BIFURCATIONS IN A POLLINATION-MUTUALISM SYSTEM WITH NECTARLESS FLOWERS

HONG WU\textsuperscript{a}, SHAN SUN\textsuperscript{b} AND YUANSHI WANG\textsuperscript{a,}\textsuperscript{*}

\textsuperscript{a}School of Mathematics
Sun Yat-sen University, Guangzhou 510275, China
\textsuperscript{b}State Key Laboratory of Glassland Agro-Ecosystems
School of Life Sciences, Lanzhou University, Lanzhou, 730000, China

Abstract. This paper considers a pollination-mutualism system in which flowering plants have strategies of secreting and cheating: secretors produce a substantial volume of nectar in flowers but cheaters produce none. Accordingly, floral visitors have strategies of neglecting and selecting: neglectors enter any flower encountered but selectors only enter full flowers since they can discriminate between secretors and cheaters. By combination of replicator equations and two-species dynamical systems, the games are described by a mathematical model in this paper. Dynamics of the model demonstrate mechanisms by which nectarless flowers can invade the secretor-pollinator system and by which a cyclic game between nectarless flowers and pollinators could occur. Criteria for the persistence of nectarless flowers are derived in terms of the given parameters (factors), including the nectar-producing cost and cheaters’ efficiency. Numerical simulations show that when parameters vary, cheaters would vary among extinction, persistence in periodic oscillations, and persistence without secretors (i.e., cheaters spread widely). We also consider the evolution of plants in a constant state of pollinator population, and the evolution of pollinators in a constant state of plant population. Dynamics of the models demonstrate conditions under which nectarless flowers (resp. selectors) could persist.

1. Introduction. Floral deception in pollination mutualisms has been intensively studied since Darwin, but the evolution of nectarless flowers is still a major puzzle in biology [22, 23, 28, 33, 42, 43]. While many flowering plants build a cooperative interaction with pollinators by providing nectar for the pollination service, there exists a proportion of plants that produces nectarless flowers to cheat pollinators [2, 42]. For example, in populations of Prosopis glandulosa (Mimosoideae), one-half of the individuals produce nectar but the others are nectarless [13]. Furthermore, some orchids have never produced nectar in their flowers [22, 29, 45]. Since nectar is full of sugars, it plays a primary role in plant-pollinator mutualisms. Thus cheaters with nectarless flowers usually have low visitation rates and low levels of fruit production, which may consequently lead to extinction of cheaters. However, in natural environments, cheaters survive stably [13, 27]. Why, therefore, could nectarless flowers/cheaters persist?

2010 Mathematics Subject Classification. 34C37, 92D25, 37N25.
Key words and phrases. Periodic solution, stable strategy, population dynamics, replicator equation, persistence.

H. Wu and Y. Wang acknowledge support from NSF of China (11571382). S. Sun acknowledges support from NSF of China (31870357).

* Corresponding author: Yuanshi Wang.
The persistence of cheaters has been studied from different points of view. First, since secretors have expensive nectar-bearing flowers whilst cheaters have nectarless flowers which are cheaper to make [2], evolutionary theory predicts that cheaters should be favored by natural selection. Second, since nectar is often concealed in flowers and cannot be directly assessed by pollinators, nectarless flowers could cheat the pollinators by having both spatial mingling and floral color similarity to full flowers [24]. Indeed, Nenitez-Vieyra et al. [28] considered intra-individual correlation between floral signal and reward (signal accuracy), and demonstrated that in *Turnera ulmifolia*, the frequency of cheating increases when the signal accuracy decreases. Third, cheaters may have strong ability of reproduction. For example, Jersáková et al. [22] displayed that the low visitation rates in orchids result in cross-pollination, which leads to dramatic increases in seed quality in almost all orchids. In order to avoid nectarless flowers, pollinators could learn prior information from their past experience and have remarkable adaptive plasticity [3]. They can learn positive correlation between floral signal and reward through associative learning [14], while they are also able to learn negative correlation between floral signal and reward through avoidance learning [18]. Cartar [6] showed that when bumble bees use a relatively sophisticated spatial memory to forage in food patches, this foraging strategy could constrain the evolution of nectarless flowers. Makino and Sakai [25] used artificial flower experiments to show that the location learning ability of bees for high reward individuals could result in nectarless flowers to evolve more difficultly than expected by Bell [2]. Nenitez-Vieyra et al. [28] demonstrated that pollinators can select for signal accuracy and their learning ability would limit the spread of nectarless flowers.

Although pollinators can learn the state of plant population and change their strategies, the plants can also evolve accordingly [19, 20]. For example, the nectarless orchids could select flowering early in the growing season when relatively more pollinators are naive and fewer nectarful plant species are flowering and/or flowering for extended periods to enhance the chance of pollinator visits [20]. Therefore, there exists a co-evolution between plants and pollinators. Bell [2] used a game theory model to describe the evolution of nectarless flowers in a single plant species. In Bell’s model, individuals of the plant species could produce either nectar-bearing flowers or nectarless ones, while individuals of pollinators either could or could not discriminate between nectarless and full flowers. The discrimination is costly because pollinators need to develop the ability of discrimination and spend time in recognizing flowers and making decisions. However, without the ability of discrimination, pollinators would receive nothing from a nectarless flower. Based on analysis of the model, Bell [2] derived a critical frequency of nectarless flowers. When frequencies of nectarless flowers are less than it, pollinators should visit both nectarless and full flowers randomly. Otherwise, they should switch to discrimination. Gilbert et al. [12] confirmed the critical frequency by real observations.

Metz et al. [26] presented a fitness measure based on a discrete time model. In the work, Metz et al. considered a multi-species system and formed a matrix process, which converges to fixed equilibria as time approaches infinity. The equilibria do not depend on initial population densities and represent the long-run growth rates of the species, which characterize reproduction successes of these species and can be defined as fitness of the species in the long-run interactions. Wang et al. [44] presented a fitness measure based on a continuous time model. In the work, Wang et al. considered a two-species system and formed a model consisting of
two differential equations. The two-species system is shown to converge to fixed numbers as time approaches infinity, which do not depend on initial population densities. The equilibria characterize the long-run growth rates of the species, which represent reproduction successes of the two species and can be defined as their fitness/payoffs in the long-run interactions. For additional relevant works, we refer to [5, 10, 30, 32, 34, 35, 36, 38, 39, 46]. To our knowledge, the co-evolution between nectarless flowers and pollinators has not been modeled by evolutionary games. In particular, the novel cyclic game between nectarless flowers and pollinators described by Bell [2] has not been characterized by models. Thus formulating evolutionary game models and analyzing properties of the co-evolution is necessary.

In this paper, we considered three evolutionary games in the plant-pollinator systems. In the game between plants and pollinators, players in the position of plants have two strategies: secreting and cheating. Accordingly, players in the position of pollinators have two strategies: neglecting and selecting. For convenience, the four types of players are called four species in this paper. Payoffs in the game are represented by the equilibria in the corresponding two-species dynamical systems. Based on the payoffs, the game between plants and pollinators can be depicted by replicator equations [41]. Stability analysis on the models demonstrates mechanisms by which the four species could coexist and by which the strategy of cheating could persist stably. Criteria for the persistence of nectarless flowers are derived in terms of the given parameters (factors). We also considered the evolution of plants in a constant state of pollinator population, and the evolution of pollinators in a constant state of plant population. Dynamics of the models demonstrate conditions under which nectarless flowers (cheaters) could persist.

The paper is organized as follows. The models are described in Section 2. Section 3 shows dynamics of the models, while the proofs are in Appendices. Section 4 analyzes periodic oscillations in the games, and discussions are in Section 5.

2. Model. In this section, we describe models characterizing games between flowering plants and pollinators. First, we describe dynamical systems which are used to characterize payoffs in the games. Then we apply replicator equations to describe the evolutionary games.

The payoff matrix for pollinators can be described by
\[
\begin{pmatrix}
  u_{11} & u_{12} \\
  u_{21} & u_{22}
\end{pmatrix}
\]
where \(u_{11}\) (resp. \(u_{12}\)) represents the payoff that a neglector gains when it meets secretors (resp. cheaters). \(u_{21}\) (resp. \(u_{22}\)) represents the payoff that a selector gains when it meets secretors (resp. cheaters).

The payoff matrix for plants is
\[
\begin{pmatrix}
  v_{11} & v_{12} \\
  v_{21} & v_{22}
\end{pmatrix}
\]
where \(v_{11}\) (resp. \(v_{12}\)) represents the payoff that a secretor gains when it meets neglectors (resp. selectors). \(v_{21}\) (resp. \(v_{22}\)) represents the payoff that a cheater gains when it meets neglectors (resp. selectors).

The entries in the game should represent the long-term fitness of the species. As far as we know, there are at least two fitness measures. One is the so-called short-term (prompt) fitness, which measures the prompt gain of each species [2]. The other is the long-term fitness, which concisely summarizes the long-run reproductive
success (growth rate) of the species [26]. Following the tenet of Darwinism, the fitness of a species with a given strategy is often represented by its reproductive success, i.e., its growth rate [17]. Thus, when we consider long-term interactions between two species, it would be more appropriate to use the long-term fitness measure than the prompt one. A long-term fitness measure is defined for a discrete-time model by Metz et al. [26]. In their model, population densities of species eventually become independent of their initial values. Thus, the limiting value as time $t$ approaches infinity, represents the long-run growth rate of the species. Therefore, the limiting state is defined as the long-term fitness of the species by Metz et al. [26]. In their paper, Metz et al. [26] also stated that the definition of fitness can be extended to continuous-time models in the same way. In this work, we consider continuous-time models in which population densities of species converge to a steady state, which is independent of their initial values. Thus, similar to the definition of fitness by Metz et al. [26], we define components of the steady state as the long-term fitness of species in the continuous-time models, which is just the extension of that given by Metz et al. [26] in discrete-time models.

$u_{ij}$ and $v_{ji}$ are given as follows. First, $u_{11}$ and $v_{11}$ can be represented by population densities at a steady state (i.e., the state consisting of converged numbers) in the neglector-secretor system, while the neglector-secretor system consists of pollinators with purely neglecting strategy and plants with purely secreting strategy. In the interactions between neglectors and secretors, neglectors provide pollination service for secretors while secretors supply food for neglectors in return. Thus the relationship between them is mutualistic. Fishman and Hadany [11] derived that the analytical expression for population-level plant-pollinator interactions can be approximated by a Beddington-DeAngelis functional response

$$\frac{\alpha NM}{1 + \alpha M + \alpha \beta N}$$

where $N$ and $M$ denote population densities of pollinators and plants, respectively. The parameter $\alpha$ is the effective equilibrium value for (un-depleted) flower-pollinator interactions that combines travel and unloading times involved in central place pollinator foraging, with individual-level plant-pollinator interactions. $\beta$ is the intensity of exploitation competition between pollinators [31].

We assume that the plants depend upon pollinators for reproduction, and the pollinators are able to exploit other plant species present, while the plant mortality rate is density-independent [11, 21, 40]. Then the neglector-secretor system can be depicted by a mutualism model with the Beddington-DeAngelis functional response:

$$\frac{dN}{dt} = N(r_1 - d_1 N + \frac{a_{12} \alpha M}{1 + \alpha M + \alpha \beta N})$$

$$\frac{dM}{dt} = M(-d_2 + \frac{a_{21} \alpha N}{1 + \alpha M + \alpha \beta N})$$

(1)

where $N$ and $M$ are population densities of neglectors and secretors, respectively. The parameter $\alpha$ and $\beta$ have the same meanings as those described above. $r_1$ denotes the intrinsic growth rate of neglectors and $r_1/d_1$ is their carrying capacity in the absence of the plants. $d_2$ represents the per-capita mortality rate of the secretors. As described by Fishman and Hadany [11], $a_{12}$ represents the neglectors’ efficiency in translating neglector-secretor interactions into fitness, and $a_{21}$ is the corresponding value for the secretors. In the next section of this paper, system (1)
Figure 1. Phase-plane panels for population dynamics of pollinator-plant systems (1)-(4), in which $l_N$ and $l_M$ denote the isoclines of pollinators ($N$) and plants ($M$), respectively. Solid and open circles denote stable and unstable equilibria. Vector fields are displayed by gray arrows, which show the direction and speed of population trajectories. Let $r_1 = 0.5, d_1 = 0.01, \alpha = 0.15, \beta = 0.8, d_2 = 0.55, a_{12} = 0.8, a_{21} = \tilde{a}_{21} = 0.9, \tilde{b}_{12} = 0.2, \tilde{d}_2 = 0.5, \tilde{r}_1 = 0.45, \tilde{\alpha} = 0.1$. (a) When secretors’ efficiency in translating neglector-secretor interactions into fitness is large, the two species can coexist at a steady state $E_{11}(u_{11}, v_{11})$. (b) When cheaters’ efficiency in translating neglector-cheater interactions into fitness is large, neglectors and cheaters can coexist at a steady state $E_{12}$. (c) When the secretors’ efficiency in translating selector-secretor interactions into fitness is large, the two species coexist at a steady state $E_{21}(u_{21}, v_{12})$ with $u_{21} < u_{11}$. (d) In the selector-cheater system, selectors approach the carrying capacity and cheaters go to extinction, which is shown by the stable equilibrium $E_{22}$.

is shown to have a globally asymptotically stable equilibrium $E_{11}(u_{11}, v_{11})$ as shown in Fig. 1a. Thus the payoffs $u_{11}$ and $v_{11}$ can be determined by system (1).

Second, $u_{12}$ and $v_{21}$ can be represented by population densities at steady states in the neglector-cheater system. Since cheaters obtain pollination service without providing rewards in return, the relationship between neglectors and cheaters is parasitic, which can be depicted by a parasitism model with a Beddington-DeAngelis functional response [1, 4, 9]:

$$
\frac{dN}{dt} = N(r_1 - d_1N - \frac{b_{12}\alpha M}{1 + \alpha M + \alpha \beta N})
$$

$$
\frac{dM}{dt} = M(-\tilde{d}_2 + \frac{\tilde{a}_{21}\alpha N}{1 + \alpha M + \alpha \beta N})
$$

where $N$ and $M$ denote population densities of neglectors and cheaters, respectively. The parameter $-b_{12}$ represents the neglectors’ efficiency in translating neglector-cheater interactions into fitness (a negative feedback). The parameter $-\tilde{d}_2$ denotes
the net per-capita growth rate of cheaters, which is equal to the growth rate minus the death rate. As shown in Revilla [37], producing nectar would have a negative effect on the plants’ growth, which implies $-\tilde{d}_2 > -d_2$ since the cheaters do not produce nectar and then their net growth rate is increased. $\tilde{a}_{21}$ represents the cheaters’ efficiency in translating neglector-cheater interactions into fitness. In some situations, we may have $\tilde{a}_{21} > a_{21}$ since low visitation rates of nectarless flowers could result in high seed quality in cheaters, as mentioned in the previous section. Other parameters have the same meanings as those in (1). In the next section of this paper, system (2) is shown to have a globally asymptotically stable equilibrium $E_{12}(u_{12}, v_{21})$ as shown in Fig. 1b. Thus the payoffs $u_{12}$ and $v_{21}$ can be determined by system (2).

Third, $u_{21}$ and $v_{12}$ can be represented by population densities at steady states in the selector-secretor system. Similar to the discussion in the neglector-secretor system, the relationship between selectors and secretors is mutualistic while selectors have to spend energy in developing the ability of discrimination and waste time in discrimination. Thus the selector-secretor system can be depicted by

$$\begin{align*}
\frac{dN}{dt} &= N(\tilde{r}_1 - d_1 N + \frac{a_{12}\tilde{\alpha}M}{1 + \tilde{\alpha}M + \tilde{\alpha}\beta N}) \\
\frac{dM}{dt} &= M(-d_2 + \frac{a_{21}\tilde{\alpha}N}{1 + \tilde{\alpha}M + \tilde{\alpha}\beta N})
\end{align*}$$ (3)

where $N$ and $M$ denote population densities of selectors and secretors, respectively. Since selectors need to develop ability of discrimination, we have $\tilde{r}_1 \leq r_1$. We also have $\tilde{\alpha} < \alpha$ because the selectors spend time in discrimination [11]. Other parameters have the same meanings as those in (1). In the next section of this paper, system (3) is shown to have a globally asymptotically stable equilibrium $E_{21}(u_{21}, v_{12})$ as shown in Fig. 1c. Thus the payoffs $u_{21}$ and $v_{12}$ can be determined by system (3).

Finally, $u_{22}$ and $v_{22}$ can be represented by population densities at steady states in the selector-cheater system. While selectors spend energy in discrimination and will not enter nectarless flowers, cheaters without visitation cannot survive. Thus, the selector-cheater system can be depicted by

$$\begin{align*}
\frac{dN}{dt} &= N(\tilde{r}_1 - d_1 N) \\
\frac{dM}{dt} &= -\tilde{d}_2 M
\end{align*}$$ (4)

where $N$ and $M$ denote population densities of selectors and cheaters, respectively. The parameters have the same meanings as those in systems (1-3). It is obvious that equilibrium $E_{22}(\tilde{r}_1/d_1, 0)$ of system (4) is globally asymptotically stable, as shown in Fig. 1d. The biological meaning is that when all floral pollinators are selectors, cheaters will go to extinction and the selectors approach their carrying capacity in the absence of the plants. Thus, we have

$$u_{22} = \frac{\tilde{r}_1}{d_1}, \ v_{22} = 0.$$

Based on the payoffs obtained above, we consider three games in the plant-pollinator systems: the co-evolution of plants and pollinators; the evolution of pollinators in a constant state of plant population; the evolution of plants in a constant state of pollinator population.
Game 1. The co-evolution of plants and pollinators

In the co-evolution of plants and pollinators, the pollinators could learn from their experience and adjust their strategies according to the frequency of nectarless flowers. That is, the frequency of neglectors varies with the frequency of cheaters. Let $M_1$ and $M_2$ be the frequencies of secretors and cheaters, respectively. Then $M_1 \geq 0, M_2 \geq 0$, and $M_1 + M_2 = 1$. The expected fitness of neglectors is $f_1 = \mu \cdot (u_{11} M_1 + u_{12} M_2)$, and that of selectors is $f_2 = \mu \cdot (u_{21} M_1 + u_{22} M_2)$, where $\mu$ is a coefficient and represents the ratio of real fitness to the expected one with $0 < \mu \leq 1$. Let $N_1$ and $N_2$ be the frequencies of neglectors and selectors, respectively. Then $N_1 \geq 0, N_2 \geq 0$ and $N_1 + N_2 = 1$. The average fitness of pollinators is

$$\bar{f} = N_1 f_1 + N_2 f_2.$$ 

The increase of $\frac{1}{N_1} \frac{dN_1}{dt}$ measures evolutionary success of the neglecting strategy, which can be depicted by the difference of $f_1$ and $\bar{f}$ \cite{17, 44}. That is, $\frac{dN_1}{dt} = N_1 (f_1 - \bar{f})$.

Similarly, the plants could change their strategies (i.e., secreting and cheating) according to the state of pollinator population. We can obtain the expression about $\frac{dM_1}{dt}$ in the same way as that about $\frac{dN_1}{dt}$. Thus the evolutionary game between plants and pollinators can be depicted by the following replicator equations

$$\frac{dN_1}{dt} = N_1 (1 - N_1) [\xi_{12} - (\xi_{12} + \xi_{21}) M_1]$$
$$\frac{dM_1}{dt} = M_1 (1 - M_1) [\eta_{12} - (\eta_{12} + \eta_{21}) N_1]$$

in which $\xi_{12} = u_{12} - u_{22}$, $\xi_{21} = u_{21} - u_{11}$, $\eta_{12} = v_{12} - v_{22}$, $\eta_{21} = v_{21} - v_{11}$ and $dt := \mu \cdot dt$. Because $N_2 = 1 - N_1, M_2 = 1 - M_1$, we will focus on $N_1$ and $M_1$ in the following discussions. It can be seen that $P(N_1^0, M_1^0)$ is an equilibrium of system (5), where

$$N_1^0 = \frac{\eta_{12}}{\eta_{12} + \eta_{21}}, M_1^0 = \frac{\xi_{12}}{\xi_{12} + \xi_{21}}.$$  

Game 2. The evolution of pollinators in a constant state of plant population

Consider the situation in which plants are in a constant state and pollinators can adjust strategies to maximize their fitness. Let $M_1^*$ be the constant frequency of secretors. Then the expected fitness of neglectors is $f_1^0 = u_{11} M_1^* + u_{12} (1 - M_1^*)$ and that of selectors is $f_2^0 = u_{21} M_1^* + u_{22} (1 - M_1^*)$. Let $N_1$ and $1 - N_1$ be the frequencies of neglectors and selectors, respectively. Similar to the first equation of (5), we obtain

$$\frac{dN_1}{dt} = N_1 (1 - N_1) (f_1^0 - f_2^0) = -(\xi_{12} + \xi_{21}) N_1 (1 - N_1) (M_1^* - M_1^0).$$  

Game 3. The evolution of plants in a constant state of pollinator population

Consider the situation in which pollinators are in a constant state and plants can adjust strategies to maximize their fitness. Let $N_1^*$ be the constant frequency of neglectors. Then the expected fitness of secretors is $g_1^0 = v_{11} N_1^* + v_{12} (1 - N_1^*)$ and that of cheaters is $g_2^0 = v_{21} N_1^* + v_{22} (1 - N_1^*)$. Let $M_1$ and $1 - M_1$ be the frequencies of secretors and cheaters, respectively. Similar to the second equation of (5), we
obtain
\[
\frac{dM_1}{dt} = M_1(1 - M_1)(d_1^0 - d_2^0) = (\eta_{12} + \eta_{21})M_1(1 - M_1)(N_1^0 - N_2^*).
\]  
(8)

**Remark 1.** The reason that the unique equilibrium \( E_{11}(u_{11}, v_{11}) \) of system (1) is used as the entries in the payoff matrices for the larger game between all four species is discussed as follows, while similar discussions can be given for other equilibria in systems (2)-(4).

In the sub-game between two pure strategies of neglecting and secreting, \( E_{11}(u_{11}, v_{11}) \) is valid as the long term expected fitnesses. The reason can be described as follows: since all pollinators are assumed to be neglectors and all plants are assumed to be secretors, following the basic tenet of Darwinism, \( u_{11}, v_{11} \) represent reproduction successes of neglectors and secretors in the game between the two pure strategies [17, 44]. Thus, in the larger game with four pure strategies (i.e., four species), the payoffs between two pure strategies of neglecting and secreting should be described by their reproduction successes in the system that all pollinators are neglectors and all plants are secretors. Thus, the payoffs should be represented by the final reproduction successes \((u_{11}, v_{11})\). The underlying reason is that it is the reproduction success that drives selection and evolution in the pollinator-plant game. Thus, using the long term expected fitnesses as payoffs in the pollinator-plant game is reasonable.

In the short term expected fitnesses, nectar and pollinated pollen that the species obtain can be used as the payoffs. However, since the nectar and pollinated pollen are only parts of the factors in species’ reproduction successes, it is oversimplified if the reproduction successes are only represented by the nectar and pollinated pollen from the viewpoint of evolutionary games [17]. Indeed, as shown in our work, the species’ reproduction successes can be affected not only by nectar and pollinated pollen, but also by species’ conversion ratio, growth/death rate, etc.

3. **Equilibrium stability.** In this section, we show equilibrium stability of models in section 2, while the definitions of \( A, B, C, \Delta; \tilde{A}, \tilde{B}, \tilde{C}, \tilde{\Delta}; \bar{A}, \bar{B}, \bar{C}, \bar{\Delta} \) and \( \text{tr}(J) \) are given in Appendix A.

Proposition 1 shows equilibrium stability of systems (1) and (3).

**Proposition 1.** (Wang et al. 2012)

(i) When
\[
a_{21} > \beta d_2 + \frac{d_1 d_2}{\alpha r_1},
\]
there is a positive equilibrium \( E_{11}(u_{11}, v_{11}) \) of system (1) with
\[
u_{11} = \frac{d_2(1 + \alpha v_{11})}{\alpha(a_{21} - \beta d_2)}, \quad v_{11} = \frac{-B + \sqrt{\Delta}}{2A}
\]
and \( E_{11} \) is globally asymptotically stable as shown in Fig.1a.

(ii) When
\[
a_{21} > \beta d_2 + \frac{\tilde{d}_1 \tilde{d}_2}{\tilde{\alpha} \tilde{r}_1},
\]
there is a positive equilibrium \( E_{21}(u_{21}, v_{12}) \) of system (3) with
\[
u_{21} = \frac{d_2(1 + \tilde{\alpha} v_{21})}{\tilde{\alpha}(a_{21} - \beta d_2)}, \quad v_{12} = \frac{-\tilde{B} + \sqrt{\tilde{\Delta}}}{2\tilde{A}}
\]
and \( E_{21} \) is globally asymptotically stable as shown in Fig.1c.
Remark 2. Proposition 1 makes sense biologically. When the secretors’ efficiency \((a_{21})\) in translating neglector-secretor interaction into fitness is large, they can coexist with neglectors at steady states as shown in Fig. 1a. When the secretors’ efficiency \((a_{21})\) in translating selector-secretor interaction into fitness is large, they can coexist with selectors at steady states as shown in Fig. 1b. Since \(\tilde{\alpha} < \alpha\) and \(\tilde{\alpha_1} \leq \alpha_1\), condition (9) is always true if (11) is true, which implies that the plant can persist in the neglector-secretor system if it can persist in the selector-secretor system. The underlying reason is that a neglector need not spend energy on discrimination, which results in its advantage over the selector and leads to the conclusion.

The following Proposition 2 show that payoffs of neglectors and secretors increase when \(r_1\) and \(\alpha\) increase. Indeed, since (1) is a mutualistic system and its right-hand sides are strictly monotonically increasing functions of \(r_1\) and \(\alpha\), we obtain Proposition 2 by the comparison theorem (Cosner 1990).

Proposition 2.

\[
\frac{\partial u_{11}}{\partial r_1} > 0, \quad \frac{\partial u_{11}}{\partial \alpha} > 0, \quad \frac{\partial v_{11}}{\partial r_1} > 0, \quad \frac{\partial v_{11}}{\partial \alpha} > 0.
\]

The following Corollary 1 shows that neglectors gain more than selectors when meeting secretors. Indeed, since \(r_1 > \tilde{\alpha_1}\) and \(\alpha > \tilde{\alpha}\), we conclude the following result by Proposition 2.

Corollary 1.

\[u_{11} > u_{21} .\]

Equilibrium stability of system (2) is given by Hwang [15, 16]. We cite the results as follows. When \(\tilde{a}_{21} > \beta \hat{d}_2 + d_1 \hat{d}_2 / \alpha r_1\), there is a positive equilibrium \(E_{12}(u_{12}, v_{21})\) of system (2) with

\[
u_{12} = \frac{\hat{d}_2 (1 + \alpha v_{21})}{\alpha (\tilde{a}_{21} - \beta \hat{d}_2)} , \quad v_{21} = \frac{-\hat{B} + \sqrt{\Delta}}{2\hat{A}} .
\] (13)

Proposition 3. (Hwang [15, 16]) When

\[\tilde{a}_{21} > \beta \hat{d}_2 + \frac{d_1 \hat{d}_2}{\alpha r_1} , \quad \text{tr}(J) < 0 \] (14)

the positive equilibrium \(E_{12}(u_{12}, v_{21})\) of system (2) is globally asymptotically stable as shown in Fig. 1c.

Proposition 3 makes sense biologically. When the cheaters’ efficiency \((\tilde{a}_{21})\) in translating neglector-cheater interaction into fitness is large, they can coexist with neglectors at steady states as shown in Fig. 1c.

Equilibrium stability of system (5) is well understood. Denote

\[
S = \{(N_1, M_1) : 0 < N_1 < 1, 0 < M_1 < 1\} .
\]

Proposition 4. (Hofbauer and Sigmund [17]) When

\[u_{11} > u_{21} , \quad u_{12} < u_{22} , \quad v_{11} < v_{21} , \quad v_{12} > v_{22} \] (15)
there is a positive equilibrium $P(N_{1}^{0}, M_{1}^{0})$ of (5). $P$ is a center and all orbits of (5) in $S$ are periodic cycles around $P$ as shown in Fig. 2. The time averages of the periodic cycles $(N_{1}(t), M_{1}(t))$ remain constant:

$$\left(\frac{1}{\omega} \int_{0}^{\omega} N_{1}(t)dt, \frac{1}{\omega} \int_{0}^{\omega} M_{1}(t)dt\right) = (N_{1}^{0}, M_{1}^{0})$$

where $\omega$ is the period.

Proposition 4 makes sense biologically. From condition (15), we obtain that the strategy of ignoring does not dominate that of selecting, while the strategy of secreting does not dominate that of cheating. This is consistent with our intuition in general situations. Thus, all strategies (species) in the system coexist in periodic oscillations as shown in the next section, and the mixed strategy $P(N_{1}^{0}, M_{1}^{0})$ is stable.

Since $1 - M_{1}^{0}$ denotes the frequency of cheaters, the following result shows the monotonicity of $1 - M_{1}^{0}$ with $\tilde{\alpha}$, which will be useful in discussions in section 5. The proof is in Appendix B.

**Proposition 5.** Assume (15) hold. The frequency of cheaters $1 - M_{1}^{0}$ at the steady state $P(N_{1}^{0}, M_{1}^{0})$ satisfies

$$\frac{\partial(1 - M_{1}^{0})}{\partial \tilde{\alpha}} < 0.$$ 

The following Proposition 6 shows coexistence of empty and full flowers, while the proof is in Appendix C.
Proposition 6. Assume conditions (11) and (14) hold. When

\[ u_{12} < u_{22}, \quad v_{11} < v_{21} \tag{16} \]

the four species of system (5) coexist. Neglectors have the same fitness \((u^0)\) as selectors, while secretors have the same fitness \((v^0)\) as cheaters. \(u^0\) and \(v^0\) are

\[ u^0 = \frac{u_{12}u_{21} - u_{11}u_{22}}{u_{12} + u_{21} - u_{11} - u_{22}}, \quad v^0 = \frac{v_{12}v_{21} - v_{11}v_{22}}{v_{12} + v_{21} - v_{11} - v_{22}}. \]

Proposition 6 demonstrates that when condition (16) holds, cheaters and secretors coexist in periodic oscillations. When in coexistence, cheaters and secretors have the same fitness, while neglectors and selectors have the same fitness.

When the state of plant population remains constant as described by system (7), Proposition 7 shows dynamics of the system. The proof can be obtained directly from the righthand side of (7).

Proposition 7. (i) If \(f^0_1 = f^0_2\), all solutions of (7) are equilibria.

(ii) If \(f^0_1 < f^0_2\), all solutions of (7) satisfy \(\lim_{t \to +\infty} N_1(t) = 0\).

(iii) If \(f^0_1 > f^0_2\), all solutions of (7) satisfy \(\lim_{t \to +\infty} N_1(t) = 1\).

Proposition 7 demonstrates the evolution of pollinators in a constant state of plant population. (i) When neglectors and selectors have the same fitness, they would coexist. (ii) When neglectors gain less than selectors, all visitors will become selectors. (iii) When neglectors gain more than selectors, all visitors will become neglectors.

When the state of pollinator population remains constant as described by (8), Proposition 8 shows dynamics of the system. The proof can be obtained directly from the righthand side of (8).

Proposition 8. (i) If \(g^0_1 = g^0_2\), all solutions of (8) are equilibria.

(ii) If \(g^0_1 < g^0_2\), all solutions of (8) satisfy \(\lim_{t \to +\infty} M_1(t) = 0\).

(iii) If \(g^0_1 > g^0_2\), all solutions of (8) satisfy \(\lim_{t \to +\infty} M_1(t) = 1\).

Proposition 8 demonstrates the evolution of plants in a constant state of pollinator population. (i) When secretors and cheaters have the same fitness, they would coexist. (ii) When secretors gain less than cheaters, nectarless flowers will spread widely. (iii) When secretors gain more than cheaters, all plants will become secretors.

Remark 3. Proposition 7 shows a phenomenon similar to that described by Bell [2]. Assume \(u_{12} < u_{22}\), i.e., \(\xi_{12} < 0\). Then the inequality \(f^1_1 < f^1_2\) can be expressed as \(M^*_1 < M^*_1\). Thus if the frequency of cheaters is large (i.e., \(M^*_1 < M^*_1\)), we have \(f^1_1 < f^1_2\) and \(N_1 \to 0\), which implies that all visitors will become selectors. If the frequency of cheaters is small (i.e., \(M^*_1 > M^*_1\)), we have \(f^1_1 > f^1_2\) and \(N_1 \to 1\), which implies that all visitors will become neglectors. If the frequency of cheaters is intermediate (i.e., \(M^*_1 = M^*_1\)), we have \(f^1_1 = f^1_2\), which implies that neglectors and selectors could coexist. While Bell’s work is based on static games through novel derivations, the results of this paper are based on evolutionary games.

4. A cyclical game. In this section, we show mechanisms by which the four species coexist in periodic oscillations, which implies that the cyclic game between nectarless flowers and pollinators described by Bell [2] occurs. We also demonstrate that some species will go to extinction when (16) does not hold.
First, we consider the situation in which condition (16) holds. By (16), we obtain \( \xi_{12}, \xi_{21} < 0 \) and \( \eta_{12}, \eta_{21} > 0 \). Let \( D_v \) be the payoff difference between neglectors and selectors (pollinators), and \( D_p \) be that between secretors and cheaters (plants). Then \( D_v \) and \( D_p \) can be expressed by

\[
D_v = u_{11}M_1 + u_{12}M_2 - (u_{21}M_1 + u_{22}M_2) = -(\xi_{12} + \xi_{21})(M_1 - M_1^0)
\]

\[
D_p = v_{11}N_1 + v_{12}N_2 - (v_{21}N_1 + v_{22}N_2) = (\eta_{12} + \eta_{21})(N_1^0 - N_1)
\]

Thus \( D_v = D_v(M_1) \) is a monotonically increasing function, and \( D_p = D_p(N_1) \) is a monotonically decreasing function. When secretors and cheaters have the frequencies \( M_1^0 \) and \( 1 - M_1^0 \) respectively, neglectors and selectors have the same payoff since \( D_v(M_1^0) = 0 \). Similarly, when neglectors and selectors have the frequencies \( N_1^0 \) and \( 1 - N_1^0 \) respectively, secretors and cheaters have the same payoff since \( D_p(N_1^0) = 0 \). Therefore, if initial frequencies of the players are at equilibrium \( P(N_1^0, M_1^0) \), then the frequencies will remain constant and the species approach a Nash equilibrium.

The biological implications of the cyclic nature in Proposition 4 are shown as follows. Assume that initial frequencies of the players are at the Nash equilibrium \( P(N_1^0, M_1^0) \). If a fluctuation decreases the amount of neglectors (i.e., \( N_1 < N_1^0 \)), then the payoffs for the pollinators will not change: each type has the same payoff, which is determined by the state of the plant population. However, the frequency of neglectors will not return to \( N_1^0 \). As to the plant population, the risk of being discriminated increases. The payoff for cheaters is less than that for secretors since \( D_p(N_1) > 0 \) as \( N_1 < N_1^0 \). Then the frequency \( M_1 \) of secretors increases. When \( M_1 > M_1^0 \), we obtain \( D_v(M_1) > 0 \), which implies that neglectors gain more than selectors. Then the frequency of neglectors increases: but the secretors gain less than the cheaters; hence more cheaters, hence fewer neglectors, and so on. This forms a cyclical game similar to “the battle of the sexes” (Dawkins 1976), as shown in Fig. 2.

Second, we consider the situation in which condition (16) does not hold. It follows from (16) that we need to discuss two cases: \( u_{12} > u_{22}, v_{11} < v_{21}; v_{11} > v_{21} \).

(i) When \( u_{12} > u_{22} \) and \( v_{11} < v_{21} \), the strategy of neglecting dominates that of selecting since \( u_{11} > u_{21} \). Thus neglectors always gain more than selectors, for example, when the cost of discrimination is sufficiently large. Then all visitors will become neglectors with \( M_1 \rightarrow 1 \). Thus all plants will become cheaters with \( N_1 \rightarrow 0 \) since \( v_{11} < v_{21} \). The condition \( v_{11} < v_{21} \) may be satisfied when the cost for plants to produce nectar is sufficiently large (e.g., \( d_2 \gg d_2 \)). Therefore, the case of \( u_{12} > u_{22} \) and \( v_{11} < v_{21} \) demonstrates a possible phenomenon in which nectarless flowers may widely spread when both costs of pollinators’ discrimination and plants’ producing nectar are large. (ii) When \( v_{11} > v_{21} \), the strategy of secreting dominates that of cheating since \( v_{12} > v_{22} \). Thus all plants will become secretors with \( N_1 \rightarrow 1 \). Then all visitors will become neglectors since \( u_{11} > u_{21} \). This case may happen when the mutualism between neglectors and secretors is sufficiently strong.

Numerical simulations show that when parameters vary, nectarless flowers can vary among extinction, persistence and widespread. Let \( r_1 = 0.5, d_1 = 0.01, \alpha = 0.15, \beta = 0.8, d_2 = 0.55, a_{12} = 0.8, a_{21} = 0.9, b_{12} = 0.2, d_2 = 0.5, \tilde{r}_1 = 0.45, \tilde{\alpha} = 0.1 \). By systems (1)-(4), we obtain \( (u_{11}, v_{11}) = (113.8, 115.2), (u_{12}, v_{21}) = (35.5, 36.1), (u_{21}, v_{12}) = (109.2, 122.4), (u_{22}, v_{22}) = (45, 0) \). Thus \( u_{11} > u_{21}, u_{12} > u_{22}, v_{11} > v_{21}, v_{12} > v_{22} \), which implies that the strategy of neglecting dominates that of selecting and the strategy of secreting dominates that of cheating. That is, all pollinators will become neglectors and all flowers will be full.
When \( a_{12} = 0.002, b_{12} = 0.05 \) and other parameters remain unchanged, we obtain \((u_{11}, v_{11}) = (51.2, 156.8), (u_{12}, v_{12}) = (44.8, 158.2), (u_{21}, v_{12}) = (45.5, 153.5), (u_{22}, v_{22}) = (45, 0)\), which implies that condition (16) holds and the four species persist in periodic oscillations, as shown in Fig. 2.

When \( a_{12} = 0.002, b_{12} = 0.03 \) and other parameters remain unchanged, we obtain \((u_{11}, v_{11}) = (51.2, 156.8), (u_{12}, v_{21}) = (47.5, 162), (u_{21}, v_{12}) = (45.5, 153.5), (u_{22}, v_{22}) = (45, 0)\). Thus \( u_{11} > u_{21}, u_{12} > u_{22}, v_{11} < v_{21}, v_{12} > v_{22} \), which implies that the strategy of neglecting dominates that of selecting and the strategy of cheating dominates that of secreting. That is, all pollinators will become neglectors and nectarless flowers will spread widely.

5. Discussion. In this paper we consider evolutionary games between flowering plants and pollinators. Stability analysis on game models demonstrates mechanisms by which nectarless flowers could persist and by which a cyclic game between nectarless flowers and pollinators could occur.

Parameters in the systems are important for persistence of nectarless flowers. We focus on the cheaters’ efficiency in translating plant-pollinator interactions into fitness, while similar discussions can be given for the others. Indeed, (a) when the efficiency is small such that the strategy of secreting dominates that of cheating (i.e., \( v_{11} > v_{21} \)), cheaters will go to extinction. (b) When the efficiency is intermediate such that condition (16) holds, i.e., both of the strategies have the same fitness, cheaters and secretors coexist. (c) When the efficiency is large such that the strategy of cheating dominates that of secreting, cheaters will spread and secretors go to extinction. Since the cheaters’ efficiency depends on both pollinators’ ability in discrimination and cheaters’ ability in survival, the animals’ learning strategies and cheaters’ cross-pollinating frequencies are important to the persistence of nectarless flowers. While Bell [2] derived a critical frequency of nectarless flowers which could result in emergence of selectors, the above results in (a-c) derived conditions which could lead to cheaters’ extinction, persistence in periodic oscillations, and persistence without secretors (i.e., cheaters spread widely). A similar discussion can be given for conditions which could lead to neglectors’ extinction, persistence in periodic oscillations, and persistence without selectors (i.e., neglectors spread widely).

Based on the expressions of payoffs in section 2 and condition (16), we derive criteria for the persistence of nectarless flowers in terms of the given parameters. For example, when the nectar-producing cost (determined by \( d_2 \) and \( \tilde{d}_2 \)) and cheaters’ efficiency (\( \tilde{a}_{21} \)) are well balanced such that payoffs in section 2 satisfy condition (16), both empty and full flowers coexist. Otherwise, one of the species will go to extinction while the other spread widely. For all we know, such criteria are not in the literature.

When plants and their pollinators are in co-evolution, Proposition 6 shows conditions under which the four species, i.e., cheaters, secretors, selectors and neglectors could coexist. The underlying reason for the coexistence is that cheaters and secretors have the same reproductive success, and so do the selectors and neglectors. Otherwise, cheaters and secretors could not coexist. Indeed, as described in section 4, (i) if selectors gain less than neglectors when meeting cheaters (e.g., the cost of discrimination is sufficiently large) and secretors gain less than cheaters when meeting neglectors, then all visitors will become neglectors and all flowers will become nectarless ones. (ii) If secretors gain more than cheaters when meeting neglectors
(e.g., the pollination mutualism is sufficiently strong), then all visitors will become neglectors, while all plants will become secretors (Proposition 6)).

When in coexistence, frequencies of the four species vary in periodic oscillations as described by Proposition 6, while the average frequencies remain constant. Thus the nectarless flowers persist in an average frequency \(1 - M^0_1\). The neglectors, which are pollinators of the nectarless flowers, have an average frequency \(N^0_1\). Here, \(1 - M^0_1\) and \(N^0_1\) are expressed by (6). While Bell [2] derived a critical frequency of cheaters by rational deduction, our result demonstrates a similar value through the evolution of nectarless flowers based on an evolutionary game model. The underlying principle of the model is the tenet of Darwinism, i.e., the evolution of species’ density with a given strategy can be described by the difference between fitness of this strategy and the average fitness of all strategies [17]. Thus, analysis on the model leads to conditions under which four strategies for pollinators and plants persist. Furthermore, the average frequency of nectarless flowers will monotonically increase when the time spent in discrimination between cheaters and secretors increases. Indeed, when the time increases, the parameter \(\alpha\) in (1) decreases [11]. It follows from Proposition 5 that the frequency of nectarless flowers increases. This monotonicity has been verified by real observations [12].

In the evolution of floral visitors with a constant state of plant population, there is a critical frequency (i.e., \(1 - M^0_1\)) of nectarless flowers. As shown by Proposition 7, when the plants have a mixed strategy and the frequency of nectarless flowers is equal to the critical value, the visitors would also have mixed strategies and both neglectors and selectors coexist. Otherwise, when frequencies of nectarless flowers are larger than the critical value, selectors will gain more than neglectors and all visitors will become selectors. When frequencies of nectarless flowers are less than the value, selectors will gain less than neglectors and all visitors will become neglectors. While a similar phenomenon has been described by Bell [2] based on the payoff of nectar, our work shows the result based on the payoff of reproductive success, and provides new insight. For example, by (6) we have

\[
1 - M^0_1 = \frac{u_{11} - u_{21}}{u_{11} - u_{21} + u_{22} - u_{12}}, \quad u_{11} - u_{21} > 0, \quad u_{22} - u_{12} > 0
\]

which implies that \(1 - M^0_1\) monotonically decreases with the increase of \(u_{22} - u_{12}\). Recall that the value of \(u_{22} - u_{12}\) represents the advantage of selectors over neglectors when they meet nectarless flowers. Then the higher the value of \(u_{22} - u_{12}\), the smaller the critical value of \(1 - M^0_1\), which implies that the easier the pollinators become selectors.

In the evolution of plants with a constant state of pollinator population, there is a critical frequency (i.e., \(1 - N^0_1\)) of selectors. As shown by Proposition 8, when visitors have a mixed strategy and the frequency of selectors is equal to the critical value, the plants will also have mixed strategies and both secretors and cheaters coexist. Otherwise, when frequencies of selectors are larger than the critical value, secretors will gain more than cheaters and all plants will become secretors. When frequencies of selectors are less than the value, secretors will gain less than cheaters and all plants will become cheaters. That is, nectarless flowers will spread widely in this situation.

While the stable Nash equilibrium in the co-evolution predicts persistence of nectarless flowers and needs to be verified by real observations, this work considered adaptive plasticity of both plants and visitors, and provide an insight on the
mechanisms by which nectarless flowers can survive. This may be helpful for understanding the complexity in the evolution of nectarless flowers.

**Appendix A.**

When \( a_{21} > \beta d_2 \), we denote

\[
A = \frac{d_1 d_2}{(a_{21} - \beta d_2)^2}, \quad B = -\frac{a_{12}}{a_{21}} - \frac{r_1}{a_{21} - \beta d_2} + \frac{2d_1 d_2}{\alpha(a_{21} - \beta d_2)^2},
\]

\[
C = -\frac{r_1}{a(a_{21} - \beta d_2)} + \frac{d_1 d_2}{\alpha^2(a_{21} - \beta d_2)^2}, \quad \Delta = B^2 - 4AC. \tag{17}
\]

Let \( \tilde{A} \), \( \tilde{B} \) and \( \tilde{C} \) be the values of \( A,B \) and \( C \) in (5) in which \( \alpha \) and \( r_1 \) are replaced with \( \tilde{\alpha} \) and \( \tilde{r}_1 \), respectively. Denote \( \tilde{\Delta} = \tilde{B}^2 - 4\tilde{A}\tilde{C} \).

Let \( \bar{A} \), \( \bar{B} \) and \( \bar{C} \) be the values of \( A,B \) and \( C \) in (5) in which \( d_2 \), \( a_{12} \) and \( a_{21} \) are replaced with \( \tilde{d}_2 \), \( -b_{12} \) and \( \tilde{a}_{21} \), respectively. Denote \( \bar{\Delta} = \bar{B}^2 - 4\bar{A}\bar{C} \).

Let \( J \) be the Jacobian matrix of system (2) at \( E_{12} \). Denote

\[
\text{tr}(J) = -d_1 u_{12} + \frac{\alpha \tilde{d}_2 (\tilde{b}_{12} - \tilde{a}_{21}) v_{21}}{\tilde{a}_{21}(1 + \alpha v_{21} + \alpha \beta u_{12})}.
\]

**Appendix B.** Proof of Proposition 5. It follows from Proposition 4 that

\[
\frac{1}{1 - M_1^q} = 1 + \frac{u_{22} - u_{12}}{u_{11} - u_{21}}.
\]

By Proposition 2, we obtain \( \partial u_{21}/\partial \tilde{\alpha} > 0 \). Thus, Proposition 5 is proved.

**Appendix C.** Proof of Proposition 6.

(i) When condition (11) holds, we obtain \( v_{12} > 0 \). Since \( v_{22} = 0 \), we have \( v_{12} > v_{22} \). By Corollary 1, we obtain \( u_{11} > u_{21} \). It follows from Proposition 4 that the result (i) is proved.

(ii) Let \( (N_1(t), M_1(t)) \) be a solution of (5) with period \( \omega \). Then frequencies of secretors and cheaters are \( M_1(t) \) and \( 1 - M_1(t) \) at time \( t \). The expected fitness of a neglector is \( u_1(t) = u_{11} M_1(t) + u_{12} (1 - M_1(t)) \), and the average fitness in a period is

\[
\bar{u}_1 = \frac{1}{\omega} \int_0^\omega [u_{11} M_1(t) + u_{12} (1 - M_1(t))] dt.
\]

By Proposition 4, we obtain

\[
\bar{u}_1 = \frac{u_{12} u_{21} - u_{11} u_{22}}{u_{12} + u_{21} - u_{11} - u_{22}} = u^0.
\]

Similarly, the average fitness \( \bar{u}_2 \) of a selector in a period can be obtained and \( \bar{u}_2 = u^0 \). For secretors and cheaters, we can show \( \bar{u}_1 = \bar{u}_2 = u^0 \) in the same way.

**Acknowledgments.** We would like to thank the anonymous reviewers for their helpful comments on the manuscript.
REFERENCES

[1] J. R. Beddington, Mutual interference between parasites or predators and its effect on searching efficiency, *J. Animal Ecol.*, **44** (1975), 331–340.
[2] G. Bell, The evolution of empty flowers, *J. Theor. Biol.*, **118** (1986), 253–258.
[3] J. M. Biernaskie, S. C. Walker and R. J. Gegear, Bumblebees learn to forage like Bayesians, *The American Naturalist*, **174** (2009), 413–423.
[4] R. S. Cantrell, C. Cosner and S. G. Ruan, Intraspecific interference and consumer-resource dynamics, *Discrete and Continuous Dynamical Systems*, **4** (2004), 527–546.
[5] J. E. Carlson and K. E. Harms, The evolution of gender-biased nectar production in hermaphroditic plants, *The Botanical Review*, **72** (2006), 179–205.
[6] R. V. Cartar, Resource tracking by bumble bees: Responses to plan-level differences in quality, *Ecology*, **85** (2004), 2764–2771.
[7] C. Cosner, Variability, vagueness and comparison methods for ecological models, *Bull. Math. Biol.*, **58** (1996), 207–246.
[8] N. Davis, *The Selfish Gene*, Macat Library, London, 2017.
[9] D. L. DeAngelis, R. A. Goldstein and R. V. O’Neill, A model for trophic interaction, *Ecology*, **56** (1975), 881–892.
[10] C. J. Essenberg, Explaining variation in the effect of floral density on pollinator visitation, *The American Naturalist*, **180** (2012), 153–166.
[11] M. A. Fishman and L. Hadany, Plant-pollinator population dynamics, *Theoretical Population Biology*, **78** (2010), 270–277.
[12] F. S. Gilbert, N. Haines and K. Dickson, Empty flowers, *Functional Ecology*, **5** (1991), 29–39.
[13] J. Golubov, L. E. Eguiarte, M. C. Mandujano, J. López-Portillo, C. Montañá, Why be a honeyless honey mesquite? Reproduction and mating system of nectarful and nectarless individuals, *American Journal of Botany*, **86** (1999), 955–963.
[14] A. Gumbert, Color choices by bumble bees (Bombus terrestris): Innate preferences and generalization after learning, *Behavioral Ecology and Sociobiology*, **48** (2000), 36–43.
[15] T.-W. Hwang, Global analysis of the predator-prey system with Beddington-DeAngelis functional response, *J. Math. Anal. Appl.*, **281** (2003), 395–401.
[16] T.-W. Hwang, Uniqueness of limit cycles of the predator-prey system with Beddington-DeAngelis functional response, *J. Math. Anal. Appl.*, **290** (2004), 113–122.
[17] J. Hofbauer and K. Sigmund, *Evolutionary Games and Population Dynamics*, Cambridge University Press, Cambridge, UK, 1998.
[18] A. I. Internicola, P. A. Page, G. Bernasconi and L. D. B. Gigord, Competition for pollinator visitation between deceptive and rewarding artificial inflorescences: An experimental test of the effects of floral color similarity and spatial mingling, *Functional Ecology*, **21** (2007), 864–872.
[19] A. I. Internicola, G. Bernasconi and L. D. B. Gigord, Should a food-deceptive species flower before or after rewarding species? An experimental test of pollinator visitation behaviour under contrasting phenologies, *Journal of Evolutionary Biology*, **21** (2008), 1358–1365.
[20] A. I. Internicola and L. D. Harder, Bumble-bee learning selects for both early and long flowering in food-deceptive plants, *Proceedings of the Royal Society B: Biological Sciences*, **279** (2012), 1538–1543.
[21] S. R.-J. Jang, Dynamics of herbivore-plant-pollinator models, *J. Math. Biol.*, **44** (2002), 129–149.
[22] J. Jersiková, S. D. Johnson and P. Kindlmann, Mechanisms and evolution of deceptive pollination in orchids, *Biological Reviews*, **81** (2006), 219–235.
[23] S. D. Johnson and L. A. Nilsson, Pollen carryover, geitonogamy, and the evolution of deceptive pollination systems in orchids, *Ecology*, **80** (1999), 2607–2619.
[24] T. L. de Jong and P. G. L. Klinkhamer, *Evolutionary Ecology of Plant Reproductive Strategies*, Cambridge University Press, Cambridge, 2005.
[25] T. T. Makino and S. Sakai, Experience changes pollinator responses to floral display size: From size-based to reward-based foraging, *Functional Ecology*, **21** (2007), 854–863.
[26] J. A. J. Metz, R. M. Nishe and S. A. H. Geritz, How should we define 'fitness' for general ecological scenarios?, *Trends in Ecology & Evolution*, **7** (1992), 198–202.
[27] M. R. Neiland and C. C. Wilcock, Fruit set, nectar reward, and rarity in the Orchidaceae, *American Journal of Botany*, **85** (1998), 1657–1671.
POLLINATION-MUTUALISM WITH EMPTY FLOWER

[28] S. Neniez-Vieyra, M. Ordoñez, J. Fornoni, K. Boege and C. A. Domínguez, Selection on signal-reward correlation: Limits and opportunities to the evolution of deceit in Turnera ulmifolia L., J. Evol. Biol., 23 (2010), 2760–2767.

[29] L. A. Nilsson, Orchid pollination biology, Trends in Ecology and Evolution, 7 (1992), 255–259.

[30] L. Oña and M. Lachmann, Ant aggression and evolutionary stability in plant-ant and plant-pollinator mutualistic interactions, J. Evol. Biol., 24 (2011), 617–629.

[31] E. R. Pianka, Evolutionary ecology, Harper and Row, New York, (1974), 133–146.

[32] G. H. Pyke, Plant-pollinator co-evolution: It’s time to reconnect with optimal foraging theory and evolutionarily stable strategies, Perspectives in Plant Ecology Evolution and Systematics, 19 (2016), 70–76.

[33] L. van der Pijl and C. H. Dodson, Orchid Flowers, Their Pollination and Evolution, University of Miami Press, Coral Gables, Fla., 1966.

[34] H. C. Qu, T. Seifan and M. Seifan, Effects of plant and pollinator traits on the maintenance of a food deceptive species within a plant community, Oikos, 126 (2017), 1815–1826.

[35] J. L. Ren, D. D. Zhu and H. Y. Wang, Spreading-vanishing dichotomy in information diffusion in online social networks with intervention, Discrete Contin. Dyn. Syst. Ser. B, 24 (2019), 1843–1865.

[36] S. Renner, Rewardless Flowers in the Angiosperms and the Role of Insect Cognition in Their Evolution. In Plant-Pollinator Interactions: From Specialization to Generalization, Nickolas Merritt Waser editor, 2006.

[37] T. A. Revilla, Numerical responses in resource-based mutualisms: A time scale approach, J. Theoretical Biology, 378 (2015), 39–46.

[38] D. R. Rodríguez and L. Torres-Sorando, Models of infectious diseases in spatially heterogeneous environments, Bulletin of Mathematical Biology, 63 (2001), 547–571.

[39] A. Smithson and L. D. B. Gigord, The evolution of empty flowers revisited, The American Naturalist, 161 (2003), 537–552.

[40] J. M. Soberon and C. Martinez del Rio, The dynamics of a plant-pollinator interaction, J. Theor. Biol., 91 (1981), 363–378.

[41] P. D. Taylor, Evolutionarily stable strategies with two types of players, J. Appl. Prob., 16 (1979), 76–83.

[42] J. D. Thakar, K. Kunte, A. K. Chauhan, A. V. Wateve and M. G. Wateve, Nectarless flowers: Ecological correlates and evolutionary stability, Oecologia, 136 (2003), 565–570.

[43] Y. S. Wang, Global dynamics of a competition-parasitism-mutualism model characterizing plant-pollinator-robin interactions, Physica A, 510 (2018), 26–41.

[44] Y. S. Wang, H. Wu and S. Sun, Persistence of pollination mutualisms in plant-pollinator-robin systems, Theoretical Population Biology, 81 (2012), 243–250.

[45] Y. S. Wang, Dynamics of a plant-nectar-pollinator model and its approximate equations, Mathematical Biosciences, 307 (2019), 42–52.

[46] Y. S. Wang, H. Wu and D. L. DeAngelis, Global dynamics of a mutualism-competition model with one resource and multiple consumers, J. Math. Biol., 78 (2019), 683–710.

Received October 2018; revised April 2019.

E-mail address: wuhong@mail.sysu.edu.cn
E-mail address: sunsh@lzu.edu.cn
E-mail address: mcswys@mail.sysu.edu.cn