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A Review of the Mathematical Models for the Impact of Seasonal Weather Variation and Infections on Prey Predator Interactions in Serengeti Ecosystem

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Abstract

Interaction between prey and predator species is a complex and non-linear process. Understanding various phenomena in the dynamics of prey-predator systems is vital to both mathematical ecology and conservation biology. Mathematical models on prey-predator systems have been the hot sport providing important information regarding the interactions of prey and predator species in various ecosystems. In this paper, a review of the available mathematical models on prey-predator systems was done. Our aim was to assess their structure, behaviour, available control strategies, population involved and their ability in predicting the future behaviour of the ecosystems. We observed diversities in the reviewed mathematical models, some model incorporated factors such as drought, harvesting and prey refuge as the factors that affect ecosystems, some ignored the contribution of environmental variations while others considered the variable carrying capacity. Most of the models reviewed have not considered the contribution of diseases and seasonal weather variation in the dynamics of prey predator systems. Some of the reviewed models do not match the real situation in most modelled ecosystems. Thus, to avoid unreliable results, this review reveals the need to incorporate seasonal weather variations and diseases in the dynamics of prey predator systems of Serengeti ecosystem.

Keywords

Prey, Predator, Weather Variation, Disease, Serengeti Ecosystem

1. Introduction

The dynamics and interactions among species in the ecosystem with their complex behaviour are the principal part of mathematical ecology and are the concern of many biological and ecological processes. An ecosystem is the biological community of all species of a given area and their physical environment [1] [2]. The application of mathematical theories and concepts in ecology has resulted in another branch of biology known as mathematical ecology. This studies the time dependent behaviour of modelled ecological systems [3] [4] [5]. These models give us significant insights for the behaviour of the system and nature. Usually these systems consider various complex communities involving various species which interact in a very complicated way and hence, challenging to analyse and draw conclusion about them. Mathematical models can govern the time evolution of species in terms of their size, age, interactions, food supply, disease and environmental conditions including seasonal and climatic variations. Since all organisms in nature are interdependent [6], the interaction existing among them influences directly and indirectly the survival of each organism and the performance of the ecosystem in general. Hence, studying the comprehensive behaviour and dynamics of the ecosystem is vital for maintaining scientific management, ecological integrity of species and conservation of the ecosystem [7] [8] [9]. There are various ways in which living things can interact, that is by commensalism, competition, predation and mutualism [10]. However, the interaction between predator and their own prey (prey-predator interactions) continues to be one of the dominant areas of research in mathematical ecology due to its universal existence, complexity and importance [11] [12]. For this reason, we believe that, this review may be of particular interest to those researchers involved in modelling this kind of biological and ecological problems allowing them to have an overview of the work which is currently being carried out. Therefore, our objective in this paper is to analyse several adaptations of prey-predator models that have been done in recent years to model different real situations that appear in the field of population dynamics.

2. Prey-Predator Interactions

It is known that, predator population always depends on their prey species as a source of food, hence for survival [13] [14]. The interaction of converting prey biomass into predator biomass through predation has the direct effect between predators and prey and has been a focus of mathematical modelling on prey-predator interactions [15] [16]. Interaction between prey-predator is complex process and non-linear process and hence understanding various biological phenomena in the dynamics of predator-prey systems is vital in ecology and conservation biology. Just under a century ago a very first endeavour to predict the dynamics of species in the ecosystem was predicted mathematically. The physician [17] and mathematician [18] were the first to develop a simple model explaining population dynamics in the context of competing species. At first

Lotka developed a simple model on animal and plant species and then he developed the application of the study of the dynamics of a prey-predator system [19]. On his behalf Volterra considered the same model simultaneously to explain the observation about the percentage of predatory fish caught during the years of World War I which had increased. This fact seemed confusing because the fishing effort had been reduced during those years. So Volterra was interested in studying that situation. To explain this behaviour, Volterra stated a simple system of ordinary differential equations.

$$\begin{aligned} \frac{\mathrm{d}N}{\mathrm{d}t} &= N\left(a - bP\right) \\ \frac{\mathrm{d}P}{\mathrm{d}t} &= P\left(-c + dN\right) \end{aligned} \tag{1}$$

where N and P are the densities of prey of prey and predator respectively, a is the growth rate of prey, c is the mortality rate of predator where as b is the predation rate and d is the conversion rate. Later Lotka-Volterra systems were generalized and considered in arbitrary dimension.

$$\frac{\mathrm{d}U_i}{\mathrm{d}t} = U_i\left(b_{i0} + \sum_{j=1}^{n} b_{ij} U_j\right), i = 1, \cdots, n \tag{2}$$

Consequently, the applications of this system started to multiply. New systems on prey-predator dynamics had been formulated but also these systems has been used for modelling many other natural phenomena such as chemical reaction [20], plasma physics [21], hydrodynamics [22] and other problems from economics and social science [23]. In a view of this, it is clear that population models in particular competition or prey-predator model are important both in their original field and in their application to many other problems from other areas. Their study is also interesting from theoretical point of view. Actually the study of prey-predator models has always been one of the hot sports in biomathematics, so there is a very big number of works on this topic, especially in dimension two. **Table 1** shows the list of some reviewed prey-predator models that considered the aspects of seasonal weather variation and disease infections.

In literature, one of the first contributions to the study of prey-predator systems was in [8] who considered the dynamics of lion, wildebeest and zebra in Kruger national park, lion being a predator while wildebeest and zebra are prey species.

$$\begin{aligned} \frac{\mathrm{d}x_1}{\mathrm{d}t} &= x_1\left(b_1 - a_{12}x_2 + a_{13}x_3\right) \\ \frac{\mathrm{d}x_2}{\mathrm{d}t} &= x_2\left(-b_2 - a_{21}x_1 + a_{23}x_3\right) \\ \frac{\mathrm{d}x_3}{\mathrm{d}t} &= x_3\left(b_3 - a_{32}x_2 + a_{33}x_3\right) \end{aligned} \tag{3}$$

where x_1, x_2 and x_3 represents the population density of wildebeest, zebra and lion respectively. Stability of the equilibrium point was analysed by eigenvalue approach. However we see that the author did not consider factors that can affect

Table 1. Summary of the characteristics of reviewed models.

Model	Seasonal weather	Disease
[6]	✓	×
[9]	×	×
[12]	×	✓
[24]	×	✓
[25]	✓	×
[26]	×	✓
[27]	×	×
[28]	×	✓
[29]	✓	×
[30]	✓	×
[31]	×	✓
[32]	×	✓
[33]	×	×
[34]	×	×
[35]	×	✓
[36]	×	✓
[37]	×	×

species such as poaching, seasonal weather variations, disease and fire. Also the study considered the linear function response ignoring the logistic growth term. The same style of modelling was also seen in [38] who developed the three species prey-predator systems as follows,

$$\begin{aligned} \frac{\mathrm{d}x_1}{\mathrm{d}t} &= x_1\left[\lambda_1 - \alpha_{12}x_2 + \alpha_{13}x_3\right] - q_1Ex_1 \\ \frac{\mathrm{d}x_2}{\mathrm{d}t} &= x_2\left[\lambda_2 - \alpha_{12}x_2 + \alpha_{13}x_3\right] - q_1Ex_1 \\ \frac{\mathrm{d}x_3}{\mathrm{d}t} &= x_3\left[\lambda_3 - \alpha_{12}x_2 + \alpha_{13}x_3\right] - q_1Ex_1 \end{aligned} \tag{4}$$

where x_1, x_2 and x_3 represents the population density of prey species one, prey species two and predator respectively. This model differ from the previous by harvesting term q_iEx_1. The author considered harvesting as an activity that can stabilize or distabilize the ecosystem.

Logistic Growth and Functional Responses

The two models above assume that prey species can grow infinitely but also the level of consumption of prey species by predator is exponential. In many cases, this may not represent the reality in many ecosystems. In order to avoid unreliable results, more general and realistic models have been suggested by considering the logistic growth to prey species and functional responses to predator

(predator's instantaneous per capita feeding rate as a function of prey abundance). Example, [9] formulated and analysed the mathematical model for the study of the interaction of lion, buffalo and Uganda kobs of the Queen Elizaberth national park in Uganda.

$$\begin{aligned}\frac{\mathrm{d}N_1}{\mathrm{d}t}&=r_1N_1\left(1-\frac{N_1}{K_1}\right)-\alpha_1N_1N_2-\left(\frac{a_1N_1}{1+b_1N_1}\right)P-EN_1\\ \frac{\mathrm{d}N_2}{\mathrm{d}t}&=r_2N_2\left(1-\frac{N_2}{K_2}\right)-\alpha_2N_1N_2-\left(\frac{cN_2}{1+d_1N_2+d_2P}\right)P\\ \frac{\mathrm{d}N_3}{\mathrm{d}t}&=-eP-\left(\frac{a_1N_1}{1+b_1N_1}\right)P+\left(\frac{cN_2}{1+d_1N_2+d_2P}\right)P\end{aligned}\tag{5}$$

Here the author assumed that prey species are growing logistically by including the constant carrying capacity, also used two kinds of function responses, the hyperbolic function response on the first prey and ratio-dependent function response on the second prey. Both local and global stability of equilibrium points was analysed. Once of the important results they obtained is that, all population would co-exist if any removal (death rate, harvesting and predation) were not below the intrinsic growth rate of every species. The same results were also obtained in [12] where was modelling the interaction of cichlid fishes, tilapia fish and Nile perch of lake Victoria ecosystem where they formulated the following model.

$$\begin{aligned}\frac{\mathrm{d}x_1}{\mathrm{d}t}&=\lambda_1x_1\left(1-\frac{x_1}{K_1}\right)-\alpha_{12}x_1x_2-\frac{\alpha_{13}x_1x_3}{1+\beta x_1}-q_1Ex_1\\ \frac{\mathrm{d}x_2}{\mathrm{d}t}&=\lambda_2x_2\left(1-\frac{x_2}{K_2}\right)-\alpha_{21}x_1x_2-\frac{\alpha_{23}x_2x_3}{1+\gamma x_2}-q_2Ex_2\\ \frac{\mathrm{d}x_3}{\mathrm{d}t}&=-wx_3+\alpha_{31}\frac{\alpha_{13}x_1x_2}{1+\beta x_1}-\alpha_{32}\frac{\alpha_{23}x_2x_3}{1+\gamma x_2}-q_3Ex_3\end{aligned}\tag{6}$$

As in [9], here the author considered the logistic growth to prey species and the Holling type II function response on predator. Here the author also assumed that every was harvested. Both [9] and [12] tried to model ecosystems by including more important factors. Other reviewed literature of the same scheme of modelling as the previous are [38] [39] [40]. Some considered prey refuge while others considered the reserved zones, time delay and alternative food.

3. Prey-Predator Interaction in Serengeti Ecosystem

According to [41] [42], Serengeti ecosystem which is in latitude 10S to 3030'S, and longitude 340E to 360E in east Africa, spanning northern Tanzania and some parts of southwestern Kenya was officially found in 1951 and is now the Tanzanians largest national park. It is extraordinary in species and it is one of the most popular wildlife reserves in the world. It has a lot of terrestrial mammal migration which makes it to be among the seven wonders of Africa [41] [42] [43]. This high diversity of the ecosystem is due to diverse habitats, including forests, kopjes, woodlands, swamps and grassland. The ecosystem comprise also of extraordinary animal species such as spotted hyenas, elephants, giraffe, thomsons gazelles, zebra, wildebeest, leopards, lion, wild dogs, impala, buffalo, Coke's hartebeest, cheetah, grant's gazelle, topi and more than five hundred species of birds [19] [41]. Despite of the vital modelling work achieved by various researchers, there has been far less quantitative focused work on predation and competition of biological species in Serengeti ecosystem particularly the interaction of wildebeest, zebra and lion which are keystone species of the Serengeti ecosystem. However, few scholars studied about the prey-predator interaction in the ecosystem such as [44] [45] [46] [47]. Example, Sagamiko *et al.* (2015) developed the following model to study the threats to Lionwildebeest Predator-Prey dynamics with Optimal control in Serengeti national park.

$$\begin{aligned} \frac{\mathrm{d}x}{\mathrm{d}t} &= rx\left(1-\frac{x}{k}\right)-\frac{wxy}{x+a}-px-\left(1-f\right)x \\ \frac{\mathrm{d}y}{\mathrm{d}t} &= -a_2 y+\frac{w_1 xy}{x+a}-cy-\left(1-e\right)y \end{aligned} \tag{7}$$

It is a two species predator-prey system where predator was lion and prey was wildebeest. They also used the optimal control theories to establish the optimal strategies for controlling the threats in the system where for poaching, the strategy was ant-poaching patrols, for retaliatory killing was construction of strong bomas and for drought they proposed then construction of dams. They found that the best result is achieved when all three controls are simultaneously used and the combined is a good approach for the scientific management of the ecosystem.

Another researcher to model prey-predator systems in Serengeti ecosystem is [19] who analysed the population dynamics of herbivores, carnivores and grasses volume using secondary data from the years 1996 to 2006. They found that, the crocodile predation on herbivore decreases the population of herbivore and the crocodile increases when the natural death rate in the absence of prey decreases. Also they found that herbivore population increase as its intrinsic logistic rate increases.

[41] also developed a comprehensive model to study the dynamics of the Serengeti-Mara ecosystem. The processes of the research involved first studying the spatial and temporal variation in climatic parameters and physiography around the Serengeti ecosystem. The relationship between rainfall and grass growth was then involved and finally, the impact of predation to those prey species. The system, even in these early stages of formulation, adequately depicted dynamics that are equivalent to those in the Serengeti ecosystem, which shows that appropriate methods were used. It was also found that the grass availability was the main factor determining the overall dynamics of wildebeest in the entire system.

[46] studied the predation and competition of Serengeti migrants captured by hierarchical models. They statistically studied wildebeest and zebra migrating

seasonally around the Serengeti-Mara ecosystem. They studied how food availability and predation determine the migration patterns of individual species in the ecosystem. They found that wildebeest tend to move with regard to food quality paying little attention to predation risks while the movement and zebra reflected a balance between the predation risk and the food quality food for sufficient biomass. Their analysis shows the way two migratory species migrates in response to different aspects in the same landscape.

More ever, [47] explains the presence of poaching in Serengeti ecosystem and protected areas which is accelerated by revenue generated from from bush meat sales. He compared the benefits and costs through monetary benefit, bodily injuries, fires and prison sentences that individual over goes over their poaching career.

3.1. Prey-Predator Systems with Seasonal Weather Variations

Seasonal weather variation plays a considerable function in changing the dynamics of prey and predator species in Serengeti ecosystem. They can affect species by influencing factors such as behaviour or distribution 48. Rainfall, temperature and humidity are the principal variables with severe impact in serengeti ecosystem [25] [29]. Variation in temperature and Rainfall indeed determines the spatial pattern of resource availability by influencing plant productivity, vegetation structure and accessibility. However, high rainfall and temperature also can lead to floods which facilitate spread of disease and parasites such as canine dispenser virus that spread among Serengeti lions in 1993 [25] [49]. Prolonged periods of low rainfall also attributes drought which leads to extinction of species and often modify the size of population. For example 75% of zebra and wildebeest deaths in Serengeti are caused by under nutrition rainfall being the most factor determining food supply [43] [44] [50]. Currently the ecosystem consists of approximately 3000 lion, 750,000 zebra and 2,000,000 wildebeest [50], but 150 lion, 265 zebra and 250 wildebeest die each year as the result of floods, drought and disease [2]. Therefore, seasonal weather variations are directly responsible for variation in the distribution and abundance of species in Serengeti ecosystem and contribute to the decline and extinction of native population that fails to respond adequately to those changes. Mathematical model can give an insight on how sturdiness and mechanism of seasonal weather fluctuation can change the dynamics of species in the ecosystem. Very few prey-predator models, in the reviewed literatures, did not find any prey-predator model in Serengeti ecosystem that incorporated seasonal weather variation. However some models involved the impact of climate variability in prey and predator systems. Example [25], studied the effects of climate change on dynamics predator-prey systems.

$$\begin{aligned} \frac{\mathrm{d}N}{\mathrm{d}t} &= r_0 N\left(1 + eg(t) - \frac{N}{K}\right) - \frac{cNP}{d+N} \\ \frac{\mathrm{d}P}{\mathrm{d}t} &= \alpha\frac{cNP}{d+N} - \delta_0 P - \frac{\delta_0 q P^2}{N} \end{aligned} \tag{8}$$

They developed a climate function, and that climatic function $r_1 = r_0\left(1+eg\left(t\right)\right)$ and $K_1 = K\left(1+eg\left(t\right)\right)$ which was used to describe how favorable the climate is assuming scale from −1 to +1. They focused on changes in variations of climate particularly a decrease in the switching rate between years with high rainfall (good years) and years with low rainfall (bad years). By considering the prey-predator dynamics, they focused on the conditions that can lead species to extinction. The researcher also developed a computer software to explore systematically a wide range of climate scenarios at a high level of aspects and the results showed that the dynamics of predator-prey interactions is sensitive to the rapid drop in growth rate caused by a switch from years with good climate (good growth years) to years with bad climate (bad growth years).

[30], studied the effects of seasonal strength and abruptness on predator prey dynamics. The study focused on abrupt seasonal forcing in modelling their dynamics. Their results highlighted that, a more abrupt seasonal forcing mostly alters the magnitude of population fluctuations and triggers period-doubling bifurcation as well as the emergence of chaos at lower forcing strength than for sine waves. The study used the sine curve to account the aspects of seasonality.

Also [48], studied climate change effects on prey-predator interactions. The purpose their study was to examine how climate change and predation risk can combine to influence herbivore stoichiometry and feeding ecology. They found that climate change can modify predator-prey interaction by affecting species characteristics and modifying consuptive and for non-consuptive predator affects. [50], studied and analyzed a system of equations for population growth with response to environmental changes. In their proposed model, they introduced a carrying capacity which depends on time and that was the main approach in explaining varying environment which resulted in studying a non-autonomous system of differential equations. This approach helped to develop the systems that reveal directly the dynamics of one or more species with their environments. This was attained by making the carrying capacity as a variable and they found that, the state of the ecosystem depends on environmental parameters that have a direct impact on population growth, leading the population to either extinction or co-existence.

[29], also studied the environmental variation as a main factor influencing prey-predator systems. The researcher investigated the impact of weather conditions on predation risk by changing the spatial behavior of the prey. In this study they used a reindeer calves in Norway and they found that deep snow and ice conditions led reindeer to move from their most pastures to the parts of lowland forests. Wolverines and Golden eagles also preyed on calves but their effect was much smaller and not associated with a specific habitat type. The link between climatic conditions, habitat use, and predation changed over the winter season and this was depending on the body weights of the calves.

3.2. Impact of Disease Infections in Serengeti Ecosystem

The occurrence of disease induced mortality has been not recorded in Serengeti ecosystem since the removal of rinderpest [1] [41]. It is therefore assumed that the population dynamics in Serengeti has not been regulated or influenced by disease. However this may not be a correct supposition as [41] states that zebra are sensitive to regular epizootics as the consequences of their social structure. He found that the female remained in close contact with each other within groups, this maximizes the probability of epizootic transmissions. Sometimes infections in the ecosystem are not straight forward as the disease related mortality is generally dependent on an animal's nutritional status [51]. For instance, for ecto-endoparasites to reach fatal number, an animal must have inadequate disease resistance which tends to occur when it is undernaurished [52]. Studying the influence of disease in the population dynamics of species in Serengeti ecosystem is potentially significant because they play a great role in stabilizing or distabilizing the ecosystem. For instance, it took more than ten years for Serengeti ecosystem to stabilize following the eruption of rinderpest disease in wildebeest as well as canine dispenser virus of 1994 in lion [6]. So far in many ecological studies of prey-predator systems with disease, it has been reported that predator take high parasites of infected prey [53] [54] [55] [56] [57]. Hence there has been a growing interest in the study of disease in prey-predator systems and mathematical modeling in both ecology and epidemiology are the important tool in understanding and analysing the dynamics of prey-predator systems. Anderson 1990 and May 1991 were the first researcher to combine the two modelling systems, ecology and epidemiology [57], while Chattopadhyay and Arino were the first who used the eco-epidemiology [58]. Since then, various mathematical models in the combined aspects of ecology and epidemiology have been formulated and analyzed [55] [56]. Models are modelled to study the dynamics of the transmission of infections among prey and predator species. Example, [28] analysed a two prey one predator system with disease in the first prey population. They developed an eco-epidemiological model using Holling type II function response, with two preys, one predator population where only first prey population is infected by an infectious disease. They observed that existence of stability switches occur around the interior equilibrium. They divided the first population into two sub-classes. Susceptible and infected and studied the dynamical behaviour of the system at various equilibrium point. They didn't consider disease infection in the predator population.

$$
\begin{aligned}
\frac{\mathrm{d}S}{\mathrm{d}t} &= rs\left(1-\frac{S+I}{K}\right)-\lambda SI-\frac{PYS}{mY+s} \\
\frac{\mathrm{d}I}{\mathrm{d}t} &= \lambda SI-\frac{cYI}{mY+I}-\gamma I \\
\frac{\mathrm{d}Y}{\mathrm{d}t} &= \delta Y\left(1-\frac{hY}{I+S}\right)
\end{aligned}
\tag{9}
$$

Also, [57] studies an eco-epidemiological model and optimal control of disease transmission between humans and animals. In their model, they introduced the optimal control problems by incorporating three controls which were categorized into curative, preventive and a combined effort of both currative and preventive strategies. This was done in order to determine the behaviour of the infections. Analitical and numerical results revealed that when a disease is not transmitted within the human population but constructed from only the animals, prevention proved to be effective and feasible.

Also [24] studied on infectious disease in prey predator. They studied in three compartments mathematical eco-epidemiological model consisting of susceptible prey, infected prey and predator. Also the study did not include treatment in prey-predator system which is included in our study.

Also [56] studied an eco-epidemiology mathematical model with treatment and disease infection in both prey and predator population. They proposed and analysed the system of differential equation using stability theory of differential equations and they compared two models, model without infected predator together with treatment classes.

[59] studied an eco-epidemiological model in the interaction between Palecanidae and Tilapia. They constructed the model and described the interaction between Tilapia and Pelecanidae with infections in Pelecanidae. The infection process were modeled by Holling type II function response and they found that disease factors in the prey population can influence predator and prey interactions. They described how disease in Tilapia may transfer to pelecanidae through predation.

[32] studied an eco-epidemiological prey-predator model where predator distinguished between susceptible and infected prey. The ratio dependent function response for both infected and susceptible was used. They found that the interaction of predator and healthy prey and the disease affects predator.

4. Conclusions

Prey-predator models are widely studied topics in biomathematics. We have reviewed recent works focusing on the modelling of harvesting, seasonal weather variation and disease. Some of the stated models show a very rich dynamics which is much more realistic that the one of the first historical models. The inclusion of seasonal weather variation in prey-predator systems can have important effects on the dynamics. It can stabilize or distabilize the systems as seen in [25] and [48]. The conclusion about the influence of disease is not the same in all the studied models. Considering the system with infections in [28] the author shows that the population of prey species increases after the application of treatment. In [26] it is shown that the increase decreases the population and can even cause extinction. We noticed that the same methods and results are used in most papers for the study of the stability of the equilibria and the qualitative behaviour of the system. Principally the authors use the standard linear stability analysis, they analyze the sign of the real part of the eigenvalues of the Jacobian matrix, sometimes using Routh Hurwitz criterion. It is important to remember that for non-hyperbolic equilibria, the computation of the eigenvalues does not allow us to conclude on the stability. We have observed that, in such cases, the equilibria were not usually studied in the papers reviewed. Other frequently used tools are the computation of Lyapunov coefficients.

In most works, there are some problems, open problems and some characteristics that would be interesting to investigate more in detail. In the following we list some problems which researchers may find interesting to address in the future, which are proposed or motivated by the works included in this review.

- Among the systems that consider the harvesting, the one proposed in [9] is the one that shows a richer dynamics. As the authors say, it is possible that by changing the functional response and taking one of ratio dependent function response, the behaviour is even more realistic, so it would be interesting to study it.
- Many systems study infections on only prey population or predator population but it would be interesting to consider models with infections both in prey and predator populations, because as stated in [57], in many ecological systems, predator takes high parasites of infected prey. Among the systems that consider infections, the model proposed in [26] shows rich dynamics as it explores infections both on prey and predator as well as possibility of treatment on both populations.
- The effect of seasonal weather variation on prey-predator systems has not been studied as far as we know. Hence there is a need to study new functions that can model the effects of seasonal weather variations on prey-predator ecosystems, (see [25] and [29]).

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Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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