ORIGINAL ARTICLE

Role of Quantity of Additional Food to Predators as a Control in Predator–Prey Systems with Relevance to Pest Management and Biological Conservation

P.D.N. Srinivasu · B.S.R.V. Prasad

Received: 29 September 2009 / Accepted: 26 October 2010 / Published online: 9 November 2010 © Society for Mathematical Biology 2010

Abstract Necessity to understand the role of additional food as a tool in biological control programs is being increasingly felt, particularly due to its eco-friendly nature. A thorough mathematical analysis in this direction revealed the vital role of quality and quantity of the additional food in the controllability of the predator–prey systems. In this article controllability of the additional food—provided predator–prey system is studied from perspectives of pest eradication and biological conservation. Time optimal paths have been constructed to drive the state of the system to a desired terminal state by choosing quantity of the additional food as control variable. The theory developed in this article has been illustrated by solving problems related to pest eradication and biological conservation.

Keywords Biological control · Additional food · Quality · Quantity · Predator · Prey · Conservation · Pest eradication · Optimal time · Mayer problem · Bang–bang · Multiple switches

1 Introduction

Controlling pest or invasive species by using natural enemies has been the attracting attention of scientists working with terrestrial ecosystems such as agro-ecosystems. These methods are also used against exotic marine species (Buttermore et al. [1994;](#page-25-0) Lafferty and Kuris [1994,](#page-26-0) [1996](#page-26-1); Miller [1985](#page-26-2); Moyle [1991](#page-26-3)). The eco-friendly nature

P.D.N. Srinivasu (\boxtimes) · B.S.R.V. Prasad

This work is supported by CSIR, Govt. of India—sanction no. 25(0159)/08/EMR-II.

Department of Mathematics, Andhra University, Visakhapatnam 530 003, India e-mail: pdns@rediffmail.com

of this approach is mainly responsible for an enhanced study in this direction. Consequently research has increased in the use of conservation biological control and other habitat manipulation techniques to fulfill the requirements of the natural enemies in agro-ecosystems (Berndt et al. [2002\)](#page-25-1). One aspect of habitat manipulation is the addition of floral resources to agro-ecosystems to provide additional food to predators, potentially enhancing their fitness and efficacy (Landis et al. [2000;](#page-26-4) Wratten et al. [2002\)](#page-27-0). These techniques could also be used to improve the success of classical biological control attempts (Gurr and Wratten [1999\)](#page-25-2). Both theoretical studies (Srinivasu et al. [2007](#page-26-5)) and experimental results (Harwood et al. [2004,](#page-25-3) [2005;](#page-25-4) Harwood and Obrycki [2005;](#page-26-6) Toft [2005](#page-26-7); Wade et al. [2008](#page-27-1); Wootton [1994\)](#page-27-2) established that provision of additional food to predators mediates indirect interactions between the species of the ecosystem, ultimately affecting the population dynamics of the predator and prey.

In the recent theoretical contributions in this direction (Srinivasu et al. [2007;](#page-26-5) Srinivasu and Prasad [2010\)](#page-26-8), the authors proposed the following model representing the predator–prey dynamics in presence of some additional food to predators.

$$
\frac{dN}{dT} = rN\left(1 - \frac{N}{K}\right) - \frac{cNP}{a + \alpha\eta A + N},\tag{1}
$$

$$
\frac{dP}{dT} = \frac{b(N + \eta A)P}{a + \alpha \eta A + N} - mP,\tag{2}
$$

where *N* and *P* represent the biomass of prey and predator, respectively. The additional food biomass is represented by *A*, which is assumed to be distributed uniformly in the habitat. *r* and *K* represent the intrinsic growth rate and carrying capacity of the prey, respectively. *m* is the death rate of the predator. If $h_1(h_2), e_1(e_2), n_1(n_2)$, respectively, represent the handling time of the predator per unit quantity of prey (additional food), the ability of the predator to detect the prey (additional food) and the nutritional value of the prey (additional food), then $c = \frac{1}{h_1}$, $b = n_1c$, $a = \frac{1}{e_1h_1}$, $\eta = \frac{n_2}{n_1} \frac{e_2}{e_1}$ and $\alpha = \frac{n_1}{n_2} \frac{h_2}{h_1}$.

The above model assumes Holling type II predator functional response (Holling [1959;](#page-26-9) Kot [2001](#page-26-10)) toward its available food and also that the number of encounters per predator with the additional food is proportional to the available additional food (Srinivasu et al. [2007\)](#page-26-5). Non-dimensionalizing the system $(1, 2)$ $(1, 2)$ $(1, 2)$ $(1, 2)$ using the transformations

$$
x = \frac{N}{a}, \qquad t = rT, \qquad y = \frac{cP}{ar} \tag{3}
$$

we obtain

$$
\frac{dx}{dt} = x\left(1 - \frac{x}{\gamma}\right) - \frac{xy}{1 + \alpha\xi + x},\tag{4}
$$

$$
\frac{dy}{dt} = \frac{\beta(x+\xi)y}{1+\alpha\xi+x} - \delta y,\tag{5}
$$

where

$$
\gamma = \frac{K}{a}, \qquad \beta = \frac{b}{r}, \qquad \delta = \frac{m}{r}, \qquad \xi = \frac{\eta A}{a}.
$$
\n(6)

From the relation $\alpha = \frac{n_1}{n_2} \frac{h_2}{h_1}$, it can be inferred that α is directly proportional to the handling time h_2 of the additional food and inversely proportional to its nutritional value n_2 . Hence the parameter α is inversely related to the quality of the additional food. Similarly, from the relation $\xi = \frac{\eta A}{a}$, it can be inferred that ξ is directly proportional to the biomass of the additional food (*A*) and thus *ξ* is a representative of the quantity of the additional food that is supplied to predators.

In Srinivasu et al. [\(2007\)](#page-26-5), it is concluded that quality and quantity of the additional food play an important role in deriving control strategies in integrated pest management. As a result studies have been undertaken in Srinivasu and Prasad ([2010\)](#page-26-8) to improve our understanding of the role of quality of the additional food on the controllability of additional food-provided predator–prey system. Relevant time optimal control strategies have been derived which find applications in pest management and biological conservation.

Having studied the role of quality as a control variable to regulate a predator–prey system, it is natural to investigate the influence of quantity on the management aspects. This is not just a mathematical curiosity but many experiments (Azzouz et al. [2004;](#page-25-5) Beach et al. [2003](#page-25-6); Siekmann et al. [2001](#page-26-11); Vandekerkhove and De Clercq [2010;](#page-26-12) Wade et al. [2008;](#page-27-1) Wu et al. [2008\)](#page-27-3) done on biological control indicate that quantity variation has direct implications on the efficacy of the management strategies. So, a study in this direction is of more practical relevance. It is important to note that varying the quantity is far more simpler and practically feasible than varying quality of the additional food. This makes the choice of quantity as a control variable pertinent.

The current study examines the role of quantity (ξ) on the controllability of an additional food—provided predator–prey system. Here $\xi(t)$ is assumed to vary in a range [*ξ*min*,ξ*max]. To achieve the objective, an appropriate (Mayer) time optimal control problem is formulated with $\xi(t) \in [\xi_{\text{min}}, \xi_{\text{max}}]$. Since the system follows two opposite directions depending on whether the parameter *α* is less (greater) than $\frac{β}{δ}$ (Srinivasu et al. [2007\)](#page-26-5), the controllability of the system is implicitly related to the parameter α (although α is assumed to be a constant). Accordingly, the optimal strategies are analyzed for three different situations with respect to *α*. The results of this study find their applications in pest management and biological conservation programs.

The section division of the article is as follows. The next section presents relevance of quantity of additional food as a control variable in the controllability of an additional food provided predator–prey system. The influence of additional food quantity on the system dynamics is present in Sect. [3.](#page-4-0) In Sect. [4,](#page-12-0) a time optimal control problem is formulated to derive control strategies that steer the system from a given initial state to a required terminal state. The properties of the optimal solution are studied and nature of optimal paths in the context of pest eradication are established in Sect. [5](#page-15-0). Finally, Sect. [6](#page-18-0) presents discussion in which four examples are included to illustrate the key findings.

2 Relevance of Quantity as a Control Variable

It is observed that quantity of the available food plays a key role in the survival, longevity, fecundity and progeny production of the species (Azzouz et al. [2004;](#page-25-5) Davis et al. [2005](#page-25-7); Fadamiro and Heimpel [2001](#page-25-8); McDougall and Mills [1997;](#page-26-13) Siekmann et al. [2001](#page-26-11); Vandekerkhove and De Clercq [2010](#page-26-12); Wade et al. [2008;](#page-27-1) Wu et al. [2008;](#page-27-3) Zhao et al. [2003\)](#page-27-4). Thus, in the context of biological control through a natural enemy, quantity of the food available to the predator plays a vital role. If the diet of the natural enemy involves food other than the pest, then the accessibility of this additional food ultimately decides the efficacy of the predator in controlling the pest. For example the mirid predator *Macrolophus pygmaeus* is a natural enemy of major economic importance for the control of white flies and other small arthropod pests in Europe (Margaritopoulos et al. [2003](#page-26-14); Perdikis and Lykouressis [2000,](#page-26-15) [2004;](#page-26-16) Perdikis et al. [1999;](#page-26-17) Vandekerkhove and De Clercq [2010\)](#page-26-12). These predators are reared on the eggs of *E. Kuehniella* for mass production and subsequent release to control the whiteflies and other pests (De Clercq [2008;](#page-25-9) Vandekerkhove and De Clercq [2010\)](#page-26-12). It is found that provision of a minimum of 40 eggs per individual predator for three days is required for optimal development and reproduction of this mirid predator. Providing the predator with lower quantities of eggs resulted in higher mortality, slower development and lower adult weights (Vandekerkhove and De Clercq [2010\)](#page-26-12). Since provision of eggs to the predator proved expensive, experiments were conducted (Vandekerkhove and De Clercq [2010](#page-26-12)) to find if pollen can be a supplementary food for this predator. It is observed that food consisting of 10 eggs and 15 mg of pollen was needed for optimal development of the predator, which was relatively a cheaper alternative (De Clercq [2008;](#page-25-9) Vandekerkhove and De Clercq [2010](#page-26-12)). Thus availability of additional food of a fixed quality appears to be vital in the development, conservation and sustainability of the species both ecologically and economically.

Also, it is observed that feeding on various sugars (in the form of plant derived food) enhances the longevity of certain predators and thus contributes to the success of biological control (Coll and Guershon [2002](#page-25-10); Harwood and Obrycki [2005;](#page-26-6) Sabelis and van Rijn [2005;](#page-26-18) van Rijn et al. [2002;](#page-26-19) Wade et al. [2008;](#page-27-1) Wratten et al. [2002\)](#page-27-0). Since the availability of these plant derived foods vary with time and space (Azzouz et al. [2004](#page-25-5); DeBach and Rosen [1974;](#page-25-11) Hendrix et al. [1992;](#page-26-20) Jervis [1998;](#page-26-21) Siekmann et al. [2001](#page-26-11); Wäckers [2004](#page-26-22), [2005](#page-26-23); Wu et al. [2008](#page-27-3)), artificial sprays are found to be a viable solution for augmentation as a pest management strategy (Wade et al. [2008,](#page-27-1) and references there in). Various experiments have been conducted to evaluate the bio-control potential of a natural enemy when it is provided with different quantities of additional food (Azzouz et al. [2004;](#page-25-5) Siekmann et al. [2001;](#page-26-11) Vandekerkhove and De Clercq [2010;](#page-26-12) Wu et al. [2008](#page-27-3)). The results of these experiments revealed that quantity of the additional food and timing of the food encounter play important roles in extending longevity, survival and fecundity of these natural enemies. Further it is observed that food of varied quantities is required at various stages of the predator in order to have optimal benefit from the predator in the biological control process. These experiments clearly illustrate the vital role played by the quantity of the additional food in the biological control attempts.

3 Influence of Additional Food Quantity on the System Dynamics

In this section we briefly review the predator–prey dynamics when the predator is provided with some additional food. Our interest is to study the controllability of the system with quantity of the additional food as a control variable. In view of this we derive some conclusions regarding asymptotic behavior of the system ([4,](#page-1-2) [5](#page-1-3)) and its dependence on the quantity parameter. Results applicable to pest management and biological conservation are presented at the end of the section.

Now, the system $(4, 5)$ $(4, 5)$ $(4, 5)$ $(4, 5)$ can be conveniently written as

$$
\frac{dx}{dt} = [g(x, \alpha, \xi) - y] f(x, \alpha, \xi), \qquad \frac{dy}{dt} = \left[\beta f(x, \alpha, \xi) \left(1 + \frac{\xi}{x} \right) - \delta \right] y,\tag{7}
$$

where

$$
f(x, \alpha, \xi) = \frac{x}{1 + \alpha \xi + x}, \qquad g(x, \alpha, \xi) = (1 + \alpha \xi + x) \left(1 - \frac{x}{\gamma}\right). \tag{8}
$$

This system always admits the trivial equilibrium *(*0*,* 0*)* and the axial equilibrium $(\gamma, 0)$. The existence of interior equilibrium is parameter dependent. The dynamics of the system ([7\)](#page-4-1) can be better understood under the following three natural cases on the ecosystem parameters:

Case A
$$
\gamma \le \frac{\delta}{\beta - \delta} < \frac{\beta + \delta}{\beta - \delta}
$$

Case B $\frac{\delta}{\beta - \delta} < \gamma \le \frac{\beta + \delta}{\beta - \delta}$
Case C $\frac{\delta}{\beta - \delta} < \frac{\beta + \delta}{\beta - \delta} \le \gamma$

The existence/non-existence of the interior equilibrium solution and its stability are discussed in Srinivasu et al. [\(2007\)](#page-26-5) and the details are briefly presented in Table [1](#page-5-0) which provides a glimpse of global behavior of the considered planar system ([7\)](#page-4-1). Since this study concentrates on the dependence of the system dynamics on the parameter *ξ* (with *α* assumed to be a constant), we shall denote the interior equilibrium of the system ([7\)](#page-4-1) by *(x*∗*(ξ),y*∗*(ξ))*.

For a fixed $\alpha > 0$ we have

$$
x^*(\xi) = \frac{\delta - (\beta - \delta\alpha)\xi}{\beta - \delta},\tag{9}
$$

$$
y^*(\xi) = (1 + \alpha \xi + x^*(\xi)) \left(1 - \frac{x^*(\xi)}{\gamma} \right).
$$
 (10)

From [\(9](#page-4-2)) we have

$$
\xi = \frac{\delta - (\beta - \delta)x^*(\xi)}{\beta - \delta\alpha}.
$$
\n(11)

From (11) (11) we observe that

$$
\beta - \delta \alpha > \text{(&)} 0 \quad \Longleftrightarrow \quad x^*(\xi) < \text{(&)} \frac{\delta}{\beta - \delta}.\tag{12}
$$

 Φ In this case $Q < 0$

 Φ In this case $Q < 0$

Equations ([9\)](#page-4-2)–[\(11](#page-4-3)) imply that an equilibrium $(x^*(\xi), y^*(\xi))$ of the system [\(7](#page-4-1)) satisfies the equation

$$
y = \frac{\beta}{\beta - \delta \alpha} \Big[1 - (\alpha - 1)x \Big] \Big(1 - \frac{x}{\gamma} \Big). \tag{13}
$$

From the analysis presented in Srinivasu et al. ([2007](#page-26-5)) and Srinivasu and Prasad [\(2010](#page-26-8)), the additional food is classified into two categories, viz., high quality and low quality. If $0 < \alpha < \frac{\beta}{\delta}$, then such a food is termed high quality, while it is termed low quality if $\alpha > \frac{\beta}{\delta}$. This classification is made based on the ability of the predator to control the prey in the presence of such additional food. Note that the high quality additional food would be superior (inferior), when compared to the prey if $\alpha \in (0, 1)$ ($\alpha \in (1, \frac{\beta}{\delta})$). Hence we have the following three cases:

Case (i) $\alpha < 1 < \frac{\beta}{\delta}$ *Case* (ii) $1 < \alpha < \frac{\beta}{\delta}$ *Case* (iii) $1 < \frac{\beta}{\delta} < \alpha$

The inter relations that exist between the prey and the predator at equilibrium for the three cases mentioned above are presented in Figs. [1–](#page-7-0)[3.](#page-8-0)

From the system analysis (Srinivasu et al. [2007](#page-26-5)) we observe that, if the system [\(7](#page-4-1)) admits an interior equilibrium in absence of additional food to the predator, then not all points lying on the curve ([13\)](#page-6-0) can become an equilibrium solution for the system in the presence of additional food. In the cases (i) and (ii), only those points on the curve [\(13](#page-6-0)) corresponding to $x \in [0, \frac{\delta}{\beta - \delta})$ become admissible equilibrium solutions (Figs. [1](#page-7-0)) and [2](#page-7-1)). On the other hand if the system [\(7](#page-4-1)), in the absence of additional food, does not admit any interior equilibrium, then unless the quantity of the additional food belongs to $(P, R) = (\frac{\delta - (\beta - \delta)\gamma}{\beta - \delta\alpha}, \frac{\delta}{\beta - \delta\alpha})$ (cf. Table [1](#page-5-0)), coexistence of prey and predator cannot be brought in. In both the cases the admissible equilibrium curve segment intersects *y*-axis at $\frac{\beta}{\beta - \delta \alpha} > 0$ (Figs. [1](#page-7-0) and [2\)](#page-7-1). While in case (i) the curve ([13\)](#page-6-0) is concave with a hump at $x = \frac{1}{2} [\gamma - \frac{1}{1-\alpha}]$ (Fig. [1\)](#page-7-0), it is monotonically decreasing with respect to *in case (ii) (Fig. [2\)](#page-7-1). In the former case the existence of a hump in the segment of* admissible equilibria brings in the possibility of having two distinct equilibria with the same *y* component. This offers two different options for the terminal state to the manager interested in continuing the state of the system at a specific predator population level. Such facility does not exist in case (ii).

In case (iii) we always have $\frac{1}{\alpha-1} < \frac{\delta}{\beta-\delta}$. If $\frac{\delta}{\beta-\delta} < \gamma$ then the segment of the curve [\(13](#page-6-0)) corresponding to $x \in (\frac{\delta}{\beta - \delta}, \gamma]$ represents the set of all admissible equi-librium points for the system [\(7](#page-4-1)) (Fig. [3\)](#page-8-0). On the other hand, if $\frac{\delta}{\beta - \delta}$ > γ then the system [\(7](#page-4-1)) does not admit any interior equilibrium point. This curve intersects *y*-axis at $\frac{\beta}{\beta-\delta\alpha}$ < 0 and always admits a hump at $x=\frac{1}{2}[\gamma-\frac{1}{1-\alpha}]$. Thus the discussion presented for such a situation in case (i) holds good here too.

From the representation of the admissible equilibrium points in Figs. [1](#page-7-0)[–3](#page-8-0), we observe that it is possible to eradicate the prey from the ecosystem only if the quality of the additional food meets the condition $\beta - \delta \alpha > 0$ (i.e., cases (i) and (ii)). This observation finds its applications in pest eradication. In case (iii) it is not possible to eradicate the prey from the ecosystem by providing additional food to the predators.

Fig. 1 This figure presents the curve ([13\)](#page-6-0) for case (i). Here *the solid line* represents the set of all admissible equilibrium solutions. Observe that the prey component of the admissible equilibria is always less than *δ ^β*−*^δ* (cf. ([12](#page-4-4)))

Fig. 2 This figure presents the curve ([13\)](#page-6-0) for case (ii). The admissible equilibrium points are represented by *solid line*. Observe that the curve of admissible equilibria is monotonically decreasing with respect to *x* and the prey component of the admissible equilibria is always less than $\frac{\delta}{\beta-\delta}$ (cf. ([12\)](#page-4-4))

Fig. 3 This figure presents the curve ([13\)](#page-6-0) for case (iii). Here *the solid line* represents the admissible equilibrium points. Observe that this curve has a hump at $x = \frac{1}{2}[\gamma - \frac{1}{1-\alpha}]$. The prey component of the admissible equilibria is always greater than $\frac{\delta}{\beta - \delta}$ (cf. [\(12](#page-4-4)))

This case can be applied to biological conservation programs where coexistence of prey and predator is desired.

The following results can be utilized to derive controllability strategies in the contexts of pest eradication and biological conservation.

Lemma 1

- (a) If the quality of the additional food satisfies $\beta \delta \alpha > 0$, then prey can be eradi*cated from the ecosystem in a finite time by providing the predator with additional food of quantity* $\xi > \frac{\delta}{\beta - \delta \alpha}$.
- (b) *If the quality of the additional food satisfies β* − *δα <* 0, *then it is not possible to eradicate prey from the ecosystem through provision of such additional food to the predators*.

Proof

(a) From the prey and predator isocline equations

$$
y = \left(1 - \frac{x}{\gamma}\right)(1 + \alpha \xi + x)
$$
 and $x = \frac{\delta - (\beta - \delta \alpha)\xi}{\beta - \delta}$

it can be easily observed that the considered system does not admit any interior equilibrium in the positive quadrant of the state space if $\beta - \delta \alpha > 0$ and $\xi > \frac{1}{\beta}$ $\frac{\delta}{\beta-\delta\alpha}$. More over the prey isocline divides the positive quadrant into two regions characterized by $\dot{x} > 0$ and $\dot{x} < 0$. Due to the positivity of \dot{y} we observe that any solution initiating in the region $\dot{x} > 0$ gets driven into the region $\dot{x} < 0$ and subsequently reaches the *y*-axis in a finite time.

(b) The proof for this case can be inferred from Table [1.](#page-5-0) Note that there are only two possibilities viz., either the system admits an interior equilibrium or does not admit one. In the former case the coexistence prevails irrespective of the stability behavior of the interior equilibrium. In the latter case all the solutions approach $(y, 0)$ eventually. Therefore, the prey continues to survive in the ecosystem if *β* − *δα <* 0.

 \Box

For the sake of simplicity let us denote the points $(0, \frac{\beta}{\beta - \delta \alpha})$, $(\frac{\delta}{\beta - \delta})$ $\frac{\beta}{\beta-\delta}[1-\frac{\delta}{(\beta-\delta)\gamma}]$ and $(\frac{1}{2}[\gamma-\frac{1}{1-\alpha}],\frac{\beta(\gamma(1-\alpha)+1)^2}{4\gamma(\beta-\delta\alpha)(1-\alpha)})$ on the curve [\(13](#page-6-0)) by (x_0, y_0) , (x_1, y_1) and (x_2, y_2) , respectively. While the point (x_1, y_1) is an admissible equilib-rium for the system [\(7](#page-4-1)) in all the three cases (i)–(iii), the point (x_0, y_0) becomes an admissible equilibrium for the system [\(7](#page-4-1)) in the cases (i) and (ii) only. If $x_2 < x_1$ $(x_1 < x_2)$ then (x_2, y_2) becomes an admissible equilibrium for the system [\(7](#page-4-1)) in case (i) (case (iii)). We have the following theorems.

Theorem 1 *If* $\alpha < 1 < \frac{\beta}{\delta}$ *and* $\gamma > \frac{1}{1-\alpha}$ *then*

- (a) *For* min $\{y_0, y_1\} < \tilde{y} < \max\{y_0, y_1\}$ *there exists a unique* $\tilde{\xi}$ *such that* $(x^*(\tilde{\xi}), \tilde{y})$ *is an admissible equilibrium for the system* [\(7](#page-4-1)).
- (b) *If* $x_2 < x_1$ *then for* max $\{y_0, y_1\} < \hat{y} < y_2$ *there exist* ξ_1, ξ_2 *with* $\xi_1 > \xi_2$ *and* $x^*(\xi_1) < x^*(\xi_2)$ *such that* $(x^*(\xi_1), \hat{y}), (x^*(\xi_2), \hat{y})$ *are admissible equilibrium points for the system* [\(7](#page-4-1)).

Proof Observe that the curve (13) (13) which attains its maximum y_2 at x_2 is concave if the parameters of the system satisfy the condition $\alpha < 1 < \frac{\beta}{\delta}$ and $\gamma > \frac{1}{1-\alpha}$. From the monotone property of the admissible equilibrium curve segment in the inter*val* $(\min \{y_0, y_1\}, \max \{y_0, y_1\})$ (cf. Fig. [4C](#page-10-0)), it follows that for $\min \{y_0, y_1\} < \tilde{y} <$ max {*y*₀*, y*₁} there exists a unique \tilde{x} and correspondingly a unique $\tilde{\xi} \in (0, \frac{\delta}{\beta - \delta \alpha}]$ (cf. [\(11](#page-4-3))) such that $x^*(\xi) = \tilde{x}$ and $(x^*(\xi), \tilde{y})$ is an admissible equilibrium for the system (7) (7) (cf. Fig. [4](#page-10-0)C). This proves the part (a) of the theorem.

If $x_2 < x_1$, then (x_2, y_2) becomes an admissible equilibrium for the system [\(7](#page-4-1)) (cf. Figs. [4](#page-10-0)A and [4B](#page-10-0)). From the concavity of the admissible equilibrium segment in the interval (min {*y*₀*, y*₁}*, y*₂*)*, it follows that for min {*y*₀*, y*₁} < \hat{y} < *y*₂ there exists \hat{x}_1 *,* \hat{x}_2 and correspondingly ξ_1 , ξ_2 with $\xi_1 > \xi_2$ such that $x^*(\xi_1) = \hat{x}_1$ and $x^*(\xi_2) = \hat{x}_2$. From the monotonicity property of ([11\)](#page-4-3) we have $x^*(\xi_1) < x^*(\xi_2)$ (cf. Figs. [4A](#page-10-0) and [4](#page-10-0)B). The points $(x^*(\xi_1), \hat{y})$ and $(x^*(\xi_2), \hat{y})$ are the admissible equilibria of the system ([7\)](#page-4-1). Thus part (b) follows. \Box

Theorem 2 *If the parameters of the system* [\(7](#page-4-1)) *satisfy any one of the following conditions*

(a)
$$
\alpha < 1 < \frac{\beta}{\delta}
$$
 and $\gamma < \frac{1}{1-\alpha}$

Fig. 4 Two quadrant graphical figure representing the relation between the admissible equilibrium curve segment in ([13\)](#page-6-0) and the control variable ξ when the parameters of the system [\(7](#page-4-1)) satisfy $\alpha < 1 < \frac{\beta}{\delta}$ and $\gamma > \frac{1}{1-\alpha}$. Frames **A** and **B** depict the situation when $x_2 < x_1$. Frame **C** shows the situation when $x_2 > x_1$.
Observe that in Frame **A** (Frames **B** and **C**) min{y₀, y₁} = y₁(y₀) and max{y₀, y₁} = y₀(

2 Springer

Fig. 5 Two quadrant graphical figure representing the relation between the admissible equilibrium curve segment in [\(13](#page-6-0)) and the control variable *ξ* when the parameters of the system ([7\)](#page-4-1) satisfy the hypothesis of Theorem [2.](#page-9-0) Frame **A** (**B**) depicts the situation when parameters of the system ([7\)](#page-4-1) satisfy the condition *a* (*b*) of Theorem [2](#page-9-0)

(b) $1 < \alpha < \frac{\beta}{\delta}$

then for $y_1 \leq \tilde{y} \leq y_0$ *there exists a unique* $\tilde{\xi}$ *such that* $(x^*(\tilde{\xi}), \tilde{y})$ *is an admissible equilibrium for the system* ([7\)](#page-4-1).

Proof Observe that the admissible equilibrium curve segment of the curve [\(13\)](#page-6-0) is decreasing in both the cases *a* and *b* with $y_1 < y_0$. Thus, for any $y_1 \leq \tilde{y} \leq y_0$ there exists a unique \tilde{x} and correspondingly a unique $\tilde{\xi}$ (cf. [\(11](#page-4-3))) such that $x^*(\tilde{\xi}) = \tilde{x}$ and $(x*(\tilde{\xi}), \tilde{y})$ is an admissible equilibrium for the system [\(7](#page-4-1)) (cf. Figs. [5](#page-11-0)A and [5B](#page-11-0)). \Box

Theorem 3 If
$$
\alpha > \frac{\beta}{\delta}
$$
 then

Fig. 6 Two quadrant graphical figure representing the relation between the admissible equilibrium curve segment in [\(13](#page-6-0)) and the control variable ξ when the parameters of the system satisfy $\alpha > \frac{\beta}{\delta}$. Frame **A** (**B**) depicts the situation when $x_1 < x_2$ ($x_1 > x_2$)

- (a) *For* $0 \leq \tilde{y} < y_1$ *there exists a unique* $\tilde{\xi}$ *such that* $(x^*(\tilde{\xi}), \tilde{y})$ *is an admissible equilibrium for the system* ([7\)](#page-4-1).
- (b) *If* $x_1 < x_2$ *then for* $y_1 < \hat{y} < y_2$ *there exist* ξ_1, ξ_2 *with* $\xi_1 < \xi_2$ *and* $x^*(\xi_1) <$ $x^*(\xi_2)$ *such that* $(x^*(\xi_1), \hat{y})$, $(x^*(\xi_2), \hat{y})$ *are admissible equilibrium points for the system* [\(7](#page-4-1)).

Proof of this theorem can be established using the ideas presented in the proof of Theorem [1](#page-9-1) and Figs. [6A](#page-12-1) and [6](#page-12-1)B.

4 Time Optimal Control Problem

In this section an optimal control problem is formulated and it is examined to study properties of optimal control strategies that drive the state of the system [\(7](#page-4-1)) to a desired position optimally (in minimum time). Let [*ξ*min*,ξ*max] represent the range for the parameter *ξ* , where *ξ*min (*ξ*max) stands for the lowest (highest) quantity of the available additional food that can be supplied to the predator. Let the initial state and the desired terminal state of the system ([7\)](#page-4-1) be (x_0, y_0) and (\bar{x}, \bar{y}) , respectively. The interest is to drive the state from (x_0, y_0) to (\bar{x}, \bar{y}) in minimum time. It is assumed that the quality representative, α is a constant (which could belong to any one of the three cases (i)–(iii)). Thus the considered problem is a time optimal control problem with *ξ* as a control variable. The problem can be stated as follows:

$$
\begin{aligned}\n&\min_{\xi_{\min} \leq \xi(t) \leq \xi_{\max}} T \\
&\text{subject to:} \\
&\frac{dx}{dt} = [g(x, \alpha, \xi) - y] f(x, \alpha, \xi), \\
&\frac{dy}{dt} = \left[\beta f(x, \alpha, \xi) \left(1 + \frac{\xi}{x} \right) - \delta \right] y, \\
&\left(x(0), y(0) \right) = (x_0, y_0) \quad \text{and} \quad &\left(x(T), y(T) \right) = (\bar{x}, \bar{y}).\n\end{aligned}
$$
\n(14)

Observe that ([14\)](#page-13-0) is a Mayer problem of minimum time (Cesari [1983](#page-25-12)). The existence of an optimal solution for [\(14](#page-13-0)) is established using *Filippov Existence Theorem* for Mayer problem (Cesari [1983](#page-25-12)) (ref. [Appendix\)](#page-21-0). Assuming that the considered problem admits a solution, the *Necessary conditions for Mayer problem of optimal control* (Cesari [1983\)](#page-25-12) are employed to obtain the nature of the optimal solutions that drive the state of the system from its initial state to the desired terminal state.

Theorem 4 *The optimal solution of* [\(14](#page-13-0)) *is a combination of bang-bang controls*.

Proof Following the necessary conditions for optimal control (Cesari [1983](#page-25-12)) the associated Hamiltonian for the considered optimal control problem [\(14](#page-13-0)) is

$$
\mathcal{H}(x, y, \xi, \lambda, \mu) = \lambda \Big[g(x, \alpha, \xi) - y \Big] f(x, \alpha, \xi) + \mu \Big[\beta f(x, \alpha, \xi) \Big(1 + \frac{\xi}{x} \Big) - \delta \Big] y, \tag{15}
$$

where λ and μ are costate variables. We know that the optimal control $\xi(t)$ (if it exists) minimizes the Hamiltonian ([15\)](#page-13-1) and along the optimal path the costate variables satisfy the following dynamic equations:

$$
\frac{d\lambda}{dt} = -\frac{\partial \mathcal{H}}{\partial x} = -\left\{ \lambda \left[g'(x, \alpha, \xi) f(x, \alpha, \xi) + \left(g(x, \alpha, \xi) - y \right) f'(x, \alpha, \xi) \right] \right\}
$$

$$
- \left\{ \mu \left[f'(x, \alpha, \xi) \left(1 + \frac{\xi}{x} \right) - \frac{f(x, \alpha, \xi)\xi}{x^2} \right] \beta y \right\},\tag{16}
$$

$$
\frac{d\mu}{dt} = -\frac{\partial \mathcal{H}}{\partial y} = -\left\{\lambda\left(-f(x,\alpha,\xi)\right) + \mu\left[\beta f(x,\alpha,\xi)\left(1+\frac{\xi}{x}\right) - \delta\right]\right\},\tag{17}
$$

 \mathcal{D} Springer

where $' = \frac{\partial}{\partial x}$. Since [\(14](#page-13-0)) is a time optimal control problem we have

$$
\mathcal{H}(x(t), y(t), \xi(t), \lambda(t), \mu(t)) = -1 \tag{18}
$$

along an optimal trajectory (Clark [2005](#page-25-13)). Differentiating the Hamiltonian ([15](#page-13-1)) with respect to the control variable *ξ* we obtain

$$
\frac{\partial \mathcal{H}}{\partial \xi} = \frac{y}{(1 + \alpha \xi + x)^2} \{ \mu \beta [1 + x(1 - \alpha)] + \lambda \alpha x \}.
$$
 (19)

Evaluating second derivative of the Hamiltonian ([15\)](#page-13-1) with respect to *ξ* we obtain

$$
\frac{\partial^2 \mathcal{H}}{\partial \xi^2} = -\frac{2\alpha}{1 + \alpha \xi + x} \frac{\partial \mathcal{H}}{\partial \xi}.
$$
 (20)

Equation [\(20](#page-14-0)) indicates that the Hamiltonian is strictly monotone with respect to *ξ* whenever $\frac{\partial \mathcal{H}}{\partial \xi} \neq 0$ and hence the optimal control strategy involves bang-bang controls. Now we are interested in finding out the existence of a singular arc in the phase space.

The considered problem [\(14](#page-13-0)) admits a singular solution if there exists an interval $[t_1, t_2]$ on which $\frac{\partial \mathcal{H}}{\partial \xi} = 0$. From [\(19](#page-14-1)) we observe that the singular solution is represented by

$$
\mu\beta\big[1+x(1-\alpha)\big]+\lambda\alpha x=0.\tag{21}
$$

Thus, along an optimal singular solution we have $\frac{\lambda}{\mu} = \frac{\beta[x(\alpha-1)-1]}{\alpha x}$. Therefore on a singular arc, if $x < \frac{1}{\alpha - 1}$, then λ and μ will be of opposite signs. On the other hand, if $x > \frac{1}{\alpha - 1}$, then both λ and μ will be of same sign. If $x = \frac{1}{\alpha - 1}$, then we have λ to be zero and μ to be arbitrary. Therefore, along a singular solution both the costate variables do not become zero simultaneously. For otherwise they fail to satisfy ([18\)](#page-14-2). Assuming that a singular solution exists, differentiating ([19\)](#page-14-1) with respect to time *t* along the singular solution and employing (7) (7) , (16) (16) and (17) (17) we obtain

$$
\frac{d}{dt}\frac{\partial \mathcal{H}}{\partial \xi} = \frac{y}{(1+\alpha\xi + x)^2} \times \frac{1}{\mu\alpha\beta\gamma} \times \left\{2(\alpha - 1)\alpha x^2 + \left[\gamma(\alpha - 1)\left[\beta - \alpha(\delta + 1)\right] - \alpha\right]x - \gamma(\beta - \delta\alpha)\right\} \n= 0.
$$
\n(22)

Differentiating (22) (22) once again with respect to t along the singular solution, we obtain

$$
\frac{d^2}{dt^2} \frac{\partial \mathcal{H}}{\partial \alpha} = \frac{y}{(1 + \alpha \xi + x)^2} \times \frac{1}{\mu \alpha \beta \gamma} \times \left\{ 4(\alpha - 1)\alpha x + \left[\gamma(\alpha - 1) [\beta - \alpha(\delta + 1)] - \alpha \right] \right\} \times \left[g(x, \alpha, \xi) - y \right] f(x, \alpha, \xi) = 0. \tag{23}
$$

 \circledcirc Springer

From [\(22](#page-14-3)) and ([23\)](#page-14-4) we infer that the singular optimal solution is a point (\hat{x}, \hat{y}) where \hat{x} is a positive root of the equation

$$
2(\alpha - 1)\alpha x^2 + \left[\gamma(\alpha - 1)\left[\beta - \alpha(\delta + 1)\right] - \alpha\right]x - \gamma(\beta - \delta\alpha) = 0,\tag{24}
$$

and

$$
\hat{y} = g(\hat{x}, \alpha, \xi). \tag{25}
$$

Observe that (\hat{x}, \hat{y}) , if exists, is a point on the *x*-isocline of [\(7](#page-4-1)) provided $\hat{x} < \gamma$. Also note from the quadratic nature of [\(24](#page-15-1)) that there exists at the most two meaningful solutions for $(24, 25)$ $(24, 25)$ $(24, 25)$ $(24, 25)$. Hence a singular solution of (14) (14) is at the most a point on the *x*-isocline of [\(7\)](#page-4-1) in the phase space and not an arc. Therefore, the solution of the considered optimal control problem is of bang–bang type only. Since we are interested in minimizing the Hamiltonian, the optimal strategy $\xi_{\text{opt}}(t)$ is given by

$$
\xi_{\text{opt}}(t) = \begin{cases} \xi_{\text{max}}, & \text{if } \frac{\partial \mathcal{H}}{\partial \xi} < 0, \\ \xi_{\text{min}}, & \text{if } \frac{\partial \mathcal{H}}{\partial \xi} > 0. \end{cases}
$$
 (26)

This completes the proof.

The following is a Corollary to the Existence Theorem presented in [Appendix](#page-21-0).

Corollary 1 If there exists an admissible path connecting the initial state (x_0, y_0) and terminal state (\bar{x}, \bar{y}) involving combination of bang–bang controls then the con*sidered time optimal control problem* [\(14](#page-13-0)) *admits a solution*.

5 Optimal Solution and Optimal Approach Paths

In this section, the properties of optimal solutions and optimal approach paths for the considered optimal control problem [\(14](#page-13-0)) are analyzed based on the observations made in the previous sections.

Observe that [\(24](#page-15-1)) is convex for $\alpha > 1$ and has two positive roots \tilde{x} , \hat{x} for $\alpha > \frac{\beta}{\delta}$ with $\tilde{x} < \frac{1}{\alpha-1}$. If $\gamma[\beta - \alpha(1+\delta)]$ and $[\gamma(\alpha-1) - 1]$ are of same sign then $\hat{x} \in$ $(\frac{1}{\alpha-1}, \gamma)$. Equation [\(24](#page-15-1)) has one negative root *x*̃ and one positive root *x*̂ for $1 < \alpha < \frac{\beta}{\delta}$ with $\tilde{x} < \frac{1}{\alpha - 1} < \hat{x} < \gamma$. For $\alpha = 1$ equation [\(24](#page-15-1)) is linear and has a negative root. For α < 1 equation ([24](#page-15-1)) is concave and does not posses any positive roots.

Let us consider the positive quadrant of the phase space containing the set of all points represented by the curve ([13\)](#page-6-0), together with the lines representing the positive solutions of [\(24](#page-15-1)), which stand for *x* component of the singular solutions (points) of the considered problem [\(14](#page-13-0)). We observe the following in respect of the three cases (i) – (iii) .

In case (i) , (24) (24) does not possess any positive roots and the curve (13) (13) divides the positive quadrant of the phase plane into two regions given by

Region Ia :=
$$
\left\{ (x, y) \middle| y < \frac{\beta}{\beta - \delta \alpha} \Big[1 - x(\alpha - 1) \Big] \left(1 - \frac{x}{\gamma} \right) \right\},
$$

$$
\Box
$$

Region Ib :=
$$
\left\{ (x, y) \middle| y > \frac{\beta}{\beta - \delta \alpha} \left[1 - x(\alpha - 1) \right] \left(1 - \frac{x}{\gamma} \right) \right\}.
$$

In case (ii), the positive root \hat{x} of [\(24](#page-15-1)) and the curve ([13\)](#page-6-0) divide the positive quadrant of the phase plane into four regions given by

Region IIa :=

\n
$$
\begin{aligned}\n\left\{ (x, y) \middle| y &< \frac{\beta}{\beta - \delta \alpha} \Big[1 - x(\alpha - 1) \Big] \Big(1 - \frac{x}{\gamma} \Big) \text{ and } x < \hat{x} \right\}, \\
\text{Region IIb} &:= \left\{ (x, y) \middle| y < \frac{\beta}{\beta - \delta \alpha} \Big[1 - x(\alpha - 1) \Big] \Big(1 - \frac{x}{\gamma} \Big) \text{ and } x > \hat{x} \right\}, \\
\text{Region IIc} &:= \left\{ (x, y) \middle| y > \frac{\beta}{\beta - \delta \alpha} \Big[1 - x(\alpha - 1) \Big] \Big(1 - \frac{x}{\gamma} \Big) \text{ and } x < \hat{x} \right\}, \\
\text{Region IId} &:= \left\{ (x, y) \middle| y > \frac{\beta}{\beta - \delta \alpha} \Big[1 - x(\alpha - 1) \Big] \Big(1 - \frac{x}{\gamma} \Big) \text{ and } x > \hat{x} \right\}.\n\end{aligned}
$$

In case (iii), we have both the roots \tilde{x} and \hat{x} of ([24\)](#page-15-1) to be positive. In this case the positive quadrant is divided into five regions by the curve ([13\)](#page-6-0) and the solutions of [\(24](#page-15-1)) which are given by

Region IIIa :=

\n
$$
\begin{aligned}\n\left\{ (x, y) \middle| y &< \frac{\beta}{\beta - \delta \alpha} \left[1 - x(\alpha - 1) \right] \left(1 - \frac{x}{\gamma} \right) \text{ and } \tilde{x} < x < \hat{x} \right\}, \\
\text{Region IIIb} &:= \left\{ (x, y) \middle| y < \frac{\beta}{\beta - \delta \alpha} \left[1 - x(\alpha - 1) \right] \left(1 - \frac{x}{\gamma} \right) \text{ and } \tilde{x} < \hat{x} < x \right\}, \\
\text{Region IIIc} &:= \left\{ (x, y) \middle| y > \frac{\beta}{\beta - \delta \alpha} \left[1 - x(\alpha - 1) \right] \left(1 - \frac{x}{\gamma} \right) \text{ and } x < \tilde{x} < \hat{x} \right\}, \\
\text{Region IIId} &:= \left\{ (x, y) \middle| y > \frac{\beta}{\beta - \delta \alpha} \left[1 - x(\alpha - 1) \right] \left(1 - \frac{x}{\gamma} \right) \text{ and } \tilde{x} < x < \hat{x} \right\}, \\
\text{Region IIIe} &:= \left\{ (x, y) \middle| y > \frac{\beta}{\beta - \delta \alpha} \left[1 - x(\alpha - 1) \right] \left(1 - \frac{x}{\gamma} \right) \text{ and } \tilde{x} < \hat{x} < x \right\}.\n\end{aligned}
$$

Note that the Region IIIb is empty if $\gamma[\beta - \alpha(1 + \delta)]$ and $[\gamma(\alpha - 1) - 1]$ are of opposite signs.

The following Theorems [5](#page-16-0) and [6](#page-17-0) can be established using procedure followed in the proofs of Theorems 3 and 4 in Srinivasu and Prasad ([2010\)](#page-26-8). Hence the proofs are omitted.

Theorem 5 *Along an optimal path*, *control can switch from ξ*min *to ξ*max (*ξ*max *to ξ*min) *in Regions* Ia, IIa, IId, IIIb *and* IIId (Ib, IIb, IIc, IIIa, IIIc *and* IIIe) *only*.

From above theorem, it follows that the optimal strategy to reach an interior point in the phase space could involve multiple switches between the extremal values (*ξ*min and *ξ*max) of the control variable. In the case of pest eradication we have the following results.

Theorem 6 *The control problem* [\(14\)](#page-13-0) *with* $\beta - \delta \alpha > 0$ *and* $x(T) = 0$ *admits a solution if* $\xi_{\text{max}} > \frac{\delta}{\beta - \delta \alpha}$. *Moreover*, $\xi_{\text{opt}}(T) = \xi_{\text{max}}$ *with* $\mu(T) < 0$.

Theorem 7 *If* $\beta - \delta \alpha > 0$ *and* $\xi_{\text{max}} > \frac{\delta}{\beta - \delta \alpha}$ *then the optimal solution of the control problem* [\(14](#page-13-0)) *with* $x(T) = 0$ *is given by* $\xi_{opt}(t) = \xi_{max}$ *on* [0*,T*].

Proof To prove this result we make use of the properties of the zero solution of the linear system (16) (16) , (17) (17) (17) which governs the co-state variables along the optimal path. This system is given by

$$
\begin{pmatrix}\n\frac{d\lambda}{dt} \\
\frac{d\mu}{dt}\n\end{pmatrix} = \begin{pmatrix}\n-a_1(t) & -b_1(t) \\
a_2(t) & -b_2(t)\n\end{pmatrix} \begin{pmatrix}\n\lambda(t) \\
\mu(t)\n\end{pmatrix},
$$
\n(27)

where

$$
a_1(t) = 1 - \frac{2x(t)}{\gamma} - \frac{(1 + \alpha\xi(t))y(t)}{(1 + \alpha\xi(t) + x(t))^2},
$$
\n(28)

$$
b_1(t) = \frac{\beta(1 + \alpha \xi(t) - \xi(t))y(t)}{(1 + \alpha \xi(t) + x(t))^2},
$$
\n(29)

$$
a_2(t) = \frac{x(t)}{1 + \alpha \xi(t) + x(t)},
$$
\n(30)

$$
b_2(t) = \frac{\beta(x(t) + \xi(t))}{1 + \alpha \xi(t) + x(t)} - \delta,
$$
\n(31)

where $x(t)$ and $y(t)$ represent the state variables along an optimal path. Let us take $\xi(t) = \xi_{\text{max}}$. Observe that $a_2(t) \ge 0$. From the hypothesis $\xi_{\text{max}} > \frac{\delta}{\beta - \delta \alpha}$, we have $b_2(t) > 0$. The term $a_1(t)$ can take either positive or negative sign depending on the values of state variables $x(t)$, $y(t)$ and parameters of the system. In particular $a_1(t) < 0$ if either $x(t) > \frac{\gamma}{2}$ or $x(t) = 0$ with $y(t) > 1 + \alpha \xi_{\text{max}}$. The term $b_1(t)$ has the same sign as that of $1 + \alpha \xi(t) - \xi(t)$.

Now let us consider the following equation representing the characteristic equation associated with the system ([27\)](#page-17-1)

$$
m^{2} + (a_{1}(t) + b_{2}(t))m + (a_{1}(t)b_{2}(t) + a_{2}(t)b_{1}(t)) = 0.
$$
 (32)

We study some needed qualitative behavior of the system (27) (27) using the concept of dependence of solutions of a system on parameters. Based on the properties of the functions $a_1(t) + b_2(t)$ and $a_1(t)b_2(t) + a_2(t)b_1(t)$, we assess the behavior of solutions of [\(27](#page-17-1)), which help in understanding the switching behavior of optimal solution of the control problem ([14\)](#page-13-0). From Theorem [6,](#page-17-0) if we assume the value of *λ* at the terminal time *T* to be negative, from the continuity of $a_1(t) + b_2(t)$ and $a_1(t)b_2(t) + a_2(t)b_1(t)$, it follows that there exists a left neighborhood of *T*, say [*a, T*], in which we have $\lambda(t) < 0$ and $\mu(t) < 0$. The proof would be complete if we can show that $a = 0$. Below we shall show that it is possible to choose the initial values for the costate variables in such a way that these variables do not change their sign in $[0, T]$, as a consequence the switching function also does not change its sign along the optimal path.

Essentially we can divide the argument into the following two cases:

Case (a) $1 + \alpha \xi(t) - \xi(t) \leq 0$ *Case* (b) $1 + \alpha \xi(t) - \xi(t) > 0$

Case (a): In this case we have $b_1(t) < 0$. Also we have the discriminant of [\(32](#page-17-2)) to be positive for all t . From this we observe that all solutions of the system (27) (27) , with initial values $\lambda(0) < 0$ and $\mu(0) < 0$, will remain only in the third quadrant of $\lambda \mu$ -space for all future times and hence the switching function does not change its sign in [0*,T*].

Case (b): In this case $b_1(t)$ being positive the discriminant of ([32\)](#page-17-2) can change its sign as *t* progresses (depending on the values of the parameters and the state variables). Thus a path of the system ([27\)](#page-17-1) initiating in the third quadrant of $\lambda \mu$ -space may leave that quadrant as time progresses. Note that at the terminal time *T* , we have $x(T) = 0$ and $y(T) > 1 + \alpha \xi_{\text{max}}$. Thus the zero solution of the system ([27\)](#page-17-1) behaves like a saddle in the vicinity of the terminal time. Therefore, it is always possible to choose the initial value for the costate variable μ sufficiently far from 0 on the negative μ -axis (with $\lambda(0) < 0$ satisfying [\(18](#page-14-2)) at $t = 0$) so that by the time the costate gets closer to negative *λ*-axis, it is influenced by the saddle nature of the zero solution. Thus, in this case also ξ_{max} proves to be the optimal strategy on [0, T]. \Box

From Theorem [7](#page-17-3) it can be inferred that in the case of pest eradication (which is possible only in the cases (i) and (ii)), the optimal policy is to provide the maximum possible quantity *ξ*max (satisfying *ξ*max *> ^δ ^β*−*δα*) of the additional food to the predators till the system becomes pest free. If the manager does not require the presence of predators in the ecosystem after the system becomes pest free, he/she may withdraw provision of additional food to the predators after the state reaches the predator axis. This strategy will automatically drive the predator to extinction (Srinivasu et al. [2007\)](#page-26-5).

6 Discussion

Providing additional food to predators is one of the established techniques in integrated pest management and biological conservation programs (Bilde and Toft [1998;](#page-25-14) Coll and Guershon [2002](#page-25-10); Harmon [2003](#page-25-15); Harwood and Obrycki [2005](#page-26-6); Murdoch et al. [1985;](#page-26-24) Sabelis and van Rijn [2005;](#page-26-18) Shannon et al. [2007;](#page-26-25) van Baalen et al. [2001;](#page-26-26) van Rijn et al. [2002](#page-26-19); Wade et al. [2008\)](#page-27-1). In such management processes as this, the key factors that decide the controllability of the ecosystem are identified as quality and quantity of additional food that is provided to the predators (Srinivasu et al. [2007\)](#page-26-5). From the theoretical studies (Srinivasu et al. [2007\)](#page-26-5), it is observed that by altering the quality and quantity of this additional food one cannot only limit the prey but also eradicate the predator from the ecosystem. In a further contribution on this topic (Srinivasu and Prasad [2010](#page-26-8)), the authors derived time optimal control strategies to drive the state of the system from an initial point to a terminal point in a minimum time using quality of the additional food as a control variable and its quantity assumed to be constant.

In this present work the controllability of an additional food—provided predator– prey system is investigated with quantity as a control variable. Here it is assumed that the quality of the additional food remains constant. This study is motivated by the results of various experiments (Azzouz et al. [2004](#page-25-5); Beach et al. [2003;](#page-25-6) DeBach and Rosen [1974;](#page-25-11) Hendrix et al. [1992;](#page-26-20) Jervis [1998](#page-26-21); Siekmann et al. [2001;](#page-26-11) Vandekerkhove and De Clercq [2010;](#page-26-12) Wäckers [2004,](#page-26-22) [2005;](#page-26-23) Wade et al. [2008;](#page-27-1) Wu et al. [2008](#page-27-3)) that were held on biological conservation control, wherein it was observed that variation in quantity plays a vital role in the efficacy of the management attempts. The results of this study clearly bring out the interdependencies on the quality and quantity of the additional food that ensures the realization of the desired objective. From the system analysis it is observed that the prey can be eradicated from the environment in a finite time by providing the predators with additional food of suitable quality and quantity (Lemma [1](#page-8-1)). From biological conservation perspective, where it is desired to have coexistence of both prey and the predator at an equilibrium, the analysis (Theorems $1-3$ $1-3$) suggests required quality and quantity of the additional food to achieve the objective.

Subsequently, an appropriate (Mayer) time optimal control problem (with quantity as a control variable) is formulated, in order to find the strategies that drive the state of the system from one point to another optimally. The existence of an optimal solution is proved using the *Filippov Existence Theorem*. From the problem formulation, we observe that the problem is non-linear in control variable. However, the analysis indicated that the associated Hamiltonian is monotone with respect to the control parameter. This property made it possible to identify the nature of the optimal strategies. Here it is observed that the optimal strategy to steer the state of the considered system to a desired position involves a combination of bang-bang controls only and does not include any singular strategy (Theorem [4\)](#page-13-4).

From the system analysis it is observed that the controllability of the system inherently depends on the quality parameter (α) and the following three cases arise:

Case (i) $\alpha < 1 < \frac{\beta}{\delta}$ *Case* (ii) $1 < \alpha < \frac{\beta}{\delta}$ *Case* (iii) $1 < \frac{\beta}{\delta} < \alpha$

It can be interpreted that case (i) represents a situation where the predator is provided with a superior quality of additional food when compared to that of prey. Case (ii) stands for a situation where the predator is provided with additional food whose quality is inferior to that of prey and still promises the hold of the predator over the prey. Case (iii) is the situation where the predator is provided with a low quality additional food. Pest eradication is possible only in cases (i) and (ii) and not in case (iii). It is found that the optimal control associated with the traversal of the state from one interior point to another could involve multiple switches. In case (i) it is noticed that both the co-state variables are of opposite signs at the switch time. For the cases (ii) and (iii) it may happen that co-state variables are of same (opposite) sign at switch time depending on the prey level at the switching point. In case of pest eradication, it is observed that the optimal control involves no switches (Theorem [7\)](#page-17-3) and the optimal

Fig. 7 This example 1 illustrates the optimal pest eradication strategy when the system parameters $(\beta = 0.4, \delta = 0.3, \gamma = 7.0, \alpha = 0.6, \xi_{\text{min}} = 1.0, \xi_{\text{max}} = 2.0)$ satisfy case (i). Since $\xi_{\text{max}} > \frac{\delta}{\beta - \delta \alpha}$, the optimal strategy is $\xi_{opt}(t) = \xi_{max}$ (Theorem [7\)](#page-17-3). This strategy drives the state from $(5.00, 1.00)$ to $(0.00, 6.45)$ in $T = 22.2$ units of time as shown in Frame **A**. The Regions Ia and Ib in this frame are the regions into which the phase space is divided in case (i). Frame **B** presents the curve $\frac{\partial \mathcal{H}}{\partial \xi}$ which is negative on [0, *T*] as required (cf. [\(26](#page-15-3))). The costate variables $\lambda(t)$ and $\mu(t)$ are presented in Frames **C** and **D**, respectively. Observe that these costate variables have remained negative in [0*,T*] as indicated by Theorem [7](#page-17-3)

policy is to provide the predators with highest quantity of additional food till the state becomes pest free.

Four different examples are presented to illustrate the optimal approach paths for problems associated with pest eradication and biological conservation. The example presented in Fig. [7](#page-20-0) illustrates the implementation of constant policy for the case of prey eradication pertaining to case (i). The parameter values considered for the example shown in Fig. [8](#page-21-1) are such that the system admits an asymptotically stable limit cycle for each $\xi \in [\xi_{min}, \xi_{max}]$. In this scenario an optimal path is constructed to move from a point lying with in both the limit cycles pertaining to the extremal control values, to a point lying outside these limit cycles. The optimal path experiences four switches in accordance with the Theorem [5](#page-16-0) to reach the terminal state. The examples presented in Figs. [9](#page-22-0) and [10](#page-23-0) exhibit solutions for biological conservation problems where the state is driven to an admissible equilibrium in minimum time and allowed to continue at the terminal state by switching to the appropriate control.

Acknowledgements We are extremely thankful to the three anonymous honorable reviewers for their critical comments and invaluable suggestions.

Fig. 8 This example 2, which also falls into case (i) with parameter values are $\beta = 0.4$, $\delta = 0.3$, $\gamma = 7.0$, $\alpha = 0.8$, $\xi_{\text{min}} = 0.5$, $\xi_{\text{max}} = 1.0$, presents an interesting instance where the optimal strategy involves four switches. Note that all the admissible equilibria of the system for *ξ* ∈ [*ξ*min*,ξ*max] are unstable (Table [1](#page-5-0)). Hence, the system admits asymptotically stable limit cycle for each *ξ* ∈ [*ξ*min*,ξ*max]. The limits cycles corresponding to *ξ*min and *ξ*max are presented in Frame **B**. The problem is to drive the system from *(*2*.*00*,* 2*.*76*)* which is located inside the both limit cycles to *(*5*.*31*,* 0*.*41*)*, located out side both the limit cycles. Applying the optimal strategy derived according to Theorem [5](#page-16-0), the state reaches the terminal point in $T = 90$ units of time after experiencing four switches, two in Region Ia and two in Region Ib as shown in Frame **A**. The four switch points are indexed according to their occurrence in the optimal path and are presented in Frame **B**. The costate variables along the optimal path are shown in Frames **D** and **E**. Frame **F** presents the optimal strategy

Appendix

The following lemma can be easily established.

 \overline{A}

redator(y)

 \overline{C} 40

 $\overline{3}$

 $\overline{\mathcal{U}}$

 $\overline{10}$

 $\overline{0}$ -10

 -20 -30

ó. $\tilde{\mathbf{z}}$

 ϵ

 $\overline{}$

 $\overline{\mathbf{3}}$

 $\overline{2}$

 $\overline{\text{II}}$ a

3

 $\overline{10}$

 $\overline{20}$

 $Time(t)$

25

15

 $\overline{30}$ $\overline{35}$ $\overline{40}$

 $\overline{2}$

 1.5

 0.5

 Ω

 $\overline{0}$ $\ddot{}$ $\overline{10}$

 $\overline{20}$ $\overline{25}$

 $Time(t)$

15

 \hat{e}

Fig. 9 This example with the parameters values being $\beta = 0.4$, $\delta = 0.3$, $\gamma = 8.0$, $\alpha = 1.1$, $\xi_{\text{min}} = 1.0$, *ξ*max = 2*.*0, falls into case (ii). Here the terminal point is chosen to be *(*1*.*91*,* 3*.*50*)*, which is an admissible (unstable) equilibrium with corresponding *ξ* value being 1*.*5571 (Table [1\)](#page-5-0). The optimal path takes $T = 35.7$ units of time to reach this equilibrium point from (7.37, 3.55). Hence there is a possibility to continue the state at the terminal value (as long as the system does not experience any perturbations) by switching the control *ξ* to 1*.*5571 at the terminal time *T* = 35*.*7. The Frame **A** presents the optimal path along with the Regions IIa, IIb, IIc and IId (described in Sect. [5](#page-15-0)). Note that the occurrence of switches in the Regions IIa, IIb is according to the Theorem [5](#page-16-0). The curve $\frac{\partial \mathcal{H}}{\partial \xi}$ along the optimal path is presented in Frame **B**. The associated plots for costate variables and optimal strategy are shown in Frames **C** and **D**, respectively

Lemma A.1 *If the parameters of the system* [\(7](#page-4-1)) *satisfy* $\xi < \frac{\delta}{\beta - \delta \alpha}$, *then the interior of the positive quadrant of the state space is invariant and all the solutions of system* [\(7](#page-4-1)) *initiating in the interior of the positive quadrant are bounded*.

A.1 General form for Mayer Problem of Optimal Control

Let *A* be a subset of the *t***x**-space \mathbb{R}^{1+n} , let *U* be a given subset of the **u**-space \mathbb{R}^m . Let $f(t, x, u) = (f_1, \ldots, f_2)$ be a given function on $A \times U$. For every $(t, x) \in A$ let $Q(t, x) = f(t, \mathbf{x}, U) \subset \mathbb{R}^n$ be the set of all $z = (z_1, \ldots, z_n)$ with $z = f(t, \mathbf{x}, \mathbf{u})$ for some $\mathbf{u} \in U$. Let *B* be a given subset of $t_1x_1t_2x_2$ -space \mathbb{R}^{2n+2} . The Mayer problem of optimal control is finding minima of the functional

$$
I[\mathbf{x}, \mathbf{u}] = g(t_1, x(t_1), t_2, x(t_2))
$$
 (A.1)

 $\overline{35}$

30

 \otimes Springer

Fig. 10 In this example 4, the system parameters are assumed to be $\beta = 0.67$, $\delta = 0.54$, $\gamma = 10$, $\alpha = 1.4$, $\xi_{\text{min}} = 0.5$, $\xi_{\text{max}} = 2.0$. Since $\alpha > \frac{\beta}{\delta}$ this example falls into case (iii). Note that all the admissible equilibria of the system for $\xi \in [\xi_{\text{min}}, \xi_{\text{max}}]$ are stable (Table [1](#page-5-0)). Here the terminal value is taken to be *(*4*.*52*,* 3*,* 44*)*, which is an admissible equilibrium with corresponding *ξ* = 0*.*5535 ∈ [*ξ*min*,ξ*max]. Hence there is a possibility to continue the state at this terminal state for all future times by switching the control *ξ* to 0*.*5535 after reaching the terminal state at *T* = 8*.*59 units. The optimal path is presented in Frame **A**, which also exhibits the Regions IIIa, IIIb, IIIc, IIId and IIIe described in Sect. [5](#page-15-0). Observe here that the optimal switches are in accordance with the Theorem [5.](#page-16-0) Frames **B** and **C** present the values of $\frac{\partial \mathcal{H}}{\partial \xi}$ and costate variables along the optimal trajectory, respectively. The optimal strategy is presented in Frame **D**

for pairs of functions $\mathbf{x}(t) = (x_1, ..., x_n), \mathbf{u}(t) = (u_1, ..., u_m), t_1 \le t \le t_2, \mathbf{x}$ absolutely continuous, **u** measurable, satisfying

$$
\frac{d\mathbf{x}}{dt} = \mathbf{f}(t, \mathbf{x}(t), \mathbf{u}(t)), \quad t_1 \le t \le t_2,
$$
\n(A.2)

boundary conditions

$$
e[\mathbf{x}] = (t_1, x(t_1), t_2, x(t_2)) \in B,
$$
 (A.3)

and constraints

$$
(t, \mathbf{x}(t)) \in A, \quad t_1 \le t \le t_2,
$$
\n(A.4)

$$
\mathbf{u}(t) \in U, \quad t_1 \le t \le t_2,\tag{A.5}
$$

in the class *Ω* of all admissible pairs *(***x***,***u***)*. By an admissible pair for the problem $(A.1-A.5)$ $(A.1-A.5)$ $(A.1-A.5)$ we mean a pair $(\mathbf{x}(t), \mathbf{u}(t)), t_1 \le t \le t_2$, **x** absolutely continuous, **u** measurable, satisfying all requirements ([A.2–](#page-23-2)[A.5](#page-23-1)). Here **x** and **u** are said to be an admissible trajectory and an admissible control, respectively.

Theorem (The Filippov Existence Theorem for Mayer Problem of Optimal Control) *If A* and *U* are compact, *B* is closed, **f** is continuous on $A \times U$, *g* is continuous on *B*, $Ω$ *is not empty, and for every* $(t, \mathbf{x}) ∈ A$ *the set* $Q(t, \mathbf{x}) = \mathbf{f}(t, \mathbf{x}, U) ⊂ \mathbb{R}^n$ *is convex, then* $I[x, u]$ *has an absolute minimum in* Ω .

Theorem (Existence Theorem) *If Ω is non-empty then the time optimal control problem* [\(14\)](#page-13-0) *has an absolute minimum*.

Proof We shall prove this result by showing that all the conditions of *Filippov Existence Theorem* are satisfied. We know that for $\xi > \frac{\delta}{\beta - \delta \alpha}$ any solution initiating in the positive quadrant reaches *y*-axis in a finite time. In view of this observation and the above Lemma [A.1](#page-22-2) we can assume that the set $A \subset \mathbb{R}^{1+2}$ for the considered problem ([14\)](#page-13-0) to be compact. To justify the existence of optimal solution it is sufficient to show that for (t, x, y) ∈ *A* the sets $Q(t, x, y) = \{(z_1, z_2) | z_1 = f_1(t, x, y, \xi), z_2 =$ *f*₂*(t, x, y, ξ), ξ* ∈ [*ξ*_{min}, *ξ*_{max}]} are convex, where $f_1 = x(1 - \frac{x}{\gamma}) - \frac{xy}{1 + \alpha \xi + x}$, $f_2 =$ *β(x*+*ξ)y* ¹+*αξ*+*^x* − *δy*.

For, let us consider

$$
z_1 = x \left(1 - \frac{x}{\gamma} \right) - \frac{xy}{1 + \alpha \xi + x}.
$$

This implies that

$$
\frac{xy}{1 + \alpha \xi + x} = x \left(1 - \frac{x}{\gamma} \right) - z_1.
$$
 (A.6)

From $z_2 = f_2(t, x, y, \xi)$ and $(A.6)$ $(A.6)$ $(A.6)$ we obtain

$$
z_2 = \beta x \left(1 + \frac{\xi}{x} \right) - \beta z_1 + \frac{\beta \xi y}{1 + \alpha \xi + x} - \delta y.
$$

Therefore

$$
\frac{\beta \xi y}{1 + \alpha \xi + x} = z_2 + \delta y + \beta z_1 - \beta x \left(1 - \frac{x}{\gamma} \right). \tag{A.7}
$$

Equation $(A.6)$ $(A.6)$ $(A.6)$ implies

$$
\xi = \frac{1}{\alpha} \left[\frac{xy}{x(1 - \frac{x}{y}) - z_1} - (1 + x) \right].
$$
 (A.8)

From $(A.7)$ we have

$$
\xi \left\{ \beta y - \alpha \left[z_2 - \beta x \left(1 - \frac{x}{\gamma} \right) + \beta z_1 + \delta y \right] \right\}
$$

= $(1 + x) \left[z_2 - \beta x \left(1 - \frac{x}{\gamma} \right) + \beta z_1 + \delta y \right].$ (A.9)

 \otimes Springer

Substituting $(A.8)$ $(A.8)$ $(A.8)$ in $(A.9)$ $(A.9)$ $(A.9)$ and after simplification, we obtain

$$
\left\{ xy - (1+x) \left[x \left(1 - \frac{x}{\gamma} \right) - z_1 \right] \right\} \beta y
$$

$$
- xy\alpha \left[z_2 - \beta x \left(1 - \frac{x}{\gamma} \right) + \beta z_1 + \delta y \right] = 0. \tag{A.10}
$$

After re-arranging the terms in $(A.10)$ $(A.10)$ we get

$$
z_2 = \frac{\beta}{\alpha x} \Big[1 - x(\alpha - 1) \Big] z_1 + \Big[y(\beta - \delta \alpha) - \beta \Big[1 - x(\alpha - 1) \Big] \Big(1 - \frac{x}{\gamma} \Big) \Big]. \tag{A.11}
$$

The above linear relation between z_1 and z_2 imply that the sets $Q(t, x, y)$ are segments that are convex. Thus, if *Ω* is non-empty then the time optimal control problem (14) (14) has an absolute minimum.

References

- Azzouz, H., Giordanengo, P., Wäckers, F. L., & Kaiser, L. (2004). Effects of feeding frequency and sugar concentration on behavior and longevity of the adult aphid parasitoid: *Aphidius ervi* (Haliday) (Hymenoptera: Braconidae). *Biol. Control*, *31*, 445–452.
- Beach, J. P., Williams, L. III, Hendrix, D. L., & Price, L. D. (2003). Different food sources affect the gustatory response of *Anaphes iole*, an egg parasitoid of *Lugus* spp. *J. Chem. Ecol.*, *29*, 1203–1222.
- Berndt, L. A., Wratten, S. D., & Hassan, P. (2002). Effects of buckwheat flowers on leafroller (Lepidoptera: Tortricidae) parasitoids in a New Zealand vineyard. *Agric. For. Entomol.*, *4*, 39–45.
- Bilde, T., & Toft, S. (1998). Quantifying food limitation of arthropod predators in the field. *Oecologia*, *115*, 54–58.
- Buttermore, R. E., Turner, E., & Morrice, M. G. (1994). The introduced northern Pacific seastar *Asterias amurensis* in Tasmania. *Mem. Qld. Mus.*, *36*, 21–25.
- Cesari, L. (1983). *Applications of mathematics series: Vol. 17*. *Optimization—theory and applications: problems with ordinary differential equations*. New York: Springer.
- Clark, C. W. (2005). *Mathematical bioeconomics—the optimal management of renewable resoruces*. New Jersey: Wiley.
- Coll, M., & Guershon, M. (2002). Omnivory in terrestrial arthropods: mixing plant and prey diets. *Annu. Rev. Entomol.*, *47*, 267–297.
- Davis, S. E., Nager, R. G., & Furness, R. W. (2005). Food availability affects adult survival as well as breeding success of Parasitic Jaegers. *Ecology*, *86*(4), 1047–1056.
- DeBach, P., & Rosen, D. (1974). *Biological control by natural enemies*. London: Cambridge University Press.
- De Clercq, P. (2008). Culture and natural enemies on factitious foods and artificial diets. In J. L. Capinera (Ed.), *Encyclopedia of entomology* (Vol. I, pp. 1133–1136). Dordrecht: Springer.
- Fadamiro, H. Y., & Heimpel, G. E. (2001). Effects of partial sugar deprivation on lifespan and carbohydrate mobilization in the parasitoid *Macrocentrus grandii* (Hymenopters: Braconidae). *Ann. Entomol. Soc. Am.*, *94*, 909–916.
- Gurr, G. M., & Wratten, S. D. (1999). Integrated biological control: a proposal for enhancing success in biological control. *Int. J. Pest Manag.*, *45*(2), 81–84.
- Harmon, J. P. (2003), Indirect interactions among a generalist predator and its multiple foods. Ph.D. thesis, St. Paul, MN, University of Minnesota.
- Harwood, J. D., Sunderland, K. D., & Symondson, W. O. C. (2004). Prey selection by linyphiid spiders: molecular tracking of the effects of alternative prey on rates of aphid consumption in the field. *Mol. Ecol.*, *13*, 3549–3560.
- Harwood, J. D., Sunderland, K. D., & Symondson, W. O. C. (2005). Monoclonal antibodies reveal the potential of the tetragnathids spider *Pachygnatha degeeri* (Araneae: Tetragnathidae) as an aphid predator. *Bull. Entomol. Res.*, *95*, 161–167.
- Harwood, J. D., & Obrycki, J. J. (2005). The role of alternative prey in sustaining predator populations. In M. S. Hoddle (Ed.), *Proc. second int. symp. biol. control of arthropods* (Vol. II, pp. 453–462).
- Hendrix, D., Wei, Y., & Leggett, J. E. (1992). Homopteran honeydew sugar composition is determined by both the insect and plant species. *Comp. Biochem. Physiol. B*, *101*, 23–27.
- Holling, C. S. (1959). Some characteristics of simple types of predation and parasitism. *Can. Entomol.*, *91*, 385–398.
- Jervis, M. A. (1998). Functional and evolutionary aspects of mouthpart structure in parasitoid wasps. *Biol. J. Linn. Soc.*, *63*, 461–493.
- Kot, M. (2001). *Elements of mathematical ecology*. Cambridge: Cambridge University Press.
- Lafferty, K. D., & Kuris, A. M. (1994). Potential uses for biological control of alien marine species. In D. Cottingham (Ed.), *Proc. conf. and workshop on nonindigenous estuarine and marine organisms, U.S. Department of Commerce, NOAA Office of the Chief Scientist*. Washington: U.S. Gov. Printing Office.
- Lafferty, K. D., & Kuris, A. M. (1996). Biological control of marine pests. *Ecology*, *77*(7), 1989–2000.
- Landis, D. A., Wratten, S. D., & Gurr, G. M. (2000). Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annu. Rev. Entomol.*, *45*, 175–201.
- Margaritopoulos, J. T., Tsitsipis, J. A., & Perdikis, D. C. (2003). Biological characteristics of the mirids *Macrolophus costalis* and *Macroplophus pygmaeus* preying on the tobacco form of *Myzus persicae* (Hemiptera: Aphididae). *Bull. Entomol. Res.*, *93*, 39–45.
- McDougall, S. J., & Mills, N. J. (1997). The influence of hosts, temperature and food sources on the longevity of *Trichogramma platneri*. *Entomol. Exp. Appl.*, *83*, 195–203.
- Miller, R. F. (1985). Sea urchin pathogen: a possible tool for biological control. *Mar. Ecol. Prog. Ser.*, *21*, 169–174.
- Moyle, P. B. (1991). Ballast water introductions. *Fishereis*, *16*, 4–6.
- Murdoch, W. W., Chesson, J., & Chesson, P. L. (1985). Biological control in theory and practice. *Am. Nat.*, *125*(3), 344–366.
- Perdikis, D., & Lykouressis, D. (2000). Effects of various items, host plants, and temperature on the development and survival of *Macrolophus pygmaeus* Rambur (Hemiptera: Miridae). *Biol. Control*, *17*, 55–60.
- Perdikis, D., & Lykouressis, D. (2004). Macrolophus pygmaeus (Hemiptera: Miridae) population parameters and biological characteristics when feeding on eggplant and tomato without prey. *J. Econ. Entomol.*, *97*, 1291–1298.
- Perdikis, D., Lykouressis, D., & Economou, L. (1999). The influence of temperature, photoperiod and plant type on the predation rate of *Macrolophus pygmaeus* on *Myzus persicae*. *BioControl*, *44*, 281–289.
- Sabelis, M. W., & van Rijn, P. C. J. (2005). When does alternative food promote biological pest control. In M. S. Hoddle (Ed.), *Proc. second int. symp. biol. control of arthropods* (Vol. II, pp. 428–437).
- Shannon, P. S., Chrzanowski, T. H., & Grover, J. P. (2007). Prey food quality affects flagellate ingestion rates. *Microb. Ecol.*, *53*, 66–73.
- Siekmann, G., Tenhumberg, B., & Keller, M. A. (2001). Feeding and survival in parasitic wasps: sugar concentration and timing matter. *Oikos*, *95*(3), 425–430.
- Srinivasu, P. D. N., Prasad, B. S. R. V., & Venkatesulu, M. (2007). Biological control through provision of additional food to predators: a theoretical study. *Theor. Popul. Biol.*, *72*, 111–120. doi[:10.1016/](http://dx.doi.org/10.1016/j.tpb.2007.03.011) i.tpb.2007.03.011.
- Srinivasu, P. D. N., & Prasad, B. S. R. V. (2010). Time optimal control of an additional food provided predator–prey system with applications to pest management and biological conservation. *J. Math. Biol.*, *60*, 591–613. doi[:10.1007/s00285-009-0279-2](http://dx.doi.org/10.1007/s00285-009-0279-2).
- Toft, S. (2005). The quality of aphids as food for generalist predators: implications for natural control of aphids. *Eur. J. Entomol.*, *102*(3), 371–383.
- van Baalen, M., Křivan, V., van Rijn, P. C. J., & Sabelis, M. W. (2001). Alternative food, switching predators, and the persistence of predator–prey systems. *Am. Nat.*, *157*(5), 512–524.
- van Rijn, P. C. J., van Houten, Y. M., & Sabelis, M. W. (2002). How plants benefit from providing food to predators even when it is also edible to herbivores. *Ecology*, *83*, 2664–2679.
- Vandekerkhove, B., & De Clercq, P. (2010). Pollen as an alternative or supplementary food for the mirid predator. *Macrolophus pygmaeus. Biol. Control*, *53*, 238–242.
- Wäckers, F. L. (2004). Assessing the suitability of flowering herbs as parasitoid food soruces: flower attractiveness and nectar accessibility. *Biol. Control*, *29*, 307–314.
- Wäckers, F. L. (2005). Suitability of (extra-) floral nectar, pollen, and honeydew as insect food sources. In F. L. Wäckers, P. C. J. van Rijn, & L. Bruin (Eds.), *Plant-provided food for carnivorous insects, a protective mutualism and its applications* (pp. 17–74). London: Cambridge University Press.
- Wade, M. R., Zalucki, M. P., Wrateen, S. D., & Robinson, K. A. (2008). Conservation biological control of arthropods using artificial food sprays: current status and future challenges. *Biol. Control*, *45*, 185–199.
- Wootton, J. T. (1994). The nature and consequences of indirect effects in ecological communities. *Ann. Rev. Ecol. Syst.*, *25*, 443–466.
- Wratten, S., Berndt, L., Gurr, G., Tylianakis, J., Fernando, P., & Didham, R. (2002). Adding floral diversity to enhance parasitoid fitness and efficacy. In R. G. Van Driesche (Ed.), *Proc. first int. symp. biol. control of arthropods* (pp. 211–214).
- Wu, H., Meng, L., & Li, B. (2008). Effects of feeding frequency and sugar concentrations on lifetime reproductive success of *Meteorus pulchricornis* (Hymenoptera: Braconidae). *Biol. Control*, *45*, 353– 359.
- Zhao, B., Qiu, J. W., & Qian, P. Y. (2003). Effects of food availability on larval development in the slipper limpet *Crepidula onyx* (Sowerby). *J. Exp. Mar. Biol. Ecol.*, *294*, 219–223.