

Juilee D. Thakar · Krushnamegh Kunte ·  
Anisha K. Chauhan · Aparna V. Watve ·  
Milind G. Watve

## Nectarless flowers: ecological correlates and evolutionary stability

Received: 2 August 2002 / Accepted: 2 May 2003 / Published online: 28 June 2003  
© Springer-Verlag 2003

**Abstract** In animal-pollinated flowers, the pollinators cannot detect the presence of nectar before entering flowers, and therefore flowers may cheat by not producing nectar. An earlier model suggested that a mixed strategy of producing nectarful and nectarless flowers would be evolutionarily stable. Here we compare nectarless flowers as a cheating strategy with three competing hypotheses namely “visit-more-flowers”, “cross-pollination enhancement” and “better contact”. We collected field data on 28 species of plants to test some of the differential predictions of the hypotheses. Nectarless flowers were detected in 24 out of 28 plant species. Correlations of percent nectarless flowers with floral and ecological variables support the cheater flower hypothesis. We further model the cost-benefits of cheating and show that an evolutionary stable ratio of nectarless to nectarful flowers can be reached. The equilibrium ratio is mainly decided by factors associated with pollinator density and pollinator learning.

**Keywords** Animal pollination · Nectarless flowers · Cheating · Pollinator learning

### Introduction

Pollination of flowers by insects is a major contributor to fitness in cross-pollinated angiosperms, and nectar is the most common reward of pollinators (Kevan and Baker 1985). However, production of nectar exerts a considerable drain on the resources of plants (Southwick 1987; Pyke 1991). If pollinators are unable to differentiate between nectarful and nectarless flowers the flowers may cheat by not producing nectar. Some species of orchids are known to produce rewardless flowers. These species

are pollinated through Batesian mimicry (Johnson 1994, 2000; Gigord et al. 2002) or through naïve pollinator visits (Gigord et al. 2002). A proportion of nectarless flowers are known to occur within rewarding species and these are thought to be cheater flowers (Bell 1986). An individual bearing nectarless cheater flowers may enjoy better fitness since it does not pay the cost of nectar. However, avoidance learning by pollinators (Smithson and MacNair 1997; Ferdy et al. 1998; Gumbert and Kunze 2001) can decrease the reproductive success of nectarless plants. The possible consequences of this have attracted empirical (Pleasants and Chaplin 1983; Golubov et al. 1999), and theoretical (Bell 1986) investigations. Bell (1986) modeled the evolution of nectarless flowers and learning among pollinating insects, assuming that discrimination occurs at the level of an individual flower, and showed that the strategy of producing a mixture of nectarful and nectarless flowers would be evolutionarily stable. The model is based on the assumption that insects can differentiate between nectarful and nectarless flowers before entering them and based on the presence or absence of this ability classifies them as “selectors” and “neglecters”. Currently no mechanism by which insects can detect the presence of nectar without entering the flower is known. In reward supplementation experiments bumble bees showed no evidence of visually assessing rewards (Smithson and Gigord 2001). Our hypothesis therefore differs from the Bell model in that we assume that the pollinator learns about an empty flower only after entering it but this learning would result in avoidance behavior later.

Nectarless flowers, however, may evolve for reasons other than cheating. Three other hypotheses have been suggested.

1. Visit more flowers: the nectarless flowers may compel pollinators to visit more flowers on the same plant (Feinsinger 1978).
2. Cross-pollination enhancement: nectarless flowers frustrate the pollinators and coerce them to visit other plants, thus reducing geitonogamy and enhancing

J. D. Thakar · K. Kunte · A. K. Chauhan · A. V. Watve ·  
M. G. Watve (✉)  
Life Research Foundation,  
10 Pranav Soc., 1000/6-C, Navi Peth, 411 030 Pune, India  
e-mail: watve@vsnl.com  
Tel.: +91-20-4338009

**Table 1** Testable predicted correlations of nectarless flowers from the alternative hypotheses: + positive correlation with the proportion of nectarless flowers; – negative correlation with the proportion of nectarless flowers; 0 no correlation/no prediction

Property	Cheater flower, Bell's model	Cheater flower, our model	Visit more flowers	Cross pollination enhancement	Better contact
Gregariousness	0	+	–	–	0
Pollinator density	0	+	–	0	+
Corolla tube length	+	0	0	0	0
Corolla color polymorphism	0	+	0	0	+
Number of flowers on a plant	0	0	+	+	0

cross-pollination (Johnson 2000). Since foraging insects tend to restrict their visits to a single species bypassing other equally rewarding species (Dukas and Real 1993) effective cross-fertilization can be achieved.

3. Better contact: the pollinator probes deeper or searches more on not finding nectar and therefore has an increased chance of contact (Smithson and Gigord 2001).

The four hypotheses are not mutually exclusive and nectarless flowers may serve more than one purpose. However, ecological conditions favoring each of them are likely to be different and therefore each of the hypotheses would predict different ecological associations. The predictions can be tested against field data to determine which of the possible selective forces have dominated the evolution of nectarless flowers. Table 1 summarizes the predictions of the hypotheses and models.

The Bell (1986) model of cheater flowers predicts that plant species with a deep concealment of nectar (deep corolla tubes) would tend to produce a higher proportion of nectarless flowers. This is not necessary in our model of cheater flowers. If pollinators possess the ability to learn from experience, they would avoid individual plants producing a larger proportion of nectarless flowers. Learning involves identification of individual plants, which would be difficult when plants occur gregariously. Moreover, in gregarious species the distance between plants, and therefore the cost of visiting different individuals, is small and thus learning to avoid a certain individual is less critical. Therefore we expect a greater tendency to cheat in gregarious species. Gregariousness increases cross-pollination naturally and the plants need not adopt specific strategies for this purpose. On the other hand, if a solitary plant bears many nectarful flowers, a pollinator visiting it is less likely to move to other plants since the cost of moving to other plants is large owing to the greater distance between them. Therefore, to achieve cross-pollination, it would be necessary for solitary plants to coerce pollinators to move to other plants by producing more nectarless flowers. Thus the “cross-pollination enhancement” hypothesis predicts that solitary species and species with a large number of flowers will have a greater proportion of nectarless flowers. The “visit-more-flowers” function of nectarless flowers also predicts that solitary plants bearing a large number of flowers will have a greater proportion of nectarless flowers. When

plants are gregarious, pollinators unable to get nectar from a few flowers can easily shift to another individual plant and therefore the “visit-more-flowers” strategy will give little rewards to the individual plant.

Pollinator density, presence of model rewarding species and corolla color polymorphism increase the probability of naïve pollinator visits and therefore are expected to enhance cheating. Naïve bumblebees spend more time on nectarless flowers than experienced bees (Smithson and Gigord 2001) therefore the “better contact” function may be served better under these conditions.

Thus, many predictions of the hypotheses contrast with each other and it should be possible now to isolate them empirically. Here we do so with data on 28 species of plants and show that the “cheater flower” hypothesis is supported empirically. We further develop a model to test the evolutionary stability of cheating.

## Materials and methods

Since the model used below and the accompanying arguments are based on the presence or absence of nectar, we used only qualitative sampling for the presence of nectar. Flowers were sampled at three localities: an urban area in Pune city and semi-evergreen forests at Tamhini and Bhimashankar in northern Western Ghats of the Pune district. Twenty-eight animal-pollinated, taxonomically and ecologically diverse species of flowering plants were sampled over a period of 1 year. For each species sampled, at least 50 flowers coming from a minimum of 5 individual plants were tested for nectar. Presence of nectar was checked for using the Diastrix strips spot test for urine sugar (Bayer Diagnostics, India). The strips indicate the presence of reducing sugars even when the amount of nectar in a sample is very small. For checking the presence of nectar, flowers were bagged overnight at the bud stage. After the flowers bloomed, the bags were removed at a time when the species sampled were most likely to have been visited by pollinators. The flowers were then plucked and the contents of the corolla tube squeezed onto the strip. The color change from blue to greenish blue, olive, brown and dark brown indicated reducing sugars in increasing amounts.

### Statistical analysis

Floral and ecological attributes of the plants were recorded in two types of data. The quantitative characters included the diameter or width of corolla, the depth of corolla tube, the number of flowers on a plant and the number of flowers in an inflorescence. These were measured on a minimum of 25 flowers and the means were ranked. Other characters, viz growth form of plant (herb, shrub, tree), gregariousness (gregarious versus solitary; gregariousness being defined as more than two-thirds of the plants in the study area being present in clusters of five or more individuals), flowering season

(months), type of corolla, color of flower and fragrance (presence-absence) were categorized. The categories were verified independently by three field botanists who were unaware of the hypotheses being tested.

For quantifiable characters we used rank correlations with the percentage of nectarless flowers. The categorical characters were analyzed using Kruskal Wallis one way analysis of variance.

## Results and discussion

Out of the 28 species of plants sampled, 24 species belonging to 23 genera and 16 families had nectarless flowers, revealing that nectarless flowers are widespread over an ecological and taxonomic range. Within a species significant differences existed between individual plants but inflorescences from the same plant did not significantly differ in the percentage of nectarless flowers. Among the species with nectarless flowers, the percentage of nectarless flowers ranged from 1.96% to 67.82% (Table 2). It was not correlated to corolla tube depth ( $r = -0.01097$ ,  $p > 0.25$ ), the number of flowers present at a given time on a plant ( $r = 0.22$ ,  $p > 0.10$ ) or the diameter of the corolla ( $r = -0.18$ ,  $p > 0.10$ ). No association was seen with the fragrance of flowers ( $H = 1.54$ ,  $K = 2$ ,  $p > 0.2$ ) or the flowering season ( $H = 5.49$ ,  $K = 7$ ,  $p > 0.30$ ). There was,

however, a positive correlation between percentage of nectarless flowers and number of flowers in an inflorescence ( $r = 0.47$ ,  $p < 0.01$ ). Tree species produced significantly less nectarless flowers ( $H = 10.66$ ,  $K = 4$ ,  $p < 0.01$ ), but most of the tree species sampled were solitary ( $\chi^2 = 8.77$ ,  $df = 3$ ,  $p < 0.02$ ). There was a significant correlation between gregariousness of plants and the proportion of nectarless flowers they produced ( $H = 8.017$ ,  $K = 4$ ,  $p < 0.02$ ).

The correlates of nectarless flowers clearly differentiate between the alternative hypotheses. Gregarious species had a greater percentage of nectarless flowers, which supports the “cheater flowers” hypothesis as against the two competing hypotheses. Although there was a positive correlation between the number of nectarless flowers and the number of flowers per inflorescence, the absence of a significant correlation with the standing number of flowers on individual plants does not support the “visit-more-flowers” hypothesis. Having many inflorescences on an individual plant is likely to make the distinction between individual plants more difficult. If animals learn to avoid one patch of flowers, they may still visit another patch on the same plant. This could enhance cheating. There was only one species in the study area with floral color polymorphism and this

**Table 2** Attributes of plant species sampled

Sr no.	Plant species	Family	Growth form <sup>a</sup>	Habit <sup>b</sup>	Flowers per plant (rank)	Flowers per inflorescence (rank)	Corolla tube depth (rank)	Fragrance	% Nectarless flowers <sup>c</sup>
1	<i>Jasminum</i> sp.	Oleaceae	J	S	21	3.5	13.5	+	27
2	<i>Barleria prionoitis</i>	Acanthaceae	S	G	8	7.5	24	-	33
3	<i>Blepharis asperim</i>	Acanthaceae	H	P	13.5	14	1	-	25
4	<i>Butea monosperma</i>	Fabaceae	T	S	27	24.5	6.5	-	15
5	<i>Carissa conjesta</i>	Apocynaceae	S	G	21	18	16	+	33
6	<i>Carvia callosa</i>	Acanthaceae	S	G	13.5	14	24	+	4
7	<i>Eicchornia crassipes</i>	Pontederiaceae	H	G	2.5	10	24	-	55
8	<i>Gardenia jasminoidis</i>	Rubiaceae	T	S	8	10	16	+	0
9	<i>Glyricidia sepium</i>	Fabaceae	T	PN	27	24.5	3.5	-	8
10	<i>Haplanthus tentaculatus</i>	Acanthaceae	H	S	2.5	10	10	-	3
11	<i>Impatiens balsamina</i>	Balsaminaceae	H	G	5	21	16	-	67
12	<i>Ixora</i> sp.	Rubiaceae	S	S	23	26	24	-	17
13	<i>Lantana camara</i>	Verbenaceae	S	G	27	27.5	6.5	-	68
14	<i>Lobellia nicotianaefolia</i>	Campanulaceae	S	S	13.5	27.5	3.5	-	27
15	<i>Mesonuron cucullatum</i>	Caesalpinaceae	S	G	25.5	23	10	-	29
16	<i>Michelia champaca</i>	Magnoliaceae	T	S	13.5	3.5	24	+	10
17	<i>Morinda tinctoria</i>	Rutaceae	T	S	6	14	10	+	29
18	<i>Mussaenda</i> sp.	Rubiaceae	T	S	8	7.5	10	-	0
19	<i>Nyctanthus arbor-tristis</i>	Oleaceae	T	S	21	3.5	13.5	+	17
20	<i>Pentas</i> sp.	Rubiaceae	H	PN	13.5	18	19	-	10
21	<i>Pentas</i> sp.	Rubiaceae	H	PN	13.5	18	19	-	10
22	<i>Quisqualis indica</i>	Combretaceae	J	S	19	21	28	-	36
23	<i>Syzygium jambose</i>	Myrtaceae	T	S	13.5	14	3.5	-	17
24	<i>Tabernaemontana divaricata</i>	Apocynaceae	T	S	18	3.5	19	-	0
25	<i>Thevetia peruviana</i>	Apocynaceae	T	S	4	3.5	24	-	0
26	<i>Thunbergia</i> sp.	Acanthaceae	J	G	13.5	14	24	-	23
27	<i>Trichodesma indica</i>	Boraginaceae	H	G	1	3.5	10	-	2
28	<i>Woodfordia fruticosa</i>	Lythraceae	S	G	25.5	21	3.5	-	17

<sup>a</sup> Growth form of the plant: H herb, J climber, S shrub, T tree

<sup>b</sup> Habit of the plant: S solitary, G gregarious, PN planted

<sup>c</sup> Digits corrected to nearest whole number

species (*Lantana camara*) had the highest proportion of nectarless flowers. Thus the data are compatible with all the predictions of the “cheater flower” hypothesis whereas the predicted correlations of the other hypotheses are not observed.

Some of the predictions have been tested based on single species observations in other studies. Johnson (2000) observed that the long-tongued fly probed fewer flowers and spent less time on rewardless *Disa pulchra* flowers as compared to the rewarding model *Watsonia lepidota*. Thus “visit more flowers” did not seem to work in this species. Brink and deWet (1980) did not observe any correlation between the length of corolla tube and the proportion of nectarless flowers as predicted by the Bell (1986) model. Smithson and Gigord (2001) showed that bumble bees spent more time searching on rewardless flowers resulting in a male advantage.

A few other predictions (Table 1) remain to be empirically tested. The percentage of nectarless flowers is expected to increase with pollinator densities. Almost all species in our sample came from a small area and the pollinator densities may not be very different. Also, we did not collect data on pollinator densities and therefore could not test the prediction. Testing this prediction would help us differentiate further between our model and Bell’s model, since in the latter the percentage of nectarless flowers is independent of pollinator density.

#### A model of insect-learning and evolution of nectarless cheater flowers

Since the Bell (1986) model is not adequately supported by field data and its assumption of “selector-neglector” dichotomy in insects is unsubstantiated, we propose an alternative, more realistic model.

We assume similar to Bell (1986) that fitness of a plant is a saturating function of the number of pollinator visits. A saturation relationship is conveniently described by a Michaelis-Menten type of equation. We assume that pollinators have a certain capacity to remember rewards obtained from individual plants and they are less likely to revisit a plant that has earlier offered low or no rewards. The number of visits a plant is likely to get is assumed to be a linear function of the proportion of nectarful flowers. However, even in the absence of nectar there would be some random visits by pollinators who are novice, exploring or were unable to learn from the previous visits (Gigord et al. 2002). The fitness gains from nectarful flowers are therefore written as,

$$R = BR + (R_{\max} - BR).N/(K + N) - C.N \quad (1)$$

where  $R$  is the reproductive success of an individual plant producing a proportion  $N$  of nectarful flowers.  $BR$  is the reproductive success gained from random visits by pollinators,  $R_{\max}$  the maximum possible reproductive success and  $K$ , a Michaelis-Menten constant. The cost of production of nectar per flower is  $C$ . Since the benefits increase with diminishing returns and the cost increases

linearly, there will be an optimum value of  $N$ , which maximizes  $R$ , and plants producing the optimum  $N$  will be selected. A necessary condition for a non-zero optimum is that the initial slope of the benefit curve should be greater than  $C$ .

The rise in  $R$  with increasing  $N$  must depend upon how efficiently pollinators learn about nectar rewards from an individual plant. The initial slope of the curve would be more if they learn fast. This however does not depend only upon the nectar production by the individual plant but the average nectarful flower production by other plants as well. The pollinators would receive higher rewards if they make a relative rather than absolute judgement. Attracting pollinators would then depend not so much on the absolute number of nectarful flowers but on the difference from the average. The slope of the  $R$  curve therefore is also decided by  $A$ , the average number of nectarful flowers produced by other plants. Since the rise of the curve is decided by  $K$ ,  $K$  should be a function of the average of the population and pollinator learning ability. We therefore write  $K = A \times L$ , where  $L$  is a constant inversely related to the pollinator learning ability. Both positive and negative learning is known in pollinators (Smithson and MacNair 1997; Ferdy et al 1998; Gumbert and Kunze 2001) and the learning ability is expected to affect the slope of the line.

Taking the maximum reproductive success unity:

$$R = BR + N.(1 - BR)/(A.L + N) - N.C \quad (2)$$

the reproductive success increases with increasing  $N$ , but saturates and declines later due to increasing cost (Fig. 1). The change in  $R$  with increasing  $N$  can be written as:

$$dR/dN = \frac{(A.L + N)(1 - BR) - (1 - BR)N}{(A.L + N)^2} - C$$

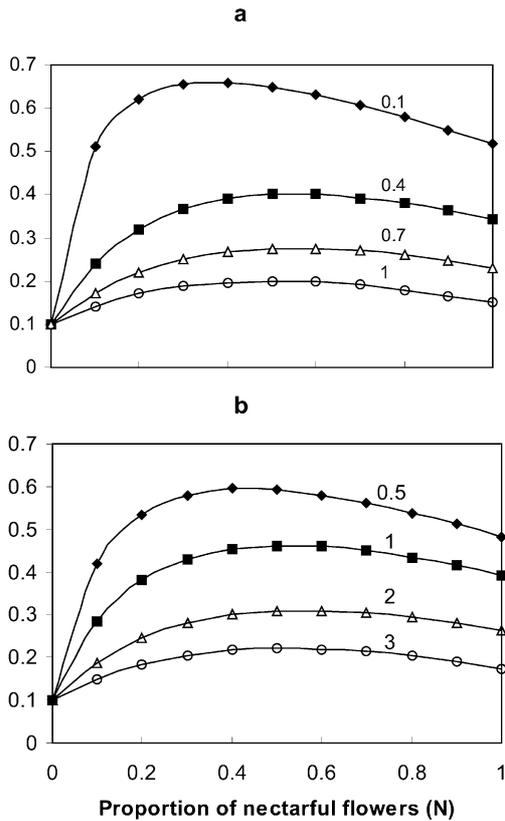
$R$  can be maximized at  $dR/dN = 0$ , therefore

$$\frac{(1 - BR).A.L}{(A.L + N)^2} = C$$

For every value of  $A$  there will be an optimum  $N$  (Fig. 2). Whenever the optimum is less than  $A$ , there will be selection for a decreased proportion of nectarful flowers and  $A$  would decrease. If  $A < N$ ,  $A$  will tend to increase. A stable equilibrium will be reached at  $A = N$ . Therefore,

$$N = \frac{(1 - BR).L}{C.(1 + L)^2}$$

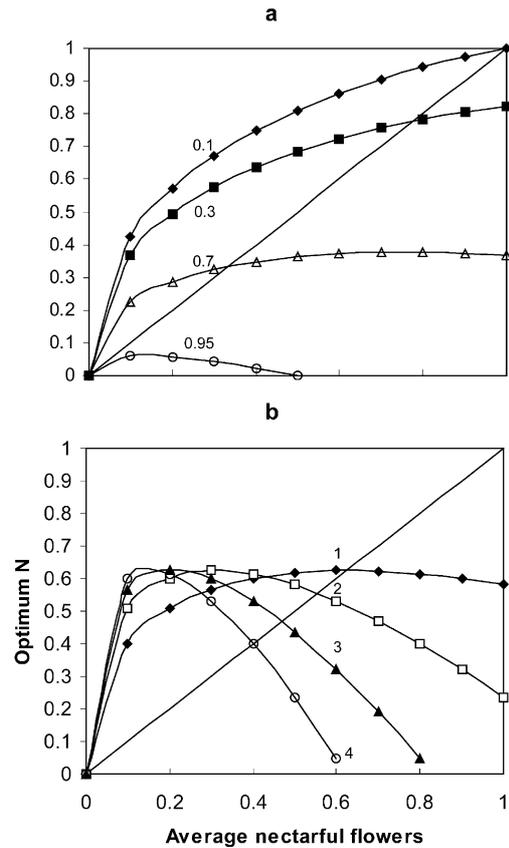
Thus  $N$ , the stable proportion of nectarless flowers decreases with  $C$ , as expected. A large  $BR$  would result in a smaller stable  $N$ . Any factor that increases visits by naïve pollinators would decrease the proportion of nectarful flowers. Interestingly, the relationship with  $L$  is non-linear. At small values of  $L$ ,  $N$  increases with  $L$  and it declines gradually for larger  $L$  values. However, a sharp distinction from a small sampling is impossible given the inevitability of sampling errors, and large samples would be costly. Therefore  $L$  is unlikely to take very small



**Fig. 1a, b** The reproductive success as a function of the proportion of nectarless flowers according to Eq. 2. The effects of the two important parameters  $A$  (the average number of nectarful flowers produced by other plants) and  $L$  (a constant inversely related to the pollinator learning ability) are shown in **a** ( $L=1$ ) and **b** ( $A=0.3$ ) respectively

values. In a realistic range a plant will have to produce more nectarful flowers if pollinator learning is faster. Several species of pollinators are known to restrict their visits to a single flowering species at a time even when other equally rewarding species are present (Heinrich 1975; Levin 1978; Waser 1986; Dukas and Real 1993). This can be viewed in a new light now. Since individual plants can differ in the proportion of nectarful flowers, it is necessary to learn and differentiate between individual plants. Multispecies foraging would make this task difficult. The evolution of single species foraging, which is crucial to cross-pollination could have evolved in response to cheating by plants.

Attempts to explain the nectarless flower phenomenon have generated many hypotheses (Feinsinger 1978; Bell 1986; Johnson 2000; Smithson and Gigord 2001). All the empirical studies trying to test such hypotheses so far have been on single species of flowering plants (e.g. Johnson 2000; Gumbert and Kunze 2001; Smithson and Gigord 2001). A multispecies correlation approach now enables us to differentiate between alternative hypotheses. In our sample of 28 species, the cheater hypothesis was better supported than the alternative hypotheses. This does not eliminate the other mechanisms but suggests that



**Fig. 2a, b** The optimum proportion of nectarful flowers ( $N$ ) changes with the standing average proportion of nectarful flowers ( $A$ ). An equilibrium will be reached at  $A=N$ . The equilibrium will be stable since at higher  $A$ ,  $N < A$  and at smaller  $A$ ,  $N > A$ . Such an equilibrium can be unstable only if the local slope of the line at the point of equilibrium is greater than 1. However, since the slope of the line  $A=N$  is 1, it cannot cut the curve at a slope greater than 1. Therefore all the equilibria in this system will be stable. The effects of the two important parameters  $BR$  and  $L$  are shown in **a** ( $L=0.5$ ) and **b** ( $BR=0.5$ ) respectively. The graphs show that evolution of all rewarding flowers, all rewarding flowers or a stable mixed strategy is possible under different conditions

cost saving by cheater flowers must be the most predominant selective force in the evolution of nectarless flowers. Other selective forces could have acted in specific situations since there is evidence for them in certain species (Smithson and Gigord 2001). Our model shows that completely rewardless, rewarding or a mixed strategy could be stable under different conditions and we expect varying proportions of nectarless flowers in a large number of animal-pollinated species.

**Acknowledgements** We thank K.N. Ganeshiah, R. Uma Shaanker and Aadish Dani for useful discussions, and Ashwini Ghate for help in field work. We also thank G.A.C. Bell for his critical comments on an earlier draft of this manuscript.

## References

- Bell G (1986) The evolution of empty flowers. *J Theor Biol* 118:253–258
- Brink DW, deWet MJM (1980) Interpopulation variation in nectar production in *Aconitum columbianum* (Ranunculaceae). *Oecologia* 47:160–163
- Dukas R, Real LA (1993) Learning constraints and floral choice behaviour in bumble bees. *Anim Behav* 46:637–644
- Feinsinger P (1978) Ecological interactions between plants and hummingbirds in a successional tropical community. *Ecol Monogr* 48:269–287
- Ferdy JB, Gouyon PH, Moret J, Godelle B (1998) Pollinator behavior and deceptive pollination: learning process and floral evolution. *Am Natl* 152:696–705
- Gigord LDB, Macnair MR, Striteski M, Smithson A (2002) The potential for floral mimicry in rewardless orchids: an experimental study. *Proc R Soc Lond B* 269:1389–1395
- Golubov J, Eguiarte LE, Mandujano MC, Lopez-Portillo J, Montana C (1999) Why be a honeyless honey mesquite? Reproduction and mating system of nectarful and nectarless individuals. *Am J Bot* 86:955–963
- Gumbert A, 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
- Heinrich B (1975) Bee flowers: a hypothesis on flower variety and blooming times. *Evolution* 29:325–334
- Johnson SD (1994) Evidence for Batesian mimicry in a butterfly pollinated orchid. *Biol J Linn Soc* 53:91–104
- Johnson SD (2000) Batesian mimicry in the non-rewarding orchid *Disa pulchra*, and its consequences for pollinator behaviour. *Biol J Linn Soc* 71:119–132
- Kevan PG, Baker HG (1985) Insects as flower visitors and pollinators. *Ann Rev Entomol* 28:407–453
- Levin DA (1978) The origin of isolating mechanisms in flowering plants. *Evol Biol* 11:185–317
- Pleasants JM, Chaplin SJ (1983) Nectar production rates of *Asclepias quadrifolia*: causes and consequences of individual variation. *Oecologia* 59:232–238
- Pyke GH (1991) What does it cost the plant to produce floral nectar? *Nature* 350:58–59
- Smithson A, Gigord LDB (2001) Are there fitness advantages in being a rewardless orchid? Reward supplementation experiments with *Barlia robertiana*. *Proc R Soc Lond B* 268:1435–1441
- Smithson A, MacNair MR (1997) Negative frequency dependent selection by pollinators on artificial flowers without rewards. *Evolution* 51:715–723
- Southwick EE (1987) Photosynthate allocation to floral nectar: a neglected energy investment. *Ecology* 65:1775–1779
- Waser NM (1986) Flower constancy: definition, cause and measurement. *Am Nat* 127:593–603