Modelling the influence of prey switching and optimal foraging on the control of banana weevil *Cosmopolites Sordidus*(Germar)

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Abstract

A mathematical model for the control of the banana weevil *Cosmopolites Sordidus* (Germar) by predatory ant species is formulated and analyzed. The model incorporates predator switching to a non-dynamic alternative food source, optimal foraging theory and self regulation in both the banana weevil and predatory-ant species! Using Lyapunov's first method, the local stability of the equilibria is established. Furthermore, conditions for the existence of the interior equilibrium are derived and its global stability established by the Bendixson–Dulac criterion with periodic orbits ruled out by the Poincare–Bendixson theorem. It is determined that intrinsic growth rates and carrying capacities rather than handling time and nutritional value have significant impact on the banana weevils–predatory ant interaction. Numerical simulations confirm the theoretical results.

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1. Introduction

One of the main challenges of the 21st century is the steady provision of food to the ever increasing global population. Overcoming this challenge partly entails protecting food crops from pests and diseases now becoming more profound due to increased international travel and trade and changing

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environmental and climatic conditions. Globally, pests are a major cause of plant yield losses. For example, Oerke and Dehne [19] estimate that about 32% of global crop yield is lost to pests.

Bananas are of particular significance in the fight against global hunger and poverty especially in least developed, low income, food deficit countries where they contribute not only to food security as a staple food crop but also to income generation as a cash crop. In Eastern Africa, one of the largest producers and consumers of bananas, the banana weevil *Cosmopolites sordidus* (Germar), is the single most significant pest of bananas. It has been credited with the decline and disappearance of the popular East African highland cooking bananas from their traditional growing areas of central Uganda and western Tanzania thereby heralding a shift to the more resistant beer varieties and other crops such as cassava, maize and potatoes [12]. Furthermore, it has been identified as the principal vector of banana *xanthomonas* wilt –the disease that has, in the past decade, ravaged plantations in the region putting millions of livelihoods at the risk of starvation and economic ruin [27].
The banana weevil is an evasive pest; the adult is free living and nocturnal while the juvenile stages (i.e. the larva and pupa) reside well inside the corm and are largely inaccessible. This lifestyle is partly responsible for the futile attempts at its complete eradication. The adult lays eggs in the leaf sheaths at the plant base and upon hatching, the larvae tunnel into the corm. Tunneling interferes with root initiation and water and nutrients uptake thereby compromising the plant stability culminating into snapping and toppling, smaller bunch sizes, delayed maturation and mat die–out.

Presently, a number of management strategies against the banana weevil are practiced namely: cultural control practices such as use of clean planting materials, trapping and crop sanitation; growing resistant varieties; use of natural enemies and application of pesticide –which is always the last advisable option given that pesticides may have adverse effects to the environment, may be unaffordable to poor farmers who form the majority in developing countries in addition to the risk of pests developing resistance to particular pesticides. Singly, these control measures may not amount to much but as a complete package in a framework called integrated pest management (IPM), some degree of success can be registered. IPM is widely employed in pest suppression and involves use of all suitable measures in combination in ways that complement each other.

Biological control measures against plant pests are highly recommended worldwide especially in mitigating the effects of pesticide use. When available, biological control is the most desirable as it is not only environmentally friendly but also requires little or no investment on the part of the farmer. The banana weevil along with its host–the banana plant, are believed to be originated in the Indo-Malay region of south east Asia from which it spread to all the world's major banana producing regions. While the pest is economically significant in other regions including East Africa, it is not so significant in it's reported area of origin. This has been attributed to the presence of co-evolved natural enemies. Biological control of the banana weevil has registered mixed results. In Cuba, myrmicine ant species reportedly reduced banana weevil numbers in heavily infested plantations [20] while in Fiji use of the predatory beetle, *Plaesius Javanus* imported from Java, Indonesia successfully controlled banana weevil infestation [26]. This success has however not been reciprocated elsewhere. Attempts to introduce these agents in other regions including East Africa failed probably due to low release numbers and failure to establish.

This notwithstanding, a number of studies to identify potential predators of the banana weevil in East Africa and elsewhere have been undertaken. Abera [2] carried out studies in Uganda to identify potentially important predators of the banana weevil and found several ant species. Two

such species, *Odontomachus troglodytes* Santschi and *Pheidole sp.2*, demonstrated ability to remove eggs from naturally infested corms and residues. In a further field trial to experimentally evaluate the impact of these two species on banana weevil in Uganda, it was discovered that ants were able to reduce the density of eggs during a full crop cycle lasting up to 30 months [1].

Ants have been proposed as potential bio control agents of the banana weevil in East Africa [13] and in parts of Asia and the Pacific islands [26]. Ants are best suited as bio control agents of insect pests of perennial crops in general and the banana weevil in particular. While other generalist predators appear to have limited ability to find banana weevil eggs, larvae and pupae underneath the corm and other plant tissue, this is not the case with ants. Ants have been observed digging through the soil and foraging inside corm tunnels. And although they are generalist predators, they are regarded as superior foragers because they are abundant, recruit each other to productive food sources and are not affected by satiation since individual ants do not forage for themselves but rather for the colony [21]. Ants can also be manipulated and deployed by moving their colony to where the pest infestation is highest. The use of service crops in enhancing ants predation rate of the banana weevil was studied by Dassou [8]. It was demonstrated, for example, that adding a service plant (*Branchiaria decumbens*) boosted banana weevil predation by generalists predators, notably, the ants of the species *selonopsis geminata* and that intercropping banana with tuber crops of the genus *xanthosoma* increased the abundance of ants of the genus *ondotomachus* and significantly reduced banana weevil damage on banana plants.

Mathematical models for predator–prey interactions are well established in literature and owe their formulation and prominence to Alfred Lotka and Vito Volterra who, in 1925, independently formulated the first predator–prey models. As well, mathematical models in which the predator feasts on multiple preys switching among them are plentiful in literature in addition to models incorporating optimal foraging theory. Krivan [14] considered a system consisting of one predator–two prey types with optimal foraging and discussed the effect of optimal diet choice on the stability of the system. It was shown that if the unprofitable prey species is close to its carrying capacity (and therefore not strongly regulated by the predator), switching may lead to reduced fluctuations in the three species system. Similarly, using numerical simulations of one predator– two prey system, Fryxell and Lundberg [9, 10] demonstrated that predators switch to the low quality prey only when they have reduced the more profitable prey to low densities and that such a switch diminishes predation pressure on the more profitable prey while at the same time buffering predator density. In Krivan and Sikder [15], it was shown that switching increases the range of parameters for which one predator–two prey systems are persistent and that while populations may fluctuate, in the long run, neither population goes extinct. Tansky [23] investigated a two-prey one predator system with a switching property and proved using Routh–Hurwitz criteria that the system generally has a stable three species co-existing equilibrium while van Leeuwen [25] developed a theory for the food intake of a predator that switches between multiple prey species. The theory is based on the behavioral assumption that a predator tends to continue feeding on the prey it consumed last in terms of morphology, defense, location, habitat, choice or behavior. From the predator's dietary history, they derived a general closed–form multi species functional response for predicting predators switching between multiple prey species. Ma [17] investigated the dynamics of a series of two–prey-one-predator models in which the predator exhibits adaptive diet choice based on different energy content and/or handling times. They showed that if the predator is efficient at exploiting its preys and has a saturating functional response, then sustained population cycles over a wide range of parameter values will be produced. In Boukal and Krivan [6], a prey-predator model with alternative food and optimal foraging is designed. Using

suitable Lyapunov functions, the authors showed that optimal foraging behavior changes the neutral stability intrinsic to Lotka–Volterra systems to the existence of a bounded global attractor.

The role of alternative prey or food species in predator–prey dynamics has been considered by many authors. For example, Banshidhar [5] studied the global stability of a predator–prey system with alternative prey incorporating logistic growth in the prey population and Holling type II response function. The existence and local stability conditions were derived and bifurcation analysis carried out with respect to the predator's search rate and handling time. Relatedly, in van Baalen *et al* [24], a predator–prey model with switching and a non–dynamics alternative prey was investigated to study the interaction between the predator and the more profitable prey. The authors showed that inclusion of a non–dynamic alternative food reduces the dimensions of the model from three to two and allows use of phase plane analysis but draw similar conclusions as in a two prey–one predator system.

In this study, a banana weevil (prey)– ants (predator) system with a non–dynamics alternative food which is also the most profitable prey is formulated with focus on the interaction between the predator and the less profitable prey. Ants largely depend on the abundant flora and fauna found in a banana ecosystem but supplement it by foraging on the banana weevil. This model differs significantly from the van Baalen *et al* [24] model in two ways: it considers the alternative food as both non–dynamic and the most profitable and, in addition, includes self regulation in both the predator and prey populations.

The rest of the paper is organized as follows: in Section 2, the model is formulated and analyzed for its equilibrium points and their stability; in Section 3, numerical simulations are presented while in Section 4, the results are discussed and some conclusions drawn.

2. Model Formulation and Analysis

2.1. The Model

Consider a habitat in which predatory ants of density, $P(t)$, feast on two food items or sources: the banana weevils of density $N(t)$ and the numerous flora and fauna abundant in a banana agroecosystem, collectively referred to as the alternative food and of fixed density A. The following assumptions are made:

1. The two food sources differ in profitability, that is, nutritional value divided by handling time.
2. Both food items are randomly distributed in the habitat.
3. The two food items are complimentary rather than substitutable.
4. The predatory ants switch between the food items on the basis of availability and encounter– which is typical of ants.;
5. The alternative food items have no dynamics of their own; they are always available in large amounts and unlimited by consumption. This simplification reduces the dimension of the system.
6. In addition, the alternative food items are regarded the most profitable on the basis of their constant availability in large amounts and lesser handling time.
7. The banana weevil is regarded as the less preferred or less profitable prey based on the inaccessibility of the edible stage (i.e. the juvenile stages which reside well inside the corm) and the larger handling time. The banana weevil is assumed to have a higher nutritional value and therefore sought after.

8. By the optimal foraging theory, at any particular time, the predatory ants' diet may contain all or one of the food items. The most profitable prey (i.e. the alternative food) is always included in the diet while the less profitable (i.e. the banana weevil), may either be included or completely ignored depending on the relative density of the most profitable prey [14, 15, 16].

9. Let $p : 0 \leq p \leq 1$ be the probability that the predatory ants encounter the banana weevil, then by the optimal foraging theory, the predatory ant will maximize its food intake by completely ignoring the alternative prey if $p = 0$, otherwise it will consume all available prey if $p = 1$. This classical result in optimal foraging theory is called the 'zero–one rule' [22, 18].

10. Let T_a and T_n time units be, respectively, the handling times for the alternative prey and the banana weevil, then the functional response (i.e. the predator's per capita consumption rate) with respect to the alternative prey and the banana weevil are respectively, $f_a(N, A) = \frac{A}{1+T_aA+pT_nN}$ and $f_n(N, A) = \frac{pN}{1+T_aA+pTnN}$.

11. Let C_a and C_n be the respective nutritional values of the alternative prey and the banana weevil, then the predator's average food intake is given by $g(N, A) = C_af_a(N, A) + C_nf_n(N, A) = \frac{C_aA+C_npN}{1+T_aA+pT_nN}$.

Assuming logistic growth of both banana weevil and the predatory ants, then the following non–linear ODE system is used to simulate the interaction between the two food sources and their predation by the ants:

$$\frac{dN}{dt} = r_1N\left(1 - \frac{N}{K_1}\right) - \frac{pNP}{1 + T_aA + pT_nN},$$

$$\frac{dP}{dt} = r_2P\left(1 - \frac{P}{K_2}\right) + \frac{(C_aA + pC_nN)P}{1 + T_aA + pT_nN},$$

(2.1)

together with $N(0) > 0$ and $P(0) > 0$.

All parameters are positive constants: r_1 and r_2 respectively represent the intrinsic growth rates of the banana weevil and predatory ants with K_1 and K_2, their respective carrying capacities.
It should be noted that when $A = 0$, system (2.1) becomes a modified Holling–Tanner model applied in enzyme–substrate kinetics with a Michaelis–Menten functional response term (see Aziz–Alaoui and Okiye [3]).

2.2. Positivity and boundedness of the solution

Denote by R_+^2 and $Int(R_+^2)$, the nonnegative quadrant and its interior respectively. Then the following results apply:

Lemma 2.1. *The positive quadrant is invariant for system (2.1).*

Proof . It can be observed from the system (2.1) that the boundaries of the nonnegative quadrant R_+^2 are invariant. Therefore the pest and predator densities $N(t)$ and $P(t)$ are positive for all $t \geq 0$ whenever $N(0) > 0$ and $P(0) > 0$. The basic existence and uniqueness theorem for differential equations ensures that the positive solutions and the axes can not intersect. $\square$

It can be shown that under some assumptions that the solutions of system (2.1) which start in R_+^2 are ultimately bounded. First the following classical Lemma whose proof is found in Aziz-Alaoui [4] is presented.

Lemma 2.2. *Let ϕ be an absolutely continuous function satisfying the differential inequality*

$$\frac{d\phi(t)}{dt} + \alpha_1\phi(t) \le \alpha_2,$$

where $(\alpha_1, \alpha_2) \in R^2, \alpha_1 \ne 0$, then $\forall\ t \ge \tilde{T} \ge 0$,

$$\phi(t) \le \frac{\alpha_2}{\alpha_1} - \left(\frac{\alpha_2}{\alpha_1} - \phi(\tilde{T})\right) exp^{-(t-\tilde{T})}.$$

Definition 2.3. *A solution $\phi(t, t_0, x_0, y_0)$ of system (2.1) is said to be ultimately bounded w.r.t R_+^2 if there exists a compact region $A \in R_+^2$ and a finite set $T(T = T(t_0, x_0, y_0))$ such that, for any $(t_0, x_0, y_0) \in R \times R_+^2$, $\phi(t, t_0, x_0, y_0) \in A$ for all $t > T$.*

The following theorem establishes the invariance and boundedness of system (2.1).

Theorem 2.4. *Let A be a set defined by*

$$A = \{(N, P) \in R_+^2 : 0 \le N \le K_1; 0 \le N + P < L_1\},$$

where

$$L_1 = \frac{K_1(r_1 + 4)}{4} + \frac{K_2[(1 + r_2)(1 + T_aA + pT_nK_1) + C_aA + pC_nK_1]}{4r_2(1 + T_aA + pT_nK_1}),$$

then

1. *A is positively invariant, and*
2. *all solutions of system (2.1) starting in R_+^2 are ultimately bounded with respect to R_+^2 and eventually enter the attracting set A.*

Proof . From Lemma 2.1, as $N(0), P(0) \in A$, it suffices to show that $(N(t), P(t)) \in A$ for all $t \ge 0$. Since $N(t) > 0$ and $P(t) > 0$ in $Int(R_+^2)$, every solution $\phi(t) = (N(t), P(t))$ of system (2.1) which starts in $Int(R_+^2)$ satisfies the differential inequality $\frac{dN}{dt} \le \frac{r_1}{K_1}N(K_1 - N)$ if the first equation of system (2.1) is considered.

Analogously, $N(t)$ may be compared with the solution of the equation $\frac{du(t)}{dt} = \frac{r_1}{K_1}u(t)(K_1 - u(t))$ namely: $u(t) = \frac{K_1u_0}{(K_1-u_0)e^{-r_1t}+u_0}$ with $u(0) = u_0$. Thus, it follows that every nonnegative solution $\phi(t)$ of system (2.1) satisfies $N(t) \le K_1$ for $t \ge 0$.

Now, to prove that $(N(t) + P(t)) = L_1$ for all $t \ge 0$, define the function: $\sigma(t) = N(t) + P(t)$. Then its derivative is:

$$\frac{d\sigma(t)}{dt} = \frac{dN(t)}{dt} + \frac{dP(t)}{dt}$$
$$= r_1N\left(1 - \frac{N}{K_1}\right) - \frac{pNP}{1 + T_aA + pT_nN} + r_2P\left(1 - \frac{P}{K_2}\right) + \frac{(C_aA + pC_nN)P}{1 + T_aA + pT_nN}.$$

Since all parameters are positive and all solutions starting in R_+^2 remain in the quadrant, then

$$\frac{d\sigma(t)}{dt} \leq r_1 N \left(1 - \frac{N}{K_1}\right) + r_2 P \left(1 - \frac{P}{K_2}\right) + \frac{(C_a A + p C_n N) P}{1 + T_a A + p T_n N},$$

holds for all N, P nonnegative.

Again, since $max_{R_+^2} \left(r_1 N \left(1 - \frac{N}{K_1}\right)\right) = \frac{r_1 K_1}{4}$, then

$$\frac{d\sigma(t)}{dt} \leq \frac{r_1 K_1}{4} - \sigma(t) + N(t) + P(t) + r_2 P \left(1 - \frac{P}{K_2}\right) + \frac{(C_a A + p C_n N) P}{1 + T_a A + p T_n N},$$

$$\frac{d\sigma(t)}{dt} + \sigma(t) \leq \frac{r_1 K_1}{4} + K_1 + P(t)[1 + r_2 \left(1 - \frac{P}{K_2}\right) + \frac{(C_a A + p C_n K_1)}{1 + T_a A + p T_n K_1}],$$

$$\frac{d\sigma(t)}{dt} + \sigma(t) \leq \frac{K_1(r_1 + 4)}{4} + P(t)[1 + r_2 \left(1 - \frac{P}{K_2}\right) + \frac{(C_a A + p C_n K_1)}{1 + T_a A + p T_n K_1}]. \qquad (2.2)$$

Let $f(P) = P(t)[1 + r_2 \left(1 - \frac{P}{K_2}\right) + \frac{(C_a A + p C_n K_1)}{1 + T_a A + p T_n K_1}]$, then $f'(P) = 1 + r_2 - \frac{2 r_2}{K_2} P + \frac{C_a A + p C_n K_1}{1 + T_a A + p T_n K_1}$.

Now the maximum value of $f(P)$ occurs when $P^* = \frac{K_2}{r_2} \left(\frac{(1 + r_2)(1 + T_a A + p T_n K_1) + C_a A + p C_n K_1}{1 + T_a A + p T_n K_1}\right)$ and therefore

$$f_{max}(P) = \frac{K_2}{4 r_2} \left(\frac{(1 + r_2)(1 + T_a A + p T_n K_1) + C_a A + p C_N K_1}{1 + T_a A + p T_n K_1}\right)^2 \qquad (2.3)$$

Using (2.3) in (2.2) yields:

$$\frac{d\sigma(t)}{dt} + \sigma(t) \leq \frac{K_1(r_1 + 4)}{4} + \frac{K_2}{4 r_2} \left(\frac{(1 + r_2)(1 + T_a A + p T_n K_1) + C_a A + p C_n K_1}{1 + T_a A + p T_n K_1}\right)^2$$

$$\leq L_1$$

where

$$L_1 = \frac{r_2 K_1 (r_1 + 4)(1 + T_a A + p T_n K_1)^2 + K_2 \left[(1 + r_2)(1 + T_a A + p T_n K_1) + C_a A + p C_n K_1\right]^2}{4 r_2 (1 + T_a A + p T_n K_1)^2}$$

Using Lemma 2.2, for all $t \geq \tilde{T} \geq 0$ with $\alpha_1 = 1$ and $\alpha_2 = L_1$, then

$$\sigma(t) \leq L_1 - (L_1 - \phi(\tilde{T})) e^{-(t - \tilde{T})} \qquad (2.4)$$

and if $\tilde{T} = 0$, then

$$\sigma(t) \leq L_1 - (L_1 - \phi(\tilde{T})) e^{-t}. \qquad (2.5)$$

Hence, since $(N(0), P(0)) \in A$, then $\sigma(t) \leq L_1$ for all $t \geq 0$. It is also shown that as $t \to +\infty$, $\sigma(t) \leq L_1$. $\square$

The proof for part (b) proceeds as follows: Since solutions of the initial value problem $\frac{dN(t)}{dt} = \frac{r_1}{K_1} N(t) (K_1 - N(t))$ satisfy $N(t) \leq K_1$ for all $t \geq 0$, then clearly, $lim_{t \to \infty} N(t) \to K_1$.

Now, to prove that $lim_{t\to\infty}(N(t) + P(t)) \leq L_1$, let $\epsilon > 0$, then there exists a $T_1 > 0$ such that $N(t) < 1 + \frac{\epsilon}{2}$ for all $t \geq T_1$. From equation (2.4) with $\tilde{T} = T_1$, for all $t \geq T_1 \geq 0$,

$$\sigma(t) = N(t) + P(t) \leq L_1 - (L_1 - \sigma(T_1))e^{-(t-T_1)}$$
$$\leq L_1 - [L_1 - \sigma(T_1)e^{T_1}]e^{-t}$$
$$\leq L_1 - [L_1 e^{T_1} - (N(t) + P(t))e^{T_1}]e^{T_1}$$
$$\leq L_1 - [L_1 - (N(t) + P(t))e^{T_1}]e^{-t}$$
$$\sigma(t) = N(t) + P(t) \leq L_1 + \frac{\epsilon}{2} - [(L_1 + \frac{\epsilon}{2}) - (N(t) + P(t))e^{T_1}]e^{-t}. \tag{2.6}$$

Let $T_2 \geq T_1$ be such that $|(L_1 + \frac{\epsilon}{2}) - (N(t) + P(t))e^{T_1}|e^{-t} \leq \frac{\epsilon}{2}$ for all $t \geq T_2$, then

$$N(t) + P(t) \leq L_1 + \frac{\epsilon}{e} - \frac{\epsilon}{2}$$
$$\leq L_1.$$

Hence $lim_{t\to\infty}(N(t) + P(t)) \leq L_1$. This completes the proof and by extension the conclusion that system (2.1) is dissipative in R_+^2.

2.3. Equilibrium points

Equilibrium points are obtained by setting the right-hand side of system (2.1) to zero. This gives four equilibria namely: $E_0(0,0)$, $E_1(K_1, 0)$, $E_2\left(0, \frac{K_2(r_2(1+T_aA)+C_aA)}{r_2(1+T_aA)}\right)$ and $E_4(N^*, P^*)$, where

$$P^* = \frac{K_2\left(r_2(1 + Ta_a) + C_aA + pN(r_2T_n + C_n)\right)}{r_2(1 + T_aA + pT_nN)^2} \tag{2.7}$$

and N^* satisfies the equation

$$r_1r_2p^2T_n^2N^3 + r_1r_2pT_n\left(2(1 + T_aA) - K_1pT_n\right)N^2$$
$$+ \left(r_1r_2(1 + T_aA)((1 + T_aA) - 2K_1pT_n) + K_1K_2p^2(r_2T_2 + C_n)\right)N$$
$$+ K_1K_2p\left(r_2(1 + T_aA) + C_aA\right) - r_1r_2K_1(1 + T_aA)^2 = 0. \tag{2.8}$$

E_0 represents the trivial equilibrium or the absence of both the banana weevil and its predator while E_1 represents the banana weevil-only equilibrium in absence of the pest. On the other hand, E_1 is the pest–free equilibrium at which the predatory ants survives only on the alternative non-dynamic food item abundant in the banana ecosystem while E_4 represents the equilibrium at which both the banana weevil and the predatory ants co-exist.

It should be noted that the equation (2.8) has at least one positive real root if:

$$\frac{K_1K_2p[r_2(1 + T_aA) + C_aA] - r_1r_2K_1(1 + T_aA)^2}{r_1r_2p^2T_n^2} < 0$$

or

$$r_2 > \frac{K_2p\left(r_2(1 + T_aA) + C_aA\right)}{r_1(1 + T_aA)^2} \tag{2.9}$$

(see [11]).

2.4. Local Stability of the Equilibria

The Jacobian matrix for system (2.1) is given by

$$
J = \begin{pmatrix} r_1(1 - \frac{2N}{K_1}) - \frac{(1+T_aA)pP}{(1+T_aA+pT_nN)^2} & -\frac{pN}{1+T_aA+pT_nN} \\ \frac{pP(1+T_aA)C_n - C_aAT_n}{(1+T_aA+pT_nN)^2} & r_2(1 - \frac{2P}{K_2}) + \frac{C_aA+pC_nN}{1+T_aA+pT_nN} \end{pmatrix}. \tag{2.10}
$$

At the trivial equilibrium, the variational matrix is given by

$$
J_{E_0} = \begin{pmatrix} r_1 & 0 \\ 0 & r_2 + \frac{C_aA}{1+T_aA} \end{pmatrix},
$$

whose eigenvalues are r_1 and $r_2 + \frac{C_aA}{1+T_aA}$. Since all parameters are positive constants, then clearly E_0 is unstable.

Similarly, the Jacobian matrix at the equilibrium, E_1, is

$$
J_{E_1} = \begin{pmatrix} -r_1 & -\frac{pK_1}{1+T_aA+pT_nK_1} \\ 0 & r_2 + \frac{C_aA+pC_nK_1}{1+T_aA+pT_nK_1} \end{pmatrix},
$$

with,

$$
trace(J_{E_1}) = -r_1 + r_2 + \frac{C_aA + pC_nK_1}{1 + T_aA + pT_nK_1}
$$

and

$$
det(J_{E_1}) = -r_1 \left(r_2 + \frac{C_aA + pC_nK_1}{1 + T_aA + pT_nK_1} \right).
$$

Clearly, the equilibrium is locally asymptotically stable for some combination of parameters and unstable otherwise. In particular, E_2 is locally asymptotically stable when

$$
r_1 > \frac{r_2(1 + T_aA) + C_aA + pK_1(r_2T_n + C_n)}{1 + T_aA + pT_nK_1}
$$

At E_2, the Jacobian matrix is

$$
J_{E_1} = \begin{pmatrix} \frac{r_1r_2(1+T_aA)^2 - pK_2[r_2(1+T_aA)+C_aA]}{r_2(1+T_aA)^2} & 0 \\ \frac{pK_2[r_2(1+T_aA)+C_aA][(1+T_aA)C_n - C_aAT_n]}{r_2(1+T_aA)^3} & \frac{-r_2(1+T_aA)-C_aA}{(1+T_aA)} \end{pmatrix},
$$

with,

$$
\begin{aligned}
trace(J_{E_2}) &= \frac{r_1r_2(1+T_aA)^2 - pK_2\left(r_2(1+T_aA)+C_aA\right)}{r_2(1+T_aA)^2} - \frac{-\left(r_2(1+T_aA)+C_aA\right)}{(1+T_aA)} \\
&= \frac{r_1r_2(1+T_aA)^2 - \left(\left(r_2(1+T_aA)+C_aA\right)\left(pK_2 + r_2(1+T_aA)\right)\right)}{r_2(1+T_aA)^2}.
\end{aligned}
$$

Clearly, $trace(J_{E_1}) < 0$ if

$$r_1 r_2 (1 + T_a A)^2 < (r_2(1 + T_a A) + C_a A)(pK_2 + r_2(1 + T_a A))$$

$$r_1 r_2 < \frac{(r_2(1 + T_a A) + C_a A)(pK_2 + r_2(1 + T_a A))}{(1 + T_a A)^2}. \qquad (2.11)$$

Similarly,

$$det(J_{E_2}) = \frac{-(r_1 r_2 (1 + T_a A)^2 - pK_2(r_2(1 + T_a A) + C_a A))(r_2(1 + T_a A) + C_a A)}{r_2(1 + T_a A)^3}$$

such that $det(E_2) > 0$ if

$$r_1 r_2 (1 + T_a A)^2 < pK_2(r_2(1 + T_a A) + C_a A)$$

$$r_1 r_2 < \frac{pK_2(r_2(1 + T_a A) + C_a A)}{(1 + T_a A)^2}. \qquad (2.12)$$

From the inequalities (2.11) and (2.12), it is clear that the pest–free equilibrium point, E_2, is locally asymptotically stable if

$$r_1 r_2 < min\left\{ \frac{pK_2(r_2(1 + T_a A) + C_a A)}{(1 + T_a A)^2}, \frac{(r_2(1 + T_a A) + C_a A)(pK_2 + r_2(1 + T_a A))}{(1 + T_a A)^2} \right\}$$

The Jacobian matrix at the co-existence equilibrium point, E_3, is given by

$$J_{E_3} = \begin{pmatrix} r_1(1 - \frac{2N^*}{K_1}) - \frac{(1+T_a A)pP^*}{(1+T_a A + pT_n N^*)^2} & -\frac{pN^*}{1+T_a A + pT_n N^*} \\ \frac{pP^*(1+T_a A)C_n - C_a A T_n}{(1+T_a A + pT_n N^*)^2} & r_2(1 - \frac{2P^*}{K_2}) + \frac{C_a A + pC_n N^*}{1+T_a A + pT_n N^*} \end{pmatrix},$$

whose

$$trace(J_{E_3}) = r_1\left(1 - \frac{2N^*}{K_1}\right) - \frac{(1+T_a A)pP^*}{(1+T_a A + pT_n N^*)^2} + r_2\left(1 - \frac{2P^*}{K_2}\right) + \frac{C_a A + pC_n N^*}{1+T_a A + pT_n N^*}$$

such that $trace < 0$ if

$$r_1\left(1 - \frac{2N^*}{K_1}\right) < \frac{(1+T_a A)pP^*}{(1+T_a A + pT_n N^*)^2} - \frac{r_2(K_2 - 2P^*)}{K_2} - \frac{(C_a A + pC_n N^*)}{1+T_a A + pT_n N^*}$$

$$< Z_1 \qquad (2.13)$$

where

$$Z_1 = \frac{K_2 pP^*(1+T_a A) - [r_2(K_2 - 2P^*)(1+T_a A + pT_n N^*) + K_2(C_a A + pC_n N^*)](1+T_a A + pT_n N^*)}{K_2(1+T_a A + pT_n N^*)^2}.$$

Likewise,

$$det(J_{E_3}) = \left(r_1(1 - \frac{2N^*}{K_1}) - \frac{(1+T_a A)pP^*}{(1+T_a A + pT_n N^*)^2}\right)\left(r_2(1 - \frac{2P^*}{K_2}) + \frac{C_a A + pC_n N^*}{1+T_a A + pT_n N^*}\right)$$

$$+ \frac{p^2 N^* P^*(1+T_a A)C_n - C_a A T_n}{(1+T_a A + pT_n N^*)^3}$$

or

$$det = r_1\left(1 - \frac{2N^*}{K_1}\right)\left(\frac{r_2(K_2 - 2P^*)}{K_2} + \frac{C_aA + pC_nN}{1 + T_aA + pT_nN^*}\right)$$
$$-pP^*\left(\frac{K_2\left(r_2(1 + T_aA) + C_aA\right) - 2r_2P^*(1 + T_aA)}{K_2(1 + T_aA + pT_nN^*)^2}\right)$$

Now, $det(J_{E_3}) > 0$ if

$$r_1(1 - \frac{2N^*}{K_1}) > Z_2, \tag{2.14}$$

where

$$Z_2 = \frac{K_2(1 + T_aA)pP^* - [K_2(C_aA + pC_nN^*) + r_2(K_2 - 2P^*)(1 + T_aA + pT_nN^*)](1 + T_aA + pT_nN^*)}{K_2(1 + T_aA + pT_nN^*)^2}.$$

From equations (2.13) and (2.14), it is deduced that the co-existence equilibrium E_3 is locally asymptotically stable if $Z_1 < r_1(1 - \frac{2N^*}{K_1}) < Z_2$ or generally, $r_1(1 - \frac{2N^*}{K_1}) < min\{Z_1, Z_2\}$.

2.5. Global Stability of the Co–existence Equilibrium

The global stability of the co-existence equilibrium is proved using the classical Poincarẽ- Bendixson theorem and periodic orbits are ruled out using the Bendixson–Dulac criteria (see [7]). To prove that E_3 is globally asymptotically stable, it must be shown that system (2.1) has no non–constant solutions using the Poincarẽ- Bendixson theorem. In this case, if E_3 is the only equilibrium in the interior of R_+^2, all solutions with $N(0), P(0) > 0$ must have an omega limit point and thus can get arbitrarily close to E_3. If E_3 is locally asymptotically stable, then any solution that gets sufficiently close to E_3 must converge to E_3 and therefore E_3 must be globally asymptotically stable.

With this background, the global stability of E_3 is established as follows: Define $H(N, P) = \frac{1}{NP}$, the Dulac multiplier. Then clearly, $H(N, P) > 0$ whenever $N, P > 0$.
Let

$$f_1(N, P) = r_1N(1 - \frac{N}{K_1}) - \frac{pNP}{1 + T_aA + pT_nN}$$
$$f_1(N, P) = r_2P(1 - \frac{P}{K_2}) - \frac{(C_aA + pC_nN)P}{1 + T_aA + pT_nN}$$

and

$$\Delta(N, P) = \frac{\partial(f_1H)}{\partial N} + \frac{\partial(f_2H)}{\partial P}$$
$$= -\frac{r_1}{K_1P} + \frac{pPT_n}{(1 + T_aA + pT_nN)^2} - \frac{r_2}{K_2N}$$

such that $\Delta(N, P) < 0$ if in particular, $\frac{pPT_n}{(1+T_aA+pT_nN)^2} < \frac{r_2}{K_2N}$, then

$$r_2p^2T_n^2N^2 + pT_n\left(2r_2(1 + T_aA) - K_2P(N + r_2(1 + T_aA)^2 > 0.\right.$$

Now, for

$$r_2p^2T_n^2N^2 + pT_n[2r_2(1 + T_aA) - K_2P]N + r_2(1 + T_aA)^2 = 0,$$

then for equal roots,

$$(pT_n(2r_2(1+T_aA) - K_2P))^2 > 4r_2p^2T_n^2(1+T_aA)^2$$

$$r_2 < \frac{PK_2}{4(1+T_aA)}. \tag{2.15}$$

It has already been shown that the equilibrium E_3 exists if the inequality (2.9) holds. From both inequalities (2.9) and (2.15), $\frac{K_2pC_aA}{r_1(1+T_aA)} < r_2 < \frac{pK_2}{4(1+T_aA)}$ such that $\Delta(N,P) < 0$ whenever $r_2 < max\{\frac{pK_2}{4(1+T_aA)}, \frac{K_2pC_aA}{r_1(1+T_aA)}\}$. Thus, the Bendixson-Dulac criterion holds in the interior of R_+^2, and non–constant solutions exist in the interior of R_+^2 and so the equilibrium, E_3, is globally asymptotically stable whenever it exists.

3. Numerical Simulations

Numerical simulations, including phase portraits, were carried out using MATLAB soft ware for different combinations of parameter values estimated from literature and the different plots are shown in the Figures 1–7.
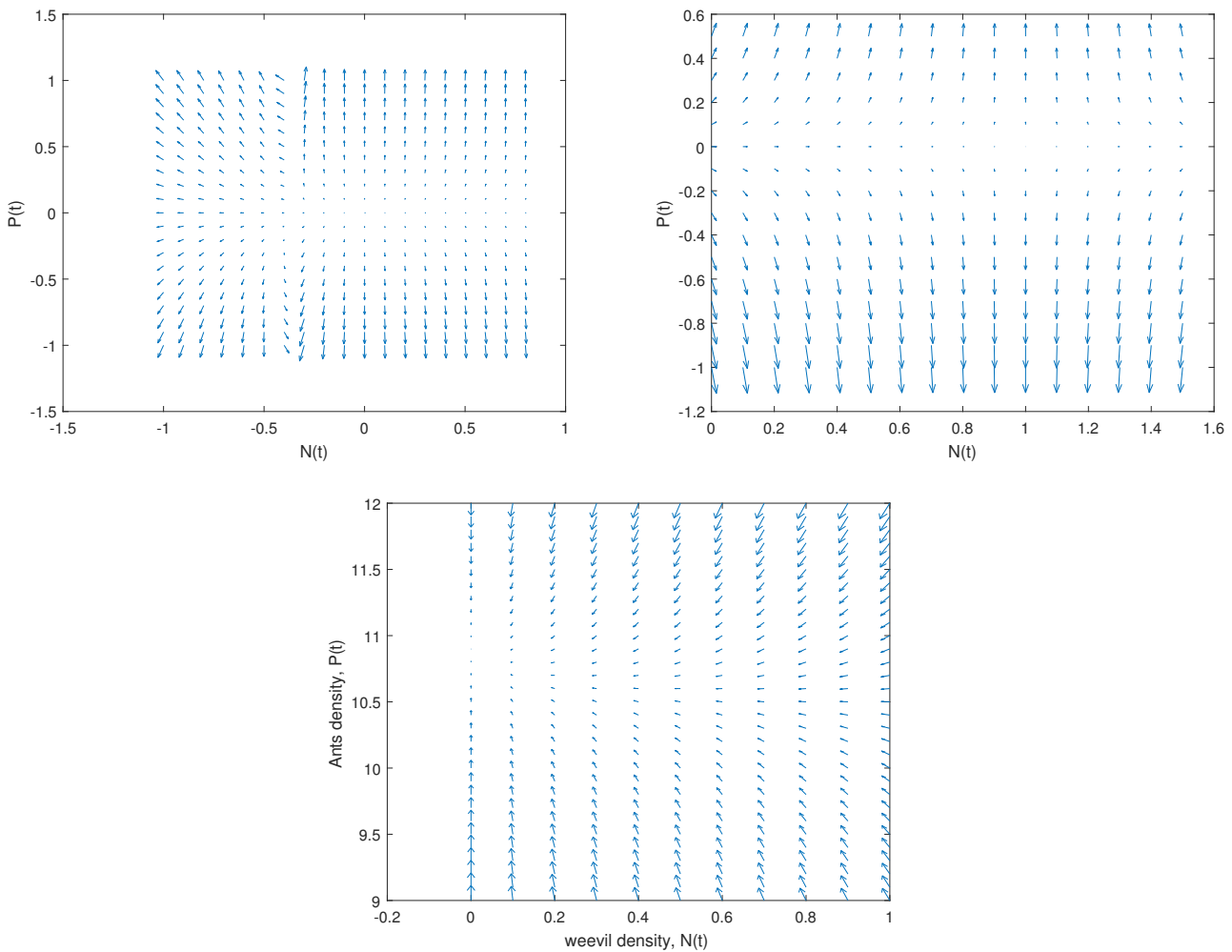

Figure 1: Directional fields for the state equilibria E_0, E_1 and E_2 for $r_1 = 1$, $r_2 = 5$, $k_1 = 1$, $K_2 = 10$, $T_a = 1$, $T_n = 5$, $p = 1$ and $c_a = c_n = 1$.
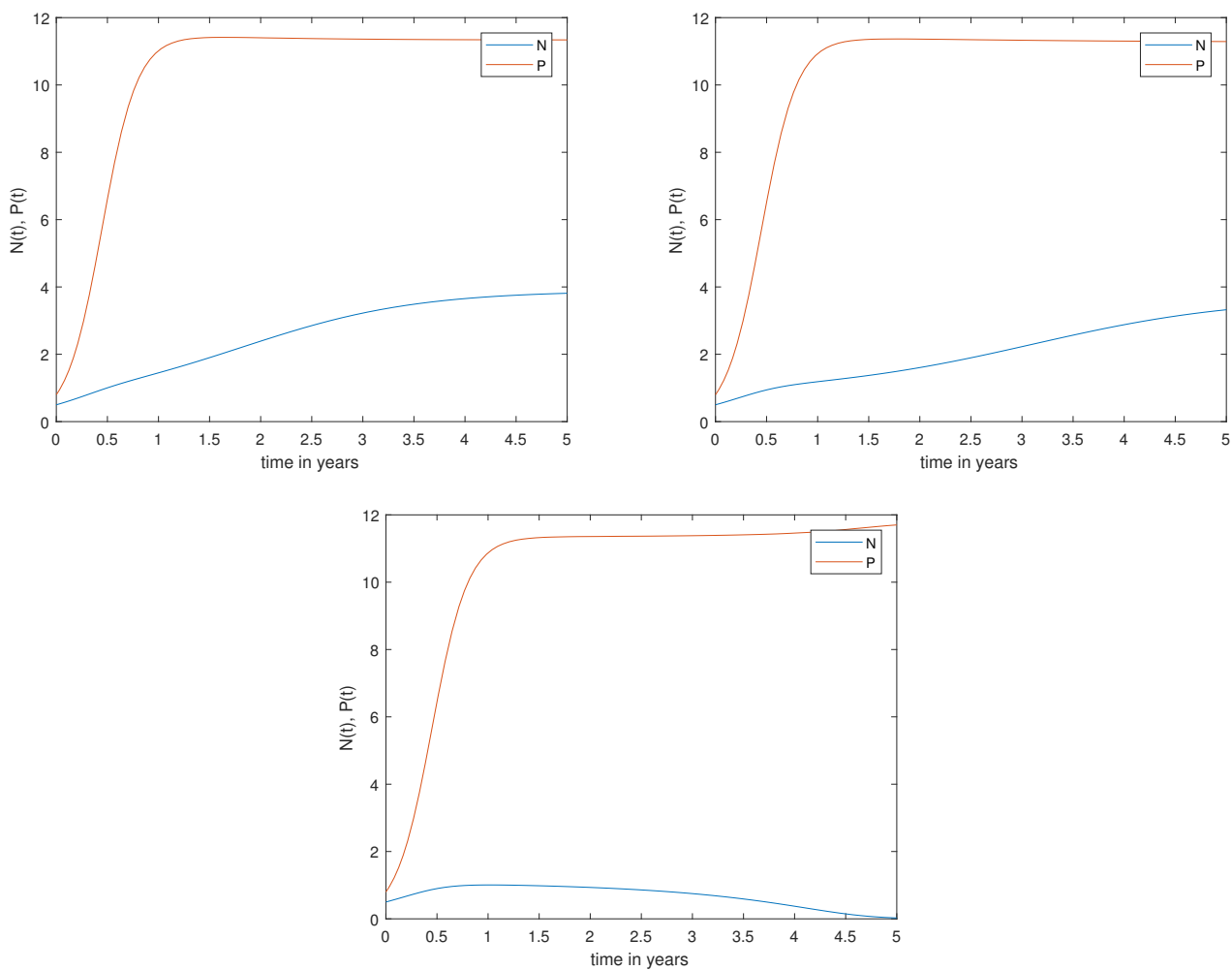
Figure 2: Illustrating the effect of optimal foraging on the banana weevil–ants interaction for $p = 0.3, 0.6, 1$ and $r_1 = 2$, $r_2 = 5$, $k_1 = 5$, $K_2 = 10$, $T_a = 1$, $T_n = 5$, $c_a = 2$, $c_n = 3$. As the probability of ants encounter with the banana weevils increases, the banana weevil population size progressively reduces to zero.

4. Discussion

A modified predator–prey model has been formulated to study the interaction between the banana weevil and its predator, the ant species, in the presence of alternative food. The model incorporates optimal foraging theory. In the absence of the predatory ants, the banana weevils grow logistically and likewise, in absence of the banana weevil, the predatory ants also grow logistically by feasting on the non-dynamic alternative food which is abundant, easily accessible and unlimited by consumption. The boundedness and invariance characters of the model are established. As well, the steady states are obtained and their stability determined. Phase plane analysis is carried out to establish the stability of the equilibria. And as well, numerical simulations are carried out to study the effect on the dynamics of the interaction between the banana weevil and its predator, for individual parameters namely: the intrinsic growth rates r_1 and r_2, the carrying capacities K_1 and K_2, the handling times T_a and T_n, the nutritional values c_a and c_n and the probability, p, that the predatory ant encounters the banana weevil. The model exhibits four equilibria: the trivial equilibrium, E_0, which represents the absence of both the banana weevil and its predator; the pest–only equilibrium, E_1, which marks the absence of the predator, the pest–free equilibrium, E_2 and the co-existence equi-
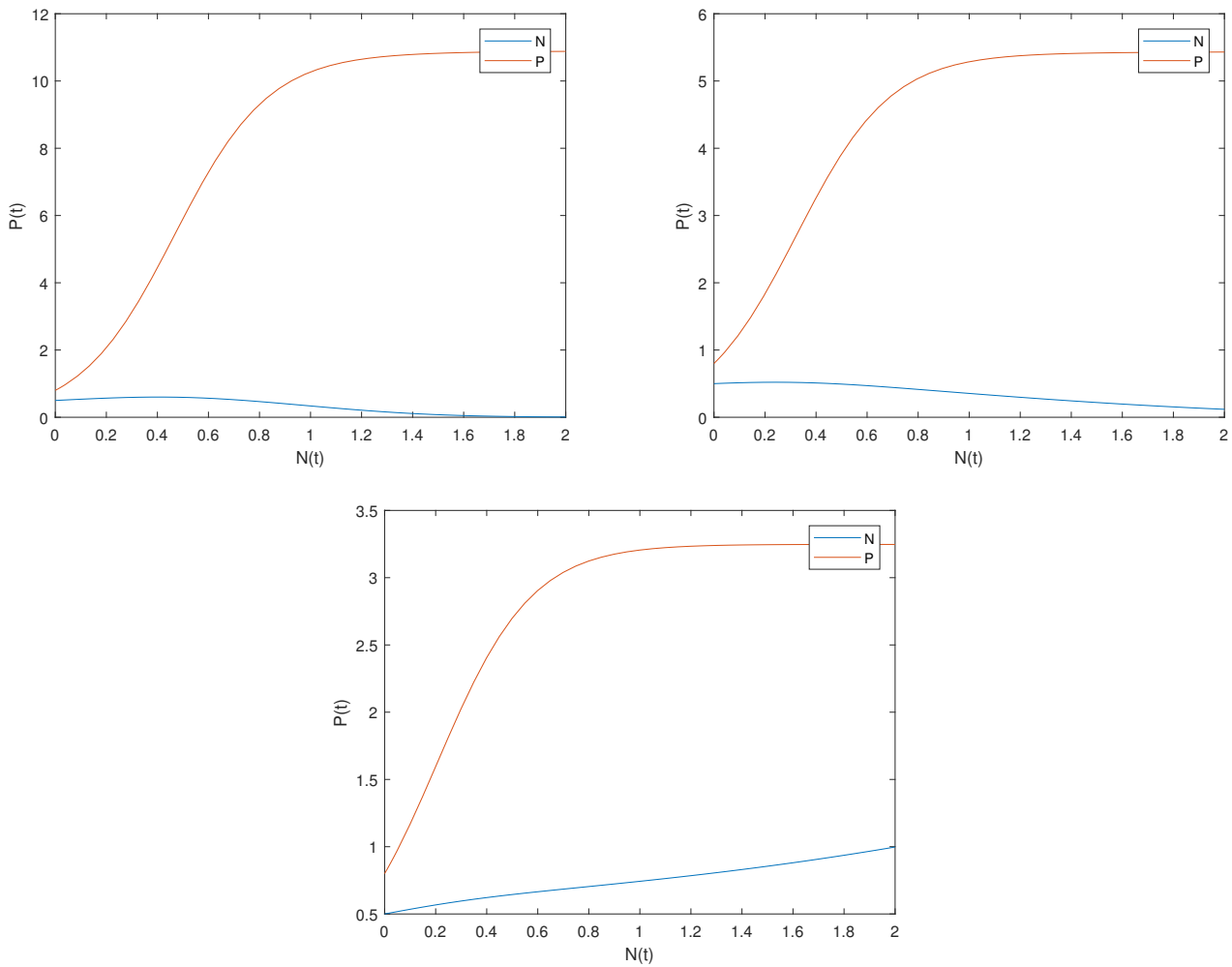
Figure 3: Demonstrating the effect of varying weevil and ants' carrying capacities on the dynamics of the model for $k_1 = k_2$, $k_1 < k_2$ and $k_1 > k_2$. When the weevil carrying capacity exceeds that of ants, both species will persist. Otherwise, the weevil population numbers will always fall to zero in finite time as a result of ants predation.

librium, E_3, at which both predatory ants and the banana weevil co-exist under certain conditions. The trivial equilibrium is always unstable as depicted in Figure 1, which is not surprising as, at this equilibrium, there are no interacting species to consider. Again from Figure 1, it can be observed that the trajectories about E_1 can be attracting in one direction and repelling in the other indicating that under particlar combinations of parameters, the equilibrium can be either stable or unstable. Figure 1 also clearly indicates that the banana weevil–free equilibrium, E_2, is always stable. This may be explained by the fact that the predatory ants always have sufficient alternative food to feed on in the absence of the banana weevils. As shown in Figures (2–7), ants' predation on the banana weevils results in suppression of the weevil numbers and for some particular combinations of parameters, may actually drive the banana weevil numbers to zero. The effect of optimal foraging on the banana weevil–ants interaction is depicted in Figure 2, where it is shown that as the probability of ants' encounter with the banana weevils increases progressively from zero to the maximum value, the weevil population size correspondingly reduces and eventually falls to zero. Relatedly, it is shown in Figure 3 that when the ants carrying capacity exceeds that of the banana weevils, predation will drive the banana weevil population size to zero and possible extinction in finite time, otherwise the two species will persist with the banana weevil at very low density compared to the ants. This
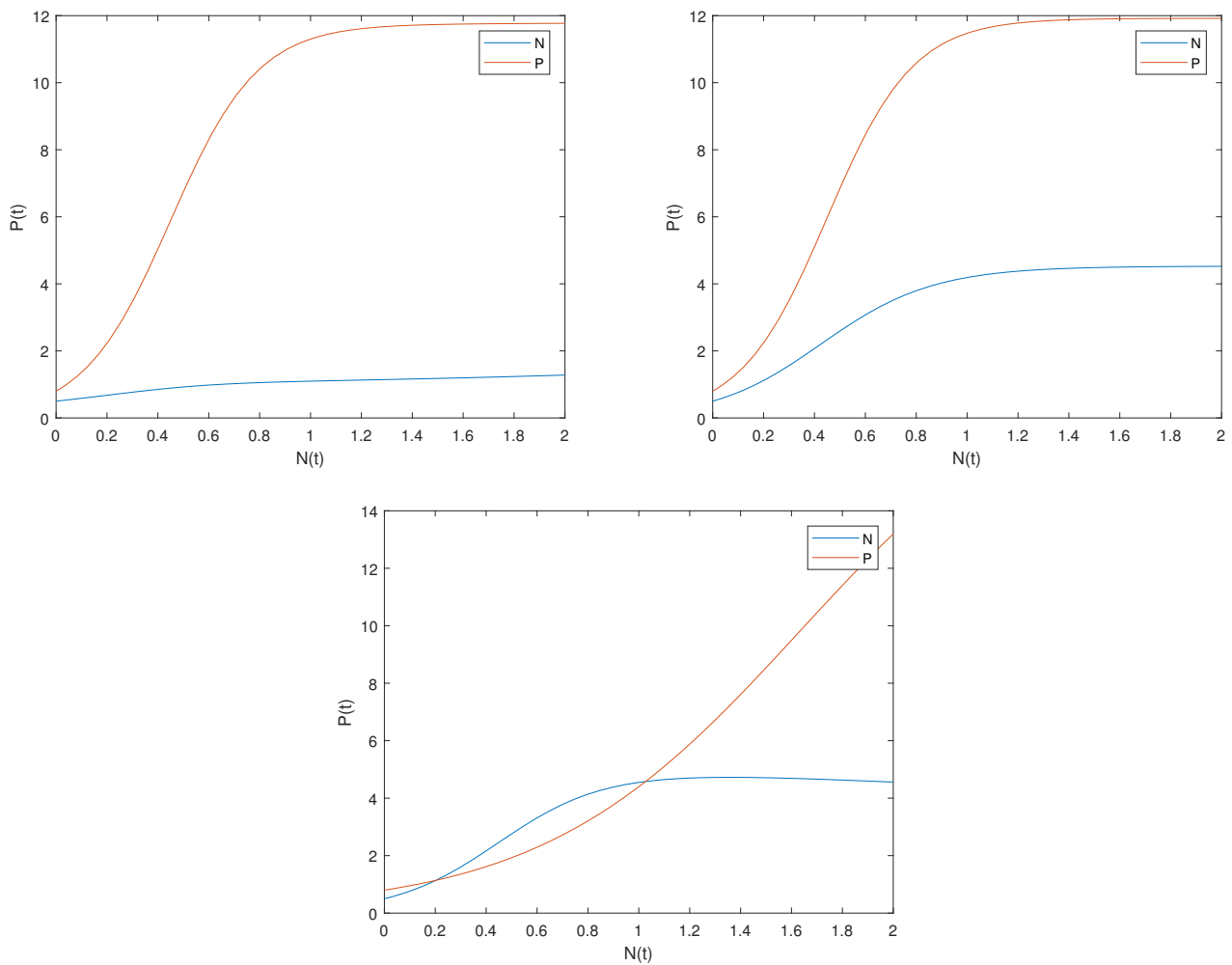
Figure 4: Simulating the weevil–ants' interaction for relative values of the intrinsic growth rates: $r_1 < r_2$, $r_1 = r_2$ and $r_1 > r_2$ for $k_1 = 5$, $T_a = 2$, $T_n = 5$, $p = 1$, $k_2 = 10$, $c_a = 2$ and $c_n = 5$. Keeping other factors constant, predation will always reduce the pest population density.
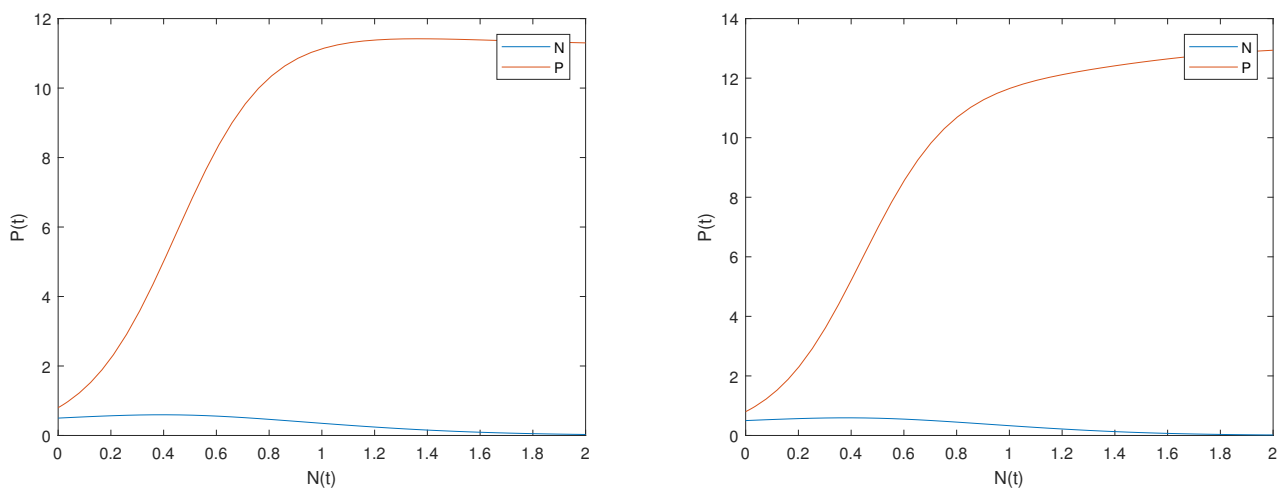

Figure 5: Illustrating the effect of weevil and alternative food's nutritional values on the long term dynamics of the model for different scenarios: $c_a < c_n$ and $c_a > c_n$ with $r_1 = 1$, $r_2 = 5$, $k_1 = 5$, $T_a = 2$, $T_n = 5$, $p = 1$ and $k_2 = 10$. It is shown that differences in nutritional values of the weevil and the alternative food have no demonstrable effect on the interaction between the pest and it's predator.
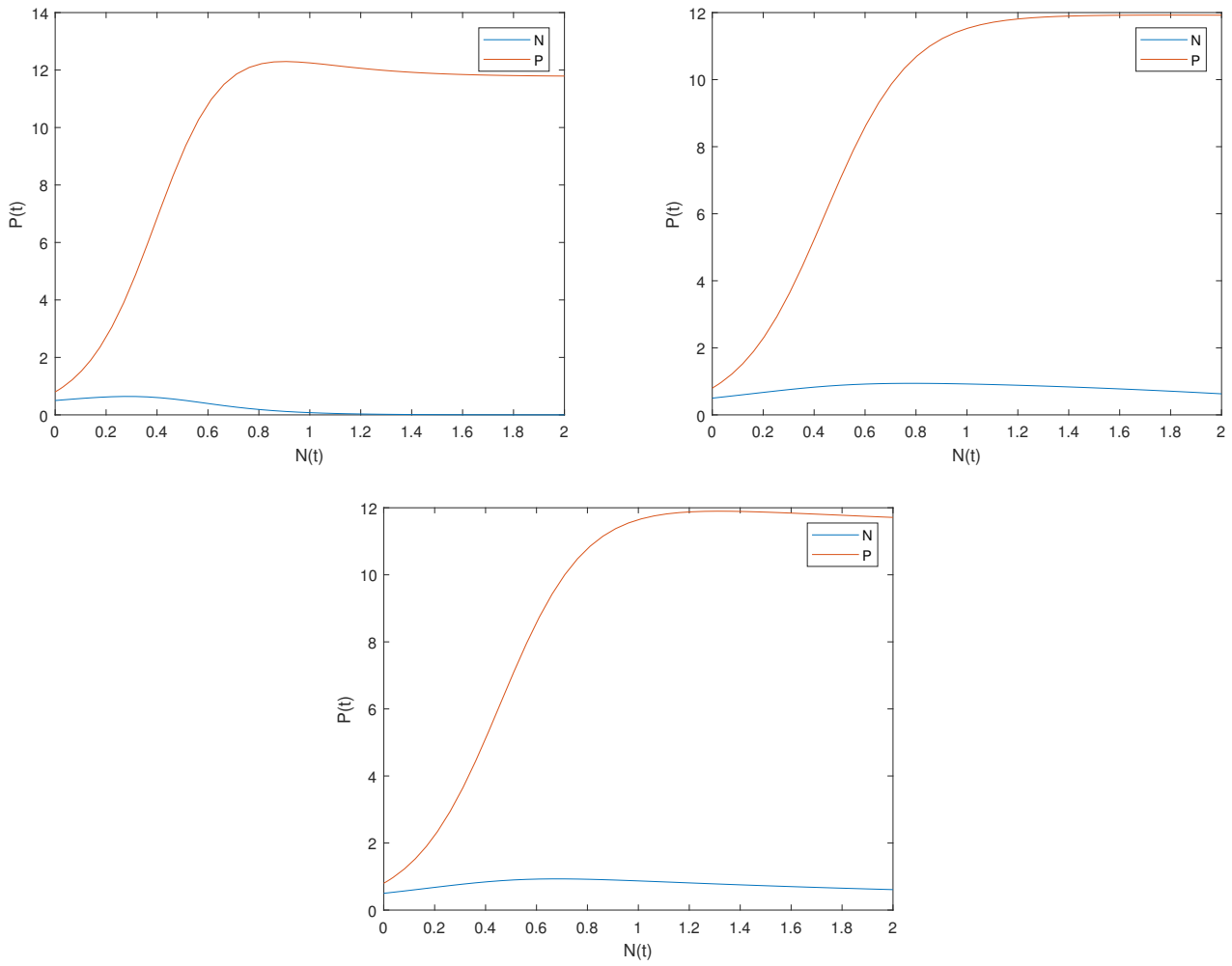
Figure 6: Simulating the effect of handling time on the dynamics of the model for different scenarios: $T_a < T_n$, $T_a = T_n$ and $T_a > T_n$ with $r_1 = 2$, $r_2 = 5$, $k_1 = 5$, $c_a = 2$, $5_n = 5$, $p = 1$ and $k_2 = 10$.
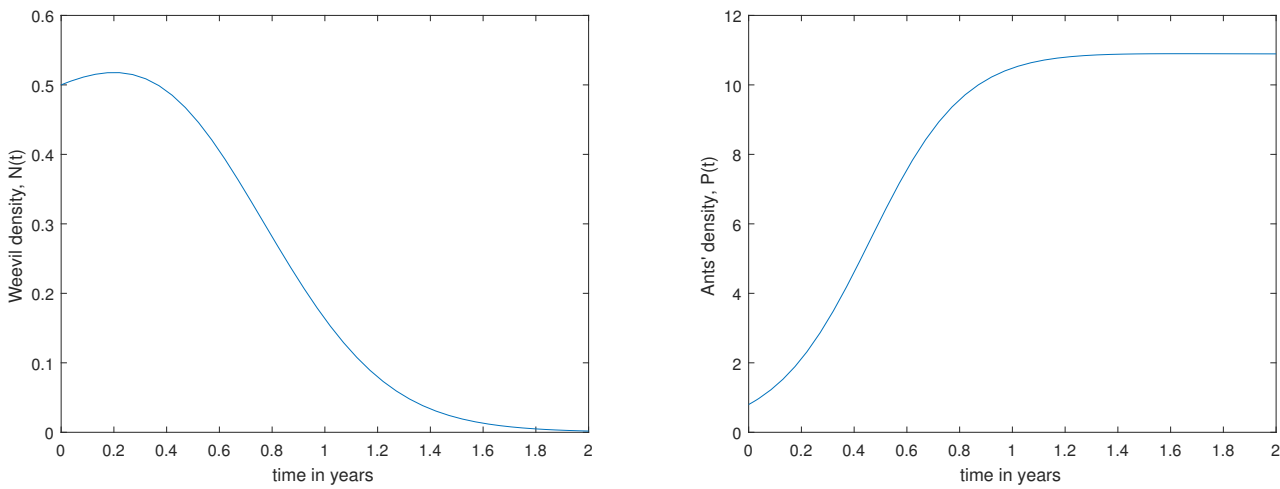

Figure 7: Variation of weevil and ant densities for $r_1 = 1$, $r_2 = 5$, $k_1 = 1$, $k_2 = 10$, $T_a = 1$, $T_n = 5$, $p = 1$ and $c_a = c_n = 1$. At appropriate parameter values, the ants population grows logistically to its carrying capacity at the expense of the banana weevil population whose size declines to zero as a result of predation.

co-existence is possible since the banana weevils have an alternative food source which is always abundant, easily accessible and unlimited by consumption. It is plausible to assume that the ants turn to feeding on the banana weevils when the weevil population size is high and upon significantly reducing it, the ants then revert to the ever abundant alternative food thereby leaving the weevil population size to build up again. In Figure 5, it is shown that differences in the nutritional values of the two food items have no demonstrable effect on the interaction between the banana weevil and its predator. This indicates that the ants predation on the banana weevil may be largely driven by abundance and/or availability rather than nutritional value–as the weevils become more abundant, their predation rate will increase until their numbers have been significantly reduced. The effect of handling time on the banana weevil–ants' interaction is depicted in Figure 6, where it is shown to have only marginal effect on the predation rate. Lastly, Figure 7 shows that at certain combination of parameters, the interaction between the banana weevil and the predatory ant species will ensure that the ant population size grows logistically to its carrying capacity at the expense of the weevil population which declines logistically to extinction in finite time.

Therefore the key parameters in the banana weevils–ants interaction are the their respective intrinsic growth rates and carrying capacities. The model predicts that encounters between the ants and weevils seem to be largely influenced by availability. One of the advantages of using ants as biological control agents of many plant pests is that their population sizes are manipulatable through such practices as colony transfer and as in the case of the banana weevils, use of service crops which increase ants density thereby increasing their predation rates [8]. These and similar practices increase the ants intrinsic growth rate and carrying capacity and so have a direct influence on the control of the banana weevils by ants. The other advantage of using ants as biological control agents is that they do not experience satiation at high prey densities and so their predation is continuous. Since the model predicts that and ants predation significants reduces banana weevil population size and given that ants have demonstrated significant ability to dig through the soil and corm in search of banana weevil eggs and larva [1, 2], it is imperative that farmers in heavily infested areas employ tactics to boost ants densities which will ultimately translate into high predation rate and eventual control of the pest through a means that is cheaper, effective and does little damage to the environment.

References

[1] AMK. Abera, CS. Gold and R. van Driesche, *Experimental Evaluation of the impacts of two ant species on banana weevil in Uganda*, Biol. Contr. 46(2008) 147–157.

[2] AMK. Abera, CS. Gold, R. van Driesche and PE. Ragama, *Composition, distribution and relative abundance of ants in banana farming systems in Uganda*, Biol. Contr. 40(2007) 168–178.

[3] MA. Aziz–Alaoui and MD. Okiye, *Boundedness and global stability for a predator–prey model with modified Leslie–Gower and Holling-Type II schemes,* Appl. Math. Lett. 16(2003) 1069–1075.

[4] MA. Aziz–Alaoui, *Study of Leslie–Gower–type tritrophic population*, Chaos Solitons and Fract. 14(8)(2002) 1275–1293.

[5] S. Banshidhar, *Global stability of predator–prey systems with alternative prey*, ISRN Biotechnol.(2013), `https://doi.org/10.5402/2013/898039`.

[6] DS. Boukal and V. Krivan, *Lyapunov functions for Lotka–Volterra models with optimal foraging behavior*, J. Math. Biol. 39(1999) 493–517.

[7] S. Busenburg, and O. van den Driessche, *A method for proving the non- existence of limit cycles*, J. Math. Analy. Appl. 172(1993) 463–479.

[8] AG. Dassou, D. Carval, S. Depigny, G. Fansi, and P. Tixier, *Ant abundance and Cosmopolites sordidus damage in plantain fields as affected by intercropping*, Biol. Contr. 81(2015) 51–57.

[9] JM. Fryxell and P. Lundberg, *Diet choice and predator–prey dynamics*, Evol. Ecol. 8(1994) 407–421.

[10] JM. Fryxell and P. Lundberg, *Individual behavior and community dynamics*, Chapman and Hall, London, UK,1997.

[11] C. Ganguli, TK. Kar and U. Das,*Consequences of providing alternative food to predator in an exploited prey-predator system controlled by optimal taxation*, Intern. J. Nonlin. Sci. 25(3)(2018) 131–150.

[12] CS. Gold, EB. Karamura, A. Kiggundu, F. Bagamba and AMK. Abera, *Geographical shifts in the highland bananas (Musa spp, group AAA-EA) production in Uganda*, Intern. J. Sust. Devel. Wor. Ecol. 6(1999) 45–59.

[13] DJ. Greathead, *Opportunities for biological control of insect pests in tropical Africa*, Revue. Zool. Afr. 100(1986) 85–96.

[14] V. Krivan, *Optimal foraging and predator–prey dynamics*, Theor. Popul. Biol. 49(1996) 265–290.

[15] V. Krivan and A. Sikder, *Optimal foraging and predator–prey dynamics II*, Theor. Popul. Biol. 55(1999) 111–126.

[16] V. Krivan and J. Eisner, *Optimal foraging and predator–prey dynamics III*, Theor. Popul. Biol. 63(2003) 269–279.

[17] BO. Ma, PA. Abrams and CE. Brassil, *Dynamics versus instantaneous models of diet choice*, Amer. Natur. 162(2003) 668–684.

[18] MW. Murdoch and A. Oaten, *Predation and population stability*, Adv. Ecol. Res., 9(1975) 11-31.

[19] EC. Oerke, HW. Dehne, *Safeguarding production losses in major crops and the role of crop protection*, Crop Prot., 23(2004) 275-285.

[20] R. Roche and S. Abreu, *Control of the banana weevil, Cosmopolites sordidus by the ant Tetramorium guineense*, Cienc. de la Agric. (Cuba) 17(1983) 41–49.

[21] PM. Room, *The relative abundances of ant species in Ghana's cocoa farms*, J. Anim. Ecol. 40(1971) 735–751.

[22] DW. Stephens and JR. Krebs, *Foraging theory: monographs in behavior and ecology* ed., Princeton University Press, Princeton, N.J, 1986.

[23] M. Tansky, *Switching effect on predator prey systems*, J. Theor. Biol. 70(1978) 263–271.

[24] M. van Baalen, V. Krivan, PCJ. van Rijn and MW. Sabelis, *Alternative food, switching predators and the persistence of predator–prey systems*, Amer. Natur.157(5)(2001) 512–524.

[25] E. van Leeuwen, A. Brannstrom, VAA. Jansen, U. Dieckmann and AG. Rossberg, *A generalized functional response for predators that switch between multiple prey species*, J. Theor. Biol. 328(2013) 89–98.

[26] DF. Waterhouse and KR. Norris, *Biological control: Pacific prospects*, Inkata Press, Melbourne, Australia,1987.

[27] E. Were, GV. Nakato, W. Ocimati, I. Ramathan, S. Olal and F. Beed, *The banana weevil, Cosmopolites Sordidus, (Germar), is a potential vector of Xanthomonas Campestris. pv. musacearum in bananas*, Canadian. J. Plant Pathol. 17(4)(2015).