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Bifurcation analysis of a predator–prey model with predators using hawk and dove tactics

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Abstract

Most classical prey–predator models do not take into account the behavioural structure of the population. Usually, the predator and the prey populations are assumed to be homogeneous, i.e. all individuals behave in the same way. In this work, we shall take into account different tactics that predators can use for exploiting a common self-reproducing resource, the prey population. Predators fight together in order to keep or to have access to captured prey individuals. Individual predators can use two behavioural tactics when they encounter to dispute a prey, the classical hawk and dove tactics. We assume two different time scales. The fast time scale corresponds to the inter-specific searching and handling for the prey by the predators and the intra-specific fighting between the predators. The slow time scale corresponds to the (logistic) growth of the prey population and mortality of the predator. We take advantage of the two time scales to reduce the dimension of the model and to obtain an aggregated model that describes the dynamics of the total predator and prey densities at the slow time scale. We present the bifurcation analysis of the model and the effects of the different predator tactics on persistence and stability of the prey–predator community are discussed.

Keywords: Hawk–dove tactics; Predator–prey model; Slow–fast dynamics; Aggregation of variables; Bifurcation analysis

1. Introduction

An important issue in population dynamics is to understand the effects of individual tactics that may adopt individuals at the population and community levels. Individuals compete for mating, food and territory. Different behavioural traits (Lott, 1991; Stamps and Buechner, 1985) occur among individuals of the same population and between different populations (Stamps and Buechner, 1985; Perret and Blondel, 1993; Pontier et al., 1995). Some phenotypic characteristics, such as aggressivity, can differ between populations. For example, in urban populations, domestic cats rarely fight while in rural populations, individuals are more likely to be aggressive for mating and to get access to some resource, (Liberg and Sandell, 1988; Pontier et al., 1995; Auger and Pontier, 1998; Pontier et al., 2000). Individuals are capable of learning and to change tactics along their life time according to the environmental conditions, to their age, to their physical conditions and to the results of previous contests (Wolf and Waltz, 1993; Liberg, 1981; Yamane et al., 1996). Behavioural plasticity allows an individual to be more flexible and to adopt the behaviour that can maximize its survival in the present environmental condition.

In previous works (Auger and Pontier, 1998; Pontier et al., 2000), we investigated the effects of aggressiveness

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on population dynamics. In these articles, individuals competed for some resource and the model was aimed at looking for the effects of this competition on the level of equilibrium density of the total population in the long term. The competition process was described by the classical hawk–dove model occurring at the fast time scale which was coupled to a population dynamics model at a slow time scale. This model was able to show the relationship between the equilibrium density of the population which was a decreasing function of the proportion of aggressive (hawk) individuals in the population and was compared to the case of the domestic cat population for which rural (low density) populations are mainly hawk and urban (high density) populations are mainly dove. However, in this previous model, the resource was assumed to be constant, i.e. at a constant level not depending for example on the predator density. The aim of this work is to take into account the interaction between the population and the resource in the frame of a predator–prey model. The resource is assumed to be a prey and the population is its predator.

The prey population grows logistically when not predated. Individual predators can use different tactics to get the resource. Predators can catch a prey and eat it, but they can also dispute a prey to another predator who has previously captured a prey. The aim of this work is to investigate the effects of individual tactics (hawk and dove) that can be used by predators on the overall stability of the predator–prey system. In a previous attempt (Auger et al., 2002) we presented such a model. In this contribution, we make explicit the process by which a predator manipulating a prey is found by a searching predator leading to a contest between the two predators. With respect to the previous work, we also incorporate a more realistic Holling type II functional response.

As in (Auger et al., 2002), we also considered two different time scales: a fast time scale corresponding to the hawk–dove game between predators and a slow time scale corresponding to prey growth and predator demography. The existence of two time scales was used to reduce the dimension of the model (a set of three ODEs for the prey, hawk predator and dove predator densities) and to obtain an aggregated model that describes the dynamics of the total predator and prey densities at the slow time scale. For the aggregation methods we refer to (Bravo de la Parra et al., 1995; Auger and Poggiale, 1998; Bernstein et al., 1999; Auger and Bravo de la Parra, 2000).

In this article, we also incorporate searching and handling activities of the predators. The handling–searching processes shall occur at the fast time scale as well as the hawk–dove game. The resulting seven-dimensional complete model is reduced to a two-dimensional aggregated model.

The question that arises naturally in this model relates to the tactics that is the most favourable for predators. Should predators be aggressive and fight to monopolize the prey resource or should predators do not dispute preys with conspecifics occasioning fightings and resulting injuries? There is not a simple answer to this question. We show in this paper that it depends on the value of the cost.

In Neat et al. (1998a, b) the role of injury and energy metabolism during fights between male ciclid fish *Tilapia zillii* is studied experimentally. Both behavioural mechanisms underly the making of the strategic decisions in animal fighting. It is concluded that the injury data and energy metabolism data suggest that escalated fighting is costly for both winners and losers, but especially so for losers.

For the temporal change of the tactic, we will assume the classical replicator dynamics which together with the hawk–dove game model gives the well known predictions; when costs were lower than the gain a monomorphic hawk predator population, and a dimorphic predator population, when the costs are larger than the gain.

We will perform a full analysis of the aggregated models by presenting complete bifurcation analysis diagrams. The resulting model resembles the well known Rosenzweig–MacArthur predator–prey model (Rosenzweig, 1971) but its long term dynamics behaviour differs significantly. For the Rosenzweig–MacArthur model, we know that if the parameter values are such that an asymptotically stable interior equilibrium exists, then it is also globally stable (Hsu et al., 1978) and if such an equilibrium is unstable, a unique globally asymptotically stable limit cycle exists (Cheng, 1981). Similar to the Bazykin model (Kuznetsov, 1998; Bazykin, 1998), where in addition to the linear predator death rate term in the Rosenzweig–MacArthur model a quadratic death term for the predator is introduced, the dynamic behaviour of our model is more complex. A stabilizing effect is found due to mutual interference between the predators. This effect is similar to that found in the Beddington–DeAngelis predator–prey model, see Beddington (1975), DeAngelis et al. (1975).

The paper is organized as follows: First we present the complete model. Then we show that by use of aggregation methods, it is possible to build a global predator–prey model governing the total prey and predator densities, by total predator density we signify the predator density obtained by summation over all individual predator categories such as searching, handling, hawk and dove sub-populations. Thereafter, we present the results of the bifurcation analysis of the aggregated models with respect to two relevant parameters, the carrying capacity and the costs for fight. The article ends with a general discussion on advantages of different tactics and their effects on the stability of the predator–prey system.