather than between-patch processes, are fundamental to illustrate the relationship between mean crowding and (4) and the implications of this relationship.

Let $N = \sum_{q=1}^Q N_q$ such that the habitat of the population is divided into Q patches of size N_q . Applying the logistic equation to the dynamics of each patch and summing over all patches gives the total state of the population as

$$\dot{N} = \sum_{q=1}^Q (rN_q - hN_q^2). \tag{5}$$

Applying this principle to (5) and dividing through by N , (5) becomes

$$\frac{1}{\sum_{q=1}^Q N_q} \dot{N} = r - h \frac{\sum_{q=1}^Q N_q^2}{\sum_{q=1}^Q N_q}. \tag{6}$$

In (6) $\sum_{q=1}^Q N_q^2 / \sum_{q=1}^Q N_q$ is equal to $m^* + 1$, where m^* is intra-specific mean crowding (Hanski, 1981; Kuno, 1988; Lloyd, 1967). Because of Iwao’s mean crowding versus mean density relationship, given in (2), it is possible to substitute $m^* + 1 = a + bm + 1$ into (6) to give

$$\frac{1}{\sum_{q=1}^Q N_q} \dot{N} = r - h(a + bm + 1), \tag{7}$$

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