

Dynamics of insect predator and mosquito prey system with mutual interference as a factor for the co-occurrence: Validating through models

Chandrani Mukherjee¹, Krishna Pada Das^{2*}, Goutam Panigrahi³

¹Department of Basic Sciences and Humanities, Seacom Engineering College, West Bengal 711302, India

²Department of Mathematics, Mahadevananda Mahavidyalaya, West Bengal 700120, India

³Department of Mathematics, NIT Durgapur, West Bengal 713209, India

* Corresponding author: Krishna Pada Das, krishnaisi@yahoo.co.in

ARTICLE INFO

Received: 9 September 2023

Accepted: 12 October 2023

Available online: 20 October 2023

doi: 10.59400/jam.v1i3.246

Copyright © 2023 Author(s).

Journal of AppliedMath is published by Academic Publishing Pte. Ltd. This article is licensed under the Creative Commons Attribution 4.0 International License (CC BY 4.0).

<https://creativecommons.org/licenses/by/4.0/>

ABSTRACT: Several models have been proposed as an extension to the classical Holling's disc equation to evaluate the predator and prey interactions and their applied aspects in biological control and population regulation of the target organisms. In a one-prey and two-predator dynamic system with mutual interference m as a quadratic parameter of predator density, an evaluation was made of the resultant impact on the prey. A simulation was carried out to see the finite-time extinction of prey and the stability of the system at origin, i.e., when all three species are extinct. We assumed the data obtained was for the interactions between the mosquito and the water bug predators that are common in the freshwater wetlands and involved in population regulation. Despite the benefits to the prey population due to interference and competition, the expected extinction of prey in a finite time is still observed. With varying magnitudes of m , the declining growth curve of the prey population shifted. The equation proposed was also compared with the Crowley-Martin functional response, and considerable differences were observed in selected instances when compared to the growth rate of the predators in a species-specific manner. The stability of the system was deduced from the eigenvalues of the Jacobian matrix at the origin to prove the extinction is stable. Our assessment supports the possible cooccurrence of predators and mosquito prey in the wetlands, with mutual interference being one of the major factors.

KEYWORDS: functional response; mutual interference; mosquito control; predator-prey interactions; water bugs

1. Introduction

In conservational biological control, the use of natural predators and pathogens is always highlighted in the regulation of the target organisms^[1,2], utilizing the natural trophic interaction^[2,3]. In this light, we are taking the water bugs (Hemiptera: Heteroptera) as potential mosquito biological control agents^[4,5], cooccurring in mosquito larval habitats^[6,7], wetlands like rice fields^[8-10] and temporary pools^[11,12], that contribute to mosquito production^[13]. Considering the generalist insect predators to be involved in several indirect interactions like the apparent competition and the intraguild predation^[14-16],

may redirect the direction of regulation of target prey. Empirical studies in the laboratory as well as in field conditions have deduced the possible species-specific differences in the interference competition and the parameters changing the predator efficacy in mosquito regulation^[17-21]. The pair-wise mutual interference^[22] shown by the predators can be considered one of the potential factors that reduces the efficacy of mosquito regulation^[23,24]. The classic Holling's disc equation only takes into account that the consumption rate of predators only depends on prey density^[25] as discussed elsewhere^[26], which is of three types, namely, type I, II, and III, with necessary modifications of the basic Holling's disc equation^[25]. Holling's type II functional response is mathematically expressed by the equation, which renders to be a function of prey density:

$$\frac{N_e}{T} = \frac{\alpha V}{1 + ahV} \quad (1)$$

where N_e is the number of prey attacked and eaten, T is the total time for foraging, V is the prey density, h is the handling time, and α is the searching rate. In this equation, the assumptions are: (a) only a single predator is present in isolation; (b) the handling time taken by the predator is equal across all prey; (c) there are no differences among the prey in terms of size, sex, and age; (d) the hunger level remains equal irrespective of the prey consumed, i.e., the hunger level remains the same from the initial till the end time of the consumption event by the predator; (e) a particular prey type remains vulnerable to the predation, i.e., being attacked by the predator; and (f) the total foraging time remains constant for all predators concerned. Irrespective of the type of functional responses, the population of the prey and the predators are supposed to fluctuate with time, keeping all other factors constant without affecting the interaction. As a result of predation, the prey population can be locally extinct, with a possible recovery in situations where the immigration of the prey individuals is found. In many other instances, the prey and predator populations may exhibit a cyclic change in number as a part of the limit cycle. One of the conditions for a limit cycle in prey-predator dynamics is the presence of an unstable interior equilibrium^[27]. When the prey population goes extinct in a finite time, the predator population also falls to zero subsequently, considering that prey is the only resource. The prey-predator dynamics, with certain initial conditions, can lead the prey population to extinction, which is determined by raising the individual number to one^[26]. As for gonochoric species and hermaphroditic species, they must fall to zero. Thus, the density of the prey species should become less than one to mathematically prove the local extinction of the target prey population. The presence of interference competition among multiple predators (in terms of abundance and terms of taxonomic identity) benefits the prey by increasing its time of decline than expected earlier increasing its survival probability. Successful prey capture in the presence of interference competition^[28-31] actually states the fitness of an individual predator. The magnitude of mutual interference may change with size, age, sex, etc. The pattern of attack is innate in predators, but the minute tricks may develop with experience. From an attack pattern of predator to survival strategies of the prey, have evolved with experience, as a young predator may face more hindrance from an experienced one, whereas, with senescence, they may lose their firmness of attack and become loose-fitting to adult predators^[32]. There are some morphological attributes to either of the sexes for reproductive purposes, which may come in the path of predation. Along with an increase in prey body size, search rate decreases generally, and for a larger predator than prey, handling time decreases^[32], which may lead to an increase in mutual interference. The interference competition reduces successful prey capture, i.e., the efficiency of a predator reduces proportionately with increasing competitors. A predator has to compete with other individuals who feed on the same resource. Other than maintenance and reproduction, it follows two components of energy expenditure: one to be spent

on subduing the prey and another to be spent on evading fellow competitors. Shedding light on the complexities of prey-predator interactions, there are different approaches, like the studies of a discrete-time prey-predator model with imprecise biological parameters and constant refuge for prey^[33], refuge proportional to predators^[34], and refuge proportional to prey and inversely proportional to predators^[35].

In the present narrative, we have considered the *Culex quinquefasciatus* Say, 1823 (Diptera: Culicidae) mosquito larvae (small and large larvae) as prey and the adults of the water bugs *Anisops bouvieri* Kirkaldy, 1904 (Heteroptera: Notonectidae), *Diplonychus rusticus* Fabricius, 1781, and *D. annulatus* Fabricius, 1781 (Heteroptera: Belostomatidae) as predators (in combination of two). They are considered to be analyzed through the existing mathematical models on prey-predator dynamics, comprised of logistic growth for prey and type II functional response on them by the predators^[26,36,37]. We introduced the mutual interference as a parameter in functional response, incorporating interference competition as a parameter. As in this system, three species interactions have been considered, with two predators feeding on single prey species, which calls for interspecific competition between them.

2. Materials and methods

In the explored model, the freshwater insects (Hemiptera: Heteroptera) are considered the predators against the mosquito as the target prey. As a result of the mutual interference among predators, a reasonable difference in the consumption rate may be observed, affecting their respective growth rates as well. To ease the calculation, we have assumed the competition between two predator species is equal and constant to nullify the significant errors due to asymmetric competition^[38]. The prey-predator dynamics are heavily affected by the presence of mutual interference among predators, as reflected in the literature available^[26,28–31,39–41].

We have considered the equation^[22,26] of three species systems, one prey and two predators, that depict their growth rates in the presence of predation, mutual interference, and competition. The prey shows logistic growth, which is formulated in the first half of the first equation, i.e., the prey growth rate equation. Both the predators show a type II functional response, as shown in the other half of the equation. As the predators feed on the same resource, there is interspecific competition between them. Putting these together in the system of equations, we considered the model proposed by Antwi-Fordjour et al.^[26], which includes the components of functional response^[25] and mutual interference together.

3. The model

Interference competition manifests when the presence of other individuals has a detrimental impact on access to resources. In the context of a species or population, this phenomenon is referred to as mutual interference, often quantified through a scaling exponent denoted as m in relation to the number of predators. We are considering the prey-predator dynamics with mutual interference, calculated using the following equation^[22]: $\frac{N_a}{PN} = QP^{-m}$, where m is the mutual interference constant, N_a is the mean number of prey consumed, P is the number of predators, N is the prey density, and Q is the value of $\frac{N_a}{PN}$ when $P = 1$.

The prey-predator model with mutual interference is constructed as an extension of the established equation^[26], with modifications as required in our case:

$$\begin{aligned} \frac{dx_1}{dt} &= rx_1 \left(1 - \frac{x_1}{k}\right) - \frac{\alpha_1 x_1 x_2^{-m_2}}{1 + \alpha_1 h_1 x_1} - \frac{\alpha_2 x_1 x_3^{-m_3}}{1 + \alpha_2 h_2 x_1} \\ \frac{dx_2}{dt} &= -\gamma_2 x_2 + \frac{d_1 \alpha_1 x_1 x_2^{-m_2}}{1 + \alpha_1 h_1 x_1} - \sigma_1 x_2 x_3 \\ \frac{dx_3}{dt} &= -\gamma_3 x_3 + \frac{d_2 \alpha_2 x_1 x_2^{-m_3}}{1 + \alpha_2 h_2 x_1} - \sigma_2 x_2 x_3 \end{aligned} \tag{2}$$

With initial conditions

$$x_1(0) = x_1^0 > 0, x_2(0) = x_2^0 > 0, x_3(0) = x_3^0 > 0^{[36,37]}$$

where x_1 is the population size of the prey species, x_2 and x_3 are the population sizes of the two predator species, respectively, at any time t , r is the intrinsic growth rate of prey, k is the carrying capacity of prey, $1/\alpha_1 h_1$ and $1/\alpha_2 h_2$ are half-saturation constants^[42] of predator 1 and 2 respectively, α_1 and α_2 are respective search rates of both predators, h_1 and h_2 are the handling time of predator 1 and 2 respectively, γ_1 and γ_2 are the death rates of predator 1 and 2 respectively, d_1 and d_2 are the conversion coefficient of functional response of predator 1 and 2 respectively, σ_1 and σ_2 are the rate at which the growth rate of predator 1 is reduced by predator 2 and vice versa, m_2 and m_3 are the mutual interference of predator 1 and 2 respectively and $0 < m_2, m_3 \leq 1$. In order to incorporate mutual interference into the functional response, we are modifying the type II functional response expression. As mutual interference reduces the energy of a predator to subdue a prey, it reduces the value of functional response. The reduction is not linear; rather, it forms a curvilinear graph, so we are raising mutual interference m to the negative power of predator density (P). The predator density is raised to the negative power of m , as mutual interference reduces access to resources, so the functional response is reduced.

The Crowley-Martin equation^[43-45] for functional response is incorporated here to describe the growth rate and compare with Equation (2) later:

$$\begin{aligned} \frac{dx_1}{dt} &= rx_1 \left(1 - \frac{x_1}{k}\right) - \frac{\alpha_1 x_1 x_2}{1 + \alpha_1 h_1 x_1 + m_2(x_2 - 1) + \alpha_1 h_1 x_1 m_2(x_2 - 1)} \\ &\quad - \frac{\alpha_2 x_1 x_3}{1 + \alpha_2 h_2 x_1 + m_3(x_3 - 1) + \alpha_2 h_2 x_1 m_3(x_3 - 1)} \\ \frac{dx_2}{dt} &= -\gamma_2 x_2 + \frac{d_1 \alpha_1 x_1 x_2}{1 + \alpha_1 h_1 x_1 + m_2(x_2 - 1) + \alpha_1 h_1 x_1 m_2(x_2 - 1)} - \sigma_1 x_2 x_3 \\ \frac{dx_3}{dt} &= -\gamma_3 x_3 + \frac{d_2 \alpha_2 x_1 x_3}{1 + \alpha_2 h_2 x_1 + m_3(x_3 - 1) + \alpha_2 h_2 x_1 m_3(x_3 - 1)} - \sigma_2 x_2 x_3 \end{aligned} \tag{3}$$

The II (small) and IV (large) instar larvae of *C. quinquefasciatus* and the consumption by the predators, the backswimmer, *A. bouvieri*, and the water bugs, *D. rusticus* and *D. annulatus*, were considered in combination for the mutual interference and the functional responses to deduce the numerical values and the evaluation of the model with reference to the impact of the mutual interference. Empirical studies on the mosquito predatory potential of these water bugs^[4,23,24,46,47], as well as the intraguild predation^[18-20,48] and apparent competition^[21], have been used to provide data input to the model for evaluation. Of particular relevance is the data on the mutual interference among the predators considered here^[23], which is used in the model to deduce the impact on the prey and the predator population.

The Holling's equation incorporating the search rate and the handling time needs to be modified to

include the interaction among all the predators of the same species, as the presence of other predators increases the time and energy expenditure of the predator, considered as mutual interference m , $0 < m \leq 1$, as an exponent of the number of predators. The magnitude of m here is calculated using the formula^[22], stated above, based on a laboratory experiment.

When the functional response is raised to the negative power of m , it reduces the number of prey captured, but $\frac{d_1 \alpha_1 x_1 x_2^{-m_2}}{1 + \alpha_1 h_1 x_1}, \frac{d_2 \alpha_2 x_1 x_3^{-m_3}}{1 + \alpha_2 h_2 x_1} > 0$ for all values of m , to satisfy the increasing growth of predators at the initial stage. When prey starts to decline and becomes zero ($x_i = 0$), theoretically the only positive term in the predator's growth dynamic becomes zero, provided this prey is the only food source for this predator. The addition of new members to the predator population stops, and the population declines shortly after the prey population comes to zero, i.e.,

$$r x_1 \left(1 - \frac{x_1}{k}\right) < \frac{\alpha_1 x_1 x_2^{-m_2}}{1 + \alpha_1 h_1 x_1} + \frac{\alpha_2 x_1 x_3^{-m_3}}{1 + \alpha_2 h_2 x_1} \tag{4}$$

But, depending on other parameters, such as r and k along with α , h , and m , the prey population can remain increasing or maintain an asymptote.

$$r x_1 \left(1 - \frac{x_1}{k}\right) \geq \frac{\alpha_1 x_1 x_2^{-m_2}}{1 + \alpha_1 h_1 x_1} + \frac{\alpha_2 x_1 x_3^{-m_3}}{1 + \alpha_2 h_2 x_1} \tag{5}$$

In the classic Lotka-Volterra equation, mutual interference has been included to provide evidence for the assumptions made for prey-predator dynamics when stability is affected by interference competition. The inclusion of parameters does not always necessarily change the nature of equilibrium. It is to see through the models if it is affecting at all; if yes, the way of changing the equilibrium is to be deduced.

To analyze the stability of Equation (2), we are presenting it through the Jacobian matrix.

Equation (2) null isoclines are determined by solving,

$$\begin{aligned} r x_1 \left(1 - \frac{x_1}{k}\right) - \frac{\alpha_1 x_1 x_2^{-m_2}}{1 + \alpha_1 h_1 x_1} - \frac{\alpha_2 x_1 x_3^{-m_3}}{1 + \alpha_2 h_2 x_1} &= 0 \\ -\gamma_2 x_2 + \frac{d_1 \alpha_1 x_1 x_2^{-m_2}}{1 + \alpha_1 h_1 x_1} - \sigma_1 x_2 x_3 &= 0 \\ -\gamma_3 x_3 + \frac{d_2 \alpha_2 x_1 x_3^{-m_3}}{1 + \alpha_2 h_2 x_1} - \sigma_2 x_2 x_3 &= 0 \end{aligned} \tag{6}$$

Now putting the Jacobian matrix(J):

$$J = \begin{bmatrix} r - \frac{2r x_1}{k} - \frac{1}{(1 + \alpha_1 h_1 x_1)^2} \alpha_1 x_2^{-m_2} & & & & \\ & \frac{1}{(1 + \alpha_2 h_2 x_1)^2} \alpha_2 x_3^{-m_3} & \frac{\alpha_1 x_1 m_2 x_2^{-m_2-1}}{1 + \alpha_1 h_1 x_1} & \frac{\alpha_2 x_1 m_3 x_3^{-m_3-1}}{1 + \alpha_2 h_2 x_1} & \frac{d_1 \alpha_1 x_2^{-m_2}}{(1 + \alpha_1 h_1 x_1)^2} \\ & & -\frac{d_1 m_2 \alpha_1 x_1 x_2^{-m_2-1}}{1 + \alpha_1 h_1 x_1} & -\gamma_2 - \sigma_1 x_3 & -\sigma_1 x_2 \frac{d_2 \alpha_2 x_3^{-m_3}}{(1 + \alpha_2 h_2 x_1)^2} - \sigma_2 x_3 \\ & & & & -\frac{d_2 m_3 \alpha_2 x_1 x_3^{-m_3-1}}{1 + \alpha_2 h_2 x_1} - \gamma_3 - \sigma_2 x_2 \end{bmatrix}$$

At origin (0,0,0),

$$J_{(0,0,0)} = [r \ 0 \ 0 \ 0 \ -\gamma_2 \ 0 \ 0 \ 0 \ -\gamma_3]$$

Here the eigenvalues $-\gamma_2$ and $-\gamma_3$ are negative, but r is positive. As all the eigenvalues are not negative, Equation (2) is unstable at origin, i.e., when all three species become zero (as prey becomes zero, both predators become zero, as discussed earlier), there persists a tendency to rebound. But the system is stable when prey falls below zero, but both predator species are more than zero. The stability of the system is calculated from the eigenvalues of the Jacobian matrix, which is calculated in “*rootSolve*”^[49] and “*popbio*”^[50] R packages, at initial numbers of individuals, at any random intermediate time interval, at a time when prey number has fallen below 1, and at steady state point, which was established using the “*rootSolve*” package function “*steady*” in the “*runsteady*” method. The eigenvalues are always negative, meaning the system is stable under those conditions. With the functions “*steady.1D*” and “*steady*” in the package “*rootSolve*”, the attribute *steady* is stated “*false*”, meaning the steady state is not reached as the equation’s initial conditions lead to the extinction of prey species, and eventually both the predators will die out due to want of prey. A dynamic system is said to be a steady state if continuous work (here, predation over the prey) is done over time. As here, prey is extinct, one species of dynamic system is out, so no further encounter can happen, and the interaction between the dynamic system is stopped. So, over time, continuous interaction comes to an end. Here, the primary condition is not fulfilled, and the system does not reach a steady state. However, the system is stable at every point except at the origin, as the eigenvalues of the Jacobian are negative at those species concentrations. The model aims to analyze the inclusion of mutual interference in prey-predator dynamics as a possible force for the coexistence and stability of the system.

4. Results

The experiments were carried out earlier to reveal that an adult water bug consumes a certain amount of the fourth instar larva of *C. quinquefasciatus*. The consumption of fourth instar larvae by these three insects concerned showed that, in numerical terms, adult *A. bouvieri* could consume 2–34 fourth instar larvae, whereas *D. rusticus* had 11–87 of the same larvae and *D. annulatus* had 33–122 of the same larvae. The difference in their consumption can be explained by their predatory efficiency, affected by their intraspecific and interspecific interactions^[23]. Concerning the evaluation of the model, we have demonstrated a numerical simulation of the model with the data available using RStudio version 4.2.2 R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL (<https://www.R-project.org/>).

The data used for the evaluation of the model:

$r = 0.1$; $k = 500$; $a_1, a_2 =$ combinations of 5.53, 526, 5.153 and 6.263, 5.323, 5.40; $h_1, h_2 =$ combinations of 12.73, 6.163, 7.12 and 39.44, 7.806, 11.243; $d_1 = 0.1$; $g_1 = 0.1$; $s_1 = 0.1$; $d_2 = 0.1$; $g_2 = 0.1$; $s_2 = 0.1$; $m_2, m_3 =$ combinations of 0.06, 0.01, 0.24, 0.35, 0.78, 0.25, 0.09, 0.31, 0.27

The pattern of declination of the prey population, from an initial density of 200 with different combinations of predators to an initial density of 5 for each predator, and mutual interference among them are shown in **Figure 1(a–e)**. Since the data did not comply with normality (neither the Shapiro-Wilk test nor Levene’s test), the Kruskal-Wallis test was performed using the R package “*rstatix kassambara/rstatix*”. The small and large larvae are taken separately as the search rate and handling time differ with different prey sizes for each combination of predators. In order to admit the change in the

growth rate of predators due to these two parameters, the system is evaluated using different sizes of prey. The difference in growth rates between two larval sizes is not subjected to a *t*-test; rather, it is only presented for evaluation in Equation (2). The results of the Kruskal-Wallis test, for most of the cases, are significantly different, i.e., the growth rate of predators is evidently affected by varying degrees of mutual interference, with some exceptions that may be a result of species-specific interaction.

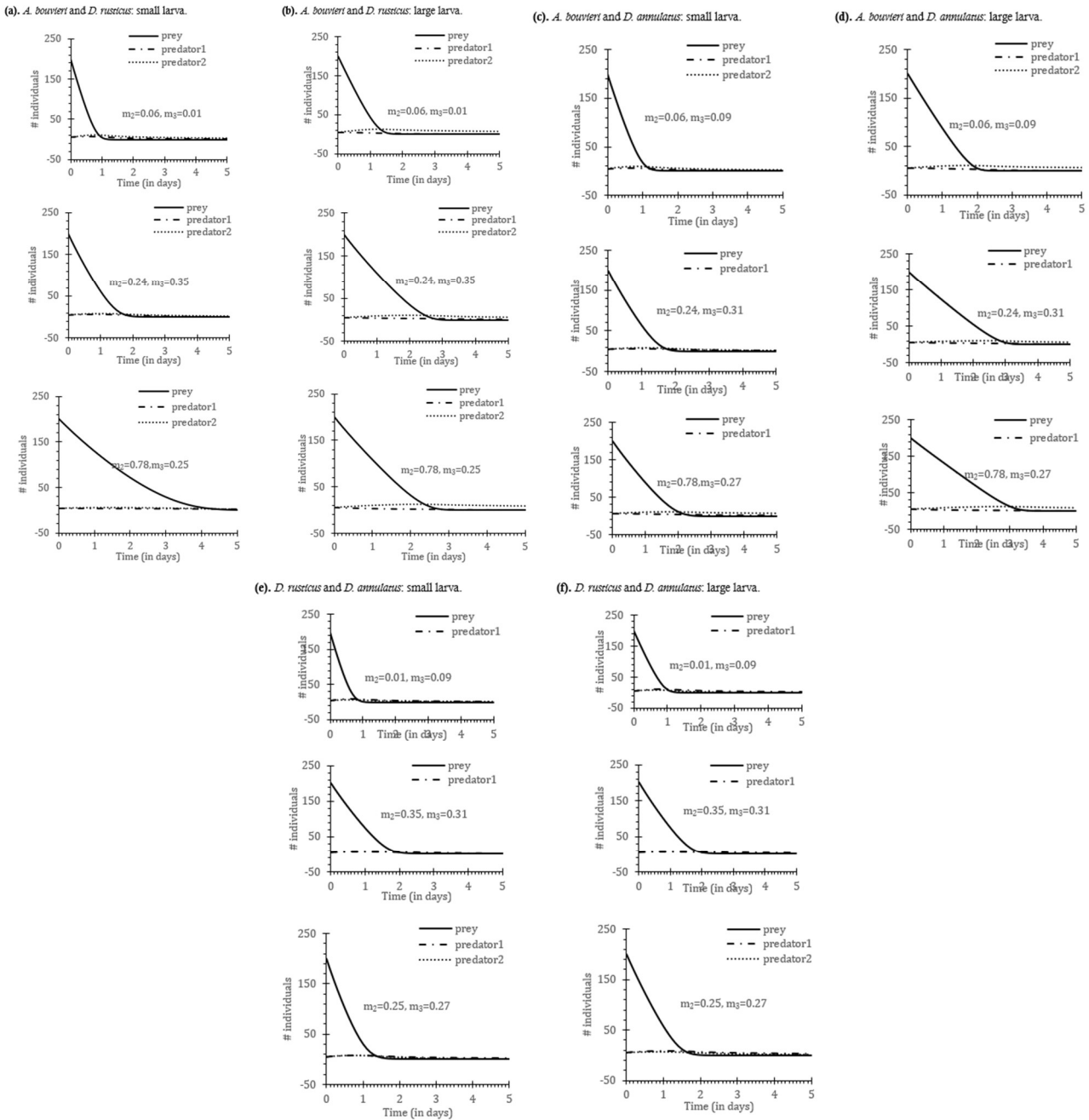


Figure 1. The representation of the different combinations of the predators and the resultant effect on the prey extinction based on the various values of the mutual interference taken separately and the size of the prey (a, c, e) small mosquito larva and (b, d, f) large mosquito larva.

As shown in the figures (Figure 2(a–c)), there is no periodic solution or limit cycle produced, as prey (V) is extinct, and with consideration that the predators under experiment were not provided other resources, they also went extinct eventually, and varying with different values of mutual interference,

prey went extinct for different numbers of predators at different time intervals. As the prey is extinct in finite time under constant predation, the interior equilibrium where all three species can be stable in positive magnitudes cannot be derived. So, the qualitative changes in the dynamical behavior of the proposed model under the effect of varying mutual interference, as concerned here, or intrinsic growth rate, do not change.

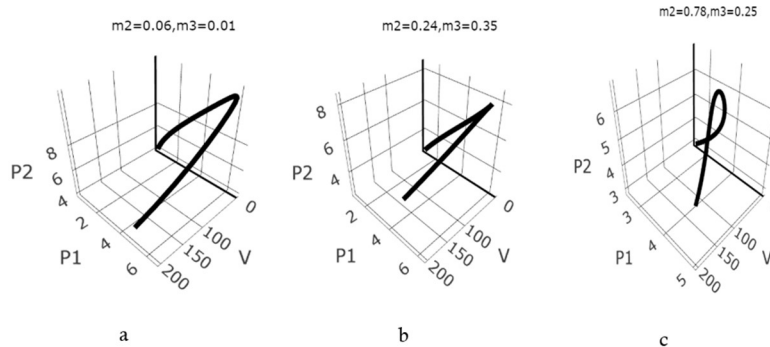


Figure 2. The graphical representation of the absence of a limit cycle as prey extinct in finite time, the prey-predator cycle does not revolve around an equilibrium.

Figure 2(a–c) represents the extinction graph for only *A. bouvieri* and *D. rusticus*, for small prey types with different combinations of mutual interference.

In addition, depictions in **Figure 3(a–c)** show the extinction of the prey species in finite time due to interaction with the predators, graphed by the growth of all three species with varying values of mutual interference. The predators are increased initially when prey is abundant, then decline as prey individuals start to decline. And this decline of predators depends on the magnitude of predators’ mutual interference; the higher the magnitude, the earlier the decline for predators, as they have to compete firmly with fellow predators in the decreased prey density for survival.

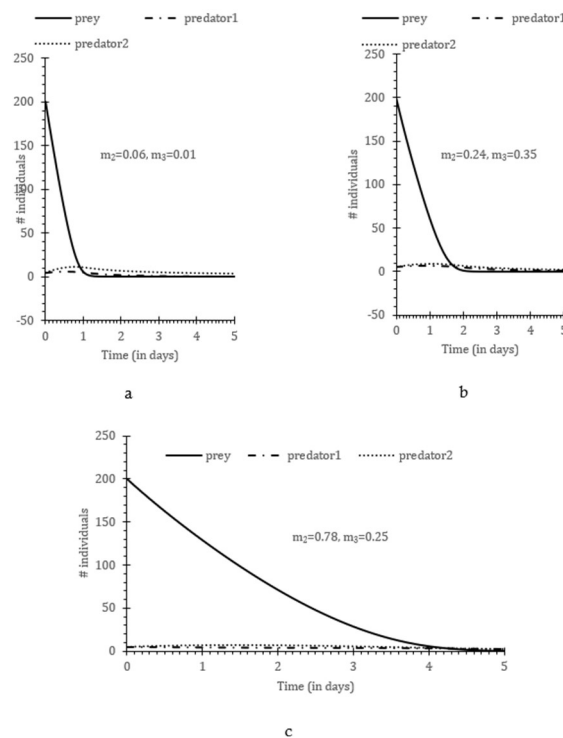


Figure 3. The graphical representation of the finite time extinction of prey population followed by predator decline.

Figure 3(a–c) represents the declination of *C. quinquefasciatus*, due to predation by *A. bouvieri* and *D. rusticus*, for small prey types with different combinations of mutual interference.

The assessment of prey extinction using average values of the mutual interference of the predators’ Figure 4(a–e). The results deduced from Figure 4(a–e) are described, but here, mutual interference is taken as the average of both predators.

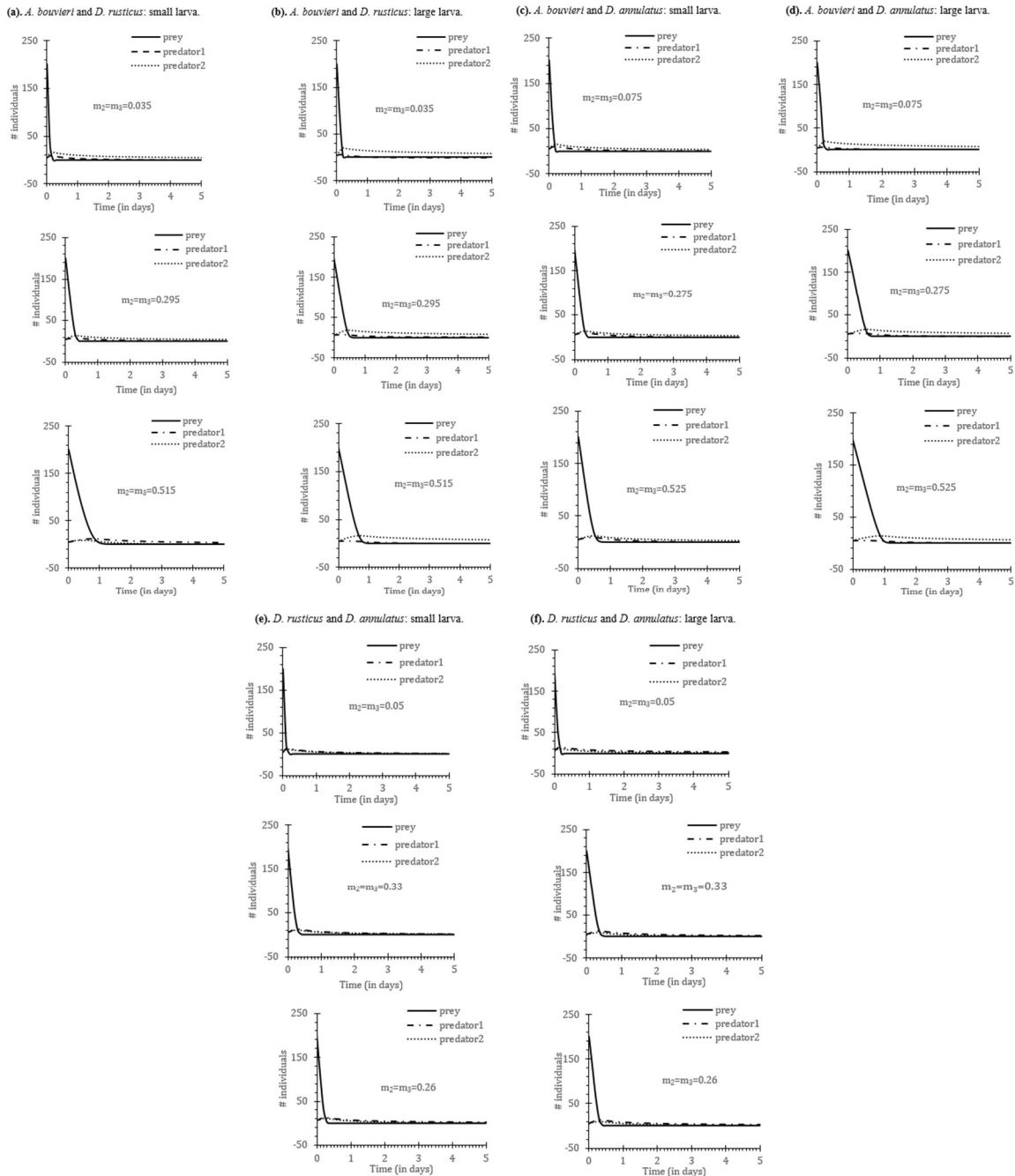


Figure 4. The representation of the different combinations of the predators and the resultant effect on the prey extinction based on the various values of the mutual interference taken as the average of both and the size of the prey (a, c, e) small mosquito larva and (b, d, f) large mosquito larva.

The mutual interferences, taken separately as combinations of a pair of species, are put in the Crowley-Martin equation (Equation (3)), the statistical significance is represented in Figure 5(a–e), and the predicted values of the prey and predators against time indicate that the prey population declines at

a constant predator density (5 for each predator species and an initial prey density of 200), but the rate of decline for the prey population varied with the mutual interference of the predators, with the same pattern of predator combination as before. A comparison of Equation (2) with Equation (3) through a two-tailed *t*-test shows that among the 36 different combinations, only 8 were found to be significantly different, suggesting that few conditions may impose a change in the population growth of the predators as a result of the mutual interferences. In all other instances, the mutual interference may impact the instantaneous predatory efficacy but not the overall growth.

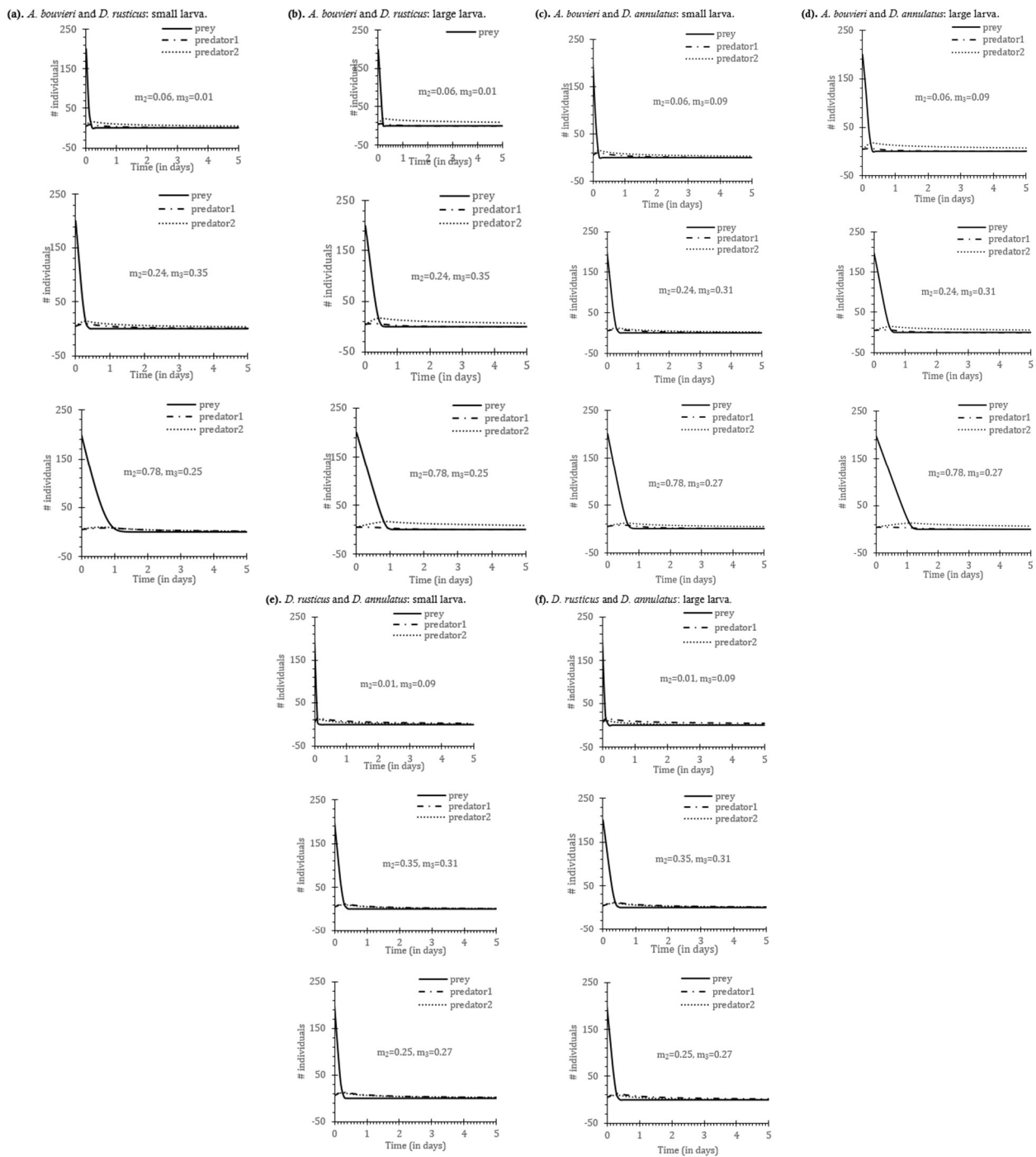


Figure 5. The representation of the different combinations of the predators and the resultant effect on the prey extinction based on the various values of the mutual interference taken separately and the size of the prey (a, c, e) small mosquito larva and (b, d, f) large mosquito larva putting in Crowley-Martin equation. The mutual interferences are taken separately as combinations of a pair of species, put in Crowley-Martin equation.

The finite time extinction of prey, i.e., analytical solution, is calculated from Equations (2) and (3) using the package “*desolve*” in R^[51], and the graphs are produced in the “*ggplot2*”^[52], “*grid*”^[53], and “*plotly*”^[54] packages in R. As the graph (Figure 6) shows, the prey population goes extinct/declines significantly from the initial prey density (V_{initial}) of 200 due to predation, whereas predators’ populations increase initially when prey is abundant, but with a decline in prey, predators’ growth rate also declines, but they maintain survival.

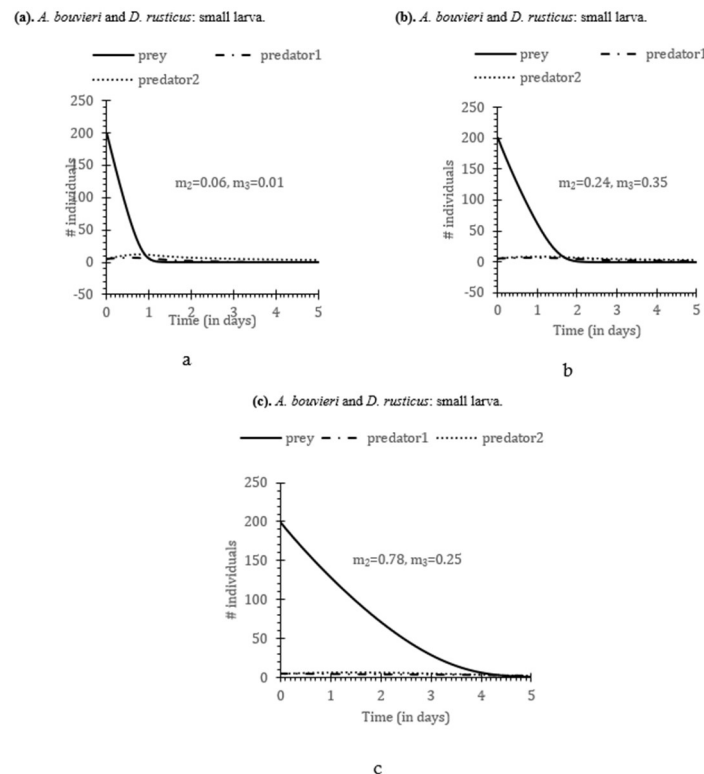


Figure 6. Different combinations of mutual interference shift the prey declination curve to the left when the magnitude of interference is low and to the right when mutual interference is high, for *A. bouvieri* and *D. rusticus*, feeding on small prey type.

Figure 6(a–c) represents the effect of the magnitude of mutual interference of predators on prey growth rate.

5. Discussion

Mutual interference between predators tends to reduce the number of prey they could have subdued with their uninterrupted potency. As an impact of the mutual interference, the functional response is reduced by a certain factor^[22,26], which may prove beneficial for the prey population. Here the population growth is assumed to be logistic in the absence of the predators, but during predation, the numerical changes in the prey follow a type II functional response, assuming prey individuals are not dying due to parasites or any epidemic. However, the numerical variations in the predator species may alter the balance achieved through interactions with multiple predators. Here, the prey population declines as the prey logistic growth is less than that captured by both the predators and aggregately, which can be due to various combinations of initial conditions. Therefore, as the prey population is declining, it is clear that the mutual interference among predators is not hindering the predator population from accumulating its required resources for growth and maintenance. But still, it intervenes in the functional response, as it affects the number of prey caught. As shown in the graph (Figure 1),

with decreased interference, the prey growth curve shifts to the left, i.e., predators catch more prey in the same time interval, so the curve comes to zero in short order, whereas, with increased mutual interference, the curve shifts to the right, implying that predators have to outdo many other members to subdue prey, so it requires more time, and the prey growth curve falls slantly to zero, requiring more time. The impact of mutual interference is influenced by the body size of the concerned prey and predators^[32,45,55]. In the present instance, the body size of the prey is also considered, for which only the handling time and search rate change (**Figure 1**), but mutual interference is the same. However, the extent of the interference in the predator pairs is considered to vary since the predators are different species and bear different body sizes. Owing to the differences in body size, the predatory efficiency would have varied, resulting in a differential level of mutual interference among the predator pairs. For instance, the average size of *A. bouvieri* is small (body length in mm, range 5.5–9; mean $7.27 \pm 0.09\text{SE}$; body weight in mg, range 1.3–40; mean $12.78 \pm 0.72\text{SE}$, $n = 83$) compared to the size of *D. rusticus* (body length in mm, range 13.1–18.1; mean $15.56 \pm 0.13\text{SE}$; body weight in mg, range 64.4–281; mean $138.47 \pm 3.75\text{SE}$, $n = 88$) and *D. annulatus* (body length in mm, range 18–25; mean $22.57 \pm 0.58\text{SE}$; body weight in mg, range 190.6–604.8; mean $434.13 \pm 31.02\text{SE}$, $n = 13$). As shown in the growth curve figures, the combination of low interference with a high search rate and less handling time shifts the curve to the left, whereas the opposite combination shifts it to the right. Thus, if the predator can subdue a prey quickly without much competition from other predators, the prey population can be reduced faster than in the presence of competitors interfering in the process. The mutual interferences increase with the increase in predator density, thereby facilitating the survival of the prey population. The mutual interference can be age-class dependent^[32,56,57]. When the predators are in their initial years, they may lack efficiency in hunting and also outdo a competitor. This is applicable to a number of insect predators, as observed in *Notonecta hoffmani*^[57,58], the predatory phytoseiid mite *Phyloseiulus persimilis*^[59], and *Callicorixa producta* (Hemiptera: Corixidae)^[60]. But with age, they learn the tactics, eventually increasing their competition efficiency, so mutual interference is increased, which means the predators take enormous time to bring the prey population to extinction.

From the results, it is apparent that the local scale extinction of the mosquito or prey is possible, but interference between the predators benefits the prey. In a situation where resources are constant, as the population grows, the resources available for individuals dwindle over time. It is assumed that there is no time lag, i.e., the population growth rates of each species change instantly with a change in any prey or predator number. Further, it is also assumed that the external environment has no influence on the rate of population growth and that there are no age, body size, or sex effects of individuals on the population growth rate. The assessment of the mutual interference involving the hemipteran predators indicates the possible impact on prey regulation, provided more than one predator is present in the habitat. Owing to the interference, the prey vulnerability is reduced, and the resultant effect benefits the prey population, i.e., the mosquito prey in the present instance. Such situations therefore provide evidence to consider the coexistence of the mosquito and the predators, but with less impact on the mosquito population.

When the magnitude of mutual interference of *D. rusticus* is less than that of *A. bouvieri*, i.e., *D. rusticus* consumes more mosquito larvae^[23], food left for *A. bouvieri* is less, considering the handling time and search rate for both species remain the same. Due to the indirect effect of the interaction chain in exploitative competition, the *A. bouvieri* population reduces. Here, in the graphs, the search rate and handling time are different for both species. Even if the search rate is more or less similar, the handling time is always much greater for *A. bouvieri* than both *D. rusticus* and *D. annulatus*. So, when the mutual

interference is less and *A. bouvieri* is expected to grow faster than both *D. rusticus* and *D. annulatus*, its higher handling time pulls back its growth rate than *D. rusticus* and *D. annulatus*.

The search rate and the handling time of the predators change, corresponding to changes in biological features like body size, age, and sex^[32,61–63]. With the change in body size of either prey or predator, the parameters defining the interaction change, which is manifested in the differential level of consumption. With aging, consumption may reduce owing to a reduction in search rate and an increase in handling time^[32]. For every change in the body morphology^[62] or the surrounding environment^[61], the behavior of the individuals varies, as do the resultant interactions. However, the changes may vary in the behavioral manifestation of predators in a species-specific manner^[63]. This can bring a difference in the magnitude of mutual interference by predators, as discussed for the model, with results depicted in the graphs on later pages. The assumption was that with increased interference, the ability of the predators to reduce prey population steeply decreases, and after numerical simulation, it was proved to be right. The declining curve for prey growth changes with different values of mutual interference. Sometimes the change is significant with respect to different species and different magnitudes of mutual interference for different numbers of individuals. When the growth is not significant with the change of mutual interference, it is mostly for the same genus (*Diplonychus sp.* here), from which it may be inferred that mutual interference is species specific to some extent. Due to morphology, species of the same genus may have similar structures that intervene in the expression of mutual interference. The predators efficiently turn down the prey population in the presence of mutual interference, only proving predatory efficacy as potent biological control agents in this combination.

6. Conclusion

Mutual interference among the predators is present at all trophic levels, with multiple consumers and multiple producers. In the part of a food web where *C. quinquefasciatus* and other mosquitoes are vulnerable to the predation of the water bugs *A. bouvieri*, *D. rusticus*, and *D. annulatus*, mutual interference is a possible way through which the competition among the predators may lead to the coexistence of both the prey and the predator. As elaborated in the models of the prey-predator interactions with functional responses and mutual interferences as the key factors, the variations in the values lead to the corresponding variations in prey growth and survival. Using the data on the mutual interference and subsequent evaluation through the established equations, we found the population variations in the mosquito prey and the water bug predators, which eventually provide evidence of the coexistence of both the predators and the prey in the concerned water bodies.

Author contributions

Conceptualization, KPD and GP; methodology, CM; software, KPD; validation, CM, KPD and GP; formal analysis, CM; investigation, KPD; resources, GP; data curation, KPD; writing—original draft preparation, CM; writing—review and editing, CM; visualization, KPD; supervision, GP; project administration, KPD; funding acquisition, GP. All authors have read and agreed to the published version of the manuscript.

Conflict of interest

The authors declare no conflict of interest.

References

1. Murdoch WW, Chesson J, Chesson PL. Biological control in theory and practice. *The American Naturalist* 1985; 125(3): 344–366. doi: 10.1086/284347
2. Barbosa PA. In: Barbosa PA (editor). *Conservation Biological Control*, 1st ed. Academic Press; 1998. 396p.
3. Murdoch WW. Population regulation in theory and practice. *Ecology* 1994; 75(2): 271–287. doi: 10.2307/1939533
4. Saha N, Aditya G, Saha GK. Prey preferences of aquatic insects: Potential implications for the regulation of wetland mosquitoes. *Medical and Veterinary Entomology* 2013; 28(1): 1–9. doi: 10.1111/mve.12003
5. Kundu M, Sharma D, Brahma S, et al. Insect predators of mosquitoes of rice fields: Portrayal of indirect interactions with alternative prey. *Journal of Entomology and Zoology Studies* 2014; 2(5): 97–103.
6. Bellows TS, Fisher TW, Caltagirone LE, et al. In: Bellows TS, Fisher TW, Caltagirone LE, et al. (editors). *Handbook of Biological Control*, 1st ed. Academic Press; 1999. 1046p. doi: 10.1016/B978-0-12-257305-7.X5046-2
7. Finke DL, Denno RF. Spatial refuge from intraguild predation: Implications for prey suppression and trophic cascades. *Oecologia* 2006; 149(2): 265–275. doi: 10.1007/s00442-006-0443-y
8. Mogi M, Memah V, Miyagi I, et al. Mosquito (Diptera: Culicidae) and predator abundance in irrigated and rain-fed rice fields in North Sulawesi, Indonesia. *Journal of Medical Entomology* 1995; 32(3): 361–367. doi: 10.1093/jmedent/32.3.361
9. Bambaradeniya C, Edirisinghe J, De Silva D, et al. Biodiversity associated with an irrigated rice agro-ecosystem in Sri Lanka. *Biodiversity and Conservation* 2004; 13: 1715–1753. doi: 10.1023/B:BIOC.0000029331.92656.de
10. Das PK, Sivagnaname N, Amalraj DD. Population interactions between *Culex vishnui* mosquitoes and their natural enemies in Pondicherry, India. *Journal of Vector Ecology* 2006; 31(1): 84–88. doi: 10.3376/1081-1710(2006)31[84:PIBCVM]2.0.CO;2
11. Fontanarrosa MS, Marinone MC, Fischer S, et al. Effects of flooding and temperature on *Aedes albifasciatus* development time and larval density in two rain pools at Buenos Aires University City. *Memórias do Instituto Oswaldo Cruz* 2000; 95(6): 787–793. doi: 10.1590/S0074-02762000000600007
12. Campos RE, Fernández LA, Sy VE. Study of the insects associated with the floodwater mosquito *Ochlerotatus albifasciatus* (Diptera: Culicidae) and their possible predators in Buenos Aires Province, Argentina. *Hydrobiologia* 2004; 524(1): 91–102. doi: 10.1023/B:HYDR.0000036122.10578.d0
13. Dale PER, Knight JM. Wetlands and mosquitoes: A review. *Wetlands Ecology and Management* 2008; 16(4): 255–276. doi: 10.1007/s11273-008-9098-2
14. Wootton JT. The nature and consequences of indirect effects in ecological communities. *Annual Review of Ecology and Systematics* 1994; 25(1): 443–466. doi: 10.1146/annurev.es.25.110194.002303
15. Blaustein L, Chase JM. Interactions between mosquito larvae and species that share the same trophic level. *Annual Review of Entomology* 2007; 52: 489–507. doi: 10.1146/annurev.ento.52.110405
16. Juliano SA. Species interactions among larval mosquitoes: Context dependence across habitat gradients. *Annual Review of Entomology* 2009; 54(1): 37–56. doi: 10.1146/annurev.ento.54.110807.090611
17. Sivagnaname N. Selective and frequency dependent predation of aquatic mosquito predator *Diplonychus indicus* Venkatesan & Rao (Hemiptera: Belostomatidae) on immature stages of three mosquito species. *Entomological Research* 2009; 39(6): 356–363. doi: 10.1111/j.1748-5967.2009.00243.x
18. Brahma S, Aditya G, Sharma D, et al. Influence of density on intraguild predation of aquatic Hemiptera (Heteroptera): Implications in biological control of mosquito. *Journal of Entomological and Acarological Research* 2014; 46(1): 6–12. doi: 10.4081/jear.2014.1977
19. Brahma S, Sharma D, Kundu M, et al. Mosquito prey vulnerability in intraguild predation between *Ranatra filiformis* and *Anisops bouvieri*: Implications in biological control. *Proceedings of the Zoological Society* 2015; 68(1): 36–44. doi: 10.1007/s12595-013-0093-0
20. Brahma S, Sharma D, Kundu M, et al. Intraguild predation in Heteroptera: Effects of density and predator identity on Dipteran prey. *Neotropical Entomology* 2015; 44(4): 374–384. doi: 10.1007/s13744-015-0286-5
21. Saha N, Kundu M, Saha GK, Aditya G. Alternative prey influence the predation of mosquito larvae by three water bug species (Heteroptera: Nepidae). *Limnological Review* 2020; 20(4): 173–184. doi: 10.2478/limre-2020-0017
22. Elliott J. Interspecific interference and the functional response of four species of carnivorous stoneflies. *Freshwater Biology* 2003; 48(9): 1527–1539. doi: 10.1046/j.1365-2427.2003.01106.x
23. Saha N, Aditya G, Bal A, Saha GK. A comparative study of predation of three aquatic heteropteran bugs on *Culex quinquefasciatus* larvae. *Limnology* 2007; 8(1): 73–80. doi: 10.1007/s10201-006-0197-6

24. Saha N, Aditya G, Bal A, Saha GK. Comparative studies on functional response of common heteropteran bugs of East Calcutta Wetlands, Kolkata, India. *International Review of Hydrobiology* 2007; 92(3): 242–257. doi: 10.1002/iroh.200610939
25. Holling CS. Some characteristics of simple types of predations and parasitism. *The Canadian Entomologist* 1959; 91(7): 385–398. doi: 10.4039/Ent91385-7
26. Antwi-Fordjour K, Parshad RD, Beaugard MA. Dynamics of a predator-prey model with generalized Holling type functional response and mutual interference. *Mathematical Biosciences* 2020; 326: 108407. doi: 10.1016/j.mbs.2020.108407
27. Case TJ. *An Illustrated Guide to Theoretical Ecology*. Oxford University Press; 2000.
28. Watt KEF. A mathematical model for the effect of densities of attacked and attacking species on the number attacked. *The Canadian Entomologist* 1959; 91(3): 129–144. doi: 10.4039/Ent91129-3
29. Hassell MP, Varley GC. New inductive population model for insect parasites and its bearing on biological control. *Nature* 1969; 223(5211): 1133–1137. doi: 10.1038/2231133a0
30. Roger DJ, Hassell MP. General models for insect parasite and predator searching behaviour: Interference. *Journal of Animal Ecology* 1974; 43(1): 239–253. doi: 10.2307/3170
31. Beddington JR. Mutual interference between parasites or predators and its effect on searching efficiency. *Journal of Animal Ecology* 1975; 44(1): 331–340. doi: 10.2307/3866
32. Hassell MP, Lawton JH, May RM. Patterns of dynamical behaviour in single-species populations. *Journal of Animal Ecology* 1976; 45(2): 471–486. doi: 10.2307/3886
33. Santra PK, Mahapatra GS. Dynamical study of discrete-time prey-predator model with constant prey refuge under imprecise biological parameters. *Journal of Biological Systems* 2020; 28(3): 681–699. doi: 10.1142/S0218339020500114
34. Mahapatra GS, Santra PK, Bonyah E. Dynamics on effect of prey refuge proportional to predator in discrete-time prey-predator model. *New Perspectives in Nonlinear Dynamics of Complex Systems* 2021; 2021: 6209908. doi: 10.1155/2021/6209908
35. Santra PK, Mahapatra GS, Phaijoo GR. Bifurcation analysis and chaos control of discrete prey-predator model incorporating novel prey-refuge concept. *Computational and Mathematical Methods* 2021; 3(6): e1185. doi: 10.1002/cmm4.1185
36. Sarwardi S, Mandal PK, Ray S. Analysis of a competitive prey-predator system with a prey refuge. *Biosystems* 2012; 110(3): 133–148. doi: 10.1016/j.biosystems.2012.08.002
37. Sarwardi S, Mandal PK, Ray S. Dynamical behaviour of a two-predator model with prey refuge. *Journal of Biological Physics* 2013; 39(4): 701–722. doi: 10.1007/s10867-013-9327-7
38. Morin PJ. *Community Ecology*. John Wiley & Sons; 2011. doi: 10.1002/9781444341966
39. Hassell MP. Mutual interference between searching insect parasites. *Journal of Animal Ecology* 1971; 40(2): 473–486. doi: 10.2307/3256
40. Meer JVD, Ens BJ. Models of interference and their consequences for the spatial distribution of ideal and free predators. *Journal of Animal Ecology* 1997; 66(6): 846–858. doi: 10.2307/6000
41. DeLong JP, Vasseur DA. Mutual interference is common and mostly intermediate in magnitude. *BMC Ecology* 2011; 11: 1. doi: 10.1186/1472-6785-11-1
42. Mulder C, Hendricks AJ. Half-saturation constants in functional responses. *Global Ecology and Conservation* 2014; 2: 161–169. doi: 10.1016/j.gecco.2014.09.006
43. Crowley PH, Martin EK. Functional responses and interference within and between year classes of a dragonfly population. *Journal of the North American Benthological Society* 1989; 8(3): 211–221. doi: 10.2307/1467324
44. Skalski GT, Gilliam JF. Functional responses with predator interference: Viable alternatives to the Holling type II model. *Ecology* 2001; 82(11): 3083–3092. doi: 10.1890/0012-9658(2001)082[3083:FRWPV]2.0.CO;2
45. Papanikolaou NE, Dervisoglou S, Fantinou A, et al. Predator size affects the intensity of mutual interference in a predatory mirid. *Ecology and Evolution* 2021; 11(3): 1342–1351. doi: 10.1002/ece3.7137
46. Sana N, Aditya G, Bal A, Saha GK. Influence of light and habitat on predation of *Culex quinquefasciatus* (Diptera: Culicidae) larvae by the waterbugs (Hemiptera: Heteroptera). *Insect Science* 2008; 15(5): 461–469. doi: 10.1111/j.1744-7917.2008.00234.x
47. Saha N, Aditya G, Saha GK. Habitat complexity reduces prey vulnerability: An experimental analysis using aquatic insect predators and immature dipteran prey. *Journal of Asia-Pacific Entomology* 2009; 12(4): 233–239. doi: 10.1016/j.aspen.2009.06.005
48. Brahma S, Sharma D, Banerjee S, et al. Influence of habitat complexity on the prey mortality in IGP system involving insect predators (Heteroptera) and prey (Diptera): Implications in biological control. *PLoS One* 2022; 17(3): e0264840. doi: 10.1371/journal.pone.0264840
49. Soetaert K, Herman PMJ. *A Practical Guide to Ecological Modelling: Using R as a Simulation Platform*. Springer; 2009. 372p. doi: 10.1007/978-1-4020-8624-3

50. Stubben C, Milligan B. Estimating and analyzing demographic models using the popbio package in R. *Journal of Statistical Software* 2007; 22(11): 1–23. doi: 10.18637/jss.v022.i11
51. Soetaert K, Petzoldt T, Setzer RW. Solving differential equations in R: Package deSolve. *Journal of Statistical Software* 2010; 33(9): 1–25. doi: 10.18637/jss.v033.i09
52. ggplot2: Create elegant data visualisations using the grammar of graphics. Available online: <https://ggplot2.tidyverse.org/reference/ggplot2-package.html> (accessed on 9 November 2023).
53. Murrell P. Recent changes in grid graphics. *R News* 2005; 5(1): 12–20.
54. Sievert C. *Interactive Web-Based Data Visualization with R, Plotly, and Shiny*, 1st ed. CRC Press; 2020. doi: 10.1201/9780429447273
55. DeLong JP. The body-size dependence of mutual interference. *Biology Letter* 2014; 10(6). doi: 10.1098/rsbl.2014.0261
56. Murdoch WW, Sih A. Age-dependent interference in a predatory insect. *Journal of Animal Ecology* 1978; 47(2): 581–592. doi: 10.2307/3802
57. Fox LR, Murdoch WW. Effects of feeding history on short-term and long-term functional responses in *Notonecta hoffmanni*. *Journal of Animal Ecology* 1978; 47(3): 945–959. doi: 10.2307/3680
58. Sih A. Stability, prey density and age/dependent interference in an aquatic insect predator, *Notonecta hoffmanni*. *Journal of Animal Ecology* 1981; 50(2): 625–636. doi: 10.2307/4079
59. Fernando MHJP, Hassell MP. Predator-prey responses in an acarine system. *Population Ecology* 1980; 22(2): 301–322. doi: 10.1007/BF02530853
60. Pajunen VI. The effect of age-dependent interference on larval development in *Callicorixa producta* (Reut.) (Hemiptera, Corixidae). *Annales Zoologici Fennici* 1982; 19(3): 221–224.
61. Abrahams MV, Mangel M, Hedges K. Predator-prey interactions and changing environments: Who benefits? *Philosophical Transactions of the Royal Society B: Biological Sciences* 2007; 362(1487): 2095–2104. doi: 10.1098/rstb.2007.2102
62. Bertossa RC. Morphology and behaviour: Functional links in development and evolution. *Philosophical Transactions of the Royal Society Lond B: Biological Sciences* 2011; 366(1574): 2056–2568. doi: 10.1098/rstb.2011.0035
63. Schmitz O. Predator and prey functional traits: Understanding the adaptive machinery driving predator–prey interactions. *F1000 Research* 2017; 6: 1767. doi: 10.12688/f1000research.11813.1