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Original Research Article

Uncertainty and predictability in population dynamics of a bitrophic ecological model: Mixed-mode oscillations, bistability and sensitivity to parameters

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A B S T R A C T

We consider a two-trophic ecological model comprising of two predators competing for their common prey. We cast the model into the framework of a singular perturbed system of equations in one fast variable (prey population density) and two slow variables (predator population densities), mimicking the common observation that the per-capita productivity rate decreases from bottom to top along the trophic levels in Nature. We assume that both predators exhibit Holling II functional response with one of the predators (territorial) having a density dependent mortality rate. Depending on the system parameters, the model exhibits small, intermediate and/or large fluctuations in the population densities. The large fluctuations correspond to periodic population outbreaks followed by collapses (commonly known as cycles of "boom and bust"). The small fluctuations arise due to a singular Hopf bifurcation in the system, and are ecologically more desirable. However, more interestingly, the system exhibits mixed-mode oscillations (which are concatenations of the large amplitude oscillations and the small amplitude oscillations) that indicate the adaptability of the species to prolong the time gap between successive cycles of boom and bust. Numerical simulations are carried out to demonstrate the extreme sensitivity of the system to initial conditions (chaos and bistability of limit cycles are observed) as well as to the system parameters (here we only show the sensitivity to the density dependent mortality rate of the territorial predator). This model throws light at the uncertainties in long term behaviors that are associated with a real ecological system. We show that even very small changes in the system parameters due to natural or human-induced causes can lead to a complete different ecological phenomenon, thus affecting the predictability of the density of the prey population. In this paper, we explain the mechanisms behind the irregular fluctuations in the population sizes in an attempt to understand the dynamics occurring in a natural population and also comment on the inherent uncertainties associated with the system.

1. Introduction

In Nature, every species live in a web of complex relationships with other species and tries to remain in an equilibrium state within the ecosystem. However, large fluctuations in the populations densities of various species, specially, in small mammals and insects, have been reported and is a subject of interest amongst environmentalists, entomologists and conservationists. A few such examples include population fluctuations in snowshoe hares in the boreal zone of North America, vole cycles in the Northern Europe and in the boreal forest arctic-tundra of Siberia, lemming cycles in the high arctic tundra of Eurasia and North America, house mice in southeastern Australia, devastating desert locusts outbreaks in Australia, and the more benign larch budmoth cycles, which have been reconstructed from the tree rings of the host subalpine larch in the European Alps with their records dating back to more than a thousand years (see Casimir, 1962; Esper et al., 2007; Korpimäki et al., 2004; Wright, 1987 and the references therein), etc. A rapid increase in the population densities of some of these species can lead to pest outbreaks, which in turn can lead to other cumulative effects such as large scale defoliation of local forests or farming losses or damage of stored food grains. Similarly, outbreaks of vector-borne diseases may lead to epidemics. These outbreaks are

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intrinsically unpredictable and often demand timely and effective responses. On the other hand, a sudden decrease in the population can bring an endangered species perilously close to an extinction. The precise mechanism behind these cycles is still an open question, but there has been a general consensus that trophic interactions or maternal effects that cause delayed negative feedback can cause such oscillations. Negative feedbacks that stem from lower trophic levels (such as host plants, prey) and/or from higher trophic levels (such as predators, diseases) are capable of producing oscillations specially if there are time lags in their effects (see Esper et al., 2007 and the references therein).

As noted earlier, the cycles of boom and bust in Nature are random and seem unpredictable. This makes it even more challenging to understand the patterns of population densities and/or predict the extreme events of outbreaks and/or collapses from field studies alone. On the other hand, even small amplitude (non-extreme events) irregular or chaotic fluctuations in population densities that may arise due to a deterministic process have been a subject of both fascination and intense debate in the ecological community. The unpredictable fluctuations in a natural population data can also be viewed as random effects due to environmental noise/and or errors in the measurement data. Documenting deterministic chaos in the wild is complicated as it is difficult to distinguish chaos from noise (Cushing et al., 2001; May, 1976). However, chaos has been documented in laboratory studies of populations of interacting species. Based on the time-series data and controlled laboratory experiments with manipulated demographic data, various nonlinear phenomena including chaos has been observed in several ecosystems (Cushing et al., 2001).

Typically an ecosystem can be divided into various trophic levels based on the size and the time needed for reproduction and growth of the individuals of each population. In almost all predator–prey interactions, the rate of production per unit biomass decreases from bottom to top along the trophic levels. For example, in the interactions between rabbits and foxes, or insects and birds, or phytoplankton and zooplankton, the lower trophic level exhibits a faster dynamics. Such time diversified predator–prey models can give us an insight to some of the features observed in the population cycles of species in the wild. Some of the studies conducted in multiple time scales ecological models include the two-trophic model involving two predators competing for their common prey (Muratori and Rinaldi, 1989; Rinaldi and Muratori, 1992; Sadhu, 2015, 2016; Sadhu and Chakraborty Thakur, 2015), the tri-trophic food chain models (Brons and Kaasen, 2010; Deng, 2001), and age-structured predator–prey models with dormancy of the predators (Kuwamura and Chiba, 2009), etc.

In this paper, we consider the model studied in Sadhu (2015, 2016) which involves two predators competing for their common prey with one of the predators (the territorial predator, say) exhibiting density dependent mortality rate, and the prey exhibiting fast dynamics, aligning with the common observation found in Nature. Typical examples would be lemmings, owls and arctic foxes, or voles, owls and weasels, or budworms and their avian predators. The model is cast into the framework of a singularly perturbed system of equations with one fast (prey dynamics) and two slow (predator dynamics) variables. As the density dependent mortality rate of the territorial predator is varied, the system exhibits a variety of rich nonlinear dynamics, including but not limited to relaxation oscillation cycles, stable and chaotic mixed mode oscillation (MMO) patterns, periodic cycles with small amplitude oscillations (SAOs), global bifurcations of limit cycles and chaos via a cascade of limit cycles bifurcations. The SAOs in our model represent the small fluctuations in the population densities of the species, whereas the relaxation

oscillations or the large amplitude oscillations (LAOs) signify the periodic outbreaks and collapses corresponding to large fluctuations in the population densities. The relaxation oscillations exhibit four phases involving two distinct time scales: due to heavy predatory exploitation, the prey population quickly collapses and remains in an endemic state on a slow time scale until the predators become scarce, after which the prey quickly regenerate allowing the predators to grow slowly. The cycle repeats itself when the exploitation pressure reaches its threshold. MMO cycles on the other hand, are concatenations of SAOs and LAOs that can be regarded as a connector between these two types of limit cycles. In these cycles, the three species coexist via SAOs over an intermediate time scale, but the fast dynamics of the prey is not completely filtered out, and is periodically revealed by the burst of an LAO.

Ecologically, an MMO orbit indicates the adaptability of a species to prolong its successive cycles of outbreaks and collapses. As observed in most outbreak events, the return time of the successive outbreak does not have a fixed periodicity, but follows an irregular pattern (see Fig. 5 in Esper et al., 2007 for the larch budmoth dynamics). Annual defoliation data collected by Virginia Department of Forestry spanning 1953–2014 Asaro and Chamberlin (2015) suggests that the population densities of gypsy moth (*Lymantria dispar L.*) and fall cankerworm (*Alsophila pometaria Harris*) seem to exhibit chaotic MMO cycles. More examples of such MMO cycles with mixed signatures can be drawn from the data pertaining to Australian locust outbreaks between 1934–2011 Casimir (1962) and Wright (1987) obtained from the Australian Plague Locust Commission Bulletin (1977–2011). The data measuring the intensities of the outbreaks suggests that the population of locusts exhibits a wide range of fluctuations varying from small to intermediate to large depending on other external factors such as rainfall, etc. The irregularities in these outbreak events can be explained to some extent by the simple model that we consider in this paper. In our model, the return time of an outbreak event can be anticipated from the occurrence of local minima in the predator populations while the prey population is in the endemic state (corresponding to one of the slow phases in an LAO cycle). An MMO orbit can exhibit different numbers of SAOs in between successive LAO peaks, and hence the return time of an outbreak event can be effectively read off from the time series of such an orbit. Thus the system of equations considered in this paper cannot only model the events of outbreaks and collapses, but can also be used to predict the occurrence of such events. Moreover, we understand that external effects of either local climate change or loss of habitat can impact relevant activities such as food consumption patterns, reproduction habits, etc., and in our model they can be incorporated by adding fluctuations (small variations) in the ecological parameters chosen (birth rates, carrying capacities, death rates, etc.). Changes in long term patterns due to sudden rapid changes in the climate is observed in the larch budmoth population (Esper et al., 2007). Minor changes in even one of the parameters used in our model can lead to such dramatic changes in the patterns of the population densities of the prey. In this paper, we will show some numerical results that elucidate the sensitivity of the system to initial conditions and parameters. It is worth mentioning that understanding the distinction between stochastic and deterministic dynamics gives us an insight of apparently irregular dynamics occurring in the wild. As Hastings et al. (1993) mentioned in their work that if fluctuations in population sizes are driven by some deterministic factors, and if those factors are understood, then it allows predictions of the dynamics over a short time scale. Management decisions are feasible in these situations. In this paper, we explain the mechanisms behind the irregular fluctuations in the population sizes driven by deterministic factors in our