



Single species models with logistic growth and dissymmetric impulse dispersal

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ARTICLE INFO

Article history:

Received 25 October 2011

Received in revised form 19 November 2012

Accepted 20 November 2012

Available online 5 December 2012

Keywords:

Single species
Impulsive dispersal
Permanence
Extinction
Periodic solution
Global stability

ABSTRACT

In this paper, two classes of single-species models with logistic growth and impulse dispersal (or migration) are studied: one model class describes dissymmetric impulsive bi-directional dispersal between two heterogeneous patches; and the other presents a new way of characterizing the aggregate migration of a natural population between two heterogeneous habitat patches, which alternates in direction periodically. In this theoretical study, some very general, weak conditions for the permanence, extinction of these systems, existence, uniqueness and global stability of positive periodic solutions are established by using analysis based on the theory of discrete dynamical systems. From this study, we observe that the dynamical behavior of populations with impulsive dispersal differs greatly from the behavior of models with continuous dispersal. Unlike models where the dispersal is continuous in time, in which the travel losses associated with dispersal make it difficult for such dispersal to evolve e.g., [25,26,28], in the present study it was relatively easy for impulsive dispersal to positively affect populations when realistic parameter values were used, and a rich variety of behaviors were possible. From our results, we found impulsive dispersal seems to more nicely model natural dispersal behavior of populations and may be more relevant to the investigation of such behavior in real ecological systems.

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1. Introduction

Due to the ubiquitous prevalence of organism movements in nature and their significant impacts on species' diversity [57], population dynamics [21] and genetic polymorphisms [22], dispersal, migration, and other types of movement in a spatio-temporally heterogeneous environment, have always attracted great interest by biologists, ecologists and biomathematicians. This includes studies of persistence and extinction [35,17,19,23,14,12,27,148,50,3,37,53,52,7,10,11,33,59,60] and stability of equilibria and periodic solutions [9,13,25,26,4–6,24,49,56,40].

Because of their distinctive significance, both as a basis for metapopulation theory and as the starting point for modeling multi-species interactions in patchy environment, single-species dispersal models have been extensively studied, and many important results have been obtained [13,14,12,25,26,28,4,5,20,53,50].

A standard single-species logistic model with continuous constant dispersal rate between two heterogeneous patches can be written as follows

$$\begin{aligned}\dot{N}_1 &= r_1 N_1 \left(1 - \frac{N_1}{k_1}\right) - m N_1 + m(1 - \delta) N_2, \\ \dot{N}_2 &= r_2 N_2 \left(1 - \frac{N_2}{k_2}\right) - m N_2 + m(1 - \delta) N_1,\end{aligned}\quad (1.1)$$

where $N_i(t)$ ($i = 1, 2$) represents the population density in the i th habitat at time t , r_i and k_i are the intrinsic rate of population increase and the carrying capacity of population i , δ is the fraction of migrants dying during migration and m is the emigration rate, a constant. Above dispersal model may be used to characterize the mobility of bird or, insect [15]. Interest for above continuous dispersal models mainly focused on the stability of equilibrium e.g., [13], and the effect of optimal dispersal rates on population size and evolution e.g. [18,25,26,28].

Habitat heterogeneity in space has long been taught not to be sufficient to promote evolution of dispersal. In particular, [25] showed that, with sufficiently high dispersal, a population will be stable if the average over the environment of the density dependent terms indicates stability. Furthermore, [26] showed that, the conditions for stability with a low dispersal rate are more stringent than those for stability with a high dispersal rate. For any dynamics leading to an equilibrium which does exhibit spatial variation, dispersal will be selected against. Hence, selection for dispersal must include other factors. [28] found that the evolution of an optimal habitat distribution may lead to a reduction in population size, and passive

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dispersal should always be selectively disadvantageous in a spatially heterogeneous but temporally constant environment.

Therefore, the question is: what are the “other factors in the above logistic dispersal model”? and is it true that passive dispersal always be selectively disadvantageous? In all of the above population dispersal models, it is assumed that migratory behavior of the modelled populations is occurring at every point in time and is occurring simultaneously between any two patches; i.e. these models are continuous bidirectional dispersal models. At the same time, authors carried into research for above models mainly by utilizing techniques of analyzing equilibrium since the model characterized here are continuous dynamic systems. Actually, real dispersal behavior is very complicated and is always influenced by environmental change and, sometimes by human activities. It usually occurs stochastically or discontinuously [44], and it is often the case that species dispersal occurs at some transitory intervals of time when individuals move among patches to search for mates, food, refuge, etc.

Animal movements between regions or patches of habitat are rarely continuous in time. They may occur during short intervals of time within seasons or within the lifetimes of animals. There are several general reasons for this.

First, the environmental conditions in the landscape matrix between habitat patches may permit normal movement patterns between patches only at certain times. This could be a result of either seasonality or random events that influence the ability of individual organisms to move between patches. For example, in marshes, high water during the wet season may restrict movement of some small mammals between drier patches, such as tree islands [45] within a seasonally flooded marsh. Conversely, fish inhabiting pools and side channels of a river system that are isolated during low water periods may be able to move back and forth among such waterbodies when water levels are higher e.g. [58,39]. In these types of cases, movement may be bidirectional when conditions permit.

Another general class of movements is connected with life cycles of organisms. Many animals may disperse long distances from their natal sites at certain stages in their life cycles, particularly between their birth and start of reproduction [16]. For example, in Florida scrub jays, the females tend to move earlier and farther [47], while among olive baboons, it is males that predominately move [41]. Juvenile male Florida panthers leave the territories of their mothers at about 14 months of age, and may travel over 100 miles to seek a territory. During the mating season, males of many species may move long distances; for example, male stoats searching for females [43]. Those movements associated with life cycles can be considered as bidirectional, as individuals may be starting from any habitat site on the landscape and moving in more or less random directions away from their natal sites.

Therefore, it is not reasonable to characterize the population movements in these cases with continuous dispersal models. This short-time scale dispersal is more appropriately assumed to be in the form of pulses in the modeling process, in order to be in much better agreement with the real ecological situation. With the developments and applications of impulsive differential equations [2,34], theories of impulsive differential equations (hybrid dynamical systems) have been introduced into population dynamics, and many important studies have been performed [3,30,32,36,51,55].

Hui and Chen [30] proposed the following single-species Lotka–Volterra model with impulsively bidirectional dispersal:

$$\begin{cases} \dot{N}_1(t) = N_1(t)(a_1 - b_1 N_1(t)), \\ \dot{N}_2(t) = N_2(t)(a_2 - b_2 N_2(t)), \\ \Delta N_1 = d_1(N_2(t^-) - N_1(t^-)), \\ \Delta N_2 = d_2(N_1(t^-) - N_2(t^-)), \end{cases} \quad \begin{matrix} t \neq n\tau, \\ \\ t = n\tau, \quad n = 1, 2, \dots, \end{matrix} \quad (1.2)$$

where a_i, b_i ($i = 1, 2$) are the intrinsic growth and density-dependent parameters of the population i , d_i is the net dispersal rate between

the i th patch and the j th patch ($i \neq j, i, j = 1, 2$). $\Delta N_i = N_i(n\tau^+) - N_i(n\tau^-)$, $N_i(n\tau^+) = \lim_{t \rightarrow n\tau^+} N_i(t)$ represents the density of the population in the i -th patch after the n -th pulse dispersal at time $t = n\tau$, while $N_i(n\tau^-) = \lim_{t \rightarrow n\tau^-} N_i(t) = N_i(n\tau)$ represents the density of the population in the i -th patch before the n -th pulse dispersal event at time $t = n\tau$ (τ the period of dispersal between any two pulse events is a positive constant). The dispersal behavior of populations between two patches occurs only at the impulsive instants $n\tau$ ($n = 1, 2, \dots$). Sufficient criteria were obtained for the existence, uniqueness and global stability of positively periodic solutions by using discrete dynamical system theory.

However, in the above impulsive dispersal models, it is assumed that the dispersal occurs between homogeneous habitat patches; i.e. the dispersal rate between any two patches is equal or symmetrical [35,25,26,28] which is really too idealized for a real ecosystem. Actually, in the real world, due to the heterogeneity of the spatio-temporal distributions in nature, movement between fragments of patches is usually not the same rate in both directions. In addition, once the individuals leave their present habitat, they may not successfully reach a new one, due to predation, harvesting, or for other reasons, so that there are traveling losses. Therefore, the dispersal rates among these patches are not always the same. Rather, in real ecological situations they are different (or dissymmetrical [14,38]). Therefore, it is our basic goal to investigate single species models with dissymmetric impulsive dispersal.

Based on the above considerations, in this paper, we will first consider the following single species model with logistic growth and dissymmetric impulsive bi-directional dispersal:

$$\begin{cases} \dot{N}_1(t) = r_1 N_1(t) \left(1 - \frac{N_1(t)}{k_1}\right), \\ \dot{N}_2(t) = r_2 N_2(t) \left(1 - \frac{N_2(t)}{k_2}\right), \\ \Delta N_1(t) = b_2 N_2(t^-) - a_1 N_1(t^-), \\ \Delta N_2(t) = b_1 N_1(t^-) - a_2 N_2(t^-), \end{cases} \quad \begin{matrix} t \neq n\tau, \\ \\ t = n\tau, \quad n = 1, 2, \dots, \end{matrix} \quad (1.3)$$

where a_i ($i = 1, 2$) is the rate of population N_i emigrating from the i th patch, and b_i ($i = 1, 2$) is the rate of population N_i immigrating from the i -th patch. Here we assume $0 \leq b_i \leq a_i \leq 1$, which means that there possibly exists mortality during migration between two patches.

Moreover, to the best of our knowledge, in all of the models investigated, whether with continuous dispersal or the discontinuous dispersal considered so far, there are hardly any papers that consider the aggregate migration, or migration of the total population as a whole. Such migration usually stems from what has been termed ‘seasonal hostility’ or the impossibility to survive or reproduce in certain locales for part of a year [42]. In practice, in real ecological systems, with alternating seasons, many kinds of birds and mammals will migrate from cold regions to warm regions in search of a better habitat to inhabit or breed. Anadromous fish will go back from ocean to their birthplaces in stream to spawn, and vice versa for some other species. An example is the annual migration of birds between the tropics and temperate or boreal regions. For example, the blackburnian warbler is a small songbird that nests in forests of the northeastern United States and southern Canada during the spring and summer, but migrates to Central and South America to live through the winter [29]. Other examples include annual migrations of ungulates among grazing areas to follow spatio-temporal changes in rainfall, or annual movements of elk from higher to lower elevations to escape cold in winter. In these cases, movement is unidirectional during each migration period and may take place over fairly short time periods.

Obviously, this kind of discontinuous periodic migration behavior occurs extensively in nature, which prompts us to model and investigate it properly. Motivated by the above considerations, in this paper, we further characterize and research the above-men-

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