

Your article is protected by copyright and all rights are held exclusively by Springer-Verlag. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your article, please use the accepted manuscript version for posting on your own website. You may further deposit the accepted manuscript version in any repository, provided it is only made publicly available 12 months after official publication or later and provided acknowledgement is given to the original source of publication and a link is inserted to the published article on Springer's website. The link must be accompanied by the following text: "The final publication is available at link.springer.com".

Dynamics of plant–pollinator–robber systems

Yuanshi Wang

Received: 2 October 2011 / Revised: 7 March 2012 / Published online: 7 April 2012
© Springer-Verlag 2012

Plant–pollinator–robber systems are considered, where the plants and pollinators are mutualists, the plants and nectar robbers are in a parasitic relation, and the pollinators and nectar robbers consume a common limiting resource with interfering competition. My aim is to show a mechanism by which pollination–mutualism could persist when there exist nectar robbers. Through the dynamics of a plant–pollinator–robber model, it is shown that (i) when the plants alone (i.e., without pollination–mutualism) cannot provide sufficient resources for the robbers' survival but pollination–mutualism can persist in the plant–pollinator system, the pollination–mutualism may lead to invasion of the robbers, while the pollinators will not be driven into extinction by the robbers' invasion. (ii) When the plants alone cannot support the robbers' survival but persistence of pollination–mutualism in the plant–pollinator system is density-dependent, the pollinators and robbers could coexist if the robbers' efficiency in translating the plant–robber interactions into fitness is intermediate and the initial densities of the three species are in an appropriate region. (iii) When the plants alone can support the robbers' survival, the pollinators will not be driven into extinction by the robbers if their efficiency in translating the plant–pollinator interactions into fitness is relatively larger than that of the robbers. The analysis leads to an explanation for the persistence of pollination–mutualism in the presence of nectar robbers in real situations.

Keywords Acyclicity · Stability · Persistence · Mutualism · Invasion

Mathematics Subject Classification 34C37 · 92D25 · 37N25

Y. Wang (✉)
School of Mathematics and Computational Science,
Sun Yat-sen University, Guangzhou 510275, People's Republic of China
e-mail: mcs wys@mail.sysu.edu.cn

1 Introduction

Floral visitors attracted to flowers consist of pollinators and nectar robbers. Pollinators provide pollen transport service, while they consume nectar, pollen and other goods. Nectar robbers take nectar away through holes bitten in flowers, without providing pollination service. The robbers have been found in nature for hundreds of years. In 1793, Sprengel recorded that bumble bees perforate nectar spurs (Sprengel 1793). In 1859 and 1876, Darwin found that bumble bees steal nectar in clover flowers (Darwin 1859, 1876). Later researchers have shown that almost all plants, whose flowers are tubular or have nectar spurs, have been robbed. Thus, nectar robbing is a widespread and costly phenomenon in the growth of flowering plants. The plants may be able to resist nectar robbing through morphological and chemical traits, but many of the traits lead to deterrence to both the pollinators and robbers (McCall and Irwin 2006). While pollinators are often regarded as mutualists with plants, the nectar robbers are also called cheaters due to their adaptation in lowering robbing impact and frequency (Wootton 1994; Werner and Peacor 2003). Mutualism theory exhibits that cooperation cannot persist when there is no effective deterrence or serious punishment on cheaters. However in real situations, the plant–pollinator mutualism persists stably. Hence, an interesting question is raised by Irwin et al. (2010, page 287, the 8th question) asking why the plant–pollinator mutualism can persist when there exist nectar robbers (cheaters).

Dynamic systems theory may provide a way to answer the question. Indeed, there has been a growing literature on the study of plant–pollinator–herbivore systems (Freedman and Waltman 1984; Liou and Cheng 1988; Waltman 1991; Hsu et al. 2001; Wang et al. 2011, etc.). Jang (2002) characterized the interactions between plants and pollinators with the Holling II functional response. Based on her model, an interaction among herbivores, plants and pollinators is proposed. Strong analysis on global dynamics of the three-species model shows that an increasing pollination visitation rate due to the presence of herbivores can promote persistence of the system. In a recent study, Oña and Lachmann (2011) described plant–pollination systems by mutualism models with various functional responses. Analysis on the model with a linear functional response shows interesting thresholds of the ants' aggressiveness level, above which the pollinators will be driven into extinction. Fishman and Hadany (2010) concluded that an analytical expression for population-level plant–pollinator interactions can be approximated by the Beddington–DeAngelis functional response, where an exploitation competition among pollinators is considered and the interactions between the plants and pollinators are obligate. Qualitative analysis and numerical simulations demonstrated that when the pollinators' efficiency in translating plant–pollinator interactions into fitness is large and the initial population densities of the two species are not too small, the plants and pollinators could persist at a steady state. As far as we know, plant–pollinator–robber systems have not been analyzed in detail. Thus, formulating models and studying features of these systems is necessary.

In this paper, we consider biological systems consisting of plants, pollinators and nectar robbers, in which the interactions between the plants and pollinators are mutualistic with the Beddington–DeAngelis functional response, and the interactions between the plants and robbers are parasitic with the Holling II functional response.

Global dynamics of a plant–pollinator model with the Beddington–DeAngelis functional response are demonstrated. Based on the dynamics of a plant–pollinator–robber model, we show that (i) when the plants alone cannot provide sufficient resources for the robbers' survival but pollination–mutualism can persist in the plant–pollinator system, the pollination–mutualism promotes reproduction of the plants and may lead to invasion of the robbers, while the pollinators will not be driven into extinction by the robbers' invasion. (ii) When the plants alone cannot support the robbers' survival but persistence of pollination–mutualism in the plant–pollinator system is density-dependent, the pollinators and robbers could coexist if the robbers' efficiency is intermediate and the initial densities of the three species are in an appropriate region. Otherwise, if the efficiency is too small, the robbers will go to extinction while the plants and pollinators coexist; if the efficiency is too large and/or the initial densities are beyond a certain level, both the pollinators and robbers will go to extinction while the plants approach their carrying capacity. (iii) When the plants alone can support the robbers' survival, the robbers are always persistent in the plant–pollinator–robber system. The pollinators will not be driven into extinction by the robbers if their efficiency in translating plant–pollinator interactions into fitness is relatively larger than that of the robbers. Otherwise, the pollinators will go extinct. Numerical simulations show that when parameters (factors) in the system vary, interaction outcomes of the three species could transition among extinction of the robbers, persistence of the three species at a steady state, persistence of the three species in periodic oscillations, and extinction of the pollinators. The analysis provides an explanation for the persistence of pollinators and nectar robbers in real situations.

The paper is organized as follows. The plant–pollinator–robber model is characterized in Sect. 2. Section 3 exhibits dynamics of the subsystems. Section 4 shows persistence of the plant–pollinator–robber system. Discussions are in Sect. 5.

2 A plant–pollinator–robber model

In this section, we describe the plant–pollinator–robber system we are concerned with and show boundedness of solutions of the model.

Since the plants provide resources for the pollinators and the pollinators supply pollination service for the plants, the relationship between them is cooperative. Let x_1 and x_2 represent population densities of the plants and pollinators, respectively. Then the plant–pollinator interaction can be approximated by the Beddington–DeAngelis functional response (Fishman and Hadany 2010)

$$\frac{\alpha x_1 x_2}{1 + \alpha x_1 + \alpha \beta x_2}.$$

Here, the parameter α is the effective equilibrium value for un-depleted plant–pollinator interaction, which combines traveling and unloading times spent in central place pollinator foraging, with individual-level plant–pollinator interactions (Fishman and Hadany 2010). β denotes the intensity of exploitation competition among pollinators (Pianka 1974).

Let r_1 represent the intrinsic growth rate of the plants and d_1 their self-incompatible degree. We obtain the equation for the growth of the plants as given by

$$\frac{dx_1}{dt} = x_1 (r_1 - d_1 x_1) + \frac{\eta \alpha x_2}{1 + \alpha x_1 + \beta x_2}$$

where the parameter η denotes the plants' efficiency in translating plant-pollinator interactions into fitness (see [Beddington 1975](#); [DeAngelis et al. 1975](#); [Fishman and Hadany 2010](#) for details). Let μ denote the corresponding value for the pollinators and let r_2 be their death rate. Then we obtain the equation for the the growth of the pollinators as given by

$$\frac{dx_2}{dt} = x_2 (-r_2 + \frac{\mu \alpha x_1}{1 + \alpha x_1 + \beta x_2})$$

For simplicity, we rewrite the plant-pollinator model as

$$\begin{aligned} \frac{dx_1}{dt} &= x_1 (r_1 - d_1 x_1) + \frac{a_{12} x_2}{1 + \alpha x_1 + \beta x_2} \\ \frac{dx_2}{dt} &= x_2 (-r_2 + \frac{a_{21} x_1}{1 + \alpha x_1 + \beta x_2}) \end{aligned} \tag{2.1}$$

where $a_{12}(=\eta\alpha)$ can be regarded as the plants' efficiency when α is fixed in our discussion, and $a_{21}(=\mu\alpha)$ is the corresponding value for the pollinators.

Let x_3 represent the population density of the robbers. Since nectar robbers are predators to plants, the plant-robber system can be depicted by the predator-prey model with the Holling II functional response

$$\begin{aligned} \frac{dx_1}{dt} &= x_1 (r_1 - d_1 x_1) - \frac{a_{13} x_3}{c + x_1} \\ \frac{dx_3}{dt} &= x_3 (-r_3 + \frac{a_{31} x_1}{c + x_1}) \end{aligned} \tag{2.2}$$

where the parameter a_{13} represents the saturation level in the Holling II functional response and c denotes the half-saturation constant, while a_{31} can be regarded as the robber' efficiency in translating plant-robber interactions into fitness. r_3 is the robbers' per-capita death rate.

Since we assume that there is no interfering competition between the pollinators and robbers, the plant-pollinator-robber system can be depicted by

$$\begin{aligned} \frac{dx_1}{dt} &= x_1 (r_1 - d_1 x_1) + \frac{a_{12} x_2}{1 + \alpha x_1 + \beta x_2} - \frac{a_{13} x_3}{c + x_1} \\ \frac{dx_2}{dt} &= x_2 (-r_2 + \frac{a_{21} x_1}{1 + \alpha x_1 + \beta x_2}) \\ \frac{dx_3}{dt} &= x_3 (-r_3 + \frac{a_{31} x_1}{c + x_1}) \end{aligned} \tag{2.3}$$

以上内容仅为本文档的试下载部分，为可阅读页数的一半内容。如要下载或阅读全文，请访问：<https://d.book118.com/755032023334011122>