The co-optimization of floral display and nectar reward

Prajakta V Belsare[1], Balasubramanian Sriram[2] and Milind G Watve[3], *

[1]Department of Zoology, University of Pune, Pune 411 007, India
[2]Indian Institute of Technology, Kanpur 208 016, India
[3]Indian Institute of Science Education and Research, Pune 411 021, India

*Corresponding author (Email, milind_watve@yahoo.com)

In most insect-pollinated flowers, pollinators cannot detect the presence of nectar without entering the flower. Therefore, flowers may cheat by not producing nectar and may still get pollinated. Earlier studies supported this 'cheater flower' hypothesis and suggested that the cost saving by cheater flowers could be the most predominant selective force in the evolution of nectarless flowers. Previous models as well as empirical studies have addressed the problem of optimizing the proportion of nectarless and nectarful flowers. However, there has been no attempt to optimize the investment in nectar production along with that in floral display. One of the key questions that arises is whether the floral display will evolve to be an honest indicator of nectar reward. We use a mathematical model to co-optimize the investments in nectar and floral display in order to achieve maximum reproductive success. The model assumes that pollinators rely on a relative rather than an absolute judgement of reward. A conspicuous floral display attracts naïve pollinators on the one hand and enhances pollinator learning on the other. We show that under these assumptions, plant–pollinator co-evolution leads to honest signalling, i.e. a positive correlation between display and reward.

1. Introduction

Pollination is an extremely important event in the reproductive life of a flowering plant. Flowers reward pollinators in the form of nectar. Pollinators visit flowers to obtain the nectar reward and, in turn, pollinate the flower. Nectar concealment is common in flowering plants (Inouye 1980; Rodriguez-Girones and Santamaria 2005, 2006) owing to which pollinators are unable to detect the presence of nectar without entering the flower. Nectar production involves considerable cost (Southwick 1987; Pyke 1991). As a result, flowers may cheat by not making nectar (Bell 1986; Thakar *et al.* 2003). Such nectarless flowers can still get pollinated (Ferdy *et al.* 1998). Some species of orchids are known to produce nectarless, i.e. rewardless, flowers (Ackerman 1986; Dafni 1984; Smithson and Gigord 2001). They are pollinated through Batesian mimicry (Dafni 1984;

Johnson 2000; Giggord *et al.* 2002). In many other species, a variable proportion of flowers are nectarless, the specific proportion presumably being the result of evolutionary optimization (Thakar *et al.* 2003; Anand *et al.* 2007). Flowers may lure pollinators by making large floral displays (Ohashi and Yahara 2002) and may not provide any reward (Ferdy *et al.* 1998).

In spite of the possibility of deception, many studies show that honest signals are stable in a wide range of systems (Leal 1999; Dunn and Cockburn 1999). This applies to floral signalling as well (Armbruster *et al.* 2005). An honest display implies that flowers having large displays are more likely to be rewarding. This raises the question as to why plants should give honest signals if they can enjoy better fitness by cheating.

Pollinators are capable of learning the reward differentials between plants (Smithson and MacNair 1997; Ferdy *et al.*

Keywords. Pollination biology; plant–animal interaction; co-evolution; cheater; pollinator learning

1998; Gumbert and Kunze 2001). It is generally assumed that a more conspicuous display will attract more pollinators. On the other hand, a less recognized consequence of display could be that it may also make the flower and the plant more conspicuous and thereby enhance pollinator learning. If pollinators are more likely to remember conspicuous individuals, they may avoid revisiting a nectarless plant. Here, we use a mathematical model based on pollinator learning, to co-optimize the investment in nectar and that in floral display in order to achieve maximum reproductive success.

Our model is based on the model by Thakar *et al.* (2003), which assumed plant fitness to be a saturating function of the number of pollinator visits. Pollinators were assumed to have a certain capacity to remember rewards obtained from individual plants so that they were less likely to revisit non-rewarding plants. However, even in the absence of nectar, there were assumed to be some random visits by pollinators that were novices, exploring or unable to learn from previous visits. We extend this model below, modifying certain critical assumptions.

2. The model

Based on the assumptions above, Thakar *et al.* (2003) wrote the following equation

$$R = BR + (R\max - BR)\frac{N}{K+N} - CN$$

where R = reproductive success of an individual plant producing a proportion N of nectarful flowers. BR is the reproductive success gained from random visits by pollinators, Rmax the maximum possible reproductive success and K, a Michaelis–Menten-like constant. The cost of production of nectar per flower is C.

Our model differs from that of Thakar *et al.* (2003) with respect to the following assumptions. The model of Thakar *et al.* assumes BR to be a constant. We assume BR to be a function of investment in individual display (D). Pollinators learn to associate the average nectar content of a species with the species-specific floral display. Therefore, BR for a given individual should increase with the average investment in nectar content (A) of a species. For a given nectar content, the display by an individual flower would be an important determinant of pollinator attraction; however, the relative rather than the absolute display should be more important. Since pollinators are more likely to choose more attractive flowers, a display that is below average is less likely to attract pollinators. Therefore, we choose a Michaelis–Menten-like form of equation where for a given A the average display acts as a Michaelis–Menten-like constant. Therefore,

$$BR = \frac{A \times D}{a + A \times D}$$

where a represents a variable denoting average display at a given average nectar content.

We set maximum reproductive fitness (Rmax) to be unity. R increases with increasing reward such that,

$$R = BR + \frac{(1 - BR) \times N^p}{A^p + N^p} - C(N + D)$$

where N = individual investment in nectar, D = individual investment in display, p = a parameter related to the pollinators' learning efficiency, and C = a proportionality constant relating investment to reproductive cost.

Substituting for BR

$$R = \frac{A \times D}{a + A \times D} + \frac{(1 - \frac{A \times D}{a + A \times D}) \times N^p}{A^p + N^p} - C(N + D)$$

$$R = \frac{A \times D}{a + A \times D} + \frac{(\frac{a}{a + A \times D}) \times N^p}{A^p + N^p} - C(N + D)$$

Pollinators are likely to learn faster from a species with conspicuous flowers than one with inconspicuous flowers. Therefore, p should be a function of a. We assume it to be a linear function where c and m are constants.

$$p = m \times a + c$$

This changes the shape of the equation depending upon the value of p. If p is 1, it follows a simple saturation curve. At higher values of p, the curve becomes increasingly sigmoid, ultimately giving rise to a sharp threshold. In spite of the change in shape, the point of inflection which lies at A remains unchanged. Pollinators are more likely to visit plants with greater-than-average nectar. Conversely, the ones offering below-average reward are likely to be deserted. With greater learning efficiency, the difference is expected to become sharper. The above equation realistically reflects such a relationship (figure 1). If pollinators are fast learners, then p is large and the curve is sharp, whereas if pollinators are poor learners, then p is small and the curve is more flat. This is established analytically in appendix article 1.

An analytical solution indicates that at small p, stable equilibrium is possible where A = optimum N and a = optimum D. At larger p, the solution becomes complex (*see* appendix article 2). We use the simulation approach to elucidate the path towards the equilibrium, if any, and the stability of the equilibrium. For a given initial condition, using the equation for R, we first determine the optimum N that maximizes R and similarly the optimum D that maximizes R. We then assume that the average nectar content (A) moves towards the optimum N and average display (a) moves towards the optimum D by a small step.

However, as soon as *A* and *a* change, the parameters get reset and optimization needs to be done again. Thus, the simulation program keeps on re-optimizing and moving the averages in the appropriate direction in search of a condition when *A* = optimum *N* and *a* = optimum *D*.

3. Results

The reproductive success equation is mainly shaped by the learning curve. At small *p* there is a single peak and only one optimum. At large *p*, on the other hand, the success curve is bimodal with two local optima (figure 2). Analytical solutions (appendix article 2) indicate that at small values of *p*, stable equilibria are possible, where *A* = optimum *N* and *a* = optimum *D*. However, at large *p*, such equilibria do not exist. In agreement with the analytical solution, simulations gave two types of equilibria. In the first type, the average successfully chased the optimum and, when *A* was equal to optimum *N* and *a* was equal to optimum *D*, the system

Figure 1. Pollination success increases with nectar investment. The shape of the relationship is decided by *p,* the pollinator learning capacity. Small *p* gives flat curves and larger values result into threshold relationships. A = 0.4 for all curves.

Figure 2. Reproductive success as a function of *N* at large *p* (*p* = 5 illustrated). The curves have two local optima and the shape is decided by *A*.

stabilized (figure 3). There was another kind of equilibrium where, when *A* crossed a critical value while moving towards optimum *N*, the optimum *N* jumped to a new value which was substantially lower than *A*; and when *A* started moving towards this optimum *N*, the optimum *N* jumped towards the higher end again. This behaviour was observed owing to the bimodality of the success curve (figure 2). At a critical *A*, the two peaks were almost identical and with a slight change in *A* the global optimum shifted. A similar behaviour was observed with *a* and optimum *D*. Thus, in the second type of equilibrium, optimum *N* and optimum *D* kept on oscillating and in effect keeping *A* and *a* around a dynamic equilibrium (figure 4). The first type of equilibrium was typically obtained at small values of *p* and type 2 equilibrium at large *p*.

The equilibrium values of *A* and *a* were mainly decided by the pollinator learning parameters *c* and *m*. The equilibrium *A* increased with *c* at small values of *m* but the trend reversed at greater values of *m*. Similarly, the equilibrium *a* increased with *c* at small values of *m* but the trend reversed at greater values of *m*. The equilibrium *A* increased till a threshold value of *p* and for higher values of *p*, equilibrium *A* decreased
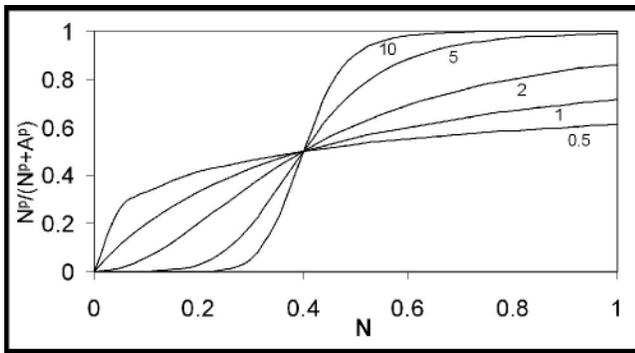

Figure 3. Simulations showing a system approaching stable equilibrium at small values of *p*.

Figure 4. System showing stable oscillations at large values of *p*.

Figure 5. The relationship between equilibrium *A* and equilibrium *a* as influenced by *p* (indicated by data labels).

(figure 5). Equilibrium *a* also had a similar relationship with *p* but the threshold was different. Figure 5 shows a dual trend in the relationship between *A* and *a* at equilibrium, which is mainly driven by *p*. In spite of the duality, there was a consistent positive correlation between *A* and *a* supporting the honest signalling hypothesis.

4. Discussion

Pollination mutualism is a complex co-evolutionary process and, in spite of extensive research inputs over several decades, a number of questions remain unanswered. Cheating by flowers and avoidance learning by pollinators is a co-evolutionary arms race, and attractive floral display can be a strategic weapon used by plants. However, since pollinators are also evolving, they can potentially make use of the display to enhance learning. The model above shows that such a process can lead to a stable equilibrium of strategies.

Although Thakar *et al.* (2003) incorporated pollinator learning in their model, in earlier work, the parameters of learning were assumed to be constant, which is a naïve assumption. If pollinator learning has adequate flexibility, it can counteract plant strategies to maximize its own returns. As an advancement over the Thakar *et al.* (2003) model, we incorporated pollinator learning efficiency as a function of the conspicuousness of flowers. This critical assumption is central to the positi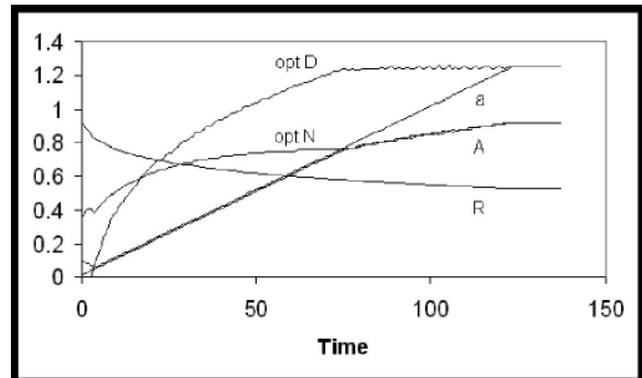ve correlation between display and reward obtained by the model. Since pollinator visits are assumed to respond to the relative rather than absolute nectar content of an individual, and since efficient learning results in a sharper response curve (figure 1), the relationship

between nectar content and reproductive success becomes bimodal at large values of *p* (figure 2). With flatter curves accompanying smaller values of *p*, on the other hand, stable equilibria are possible. At large *p* the bimodality results into two possible optima and a dynamic equilibrium with shifting optima is obtained. An alternative possibility is that there might be dispersive selection in the population where a proportion of individuals reaches one optimum and others reach the other optimum. In this case, frequency-dependent selection can ensure optimum proportions of the two types. In either case, evolutionary equilibria do exist for both nectar content and floral display, the most important determinant of the equilibrium being pollinator learning efficiency.

The most important result of the model is that a positive relationship exists between floral display and nectar content (figure 5). At low values of *p*, the relationship is convex and at large values concave, the nature of which is mainly decided by pollinator learning efficiency. There appears to be a critical learning efficiency that pushes the evolution of plants towards more nectar. Interestingly, at higher learning efficiencies, there is a reduction in the equilibrium nectar content. This happens because the success curve (figure 1) becomes a threshold relationship. Plants with slightly higher nectar content than the average gain almost the same reproductive success as ones having a much larger *N*. It is expected, therefore, that this will give rise to an optimum level of learning in pollinators. At present, we have not modelled the evolution of learning efficiencies in pollinators and, especially, have not incorporated the cost of learning. With some cost of increasing learning efficiency, the optimum could be somewhat lower than what this model shows.

We should therefore expect a mosaic of cheating and honesty in plant–pollinator co-evolution. On the one hand, plants will have a variable proportion of nectarless or cheater flowers optimized according to the local ecological conditions, and on the other, the display should reflect the reward with some degree of honesty. These predictions of the model are compatible with the observations that a substantial proportion of species have some proportion of nectarless flowers (Thakar *et al.* 2003, Anand *et al.* 2007) and there is detectable honesty in signalling as well (Armbruster *et al.* 2005).

References

Ackerman J D 1986 Mechanism and evolution of food-deceptive pollination systems in orchids; *Lindleyana* **1** 108–113

Anand C, Umranikar C, Shintre P, Damle A, Kale J, Joshi J and Watve M G 2007 Presence of two types of flowers with respect to nectar sugar in two gregariously flowering species; *J. Biosci.* **32** 769–774

Armbruster W S, Antonsen L and Pelabon C 2005 Phenotypic selection on *Dalechampia* blossoms: honest signaling affects pollination success; *Ecology* **86** 3323–3333

Bell G 1986 The evolution of empty flowers; *J. Theor. Biol.* **118** 253–258

Dafni A 1984 Mimicry and deception in pollination; *Ann. Rev. Ecol. Syst.* **15** 259–278

Dunn P O and Cockburn A 1999 Extrapair mate choice and honest signaling in cooperatively breeding superb fairy-wrens; *Evolution* **53** 938–946

Ferdy J B, Gouyon P H, Moret J and Godelle B 1998 Pollinator behavior and deceptive pollination: learning process and floral evolution; *Am. Nat.* **152** 696–705

Gigord L D B, Macnair M R, Striteski M and Smithson A 2002 The potential for floral mimicry in rewardless orchids: an experimental study; *Proc. R. Soc. London B*. **269** 1389–1395

Gumbert A and Kunze J 2001 Colour similarity to rewarding model plants affects pollination in a food deceptive orchid, *Orchis boryi*; *Biol. J. Linn. Soc.* **72** 419–433

Johnson S D 2000 Batesian mimicry in the non-rewarding orchid *Disa pulchra,* and its consequences for pollinator behaviour; *Biol. J. Linn. Soc.* **71** 119–132

Inouye D W 1980 The effect of proboscis and corolla tube lengths on patterns and rates of flower visitation by bumble-bees; *Oecologia* **45** 197–201

Leal M 1999 Honest signalling during prey–predator interactions in the lizard *Anolis cristatellus*; *Anim. Behav.* **58** 521–526

Ohashi K and Yahara T 2002 Visit larger displays but probe proportionally fewer flowers: counterintuitive behaviour of nectar-collecting bumble bees achieves an ideal free distribution; *Func. Ecol.* 16 492–503

Pyke G H 1991 What does it cost the plant to produce floral nectar?; *Nature (London)* **350** 58–59

Rodriguez-Girones M A and Santamaria L 2005 Resource portioning among flower visitors and evolution of nectar concealment in multi-species communities; *Proc. R. Soc. London B* **272** 187–192

Rodriguez-Girones M A and Santamaria L 2006 Models of optimum foraging and resource partitioning: deep corollas for long tongues; *Behav. Ecol.* **17** 905–910

Smithson A and MacNair M R 1997 Negative frequency dependent selection by pollinators on artificial flowers without rewards; *Evolution* **51** 715–723

Smithson A and Gigord L D B 2001 Are there fitness advantages in being a rewardless orchid? Reward supplementation experiments with *Barlia robertiana*; *Proc. R. Soc. London B* **268** 1435–1441

Southwick E E 1987 Photosynthate allocation to floral nectar: a neglected energy investment; *Ecology* **65** 1775–1779

Thakar J D, Kunte K, Chauhan A K, Watve A V and Watve M G 2003 Nectarless flowers: ecological correlates and evolutionary stability; *Oecologia* **136** 565–570

The co-optimization of floral display and nectar reward

Prajakta V Belsare, Balasubramanian Sriram and Milind G Watve

Appendix

Article 1

Here, we attempt to establish analytically the relationship of R with N as affected by p.

$$R = f(p), \text{ i.e.}$$

$$R = BR + \frac{(1 - BR) \times N^p}{A^p + N^p} - C(N + D)$$

$$R' = \frac{N^p}{A^p + N^1} \text{ and compute } dR'/dp.$$

$$\ln R' = \ln N^p - \ln(A^p + N^p)$$

now differentiating with respect to p

$$\frac{1}{R'}\frac{dR'}{dp} = \frac{1}{N^p}\frac{dN^p}{dp} - \frac{1}{(N^p + A^p)}\frac{d(N^p + A^p)}{dp}$$

applying

$$\frac{dx}{dp} = x \ln N = N^p \ln N$$

thus we get

$$\frac{1}{R'}\frac{dR'}{dp} = \frac{1}{N^p}N^p \ln N - \frac{1}{(N^p + A^p)}(A^p \ln A + N^p \ln N)$$

$$\frac{1}{R'}\frac{dR'}{dp} = \frac{A^p}{(A^p + N^p)} \ln \frac{N}{A}$$

$$\frac{dR'}{dp} = \frac{A^p N^p}{(A^p + N^p)^2} \ln \frac{N}{A}$$

$$\Rightarrow \frac{dR}{dp} = \frac{(1 - BR)A^p N^p}{(A^p + N^p)^2} \ln \frac{N}{A}$$

Thus, for $N > A$ as per the assumption in the simulations, we find that the rate of change in R with respect to p is positive tending towards 0 as $N \to A$ and for $N < A$ the rate of change is negative. This results in the curves shown in figure 1.

Article 2:
Analytical treatment of the optimization problem

R is a function of N and D. Thus, we are interested in finding the optimum value of R in the surface obtained by plotting R versus N and D. We assume $C = 1$ for simplicity of solutions.

We optimize in two dimensions.

To do this, we compute

$$\frac{dR}{dD}, \frac{dR}{dN}, \frac{d^2R}{dD^2}, \frac{d^2R}{dN^2}, \frac{d^2R}{dDdN} = \frac{d^2R}{dNdD}.$$

Next, we put $\frac{dR}{dD} = 0 \text{ and } \frac{dR}{dN} = 0$ to obtain the critical point.

In order to obtain the nature of the critical point, we compute the Hessian determinant $(H = (\frac{d^2R}{dD^2} \cdot \frac{d^2R}{dN^2} - (\frac{d^2R}{dDdN})^2))$ to check its sign and check for the sign of $\frac{d^2R}{dD^2}$.

Thus, $\dfrac{dR}{dD} = \dfrac{aA^{p+1}}{(a + A \times D)^2(A^p + N^p)} - 1,$

$$\frac{dR}{dN} = \frac{apA^p N^{p-1}}{(a + A \times D)(A^p + N^p)^2} - 1,$$

$\frac{dR}{dD} = 0 \text{ and } \frac{dR}{dN} = 0$ yields the critical point which is computed numerically for different values of p. Thus, the values of N and D are obtained.

$$\frac{d^2R}{dD^2} = \frac{-2aA^{p+2}}{(a + A \times D)^3(A^p + N^p)} < 0$$

$$\frac{d^2R}{dN^2} = \frac{apA^p N^{p-2}(A^p(p-1) - N^p(p+1))}{(a + A \times D)(A^p + N^p)^3},$$

$$\frac{d^2R}{dDdN} = \frac{-apA^{p+1}N^{p-1}}{(a + A \times D)^2(A^p + N^p)^2}$$

Therefore

$$H = (2A^{3p+2} N^{p-2}a^2p(1-p)A^{2p+2}N^{2p-2}a^2p(p+2))/((a+A\times D)^4 (A^p+N^p)^4)$$

Thus for all $p = \in (0,1)$ $H > 0$ and as $\frac{d^2R}{dD^2} < 0$ maxima is possible for every p in this range at the critical points. At equilibrium $A = N$ and substituting this in H we get

$H = 2A^{4p}a^2p(1-p) + A^{4p}a^2p(p+2)/(16a^4(1+A)^4(A^P)^4)$

$H = (2p(1-p)+p(p+2))/(16a^2(1+A)^4) = (4p-p^2) / (16a^2(1+A)^4)$

Thus, for all $p > 4$ H < 0 and $p < 4$ H > 0.

This implies that at critical points less than 4, we get maxima when stability is achieved when $N = A$, and for all critical points greater than 4, we get a saddle point as the sign of the Hessian changes at 4. The precise position of the critical p will change if we change the assumed parameters. The behaviour that there will be stability below a critical p remains invariant.