

Prey preference and mutual interference may alter prey–predator dynamics: inference using an ecological model

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SUMMARY

The regulation of pests and vectors using their predators promotes conservation and sustenance of environmental quality. In such prey–predator interactions, local extinction of the prey population is observed, while predators may exhibit mutual interference and prey preference. A mathematical equation, considering a 2-prey and 1-predator system, was used to evaluate and justify this proposition, assuming logistic growth for the prey and a functional response of the predator. Empirical evidence from two distinct prey–predator systems was also considered: (i) a snail and limpet as prey and the malacophagous leech *Glossiphonia weberi* as predator, and (ii) vector mosquito larvae and chironomid midge larvae as prey against the predatory larvae of the mosquito *Lutzia fuscana*. The results highlight prey population decrease at varying time points depending on species composition and the prey preference. The growth of the preferred prey declined earlier, signifying the effect of apparent competition facilitating the alternative prey, followed by a decrease in the predator population. Instances with both mutual interference and prey preference produced a greater decline in the prey population than the instance where only mutual interference acted on the system. As an extension, it may be inferred that target prey regulation in biological control will be influenced by the predators' preference and mutual interference.

Key words: prey–predator interactions, *Physella acuta*, *Anopheles stephensi*, *Culex quinquefasciatus*, *Lutzia fuscana*, mutual interference, apparent competition, prey preference

1. Introduction

Prey–predator population dynamics has been a key subject in ecology, with

diverse consequences obtained with different combinations of species (Taylor, 1990; Holt, 1984; Cuddington and Yodzis, 2002). Additionally, biotic parameters such as intrinsic growth rate, carrying capacity and initial species density (Tanner, 1975; Holt, 1984) equally affect the prey–predator system in reaching an equilibrium or a limit cycle (Case, 2000), and sometimes also the system faces extinction given certain initial conditions (Chakraborty et al., 2024). In prey–predator dynamics, multiple factors can be incorporated into the system and explored through mathematical equations. A predator with a higher attack rate may induce faster prey decline in a prey–predator system (Holt, 1977, 1984). However, the presence of prey refuges may help the prey population to survive longer (Sarwardi et al., 2012, 2013), and if the predator population exhibits mutual interference, the survival of the prey population is favoured (Chakraborty et al., 2024). Extending these ideas, an exploration of prey–predator interactions was made, using two prey and one predator, with mutual interference as a key component. A type II functional response of the predator was considered, along with a preference for one prey over the alternative prey. As a foundation, the study assumes that the prey preference reduces the population of the preferred prey relative to the other, creating a situation similar to apparent competition (Holt, 1977; Holt and Bonsall, 2017).

The use of predators in the biological control of mosquitoes (Lord, 2007; Saha et al., 2012; Benelli et al., 2016) and invasive snails (Berg, 1973; Madsen, 1990; Sulieman et al., 2015; Guo et al., 2017; Paul et al., 2021; Saglam et al., 2023) has attracted the attention of scientists in recent years, as it can achieve the required result without affecting the natural habitat, unlike the use of hazardous chemicals and other pesticides. This study takes the snails *Ferrissia baconi* (Bourguignat, 1854) (Mollusc: Planorbidae) and *Physella (Physa) acuta* (Draparnaud, 1805) (Mollusc: Pulmonata) as prey, together with *Glossiphonia weberi* (Blanchard, 1897) (Hirudinea: Glossiphoniidae) as predator, in the first combination. Four other combinations consisted of *Culex quinquefasciatus* (Say, 1823) (Diptera: Culicidae), *Anopheles stephensi* (Liston, 1901) (Diptera: Culicidae) and chironomid larvae as prey against the predator *Lutzia fuscana* (Wiedemann,

1820) (Diptera: Culicidae). Leeches are adapted to swallow live prey species whole, as demonstrated by the dumping of limpet shells in containers after being preyed on by *G. weberi* (Aditya and Raut, 2004). *G. weberi* attaches itself to the shell of *P. acuta* and positions the anterior sucker through the prey's aperture (Aditya and Raut, 2005). Using its mandible, *L. fuscana* consumes the whole larvae, except for the siphon in the case of *A. stephensi* and chironomid larvae (Pramanik and Aditya, 2009).

This article describes the results obtained for a two-prey and one-predator system in the presence of mutual interference and prey preference, even after indirect promotion of the prey's population growth, determining whether the predator species can bring down the prey population sufficiently to be proposed as a potent biological control agent. A range of data was generated to highlight the prey preferences of the predators, and further assessment was made using the mutual interference of the predators as a factor, defining the growth of the prey and predators. Considering biological control as a key issue in the regulation of target pests and vectors, the present analysis will provide insights on the mutual interference and prey preferences as factors governing the dynamics of local growth of prey and predators. Mosquitoes (Diptera: Culicidae) transmit malaria, dengue, Japanese encephalitis, yellow fever, Bancroftian filariasis, Eastern Equine encephalitis, and West Nile viruses (El-Setouhy and Ramzy, 2003; Mittal, 2003; Sudeep et al., 2015; Lockaby et al., 2016; Tyagi, 2018; Shocket et al., 2020), whereas the snail *P. acuta* (Mollusc: Pulmonata) acts as a potent intermediate host for several food-borne trematode diseases such as echinostomiasis and fascioliasis, caused by *Posthodiplostomum* sp., *Echinostoma* spp., and *Trichobilharzia physellae* (Bispo et al., 2025), *Angiostrongylus cantonensis* (Kim et al., 2014; Yun-hai and Yi, 2022) and *Fasciola* spp. (Qureshi et al., 2015). *F. baconi* and *F. tenuis* (Mollusc: Planorbidae) are potent intermediate hosts for *Schistosoma haematobium*, causing schistosomiasis (Aditya and Raut, 2004; Mukhopadhyay et al., 2017). Reports state that about one million people die annually due to mosquito-borne diseases (World Health Organization 2012). Around 200 million individuals

worldwide are affected annually by schistosomiasis, with almost 85% of cases occurring in Africa, while India remains non-endemic to the disease (Kali, 2015). Around 40 million people annually worldwide are affected by food-borne trematode infections (World Health Organization 2018), prevalent in East and Southeast Asia and in Central and South America (Ghatani et al., 2018). While several empirical studies on mosquito biocontrol are available, there has been little work on assessing the efficacy of mosquito predators using mathematical models. The present study will reveal information on mutual interference and apparent competition that may help understand the key issues of two-prey and one-predator interaction dynamics.

2. Materials and methods

Collection of study materials

P. acuta snails collected in the field were reared in the laboratory in glass aquaria (18 x 18 x 18 cm³) filled with water stored for at least 4 days, at a density of 6 individuals per litre, with mashed lettuce leaves as food, *ad libitum*. Continuous monitoring of the aquaria enabled the collection of 0-day-old egg capsules, from which the newly hatched snails were further reared (for a time of around 2–3 weeks) to a size of 2 mm prior to their use in the experiment, as described in previous studies (Nandy et al., 2024; Mandal et al., 2024). The malacophagous leech *G. weberi* and the limpet *F. baconi* were obtained from various wetlands (Aditya and Raut, 2004), mostly with *Vallisneria* sp. as a macrophyte, and segregated and used for the experiment. In the laboratory, *G. weberi* was maintained in glass aquaria containing a few leaves of *Vallisneria* sp. as a refuge and a few individuals of *F. baconi* and *P. acuta* as food. In a separate glass aquarium, the limpets were maintained with *Vallisneria* sp. as a refuge for food and shelter. Constant monitoring of the organisms in the laboratory was continued during the acclimatization period of 10 days.

Mosquito larvae (both instars III and IV) were obtained from a laboratory culture (~30 generations) of *A. stephensi* and *C. quinquefasciatus* (DattaMudi et

al., 2023), while chironomid larvae were collected from rice fields (near the suburban areas of Kolkata, India) and brought to the laboratory for segregation and rearing. The field-collected *L. fuscana* were segregated in the laboratory for the selection of instar IV larvae for the purpose of the experiment. The larvae of *L. fuscana* are predatory in nature and consume the larvae of other mosquitoes and chironomid midges (Jin et al., 2006; Pramanik and Aditya, 2009; Pramanik et al., 2016). A survey of larval habitats such as sewage drains, earthen pots and rice fields was carried out for the collection of *L. fuscana* larvae in adequate numbers. In the laboratory, the larvae were segregated based on their length into two size groups: instar III larvae (smaller) and instar IV larvae (larger). Since it was not possible to confirm the instar stages of all larvae, the size of the larvae was used as a surrogate of the instar stage. The larvae in the laboratory were continually monitored, with the water changed every 24 hours.

Laboratory experiments

Experimental observations on predation:

(i) In the predation experiments with gastropods and the malacophagous leech, equal numbers of *P. acuta* and *F. baconi*, amounting to a total of 20, were offered to two *G. weberi* (7–8 mm in length in rest condition). A plastic container with 500 ml capacity was filled with aged tap water, and the prey and the predator were placed in the container, forming the treatment arena. Observations at the end of 48 hours were taken with reference to the number of prey consumed by *G. weberi*. Following counting of the prey killed, the requisite numbers of prey were replaced to restore the total count to 20 with equal numbers of *P. acuta* and *F. baconi*. Unconsumed prey were not used in the successive replicates. Further observations were made on the prey consumed by *G. weberi* after 48 hours. A total of 24 observations were made (8 replicates with 3 consecutive observations for each) for the prey consumed by the leech, and the data was subjected to prey preference analysis. In all instances, the predator and prey individuals were used only once in the experiment (supplementary file ‘snail’).

(ii) The experiments with dipteran larvae were carried out using the same ratio of the prey larvae as above, but with greater numbers, namely 50 each of the mosquito and chironomid larvae, amounting to 100 prey larvae for consumption by 10 instar IV predatory larvae of *L. fuscana*. The consumption of the prey by the predators was observed for a 24-hour period and recorded. For both the small and large prey larvae, instar IV larvae of *L. fuscana* were used. Separate experiments were carried out using small- and large-sized larvae of *Anopheles* and *Culex* mosquitoes and chironomid larvae. The small *Culex* larvae (4.09 ± 0.052 mm) and *Anopheles* larvae (3.50 ± 0.02 mm) were considered as instar III, and the large *Culex* larvae (5.87 ± 0.09 mm) and *Anopheles* larvae (5.34 ± 0.09 mm) were considered as instar IV, whereas *L. fuscana* of length 8.32 ± 0.2 mm were considered to be instar IV, and the chironomid larvae (4.2 ± 0.21 mm) were also considered as instar IV (Pramanik et al., 2016, 2017; Dutta Mudi et al., 2024). A total of 12 observations were made (4 replicates with 3 consecutive observations for each) for the prey consumed by *L. fuscana*, and the data was subjected to prey preference analysis (supplementary file ‘mosquito’). In all instances, the unconsumed prey were not used in the successive replicates. The prey and predator larvae were used only once in the experiment.

3. Analysis

The data on prey consumption by the predators were used as input to derive the prey preference values (Murdoch, 1969; Manly et al., 1972; Chesson, 1978) using the formula: $(\partial) = \frac{P_1/P_2}{R_1/R_2}$, where R_1 and R_2 represent the prey abundance in the environment, while P_1 and P_2 represent the prey abundance in the predator's diet. A two-tailed paired t-test (with $P = 0.05$) was used to justify the significance of the prey preference values and the lower and upper confidence interval. The effect size was estimated through derivation of Cohen's d and applying the formula: Effect size = $d/\sqrt{(d^2 + 4)}$, where $d = |m_1 - m_2|/\sqrt{s_{pooled}}$, where m_1 and m_2

are the mean values of the prey preference (Manly's alpha) and S_{pooled} is the pooled standard deviation of prey preference 1 and prey preference 2. The upper confidence limit and the lower confidence limit for the obtained preference value were calculated (at CI 95%), and the results are presented for the predators *L. fuscana* and *G. weberi* against the prey combinations (Zar 1999). The data presented in graphical form were created using RStudio Team (2020) (RStudio: Integrated Development for R. RStudio, PBC, Boston, MA, URL <http://www.rstudio.com>) and the plotly package (v4.9.3; Sievert 2020) respectively, and all other figures were created using MS Excel. The parameters taken for the model were used in the RStudio for deSolve package (Soetart et al. 2010) to solve the ordinary differential equation proposed.

The model

This article takes into account the prey–predator dynamics with mutual interference and prey preference, calculated with the equation (Elliott 2003): $\frac{N_a}{PN} = QP^{-m}$, where m is the mutual interference constant, N_a denotes the mean number of prey consumed, P is the number of predators, N is the prey density, and Q represents the value of $\frac{N_a}{PN}$ when $P = 1$; the other equation for prey preference (Murdoch, 1969; Manly et al., 1972; Chesson, 1978) gives the prey preference coefficient for prey type 1 (∂) = $\frac{P_1/P_2}{R_1/R_2}$, where, P_1 and P_2 are the prey abundance in the predator's diet, and R_1 and R_2 are the prey abundance in environment. When the prey preference coefficient for prey type 1 (∂) is greater than 1, it indicates the predator's choice of prey type 1, and when ∂ is less than 1, the predator prefers prey type 2 over type 1.

The 2-prey and 1-predator system incorporating mutual interference and prey preference is constructed as per the established equations (Post et al., 2000; Antwi-Fordjour et al., 2020; Chakraborty et al., 2024):

$$\frac{dx_1}{dt} = r_1 x_1 \left(1 - \frac{x_1}{k_1}\right) - \frac{\alpha_1 x_1 x_3^{-m_1}}{1 + \alpha_1 h_1 x_1} \partial_1$$

$$\begin{aligned}\frac{dx_2}{dt} &= r_2 x_2 \left(1 - \frac{x_2}{k_2}\right) - \frac{\alpha_2 x_2 x_3^{-m_2}}{1 + \alpha_2 h_2 x_2} \partial_2 \\ \frac{dx_3}{dt} &= -\gamma x_3 + \frac{c_1 \alpha_1 x_1 x_3^{-m_1}}{1 + \alpha_1 h_1 x_1} \partial_1 + \frac{c_2 \alpha_2 x_2 x_3^{-m_2}}{1 + \alpha_2 h_2 x_2} \partial_2\end{aligned}\quad (1)$$

with initial conditions $x_1(0) = x_1^0 > 0, x_2(0) = x_2^0 > 0, x_3(0) = x_3^0 > 0$ (Sarwardi et al., 2012, 2013) where x_1 and x_2 refer to the population size of the prey species 1 and 2 respectively, x_3 is the population size of the predator species, at any time t , r_1 and r_2 are the intrinsic growth rates of prey 1 and 2 respectively, k_1 and k_2 are the carrying capacities of prey 1 and 2 respectively, $1/\alpha_1 h_1$ and $1/\alpha_2 h_2$ denote the half saturation constants (Mulder and Hendriks, 2014) of the predator for prey 1 and 2 respectively, α_1 and α_2 are search rates of the predator for prey 1 and 2 respectively, h_1 and h_2 denote the handling time of the predator for prey 1 and 2 respectively, γ refers to the death rate of predator, c_1 and c_2 signify the conversion coefficient of functional response of the predator for prey 1 and 2 respectively, m_1 and m_2 signify the mutual interference of the predator for prey 1 and 2 respectively, $0 < m_1, m_2 \leq 1$, and ∂_1 and ∂_2 are the prey preferences of the predator for prey 1 and 2 respectively.

Equation (1) has been non-dimensionalized, considering:

$$\begin{aligned}x_1 &= kx, x_2 = \frac{k_1 r_1 y}{r_2}, x_3 = \frac{c_1 z}{r_1}, \tau = rt \\ \frac{dx}{d\tau} &= x(1 - x) - \frac{\alpha_1 x z^{-m_1}}{A_1 + x} \\ \frac{dy}{d\tau} &= by(1 - y) - \frac{\alpha_2 y z^{-m_2}}{A_2 + x} \\ \frac{dz}{d\tau} &= \frac{\alpha_1 x z^{-m_1}}{A_1 + x} + \frac{\phi y z^{-m_2}}{A_2 + y} - \varepsilon z\end{aligned}\quad (2)$$

where $\alpha_1 = \frac{\partial_1 h_1 r_1^{-m_1}}{c_1^{-m_1}}$, $\alpha_2 = \frac{\partial_2 h_2 r_1^{-m_1}}{c_1^{-m_1}}$, $A_1 = \frac{1}{\alpha_1 h_1 k_1}$, $A_2 = \frac{1}{\alpha_2 h_2 k_2}$, $r_1 = \frac{b}{r_2}$, $\phi = \frac{\alpha_2 c_2}{c_1}$, $\varepsilon = \frac{\gamma}{r_1}$

The Jacobian matrix for equation (2) is

$$J = \begin{bmatrix} 1 - 2x - \frac{\alpha_1 z^{-m_1}}{(A_1+x)^2} & 0 & \frac{xm_1\alpha_1 z^{-m_1-1}}{A_1+x} \\ 0 & b - 2by - \frac{\alpha_2 z^{-m_2}}{(A_2+y)^2} & \frac{ym_2\alpha_2 z^{-m_2-1}}{A_1+x} \\ \frac{\alpha_1 z^{-m_1}}{(A_1+x)^2} & \frac{\phi z^{-m_2}}{(A_2+y)^2} & -\frac{xm_1\alpha_1 z^{-m_1-1}}{A_1+x} - \frac{ym_2\alpha_2 z^{-m_2-1}}{A_1+x} - \varepsilon \end{bmatrix}$$

4. Model prediction and empirical patterns

In accordance with the proposition of the model, the predictions are: (i) local extinction of both prey despite the prey preference and mutual interference among the predators; (ii) a possible faster decline in the preferred prey may be anticipated under the concomitant interactions of preference and mutual interference. As a consequence, the use of the selected predators for the biological control of the target prey (preferred prey) may be possible though the comorbidity of the cooccurring prey; (iii) a faster decline of the preferred prey will indicate that the predators are consuming the target prey in the presence of the alternative prey, which is one of the desired requirements for the selection of a biological control agent (Berg, 1973; Benelli et al., 2016). In the present context, the predators are promoted for biological regulation of snails (for the leech *G. weberi*; Aditya and Raut, 2004, 2005) and mosquitoes (for *L. fuscana*; Pramanik and Aditya 2009) respectively. However, the predators are generalist and consume a wide range of prey (Aditya and Raut, 2004, 2005; Paul et al., 2021, 2022; Datta Mudi et al., 2025), which may reduce the predatory ability; (iv) in this study, in the theoretical model and the empirical observations, the prey preference and the mutual interference were addressed with a view to promoting the use of the predators as biological control agents.

The data obtained from the empirical studies, particularly those related to the prey preference and mutual interference, were used in the theoretical models. Subsequently, the model was evaluated in concurrence with the data obtained on the prey preference and mutual interference. As indicated in the formula used to determine the prey preference (Chesson, 1978) and the mutual interference

(Elliot, 2003), figures for prey consumption by the predators were used as input data. The mathematical model was derived from the original description of Antwi-Fordjour et al. (2020).

5. Results and discussion

Theoretical framework

Existence and positive invariance:

For $t > 0$, letting $X = (x, y, z)^T$, $F: \mathbb{R}^3 \rightarrow \mathbb{R}^3$, $F = (F_1, F_2, F_3)^T$, system 1 can be rewritten as $\frac{dx}{dt} = F(x)$. Here, $F_i \in C^\infty(\mathbb{R})$, for $i = 1, 2, 3$, where, $F_1 = x(1 - x) - \frac{\alpha_1 x z^{-m_1}}{A_1 + x}$, $F_2 = by(1 - y) - \frac{\alpha_2 y z^{-m_2}}{A_2 + x}$ and $F_3 = \frac{\alpha_1 x z^{-m_1}}{A_1 + x} + \frac{\phi y z^{-m_2}}{A_2 + y} - \epsilon z$. The vector function F is a smooth function of the variables (x, y, z) in the positive octant, $\Omega = \{(x, y, z); x > 0, y > 0, z > 0\}$; local existence and uniqueness for the solution for system 1 are confirmed.

Boundedness:

From the first equation of system 2, the following inequality can be deduced

$$\begin{aligned} \frac{dx}{d\tau} &\leq x(1 - x), \limsup_{\tau \rightarrow +\infty} x(\tau) \leq 1, \\ \frac{dy}{d\tau} &\leq by(1 - y), \limsup_{\tau \rightarrow +\infty} y(\tau) \leq 1 \end{aligned}$$

The predator populations depend on the prey population for their existence, hence, only the prey are considered for boundedness analysis.

Equilibria and their feasibility:

The equilibria for system 2 are

- At the origin, $E_0 = (0, 0, 0)$
- At four boundary points, $E_1 = (1, 0, 0)$, $E_2 = (x_2, y_2, 0)$, $E_3 = (x_3, 0, z_3)$ and $E_4 = (0, y_4, z_4)$
- At the interior equilibrium, $E^* = (x^*, y^*, z^*)$

On analyzing $E_0 = (0,0,0)$, the eigenvalues are, $1, b, -\varepsilon$, making the system unstable at the origin, but it is feasible. For $E_1 = (1,0,0)$, the eigenvalues are $-2, b, -\varepsilon$, making the system unstable. For $E_2 = (x_2, y_2, 0)$, the solution becomes, $x_2 = 1$ or 0 , and $y_2 = 1$ or 0 . The eigenvalues are $(1 - 2x_2, b - 2by_2, -\varepsilon)$, making the E_2 equilibrium stable only when $x_2 > \frac{1}{2}$ and $y_2 > \frac{1}{2}$. For $E_3 = (x_3, 0, z_3)$, the solution becomes, $x_3 = \frac{1 \pm \sqrt{1-4\varepsilon z}}{2}$, where, and $z_3 = \left\{ \frac{\varepsilon(A_1+x)}{x\alpha_1} \right\}^{-\frac{1}{1+m_1}}$. The eigenvalues are $(1 - 2x_3 - \frac{x_3\alpha_1 z_3^{-m_1}}{(A_1+x_3)^2}, -\frac{\alpha_2 z_3^{-m_2}}{A_2^2}, -\varepsilon - \frac{m_1 x_3 \alpha_1 z_3^{-m_1-1}}{A_1+x_3})$, making the E_3 equilibrium stable only when $1 < 2x_3 + \frac{x_3\alpha_1 z_3^{-m_1}}{(A_1+x_3)^2}$. For $E_4 = (0, y_4, z_4)$, the solution becomes, $y_4 = \frac{b\phi \pm \sqrt{(b\phi)^2 + 4b\phi\varepsilon z}}{2b\phi}$ and $z_4 = \left\{ \frac{\varepsilon(A_2+y)}{y\phi} \right\}^{-\frac{1}{1+m_2}}$. The eigenvalues are $(-\frac{\alpha_1 z_4^{-m_1}}{A_1^2}, 1 - 2by_3 - \frac{\alpha_2 z_4^{-m_2}}{(A_2+y_3)^2}, -\varepsilon - \frac{m_2 y_4 \phi z_4^{-m_2-1}}{A_2+y_4})$, making the E_4 equilibrium stable only when $1 < 2by_3 + \frac{\alpha_2 z_4^{-m_2}}{(A_2+y_3)^2}$. For $E^* = (x^*, y^*, z^*)$, the solution becomes $x^* = \frac{(1-A_1) \pm \sqrt{(A_1-1)^2 - 4(\alpha_1 z^{*-m_1} - A_1)}}{2}$ and $y^* = \frac{b(1-A_2) \pm \sqrt{b^2(A_2-1)^2 - 4b(\alpha_2 z^{*-m_2} - bA_2)}}{2b}$, and $z^* = \frac{x^*(1-x^*) + \beta by^*(1-y^*)}{\varepsilon}$, where $\beta = \frac{c_2}{c_1}$ and $\beta\alpha_2 = \phi$. The interior equilibrium is stable under the conditions, $1 < 2x^* + \frac{\alpha_1 z^{*-m_1}}{(A_1+x^*)^2}$ and $1 < 2by^* + \frac{\alpha_2 z^{*-m_2}}{(A_2+y^*)^2}$.

6. Empirical analysis

Figure 1a shows the range of prey preference of *G. weberi* predating on *F. baconi* and *P. acuta*, whereas Figure 1b shows the amount of prey consumed by the predator. Figures 2 and 3 show the range of prey consumed by *L. fuscana* over the combination of the *C. quinquefasciatus* and chironomid larvae (small and large) and *A. stephensi* and chironomid larvae (small and large), and the prey preference of *L. fuscana* for the same combination of prey and predator, respectively. For *G. weberi* predating on *F. baconi* and *P. acuta*, the predator consumed on average 1.33 ± 0.25 SE (range 0–3) *F. baconi* and 6.29 ± 0.14 SE (range 5–8) *P. acuta*, when 10 individuals of each species were provided. For *L. fuscana* predating on *C. quinquefasciatus* and chironomid larvae (small),

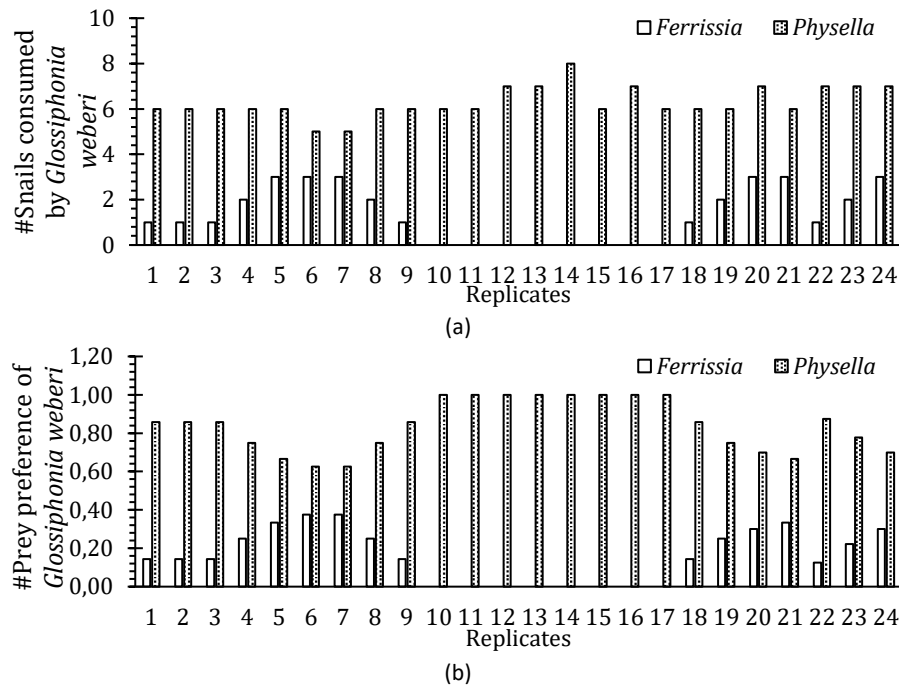


Figure 1: The prey consumed (a) and prey preference (b) of the malacophagous leech *G. weberi* for the two gastropods *F. baconii* and *P. acuta* in 24 replicates. Data represent the observations for a period of 24 hours with 2 predators and an equal number of the two prey in the treatment arena. Unconsumed prey were not used in future replicates, and in each replicate different prey and predator individuals were used. The prey preference was calculated based on Manly's alpha

the predator consumed on average 13.67 ± 0.37 SE (range 12–16) *C. quinquefasciatus* and 25.25 ± 0.25 SE (range 24–27) chironomid larvae, when 50 individuals of each species were provided. For *L. fuscana* predating on *C. quinquefasciatus* and chironomid larvae (large), the predator consumed on average 8.42 ± 0.42 SE (range 7–12) *C. quinquefasciatus* and 17.17 ± 0.65 SE (range 15–22) chironomid larvae, when 50 individuals of each species were provided. For *L. fuscana* predating on *A. stephensi* and chironomid larvae (small), the predator consumed on average 16.67 ± 0.45 SE *A. stephensi* (minimum 14, maximum 19) and 27.33 ± 0.43 SE chironomid larvae (minimum 25, maximum 30), when 50 individuals of each species were provided. For *L. fuscana* predating on *A. stephensi* and chironomid larvae (large), the predator consumed on average

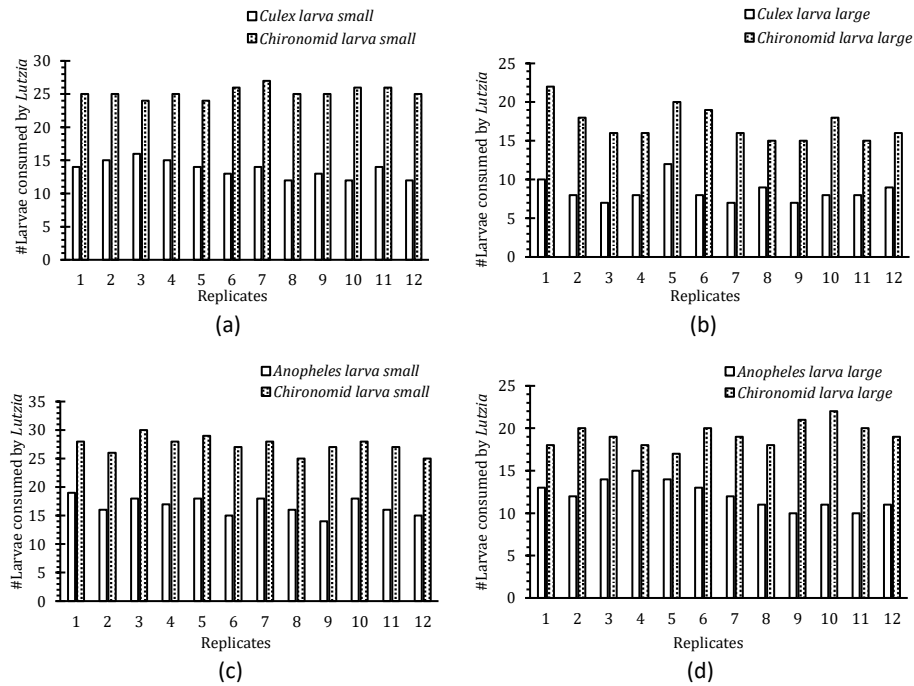


Figure 2: The prey consumption of *L. fuscana* over *C. quinquefasciatus* and chironomid larvae small (a) and large (b), and for a second combination of *A. stephensi* and chironomid larvae small (c) and large (d). Data represent the observations for a period of 24 hours with 2 predators and an equal number of the two prey in the treatment arena. Unconsumed prey were not used in future replicates; prey and predator individuals were used only once in the experiment

12.16±0.47 SE (range 10–15) *A. stephensi* and 19.25±0.41 SE (range 17–22) chironomid larvae, when 50 individuals of each species were provided. The growth of *G. weberi*, *F. baconi* and *P. acuta* and their growth patterns following Equation (1) are presented in Figure 4a and b, respectively. Figure 5a and c show the growth of *L. fuscana*, *C. quinquefasciatus* and chironomid larvae, and Figure 5b and d show their respective growth patterns in the same prey–predator combination (small and large larvae, respectively). Figure 6a and c show the growth of *L. fuscana*, *A. stephensi* and chironomid larvae, with their growth patterns shown in Figure 6b and d (small and large larvae, respectively). For all of the growth curves, the preferred prey declined earlier. In both instances for the mosquito larvae as prey, the large larvae showed more susceptibility to predation,

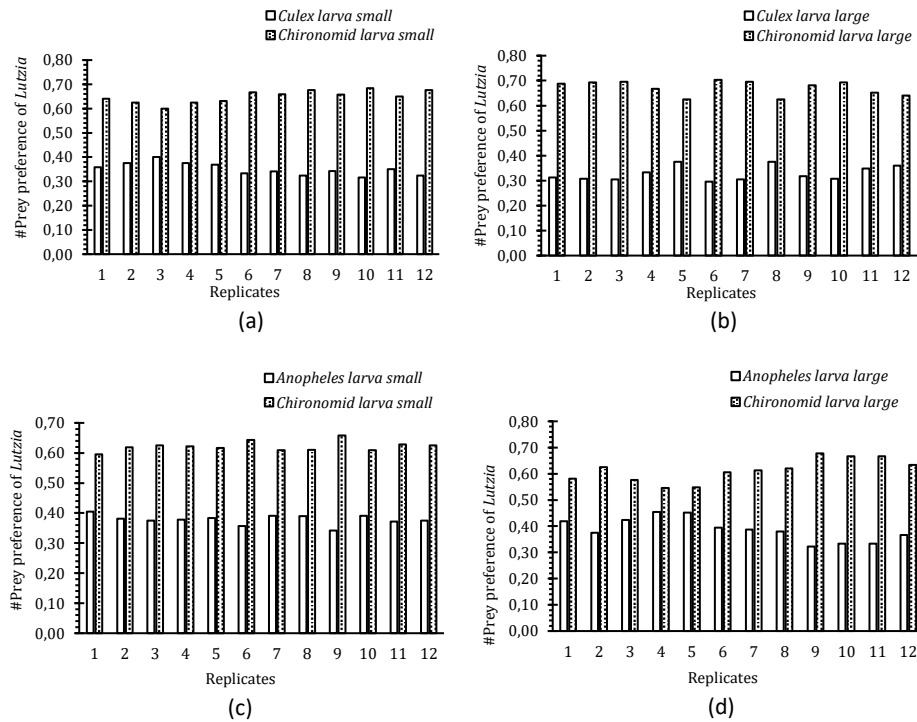


Figure 3: The prey preference of *L. fuscana* over *C. quinquefasciatus* and chironomid larvae small (a) and large (b) and for a second combination of *A. stephensi* and chironomid larvae small (c) and large (d). Data represent the observations for a period of 24 hours with 2 predators and an equal number of the two prey in the treatment arena. Unconsumed prey were not used in future replicates, and in each replicate different prey and predator individuals were used. The prey preference was calculated based on Manly's alpha

with an increase in magnitude of preference for the same species, which brought the population down to zero in a shorter time than in the case of small larvae (Figures 5a and c and Figures 6a and c).

For every combination, the prey preference remained significant (Table 1), substantiating the claim that a differential level of vulnerability to the predator is observed for the prey pairs. This also affected the population growth of the mosquitoes taken as prey in four combinations of small and large *C. quinquefasciatus*, *A. stephensi* and chironomid larvae (Table 2). As shown in Figure 7, a significant difference in prey and predator growth was observed with

Table 1: The significant difference (d) in prey preference by the predators (*L. fuscana* for *C. quinquefasciatus*, Chironomid larvae and *A. stephensi*, and *G. weberi* for *F. baconi* and *P. acuta*), when offered two prey in equal numbers. All *p* values are significant (<0.01). The confidence interval around the value and the two tailed t-values are shown with the respective df values. The effect size, calculated based on Cohen's d, are also shown against each prey pair

Predator-prey pair	d (mean± SE)	Confidence interval	t-score	Effect size	Cohen's d
<i>C. quinquefasciatus</i> larvae, small	0.3507±0.0073	UCL-0.3668, LCL-0.3346	$t_{(2),24}=31.3682$	0.987	12.3036
Chironomid larvae, small	0.3285±0.0083	UCL-0.6654, LCL-0.6332			
<i>C. quinquefasciatus</i> larvae, large	0.6715±0.0083	UCL-0.3468, LCL-0.3102	$t_{(2),23}=30.3244$	0.9867	12.15
Chironomid larvae, large	0.6715±0.0273	UCL-0.6898, LCL-0.6532			
<i>A. stephensi</i> larvae, small	0.3729±0.0048	UCL-0.3888, LCL-0.3677	$t_{(2),22}=31.815$	0.9908	14.6214
Chironomid larvae, small	0.6217±0.0048	UCL-0.6323, LCL-0.6111			
<i>A. stephensi</i> larvae, large	0.3868±0.0128	UCL-0.415, LCL-0.3585	$t_{(2),22}=12.4783$	0.9308	5.0942
Chironomid larvae, large	0.6132±0.0128	UCL-0.6415, LCL-0.5850			
<i>F. baconi</i>	0.1595±0.0278	UCL-0.2171, LCL-0.1019	$t_{(2),47}=17.662$	0.9284	4.9956
<i>P. acuta</i>	0.8405±0.0279	UCL-0.8981, LCL-0.7829			

Table 2: The results of the t-test compared for changes in growth rate for the prey species (small and large) along with the predator, in the presence of prey preference and mutual interference, with the data derived from solving Equation (1). For the predator *L. fuscana*, the comparison is between small and large prey consumption of the mosquito and chironomid larvae. The larval stages showing significant differences have been highlighted in bold

Species	t-value	p-value
<i>Culex quinquefasciatus</i> larvae	$t_{(2),956}=3.096$	0.002
Chironomid larvae	$t_{(2),1007}=2.204$	0.03
<i>Lutzia fuscana</i>	$t_{(2),1110}=0.957$	0.39
<i>Anopheles stephensi</i> larvae	$t_{(2),1301}=1.4204$	0.16
Chironomid larvae	$t_{(2),1129}=3.518$	0.00045
<i>Lutzia fuscana</i>	$t_{(2),1345}=0.617$	0.54

mutual interference and prey preference in this prey-predator interaction. The influence of prey-predator interaction and prey preference has been proved empirically (Elliott 2003; Saha et al. 2007) and theoretically (Chakraborty et al. 2024) for aquatic insect predators and mosquito and chironomid as prey. In the

present context, the result showed that a significant difference is present for the alternative prey's population growth (Table 3).

Table 3: The significant difference in the growth of the species in the presence of both mutual interference and prey preference against the prey–predator dynamics affected only by the mutual interference, with the data derived from solving Equation (1). The species affected significantly are shown in bold

Species	t-score	p-value
<i>Ferrissia baconi</i>	$t_{(2),500} = \mathbf{12.79}$	<0.05
<i>Physella acuta</i>	$t_{(2),500} = 1.3435$	0.18
<i>Glossiphonia weberi</i>	$t_{(2),500} = 0.68045$	0.5
<i>Culex quinquefasciatus</i> small larvae	$t_{(2),500} = \mathbf{4.7261}$	<0.05
Chironomid small larvae	$t_{(2),500} = 2.1252$	0.33
<i>Lutzia fuscana</i>	$t_{(2),500} = 0.0884$	0.93
<i>Culex quinquefasciatus</i> large larvae	$t_{(2),500} = 0.75972$	0.45
Chironomid large larvae	$t_{(2),500} = 1.7014$	0.09
<i>Lutzia fuscana</i>	$t_{(2),500} = 0.044$	0.96
<i>Anopheles stephensi</i> small larvae	$t_{(2),500} = \mathbf{4.8664}$	<0.05
Chironomid small larvae	$t_{(2),500} = \mathbf{2.6543}$	0.008
<i>Lutzia fuscana</i>	$t_{(2),500} = 0.10999$	0.91
<i>Anopheles stephensi</i> large larvae	$t_{(2),500} = \mathbf{4.3397}$	<0.05
Chironomid large larvae	$t_{(2),500} = 1.8587$	0.06
<i>Lutzia fuscana</i>	$t_{(2),500} = 0.12551$	0.9

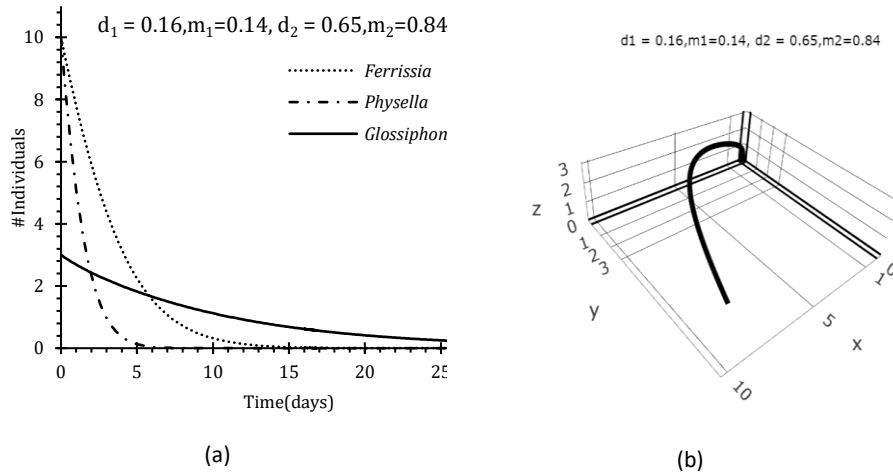


Figure 4: The growth curve (a) and growth pattern (b) of *F. baconi* and *P. acuta* as prey along with the predator species *G. weberi*. The predator shows a preference for *P. acuta*, reducing its population earlier than *F. baconi*

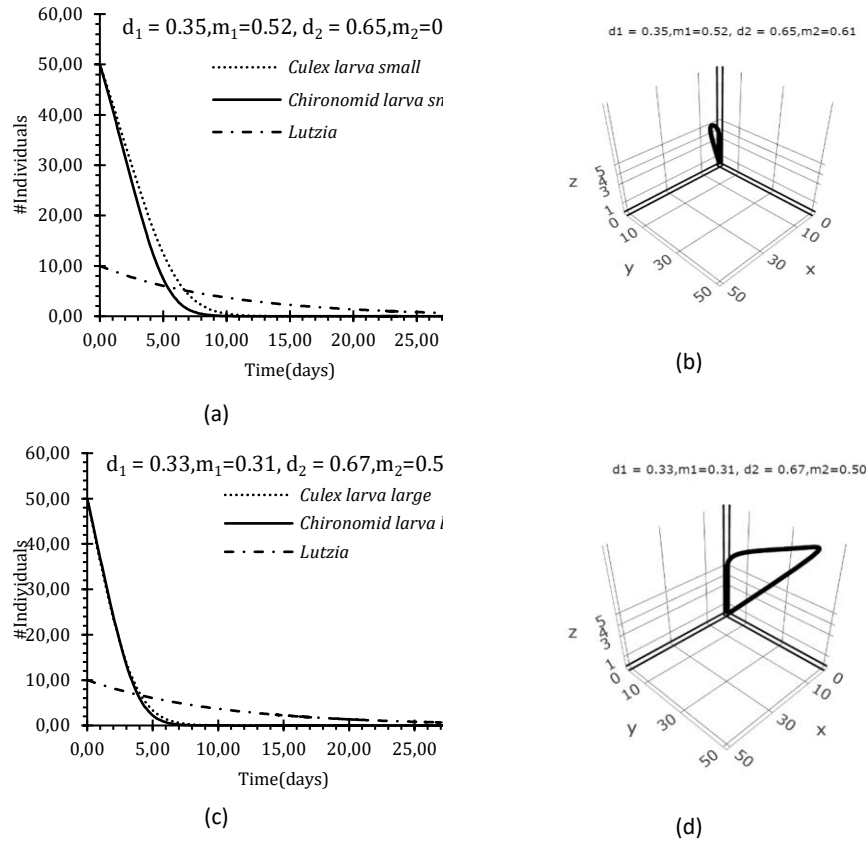


Figure 5: The growth curve (a,c) and growth pattern (b,d) of *C. quinquefasciatus* and chironomid larvae small and large, as prey along with the predator species *L. fuscana*. In this scenario, despite the preferences acting on the system, the mutual interference, being similar, facilitates the growth of the preferred prey. In the presence of both indirect interactions, the prey decline due to prey preference is balanced by the mutual interaction

This implies that the preferred prey requires an extended time period for reaching the growth of the alternative prey in a two-prey and one-predator system. In a biological sense, owing to the predation of the preferred prey at a higher rate, its population growth is smaller than that of the alternative prey. The preferred prey *P. acuta* declined later than the alternative *F. baconi* in the presence of only mutual interference, maybe because their faster locomotion helped them to evade the predators more efficiently. The small larvae of both *C. quinquefasciatus* and *A. stephensi* exhibited a decline earlier than the preferred prey when the system

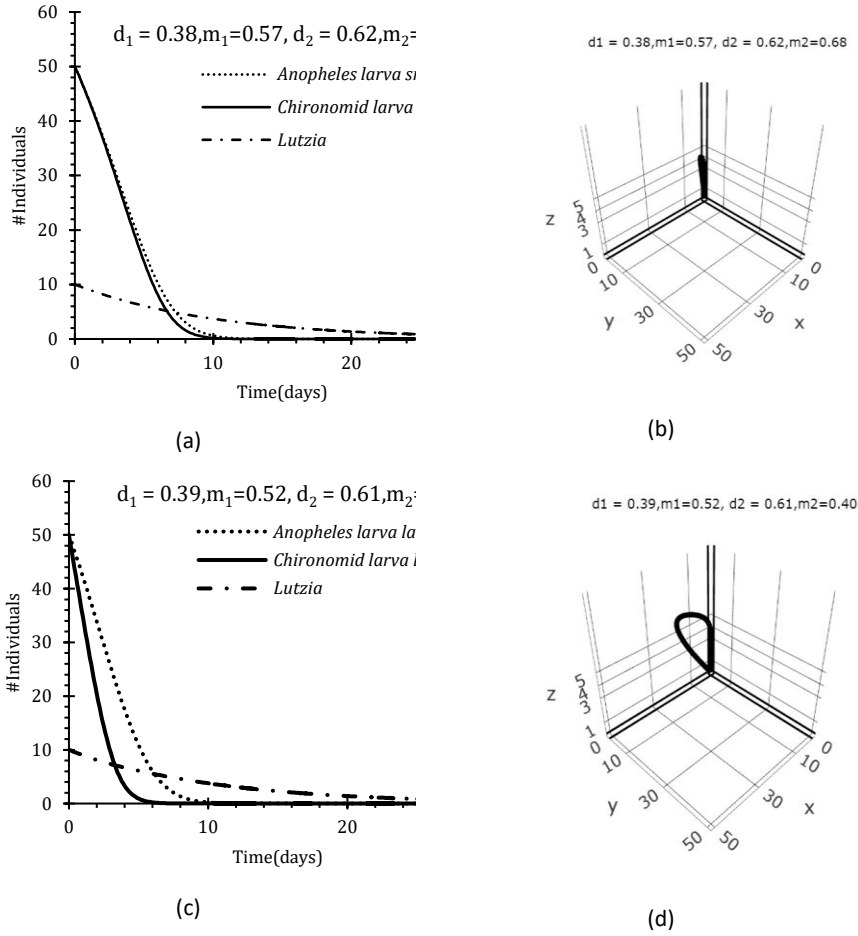


Figure 6: The growth curve (a,c) and growth pattern (b,d) of *A. stephensi* and chironomid small and large larvae as prey along with the predator species *L. fuscana*. In this scenario, the small larvae show a similar time to decline, whereas the large chironomid larvae declined earlier due to the presence of prey preference, assumed to be due to their larger size, which makes them easier to capture

dynamics were not guided by prey preference, implying that their smaller size made them more prone to predation than the larger chironomid larvae, whereas the large larvae of *C. quinquefasciatus* and *A. stephensi* declined in a similar time to chironomid larvae (Figure 7). The values of the parameters used in the validation of the proposed model are noted in Table 4.

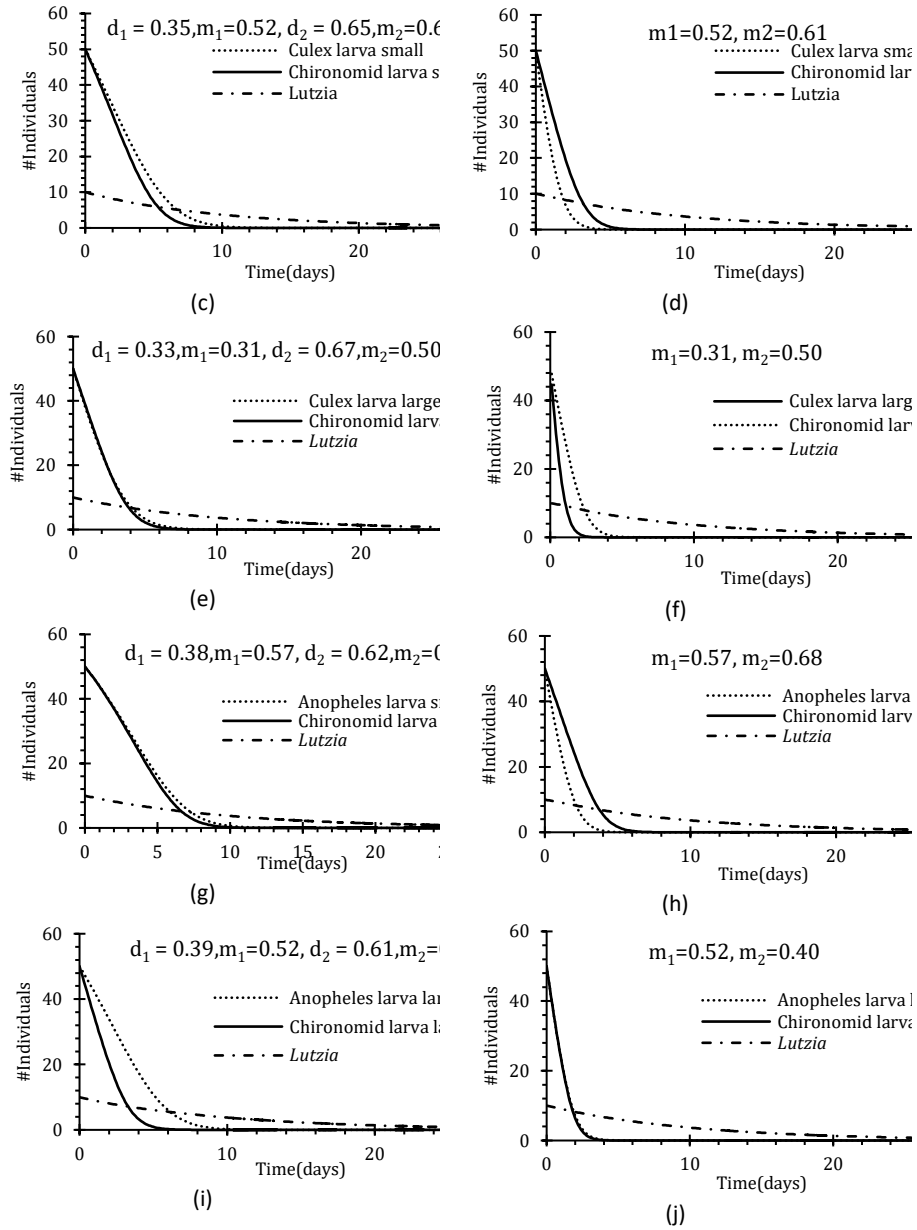


Figure 7: The growth of the prey populations in 5 different combinations, affected by both the indirect interactions, compared with that affected only by intraspecific interference among the predators. The time of decline for the alternative prey population is significantly accelerated in the absence of prey preference

Table 4: The parameters taken for validation of Equation (1). Some parameters were kept unchanged for each combination to nullify their individual effect. The handling time was taken per hour in each day, and all other parameters have universal units. x_1 and x_2 refer to the population size of the prey species 1 and 2 respectively, x_3 is the population size of the predator species, at any time t , r_1 and r_2 are the intrinsic growth rate of prey 1 and 2 respectively, k_1 and k_2 are the carrying capacity of prey 1 and 2 respectively, $1/\alpha_1 h_1$ and $1/\alpha_2 h_2$ denote the half saturation constants (Mulder and Hendriks 2014) of the predator for prey 1 and 2 respectively, α_1 and α_2 are search rates of the predator for prey 1 and 2 respectively, respectively, h_1 and h_2 denote the handling time of the predator for prey 1 and 2 respectively, γ refers to the death rate of the predator, c_1 and c_2 signify the conversion coefficient of functional response of the predator for prey 1 and 2 respectively, m_1 and m_2 signify the mutual interference of predator for prey 1 and 2 respectively, $0 < m_1, m_2 \leq 1$, and ∂_1 and ∂_2 are the prey preferences of the predator for prey 1 and 2 respectively

No.	Combinations						r ₁	r ₂	k ₁	k ₂	
1	<i>F. baconi</i> , <i>P. acuta</i> , <i>G. weberi</i>						0.13	0.15	5000	5000	
2	<i>C. quinquefasciatus</i> , Chironomid small larvae, <i>L. fuscana</i>						0.11	0.11	5000	5000	
3	<i>C. quinquefasciatus</i> , Chironomid large larvae, <i>L. fuscana</i>						0.11	0.11	5000	5000	
4	<i>A. stephensi</i> , Chironomid small larvae, <i>L. fuscana</i>						0.13	0.11	5000	5000	
5	<i>A. stephensi</i> , Chironomid large larvae, <i>L. fuscana</i>						0.13	0.11	5000	5000	
No.	a ₁	h ₁ (h ⁻¹ d ⁻¹)	∂ ₁	m ₁	a ₂	h ₂ (h ⁻¹ d ⁻¹)	∂ ₂	m ₂	γ	c ₁	c ₂
1	3.53	13.25	0.16	0.14	2.26	8.94	0.84	0.71	0.1	0.01	0.01
2	5.23	6.23	0.35	0.52	4.69	10.3	0.65	0.61	0.1	0.01	0.01
3	5.23	6.23	0.33	0.31	4.69	10.3	0.67	0.50	0.1	0.01	0.01
4	5.68	7.21	0.38	0.57	5.12	11.2	0.62	0.68	0.1	0.01	0.01
5	5.68	7.21	0.39	0.52	5.12	11.2	0.61	0.40	0.1	0.01	0.01

Mutual interference seems to play an interesting role in prey–predator dynamics, shaping their growth patterns and local stability in a spatiotemporal scale (Arditi et al., 2004). As a consequence, the prey population and the food web structure is retained with little perturbation. Besides, preference for one prey type, in a multiple prey system, favours an increase in population of the other prey, recognized as a phenomenon of apparent competition. In two-prey apparent competition a steep decline of the preferred prey population is coupled with the increased chance of survival and growth of the alternative prey (Holt, 1977). The mathematical equation proposed (Equation (1)) shows the prey–predator interaction for stability of the system, when one prey is favoured by mutual interference while a certain prey is reduced as an effect of apparent competition.

The predator *L. fuscana* captures the mosquito larvae at the neck, the slender body or the siphon, using its mandible; an attack at the neck or body leads to successful prey capture, but an attack at the siphon is weaker, favouring evasion by the prey. This may be a firm reason for the lower number of successful prey

captures than of chased prey. This may not affect the mutual interference or the prey preference, but the efficacy of the predator is reduced, favouring the prey population. The chironomid larvae are the preferred prey for *L. fuscana* over *C. quinquefasciatus*, due to the absence of the siphon. For the combination including *A. stephensi* and chironomid larvae as prey, where both of them lack a siphon, *L. fuscana* prefers chironomid larvae, maybe due to the evolved evasion techniques of *A. stephensi*. The malacophagous leech prefers *P. acuta* over the limpet, as it can attach itself to the larger shell of *P. acuta* and easily enters the anterior sucker through its aperture, as opposed to attaching itself to the waxy body of *F. baconi*. The time for unsuccessful attempts reduces the predator's efficacy in terms of a decreasing search rate (α) with an increased handling time (h), favouring the prey population. With every successful prey capture, the prey density decreases in the spatiotemporal dynamics, and the predator also approaches satiation, collectively reducing the search rate. It can be said that, besides mutual interference, the functional response alone favours the prey population, leading to the coexistence of prey and predator species.

Mutual interference is interpreted from the predator's perspective, and apparent competition from the prey's perspective. Due to the presence of mutual interference, the decline in the preferred prey population may be delayed (Chakraborty et al., 2024). When mutual interference is coupled with prey preference, the effective decline of the prey population is faster in comparison with situations where prey preference is the sole factor (without any interference). The growth affected by both mutual interference and prey preference was significantly different from the growth affected by only mutual interference (Table 3). Thus, effectively, the preference of a predator appears to be important in determining the fate of the prey, irrespective of the apparent competition. In nature, prey preference is an obvious feature that regulates the relative abundance of different prey, and effectively shapes the food web structure. In empirical studies it was observed that the relative consumption of the predators varied with the two prey, implying some preference (Holt 1977, 1984; Holt and Bonsall 2017). Extrapolating the observations to natural habitats, it will be obvious that

the prey preference of a predator may play a significant role in prey–predator dynamics. This is relevant to proposals for the effective regulation of mosquitoes or disease-transmitting snails in freshwater habitats. Biological control of mosquitoes using predators is often limited with regard to the type of preference exhibited and the habitat similarity. In instances where mosquito larval predators have been proposed, the preference of the predator become a significant contributor to the effective reduction of the mosquito. This applies also to invasive and disease-transmitting snails. Considering *P. acuta* as an invasive species, a preference for the snail over the limpet will enable positive regulation, while the reverse will promote the presence of the invasive snails in freshwater habitats.

7. Conclusion

A successful biological control programme needs to be ecologically feasible and economically viable to sustain the long-term regulation of the target species (Guo and Zhang 2015). Use of natural enemies like the malacophagous leech *G. weberi* against the disease-transmitting invasive snail *P. acuta* and the limpet *F. baconi*, and the predatory larvae of the mosquito *L. fuscana* against the larvae of the vector mosquitoes *A. stephensi* and *Cx. quinquefasciatus* qualify as cost-effective and ecologically sustainable modes of biological regulation. A two-prey–one-predator system as considered in this article presents the potential prey–predator interactions underlying the biological regulation. It appears that the regulation of the target prey in the respective cases was dependent on the mutual interference and the prey preference exhibited by the predators, as substantiated through the model constructed. Observations of the empirical study and the inferences of the theoretical framework justify the conclusion that the use of natural enemies can lead to local extinction of the target prey, but this varies with the extent of prey preference and mutual interference as ecological factors. The result of local prey extinction comes from laboratory observations combined with efforts to model them using the proposed equation. In natural conditions, however, several factors

interfere with this two-prey–one-predator system, as the predators may find other suitable prey even in the presence of those taken into consideration. The presence of prey refuges cannot be neglected, as this also enhances prey population survival. Considering all of these factors, vigorous field study is needed for the prey–predator system under analysis. The data from field observations should be modelled using the same equation to compare the result with the laboratory data observed. After comparing the field data with laboratory observations, the model can be validated. Further studies on these and other species combinations may be carried out in natural habitats to validate the theoretical results, leading to successful biological control.

Acknowledgement

The authors gratefully acknowledge the Head of the Department of Zoology, University of Calcutta, Kolkata, India for the facilities provided in carrying out this work.

Declarations

No specific funding was received for this research work. Conceptualized by GA; data search SC, SB, SB, NS, and GKS and model initiation by SC, GA; model selection and preparation SC; model evaluation SC; validation SC; manuscript preparation SC, GA. As authors we declare no conflict of interests. The experimental data and the calculation details, if required, may be provided upon authentic request.

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