Capítulo 8

Deceptive Pollination vs. Learning

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Abstract: In this work we propose and discuss a model describing the interaction between two species: a plant that gets pollinated by an insect population. The plants attract the insects deceiving them and not delivering any reward. We are interested in analyzing the effect of learning by the insect population due to unsuccessfully visiting the plants. The main focus is the existence and stability of the equilibria of the corresponding differential equations system, and the conditions for the existence of periodic solutions. In particular we look for conditions for the simultaneous coexistence of both species, or for their extinction as a function of the biological cost of the deceptiveness for the pollinators.

Keywords: Deceptive pollination, Learning, Stability, Hopf Bifurcation, Coexistence.

Resumen: En el siguiente trabajo proponemos un modelo matemático que describe la interacción de dos especies, una población de plantas y una población de polinizadores. La vía para la reproducción de las plantas es por medio de la polinización por engaño. Además, suponemos que los polinizadores tienen forma de aprender y detectar el engaño. El modelo matemático es un sistema de dos ecuaciones diferenciales ordinarias no lineales. Exploramos el efecto del costo biológico de ser engañado y su efecto sobre la posible existencia de niveles de equilibrio de ambas especies o de su extinción. Se estudian

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algunas propiedades de existencia y estabilidad de puntos de equi-
librio y se dan condiciones para la existencia de órbitas periódicas;
donde ambas poblaciones coexisten.

Palabras clave: Polinización por engaño, Aprendizaje, Estabilidad,
Bifurcación de Hopf, Coexistencia.

8.1   Introduction

The majority of plants in almost any habitat are flowering plants. Their diver-
sity and abundance relays heavily on their interaction with pollinating animals,
insects in particular [Abrol2012]. Despite the existence of abiotic pollination
[Abrol2012], the mutualistic relation between angiosperms and pollinating in-
sects remains a very important ecological element in the conservation of natural
as well as of agricultural environments [Kearns1998]. The economic as well as
the environmental relevance of pollination has been underlined in recent studies
on the worldwide decline of bees and bumblebees [Biesmeijer2006]. This problem
makes it urgent to gather more knowledge on the coevolution between plants and
pollinators in order, among other things, to be able to proceed with ecological
restoration, if needed [Mitchell2009].

Many flowers reward the pollinators through nectar [Dafni1984], pollen or
both. C. K. Sprengel [Sprengel1793], the founder of the modern study of flowering
plants was the first to observe that plants do not always reward their pollinators.
He worked on the genus Orchis. In his observations he noticed that the pollina-
tion process was a deceptive one. The insects were attracted by false signals of
reward. Even though the plants are forced to reproduce a perfectly false sensory
impression in the insects' nervous system, such a mechanism actually evolved.
Compared with other genera, Orchids are known by their diverse number of forms
of pollination, in particular by their great number of species relaying in deceptive
pollination [Jersáková2006]. Despite having been studied intensively since Dar-
win's time, the evolutionary mechanisms of deceptive pollination in orchids and
other plants still keep many secrets [Jersáková2006]. The different forms of trick-
ery include food deception, sexual deception, flower mimetism, shelter imitation,
pseudo-antagonism, etc. [Jersáková2006]. Food deception for instance has been
reported in more than 30 genera, and sexual deception in more than 18 genera
[Jersáková2006]. Here we present a mathematical model of the interaction of two
species, plants and insects. The plant species gets pollinated by deception. We
assume an alternate source of food for the insects' population, but the plants are
assumed dependent on the insects for reproduction.

We also assume that intraspecific competition among plants is intense. An
important element is the fact that we model learning by the insects, leading to a

reduction of visits after repeated failure to obtain a reward from the plant.

We present results on the existence and stability of nontrivial stationary states, which represent coexistence of both species. We analyze the possibility of sustained oscillations around such equilibrium states.

The work is organized as follows: section 2 we present the model for deceptive pollination and learning. In section 3 we analyze the condition for different outcomes. Section 4 presents some conclusions and the biological interpretation of the results.

8.2 The model

We consider two species: a plant population, and a pollinator population, denoted for any time t by $x(t)$ and $y(t)$, respectively. The main hypotheses on the system for obtaining the system of differential equations are:

1) The plant population depends exclusively on the pollinator for survival.

2) Intraspecific competition among plants is stronger than the natural death rate.

3) Pollinators look for the false rewards offered by the plants, but have access to alternative sources of food. Growth of the insects' population is assumed logistic.

4) Reproduction of the plants occurs through deceptive pollination, i.e. the plants send false signals to the insects, imitating some rewarding conditions, such as food, sexual, shelter, etc.

5) Pollinators perceive the number of unsuccessful visits to the plants and adjust their behavior accordingly.

6) The interaction plant-pollinator is a parasitic one, and we describe it with a term of the form $\frac{sxy}{1+\beta(x)+\gamma y}$. Further down we give a more detailed description of the parameters involved.

Starting with the dynamics of the plant population, its dependency on the pollinations is modeled by assuming an exponential decay, d, in the absence of any interaction, i.e., we assume a term of the form

$$\frac{dx}{dt} = -dx \qquad (8.2.1)$$

Due to intraspecific competition, μ_1, for instance in orders to attract pollinators, the plants increase their speed of decay, which adds a quadratic term to the equation (8.2.1):

$$\frac{dx}{dt} = -dx - \mu_1 x^2 \qquad (8.2.2)$$

For the dynamics of the pollinators, in the absence of plants, we use the logistic equation

$$\frac{dy}{dt} = ry - \mu_2 y^2 \qquad (8.2.3)$$

Equation (8.2.2) describes the dynamics of the plants in the absence of pollinators, and equation (8.2.3) describes the dynamics of the pollinators in the absence of plants. The parameter μ_2 represents the intraspecific competition among pollinators.

Modeling the interaction between the species will add a term that will increase the reproduction of the plants and, in a similar way, will decrease the reproduction potential of the pollinator. Such term will be a function of the number of encounter between plants and pollinators. So we start with a basic mass-action law to describe the number, c_1, of encounters between a plant and a pollinator, $c_1 xy$. In a fraction of those encounters per unit of time, the pollinator will be deceived. The term describing that has the form $mc_1 xy$, m being the probability that the plant does not deliver any reward. k represents the net benefit received by the plant in each visit.

Taking this into consideration, a first way of modeling the interaction would be with the equations

$$\begin{array}{rcl} \frac{dx}{dt} & = & -\mu_1 x^2 + kmc_1 xy \\ \frac{dy}{dt} & = & ry - \mu_2 y^2 - mc_1 xy \end{array} \qquad (8.2.4)$$

This model has an undesirable behavior. Its solutions can tend to infinity. So, to avoid that we take into considerations the fact that an ever increasing number of pollinators cannot simply produce the same benefit for the plants, since the number of flowers to pollinate remains finite. There is a saturation of the environment with pollinators. Also, if the number of plants increases the damage to the pollinator cannot increase without bounds, since they cannot visit all the plants. So we propose a saturation of the form $\frac{1}{1+\beta(x)+\gamma y}$. In this expression the function $\beta(x)$ represents the reaction of the pollinator to the deceptiveness of the plant. $\beta(x)$ is taken as an nonnegative increasing function of x. The more the pollinator is deceived, the less often it will visit the plant. The parameter γ models the intensity of competition among pollinators for exploiting the benefits offered by the plants.

Now we obtain the final form for the system:

$$\begin{array}{rcl} \frac{dx}{dt} & = & -\mu_1 x^2 + \frac{a}{1+\beta(x)+\gamma y} xy \\ \frac{dy}{dt} & = & ry - \mu_2 y^2 - \frac{c}{1+\beta(x)+\gamma y} xy \end{array} \qquad (8.2.5)$$

where a and c in (8.2.5) are obtained as the corresponding values kmc_1 and mc_1 in equation (8.2.4). Due to the biological interpretation of the variables, we restrict the analysis to the region $x \geq 0$ and $y \geq 0$.

8.3 Stability analysis

Since system (8.2.5) is a nonlinear one, we analyze it qualitatively. Let us start with the steady state equations $\frac{dx}{dt} = \frac{dy}{dt} = 0$, for all time t. We will denote by $E(x^*, y^*)$ any equilibrium solution of this system. They represent states in which the number of individuals in both species is in equilibrium. If both, x^* and y^* are different from zero, we call the equilibrium $E(x^*, y^*)$ a nontrivial one, otherwise we call it trivial equilibrium. System (8.2.5) has two trivial equilibria $E(0, 0)$ and $E(0, \frac{r}{\mu_2})$; the first one represents the absence of plants and pollinators, and the second one represents the absence of plant, but a pollinator population in a nonzero equilibrium.

Of special interest are the nontrivial equilibria, since they represent states in which both species coexist. Let us look for them, solving the corresponding equations of system (8.2.5)

$$y^* = \frac{\mu_1 x^* (1 + \beta(x^*))}{a - \gamma \mu_1 x^*} \tag{8.3.1}$$

$$cx^* = \frac{a(1 + \beta(x^*))}{(a - \gamma \mu_1 x^*)^2} \{ r(a - \gamma \mu_1 x^*) - \mu_1 \mu_2 x^* (1 + \beta(x^*)) \} \tag{8.3.2}$$

Equation (8.3.2) gives the equilibrium value of x^* and equation (8.3.1) the corresponding value of y^*. Observe that x^* belongs to the interval $(0, \frac{a}{\gamma \mu_1})$. Considering the left side of (8.3.2) as a function of x, $l(x)$, and the right side as a function $g(x)$, the equilibrium is represented by the intersection of a straight line with the function g depicted below. Figure 1 shows a typical shape for the function $g(x)$.
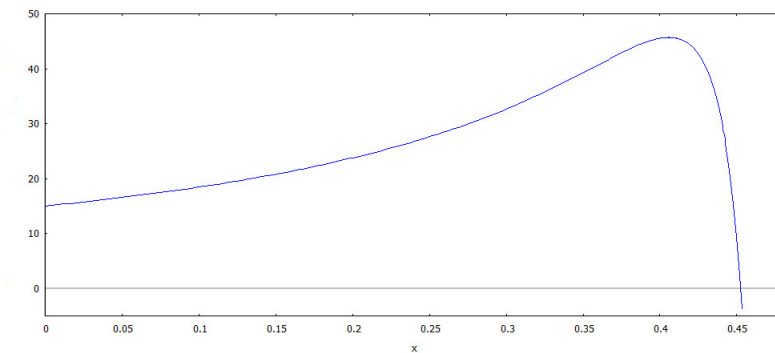
Figura 8.1: Graph of $g(x)$.

The following results are proved in a separated paper, Vázquez V. and Barradas I. [Vázquez]; here we will focus on their biological interpretation.

In what follows we assume that the function $g(x)$ has a unique inflexion point, x_{in}, with positive slope for the function $g(x)$ as depicted by Figure 8.1.

Not many functions β fails this condition, and even then, they do not fail it for a wide range of parameters; we will comment on it later on. Here we will focus on the parameter c, the measure of the damage or biological cost for the pollinator after being fooled by a deceiving plant.

Theorem 8.3.1 *Assume:*

1) g increasing and convex at $x = 0$,

2) $c \leq \mu_1$, and

3) $g'(x_{in}) \leq \frac{g(x_{in})}{x_{in}}$,

then system (8.2.5) has a unique equilibrium point, $E(x^*, y^*)$, which is globally asymptotically stable.

Condition 3 of the theorem is needed for the uniqueness of the equilibrium point, as can be seen from the intersection of the straight line with the curve g in Figure 8.2.
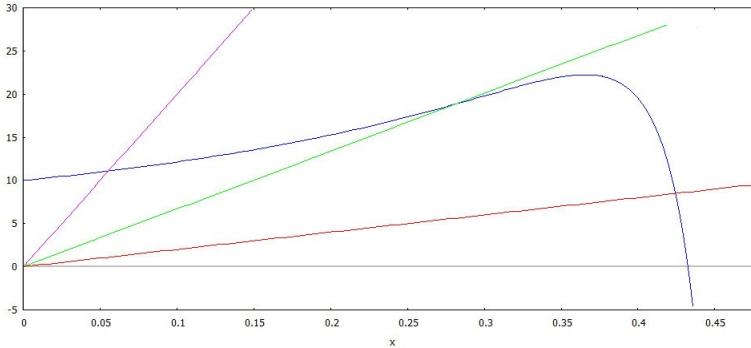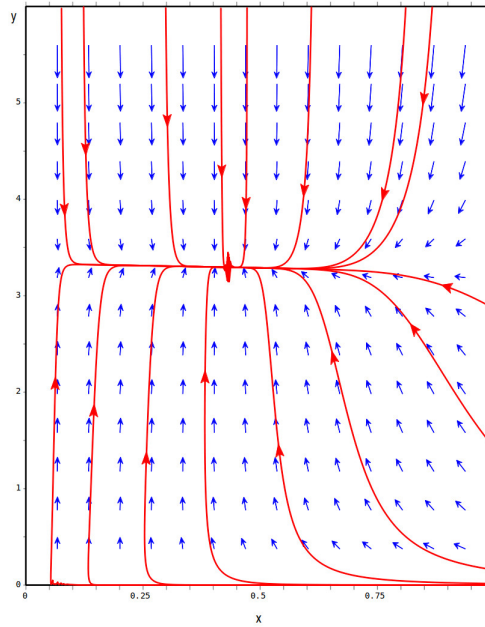

Figura 8.2: Unique equilibrium point.

Theorem 8.3.1 assures that if the biological cost for the pollinator, c, which can also be seen as the damage caused by the plant; is small enough compared with the death rate of the plant, μ_1, the system always tends to stabilize at an equilibrium level. In particular, the system is able to maintain itself, and even more, after small perturbations in the environment, it will returns to its original equilibrium level, x^*. The level of equilibrium for the pollinator depends on the biological cost, c; it increases as c decreases.

For smaller values of c, i.e., a lesser deceptive pollination level, the plant will attain a bigger level of occupancy, benefiting both species. Figure 8.3 shows a simulation for the global stability of the equilibrium for $\beta(x) = 0.1x$.

Many phenomena in nature repeat themselves periodically, and individuals adapt to the corresponding biological facts. Everyday variables change trough

Figura 8.3: Unique equilibrium point.

day and night, as well as through the seasons. The biological rhythms are only a small example of that. The next result shows under which conditions the system can present a sustained oscillation.

Theorem 8.3.2 *Assume system (8.2.5) has a unique equilibrium point, and the following hypotheses hold true:*

1) $\beta''(x_{in}) \leq 0$,

2) $x^{c_0} \beta''(x^{c_0}) + 2\beta'(x^{c_0}) > 0$,

3) $\mu_2 \geq 2a$,

then, system (8.2.5) has a periodic orbit around the equilibrium $E(x^*, y^*)$.

x^{c_0} in condition 2 of the theorem satisfies the equation $\frac{g(x^{c_0})}{x^{c_0}} = c_0$, c_0 is called the bifurcation value [Edelstein2005].

The first two conditions in Theorem 8.3.2 are technical ones, and they are required for the so called Hopf Bifurcation to occur [Edelstein2005]. The interpretation of the third condition is that the intraspecific competition among pollinators is big enough compared to the benefit it provides to the deceptive plant. In such case both species oscillate around an equilibrium level. The mechanics for this oscillation looks like the following: an increasing number of pollinator
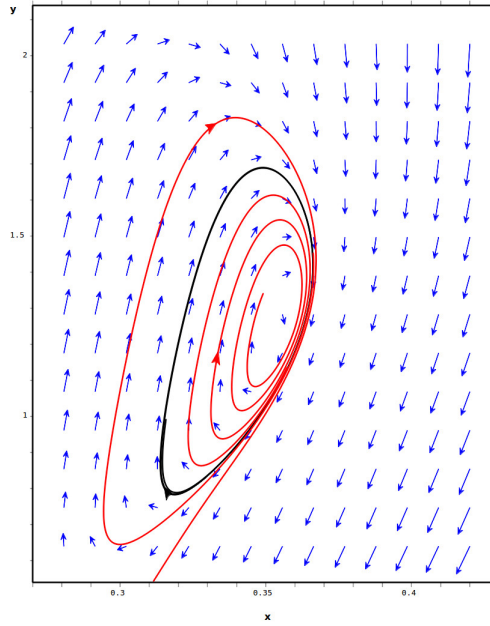
Figura 8.4: Periodic orbit.

induce an increase in the number of plants. Once the number of plant increases, the number of unsuccessful visits by the pollinators also increases, which induces a reduction in the number of visits. The reduced number of pollination events finally leads to a reduction in the number of plants. Figure 8.4 shows a simulation for $\beta(x) = 0.1x$.

Combining the interpretation of Theorems 8.3.1 and 8.3.2 we see that for low levels of deception both species coexist and stabilize at the equilibrium but, for bigger values of c, i.e., a bigger biological cost for the pollinator, the systems starts to oscillate. This oscillation increases in amplitude, making it possible that the plant as well as the pollinator population approach very low levels. Any addition perturbation could make them go extinct.

These results can be generalized to a bigger number of steady states. Figure 8.5 shows such an example; each straight line shows a different case and the possibility of one or multiple steady states.

In the general case a theorem can be stated that guarantees the existence of a tangency point, x^{T_2}, between g and the straight line with slope c, closest to, x^M, the maximum of g. The theorem is then formulated in terms of such points.

Theorem 8.3.3 *Assume the following conditions hold true:*

1) $\frac{g(x_{in})}{x_{in}} < g'(x_{in}),$
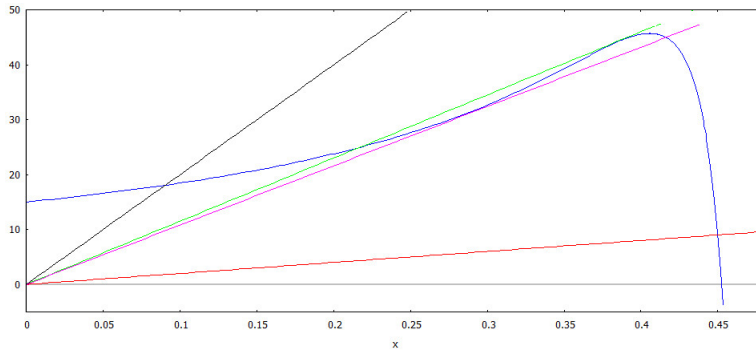
Figura 8.5: Single Equilibrium point vs. multiple points.

2) $\frac{x^{T_2}\beta'(x^{T_2})}{1+\beta(x^{T_2})} \leq 1,$

3) $x^{c_0}\beta''(x^{c_0}) + 2\beta'(x^{c_0}) > 0,$ and

4) $\mu_2 \geq 2a,$

then, there is a periodic orbit around the equilibrium $E(x^*, y^*)$ and it hold true that $x^{T_2} < x^* < x^M$.

The first condition of the theorem is necessary to ensure the existence of multiple equilibrium points, as can be seen in Figure 8.5. Conditions 2 and 3 are technical ones, and they are required for the so called Hopf Bifurcation to occur [Edelstein2005]. The interpretation of the fourth condition is the same as that of Theorem 8.3.2.

The main biologically relevant difference between this case and Theorem 8.3.2 is the fact that the oscillation assured in Theorem 8.3.3 can disappear under some disturbances. Figure 8.6 shows a case of a unstable periodic solution for $\beta(x) = 0.1x$. Vázquez V. and Barradas I. [Vázquez]; work similar examples for different functions $\beta(x)$.

8.4 Conclusions

The main purpose of this work was to present and analyze a mathematical model for deceptive pollination, which happens to by obligatory for the plant population to reproduce. Further, we assume that pollinators are able to learn from unsuccessful visits, reducing the number of pollinated plants. This interaction is modeled by function β in system (8.2.5).

The main results outlined in the theorems describe the possible behaviors depending on the parameter c, which represents the biological cost for the pollinator being deceived. At low levels of deceptiveness, the pollinators sustain a reduction
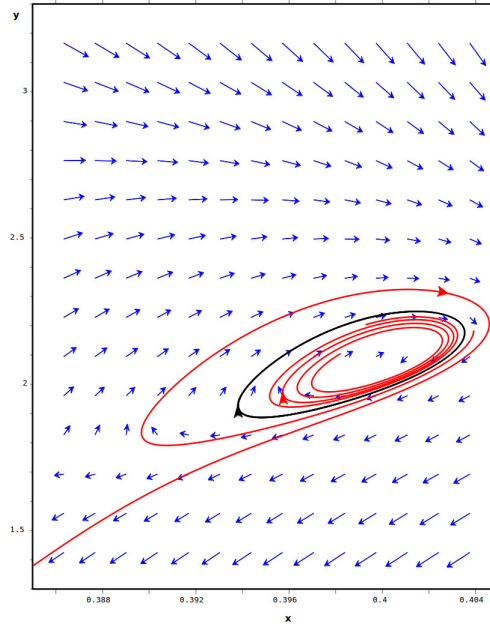
Figura 8.6: Periodic orbit.

on the numbers of individuals at equilibrium. The equilibrium is a global attractor, which means that for almost any initial condition or small disturbances, the system tends to return to the equilibrium level. In particular, even though the plants depend exclusively on the deceptive pollination, it is always possible for the plant to parasitize the pollinator population.

For an increasing level of deceptiveness, that equilibrium can turn unstable, giving way to an undamped oscillation around the equilibrium. The oscillations, once they appear, turn to be stable, attracting any other solution.

For even greater values of c, the biological cost of being fooled, the oscillations turn wilder, allowing the number of individuals to increase above the equilibrium, but also reducing the numbers far below the equilibrium. If such variations bring the number of individuals to very low levels, any additional disturbance could lead to extinction of any or both of the species involved.

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