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Ecological and evolutionary dynamics of two-stage models of social insects with egg cannibalism

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ABSTRACT

Cannibalistic interactions between different developmental stages in a population are prevalent among many groups of animals and social insects. Cannibalism plays an important role in the population outcomes and represents an adaptive strategy in which parents consume some offspring to increase their current and/or future reproductive success. To understand how egg cannibalism affects ecological dynamics and evolutionary outcomes, we propose a simple two-stage ecological model and its evolutionary model by using the framework of evolutionary game theory. Our analytical study shows that: 1. At the population level, a large rate of egg cannibalism can lead to a forward transcritical bifurcation, characterized by the emergence of a globally stable interior equilibrium, while a small rate of egg cannibalism can lead to a backward subcritical bifurcation, which generates *strong Allee effects*. 2. When the environment is harsh, egg cannibalism can prevent extinction in both the ecological and the evolutionary setting. In addition, evolution preserves *strong Allee effects* by choosing the trait with the smaller cannibalism rate. 3. Evolution may decrease or increase the fitness of the colony by decreasing or increasing the total population size. 4. The trait function is very important since it can affect permanence of the system. These results suggest that cannibalism behavior is indeed an adaptive strategy when the availability of food is scarce and the nutrient is limited. Additionally, cannibalism may be averted by defensive behaviors or other adaptations that serve to their age distribution, and it may be also a mechanism that can generate *strong Allee effects*.

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1. Introduction

Cannibalistic interactions between different developmental stages in an animal population are prevalent among many groups of animals [11,29,31,34]. One form of this cannibalism that is common among social insects is the cannibalism of conspecific eggs by larvae or higher developmental stages. It has been shown that these interactions are not only a response to severe food shortages or other dire circumstances but are often a part of typical intraspecies interactions [13]. Cannibalism is, in fact, such a standard part of the trophic structure, that in certain species, say of ants and stinging bees, workers produce non-viable eggs (called "trophic eggs") [11,12] whose sole purpose is to be consumed. But cannibalism of viable eggs is also pervasive among social insects [20,43] and is an important factor in population dynamics.

Cannibalism is more than just a relatively uncommon feature of a predator's foraging behavior. Across several field and laboratory studies as well as in model analysis, it has been demonstrated to be an important mechanism that can benefit the colony fitness by improving growth rate, survivorship, vigor, longevity, and fecundity [31]. Depending on the model under study, cannibalism has been shown to either stabilize [4,8,22] or destabilize [9,19,24] the population dynamics. It can induce self-regulation of the cannibalistic species [4], a stabilizing effect, and it can provide a cannibalistic species with the ability to survive an acute catastrophic event that may have been fatal in the absence of cannibalism [16], the so-called "lifeboat mechanism".

The study of cannibalism builds primarily on the foundation of age-structured or stage-structured models because cannibalism tends to occur between individuals at different stages in their life cycle, not between individuals in the same stage. In 1970, Tognetti and Mazanov [37] proposed a single-species growth model with stage structure consisting of immature and mature stages linked through a discrete time delay. Their study shows that all populations with positive initial functions tend to a constant population level, either directly or through an oscillatory process. Diekmann, Nisbet, and Gurney [9] used very general assumptions on how age-structure affects cannibalism and derived an age-structured Volterra integral equation model for the dynamics of an age-structured cannibalistic species. Their model contained a Hopf bifurcation, which supported the previously held assumption that cannibalism may promote oscillations. In 1989, Wood, Blythe, and Gurney [44], and in 1990, Aiello and Freedman [1] introduced similar simple models of two-stage delay population models, and gave standard stability results. Cushing [4] used a discrete-time two-stage juvenile–adult model with cannibalism to show that cannibalism can induce important dynamics including oscillations, hysteresis, and resistance to extinction events. In 1994, Freedman et al. [14] proposed and analyzed a similar model but with the inclusion of cannibalism. This model was admittedly only a first step, and in 1997, Peng [28] improved the model, which was focused on the stage of juveniles being cannibalized by the stage of adults. Others [16,22,24] analyzed cannibalism in the presence of a Lotka–Volterra predator–prey system where cannibalism took place in the predators, but these methods lack either age-structure, delayed maturation, or analytic results. Recent work by van Kooten et al. [40] show how hatching size determines dynamics through its effect on the relative strength of cannibalistic mortality and resource competition as mechanisms of population regulation. Nevertheless, ecological models with cannibalism provide us useful insights on the potential effects of cannibalistic behavior on population dynamics.

Cannibalism appears to be a result of genetic features and is induced by environmental factors [29]. In some species, cannibalistic genes may contribute to both the fitness of the individual and the population [29]. This behavior is expected to evolve in conditions of food scarcity, crowding of conspecifics, vulnerable individuals, age structure, and selection [13,34]. All of these environmental factors influence the intensity of this cannibalism behavior. Moreover, it has been stressed that the evolutionary effect of a cannibalistic confrontation depends on the degree of the genetic relationship between cannibal and victim, i.e. as the relationship becomes more distant, the cannibal requires a smaller advantage over the prey before it performs this behavior [13]. Additionally, another factor governing cannibalism evolution is having an optimal diet. The need for protein may be the reason why cannibalism is a common behavior among herbivores and granivores [29]. The energy obtained by eating conspecifics may permit the survival of individuals during