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Dynamics of generalist predator in a stochastic environment: Effect of delayed growth and prey refuge

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ABSTRACT

In this paper, an attempt has been made to understand the dynamics of a prey–predator system with multiple time delays where the predator population is regarded as a generalist type. In this regard, we consider a modified Holling–Tanner prey–predator system where a constant time delay is incorporated in the logistic growth of the prey to represent a delayed density dependent feedback mechanism and the second time delay is considered to account for the length of the gestation period of the predator. Predator's interference in prey–predator relationship provides better descriptions of predator's feeding over a range of prey–predator abundances, so the predator's functional response is considered to be Type II ratio-dependent and foraging efficiency of predator largely varies with the refuge strategy of prey population. In accordance with previous studies, it is observed that delay destabilizes the system, in general and stability loss occurs via Hopf-bifurcation. In particular, we show that there exists critical values of the delay parameters below which the coexistence equilibrium is stable and above which it is unstable. Hopf bifurcation occurs when the delay parameters cross their critical values. Also, environmental stochasticity in the form of Gaussian white-noise plays a significant role to describe the system and its values. Numerical computation is also performed to validate and visualize different theoretical results presented. The analysis and results in this work are interesting both in mathematical and biological point of views.

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1. Introduction

To study the effect of environmental noise on population dynamics, researchers [1,2] have used Gaussian white-noise as a model of environmental variations. May [2] analyzed a biological system under stochastic fluctuation considering white noise for population and observed that when the population deviates more from equilibrium point, the system shows irregular behavior (i.e., instability). Ripa et al. [3] examined the effect of environmental noise on populations and presented a general theory of environmental noise in ecological food webs. Upadhyay et al. [4] investigated the influence of environmental noise on a fairly realistic ecological model with generalist top predator and shown the importance of the noise amplitude, the trophic level and the susceptibility of populations to environmental noise. Schwartz et al. [5] studied the effect of delay on the rates of noise-induced switching between co-existing stable states and noise-induced extinction in a population dynamic model.

Modeling of interacting population has begun to supplement models of evolutionary processes in addition of stochasticity at some level of interactions while sometimes the origin of stochasticity can be related to the finiteness of population size [6,7],

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uncertainties also may enter under the assumption of irrationality and errors in decision-making [8–10]. Examples range from stochastic gain in population dynamics [11] and eradication of coexistence in the cyclic Lotka–Volterra model [12] to cooperation promotion in the spatial prisoner dilemma game [13]. Perc et al. [14,15] have studied a six-species Lotka–Volterra type predator–prey model in stochastic environments. They have studied this model in structured populations in cyclical interactions with alliance-specific heterogeneous invasion rates and Noise-guided evolution within cyclical interactions where it was shown that defensive alliances can emerge if the chain length is more than 3. Moreover, predator–prey interactions can emerge spontaneously in evolutionary settings relevant to public goods, as reported in Correlation of positive and negative reciprocity fails to confer an evolutionary advantage [16]. They have studied a spatial public goods game, where in addition to the three strategies of defection, rewarding and punishment, a fourth strategy that combines the latter two competes for space. The impact of reward on the evolution of cooperation in the spatial public goods game is investigated and found that moderate rewards may promote cooperation better than high rewards, which is due to the spontaneous emergence of cyclic dominance between the three strategies [17]. Recently, Szolnoki et al. [18] introduced a spatial ultimatum game with discrete strategies and shown the occurrence of traveling waves and cyclic dominance where one strategy in the cycle can be an alliance of two strategies. While empathy and spatiality may lead to the evolution of fairness that would be driven by pattern formation. Finally, this subject received a recent comprehensive review on cyclic dominance in evolutionary games by Szolnoki et al. [19], focusing the pattern formation, the impact of mobility and the spontaneous emergence of cyclic dominance. Also, they highlighted the importance and usefulness of the statistical physics for the successful study of large-scale ecological systems. The potential applicability of the proposed theory extends also to the physics of social systems [20] as well as to statistical mechanics of evolutionary and coevolutionary games as reviewed in collective behavior and evolutionary games - an introduction [21].

Complex dynamical behavior arises as a consequence of time delay in a biological systems (with significant time delay) may exhibit limit cycle oscillations and chaos [22]. The larger value of gestation time delay cause individual population density to fluctuate and hence the system becomes unstable. As the estimated length of delay to preserve stability and the critical length of time delay for Hopf-bifurcation are dependent on the system's parameter, it is possible to impose some control, which will prevent the possible abnormal oscillation in the population density. Zhao et al. [23] studied a ratio-dependent model with two time delays and obtained the estimated length of gestation delay which would not affect the stable co-existence of both the species at their equilibrium value. Dynamics of a non-delayed ratio-dependent model with constant and quadratic predator harvesting and the bifurcation of ratio-dependent system with constant rate harvesting has been reported in [24–27]. The system exhibits interesting dynamics around the coexistence equilibria, including multiple bifurcation periodic solution and homoclinic orbit. Ruan and Wei [28] studied the periodic solutions of a planar systems with two delays. Nindjin and Aziz-Alaoui [29] analyzed a prey–predator model with modified Leslie–Gower and Holling type II scheme with time delay and obtained a sufficient condition for global stability. In 2008, Yafia et al. [30] obtained the limit cycle for small and large delay in the model with Leslie Gower and Holling type II scheme. Xu and Ma [31] studied the stability and Hopf-bifurcation in a ratio-dependent system with stage-structure. Xu et al. [32] studied the stability and bifurcation of a ratio-dependent model with time delay due to gestation of the predator. Recently, Feng [33] studied the dynamics of a delayed ratio-dependent model with quadratic harvesting. Karaoglu and Merdan [34] studied a detailed Hopf-bifurcation analysis of a ratio-dependent predator-prey system involving two different discrete delays.

There has been a great deal of research on the effect of prey refuges on the population dynamics: (i) first, it affects positively the growth of prey and negatively that of predator, comprise the reduction of prey mortality due to decrease in predation success, (ii) second the trade-off and byproducts of the hiding behavior of prey which could be detrimental for all the interacting population, and (iii) third, the refuges which protect a constant number of prey, have a stronger stabilizing effect on population dynamics than the refuges, which protect a constant proportion of prey. Magalhães et al. [35] carried out a greenhouse experiment on larvae of western flower thrips, *Frankliniella occidentalis* use the web produced by spider mites as refuge from predation by predatory mite, *Neoseiulus cucumeris* to incorporate the benefits of refuge use and develop a prey-predator model. This model predicted a minor effect of the refuge on the prey density at equilibrium. Jana et al. [36] described a time delayed prey-predator system incorporating prey refuge with Holling type II functional response. Ko and Ryu [37] investigated the asymptotic behavior of spatially inhomogeneous solution and local existence of periodic solution under the homogeneous Neumann boundary condition in a model with Holling type II functional response incorporating a prey refuge. Guan et al. [38] investigated the spatiotemporal dynamics of a 2D prey–predator model based on modified version of Leslie–Gower scheme incorporating a prey refuge. Lian et al. [39] studied the effect of time delay and cross diffusion on the spatiotemporal dynamics of a modified Leslie–Gower model incorporating a prey refuge.

In this work, we have designed a modified Holling–Tanner predator-prey model under ratio-dependent scheme with prey refuge and two time delays. The predator population is regarded as generalist type predator which switches to an alternative food option as and when it faces difficulty to find its favorite food. The positive aspects of this formulation of prey–predator interaction is that it takes care of our inability to write down growth equations for all the species on which the generalist predator feeds upon [40]. A constant time delay is incorporated in the logistic growth of prey population to represent a delayed density dependent feedback mechanism and second time delay is considered to account for the length of the gestation period of the predator. We have also analyzed the deterministic model incorporating the environmental fluctuation in the natural growth rate of prey and predator in the form of Gaussian white noise. The paper is organized in a following way: in the next section, we develop the model system and analyzed it for both delay and non-delay case. The global stability analysis of the delay model system is presented in Section 3. In Sections 4 and 5, we perform the stochastic scenario of non-delayed and delayed system respectively. Numerical results are presented in Section 6. Conclusion and discussion are presented in the last section.

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