Applied Mathematics and Computation 273 (2016) 664–677

Contents lists available at ScienceDirect

Applied Mathematics and Computation

journal homepage: www.elsevier.com/locate/amc

Transition of interactions between a cuckoo and its host: Fluctuating between parasitism and mutualism

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ARTICLE INFO

Keywords:
Cooperation
Persistence
Coexistence
Stability
Bifurcation

ABSTRACT

This paper considers crow–cuckoo–cat systems in which crows are the host, cuckoos are the parasite, cats are the predator of crow nests, and cuckoo chicks in the nests reveal a mix of caustic and repulsive compounds that repel and deter cats. An over 16-year observation on the crow–cuckoo–cat system shows that the parasite and its host can be mutualistic in the presence of predators (Canestrari et al., 2014). In order to exhibit mechanisms by which the mutualism occurs, a crow–cuckoo–cat model is formed in this work. Global dynamics of the model demonstrate that cats' predation ability and converting efficiency are crucial to the occurrence of mutualism. When the predation/efficiency is low, cats would be driven into extinction by cuckoos. When the predation/efficiency is intermediate, the three species coexist and interaction outcomes between crows and cuckoos change from parasitism to commensalism and mutualism as the deterrence effect increases. When the predation/efficiency is high, cats would drive cuckoos into extinction if the deterrence is weak. If the deterrence is strong, either cuckoos or cats go extinct, where the species with higher initial density persists. Therefore, results in this work show the empirical observation by Canestrari et al. (2014), and predict situations that have not been observed by Canestrari et al. (2014). Numerical simulations display that the crow–cuckoo–cat model fits the observation well.

1. Introduction

An over 16-year observation on carrion crows (*Corvus corone corone*) and the great spotted cuckoo (*Clamator glandarius*) shows that a parasite (cuckoo) can provide a benefit to its host (crow) by deterring crow nest predators [4]. The cuckoo is called a parasite of the crow since it lays eggs in the nest of the crow, which breeds the unrelated chicks and suffers the loss of its brood. Canestrari et al. [4] studied crow nests in northern Spain and found that the nests parasitized by cuckoos are more successful in crows' raising their own chicks than non-parasitized nests. This is due to predator repellence by a malodorous cloacal secretion that parasitic chicks release. The cuckoo secretion is a mixture of caustic and repulsive compounds, which are known to repel crow nest predators such as corvids, raptor birds and quasi-feral cats. A cat is called quasi-feral if it is free-ranging and hunts year-round but could be attracted with food. For convenience, we use cats to represent the predators in this work.

The long-term observation by Canestrari et al. [4] displays that although cuckoos decreased host reproductive success during seasons with low nest predation, parasitized nests produced more fledglings than non-parasitized nests during seasons with

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http://dx.doi.org/10.1016/j.amc.2015.10.067
0096-3003/

high nest predation. Thus, interaction outcomes between the crow and cuckoo fluctuate between parasitism and mutualism each season, depending on the intensity of predation pressure. While the novel mutualism between the parasite and its host is observed, mechanisms by which the mutualism can occur need to be demonstrated.

Parasitism/predation systems of two species have been studied by a series of significant works. Volterra [18] established a predator–prey model to describe interactions between the predator fish and prey fish in Adriatic during the First World War. Functional responses in the model are linear and all positive solutions (except the equilibrium) are shown to be periodic. Since the time averages of all periodic solutions correspond to components of the unique positive equilibrium, dynamics of the model well characterize the mechanism by which the amount of predator fish during the First World War was considerably higher than those in the years before. The model is also called the Lotka–Volterra predator–prey model because of the important contribution of Lotka [14]. Moreover, the model is extended to describe the predation system where there exists intraspecific competition in each species. The extended model is structurally stable and all of its positive solutions converge to an equilibrium (see for example, [10]).

The two-species model is expanded to describe predation systems with multiple species. Freedman and Waltman [7] considered a general predator–prey system of three species, in which two predators have a common prey. A general mathematical criterion is given for persistence of the three-species system. Cantrell et al. [5] studied a specific two-consumer and one-resource system in which there is no interaction between the consumers. Theoretical analysis and numerical simulations showed that the two consumers can coexist upon the single resource at steady states or in periodic oscillations as the environmental condition varies. Lisena [13] considered a two-predator and one-prey system with periodic coefficients, in which there is competition between the predators. Suitable average conditions are given to extinction of the competitively inferior species. For more relevant works, see Armstrong and McGehee [1], Smith and Thieme [15], Hsu et al. [11], Wang and Wu [16], Wang et al. [17], etc. While these works focus on coexistence of consumers, there is little work on parasitism-predation models in which the parasite and its host can be mutualistic in the presence of predators. Thus, modelling the crow–cuckoo–cat system and exhibiting mechanisms by which the mutualism between the crow and cuckoo can occur is necessary.

Motivated by the empirical observation and Lotka–Volterra predator–prey model, we expand the model to describe the parasitism-predation system consisting of crows, cuckoos and cats. In the system, crows are the host, cuckoos are the parasites, cats are the predators of crows, and cuckoo chicks reveal a mix of caustic and repulsive compounds that repel and deter cats. Global dynamics of the crow–cuckoo–cat model demonstrates that cats' predation ability and converting efficiency are crucial to the occurrence of the mutualism between crows and cuckoos. When the predation/efficiency is low, cats would be driven into extinction by cuckoos. When the predation/efficiency is intermediate, the three species coexist and interaction outcomes between crows and cuckoos change from parasitism to commensalism and mutualism as the deterrence effect increases. When the predation/efficiency is high, cats would drive cuckoos into extinction if the deterrence is weak. If the deterrence is strong, either cuckoos or cats go extinct, where the species with higher initial density persists. Therefore, results in this work show the empirical observation by Canestrari et al. [4], and predict situations that have not been observed by Canestrari et al. [4]. Simulations illustrate the results.

The paper is organized as follows. The crow–cuckoo–cat model is formed in Section 2. In Section 3, we consider stability of equilibria and in Section 4, we show persistence of the system. We exhibit occurrence of mutualism in Section 5, and a discussion of the results is in Section 6.

2. The crow–cuckoo–cat model

In this section, a three-species model is formed to characterize the crow–cuckoo–cat system. Since cuckoo chicks consume food provided by adult crows, the crow-cuckoo interaction is parasitism, which can be described by a parasitism model. On the other hand, since cats kill and eat crows, the crow–cat interaction is predation, which can be depicted by a predator–prey model. Then the two models are combined to form a crow–cuckoo–cat model, and boundedness of solutions of the three-species model is shown.

In the crow–cuckoo interaction, immature cuckoos are bred by crows, which results in a loss of crows in their own brood. Thus the crow-cuckoo interaction is parasitic and we apply the Volterra type model to depict the interaction

$$\frac{du}{dt} = r_1 u\left(1 - \frac{u + \beta_1 v}{K}\right)$$
$$\frac{dv}{dt} = v(-r_2 + \alpha_1 u - \gamma_1 v)$$

where variables u and v denote population densities of crows and cuckoos, respectively. Parameter r_1 represents the intrinsic growth rate of crows, while K is the carrying capacity. Parameter β_1 denotes the quantity of resources consumed by a cuckoo, and α_1 is the efficiency of the cuckoo in converting the consumption into fitness. Parameter r_2 is the mortality rate of cuckoos, while γ_1 represents the intraspecific competition.

In the crow–cat interaction, cats are predators and crows are their prey, which can be described by

$$\frac{du}{dt} = r_1 u\left(1 - \frac{u}{K}\right) - \beta_2 u w$$
$$\frac{dw}{dt} = w(-r_3 + \alpha_2 u - \gamma_2 w)$$