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A Model to Predict the Influence of Insect Flower Constancy on Interspecific Competition between Insect Pollinated Plants

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Honeybees and bumblebees, among the most important pollinators in many plant communities, are known to exhibit flower constancy. When foraging, bees do not sample flowers randomly as they encounter them, but rather they exhibit a strong preference for one species of flower, and will ignore other species that they encounter. The species favoured depends on previous foraging success: if a species of flower has previously provided a high reward, it will be favoured to the exclusion of others. Various models have been developed to describe the optimal foraging pattern of flower feeding insects, which explain, at least in part, observed behaviour. However, they do not consider the importance consequences of flower constancy for competition between plants dependant upon insects for pollination. Bees are most likely to favour a common species which they encounter frequently, and will fly directly between individuals of the favoured species, and thus provide efficient pollination. Conversely, they are unlikely to develop a preference for a scarce flower which necessarily is rarely encountered.

A simple two-flower species model is developed which predicts the proportion of insects which will favour each of the two species for particular flower densities, assuming that individual insects favour the species which provides them with the greatest reward per time.

The model predicts that scarce plant species will receive no pollinators below a threshold density of reward, and that scarce plants must provide a relatively huge reward per flower to achieve pollination. The threshold is lowered at high insect densities when the reward offered by the more common species becomes depleted. The implications of flower constancy to plant communities are discussed.

1. Introduction

The term "flower constancy" describes preference for a particular flower species in insects foraging for nectar or pollen. It is well documented in the honeybee, *Apis mellifera* (Hymenoptera: Apidae) (reviewed in Waddington, 1983; Barth, 1985). Individual bees may visit up to 500 individual flowers on a single trip from the hive, with 93–98% of all visits to the same flower species (Grant, 1950; Free, 1963). The species visited varies between individuals, between hives, and over time in the same individuals, in response to changing nectar availability in different flower species (Barth, 1985). Bees rapidly learn to associate nectar availability with a particular flower species, and can use colour, scent, and shape to identify the correct species (Wehner, 1967; Koltermann, 1969; Menzel & Erber, 1978). Bees can convey scent preferences to other members of the hive (Barth, 1985). When nectar availability switches so that it is no longer available from the favoured species, bees can learn new preferences within eight to ten visits (Koltermann, 1969). Bees can also learn to distinguish between flowers of the same species according to their age, and to favour the age group which provides the highest reward (Giurfa & Núñez, 1992).

Although studies of insect pollinators are heavily biased towards Hymenoptera, principally honeybees and bumblebees, it seems likely that flower constancy is more widespread. Two butterfly species have recently been found to exhibit flower constancy, *Pieris*

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rapae (Lepidoptera: Pieridae) (Lewis, 1989) and *P. napi* (Goulson & Cory, 1993). Clearly studies of other pollinating insects are necessary to establish the generality of this phenomenon.

Alternative theories have been proposed to explain the occurrence of flower constancy. Barth (1985) suggests that if experience has demonstrated that a particular flower species is a good source of nectar, and providing that the flower is sufficiently abundant, an insect should not waste time visiting other flowers which provide an unknown reward (effectively a form of risk aversion). However, most discussion of the causes of flower constancy focus on learning constraints: learning to locate nectar in a particular flower species takes time, so that handling time declines in successive visits (for example, Laverty & Plowright, 1988; Lewis, 1986; 1993). Hence handling time is minimized if only one species of flower is utilised. Both bees (Heinrich *et al.*, 1977; Gould, 1985) and butterflies (Stanton, 1984; Lewis, 1986) have a limited memory: knowledge of how to manipulate one flower type can be lost simply because it is replaced by information about a new flower type. As memory capacity decreases so constancy is favoured (Waser, 1986).

Flower constancy has been modelled with some success: traditional models assume bees maximize reward per time (for example Oster & Heinrich, 1976). More recently attention has focused on risk aversion, in which bees avoid flower species which provide a variable reward (Real, 1981). Explanations for this are a subject of debate, for somewhat contradictory predictions have been produced in alternative models: Possingham *et al.* (1990) claim that, as there is a decelerating relationship between time spent on a flower and nectar volume (Harder, 1986), then bees should favour flowers which provide a variable reward, while Harder & Real (1987) and Real *et al.* (1990) suggest that bees base foraging decisions on short sampling periods, and consequently favour flowers which provide less variable rewards. However, in an empirical test of alternative foraging models, namely flower constancy, reward maximisation and risk aversion, Wells & Wells (1983) found that only flower constancy was consistent with honeybee behaviour.

Fidelity of individual insects to particular flower species is advantageous to the favoured plant, for the insect will fly directly between flowers of this species and thus provide an efficient pollination system. Conversely, flowers which are scarce will not be pollinated efficiently, if at all, for flower constancy should not develop in favour of rare flowers, unless they provide a large nectar reward. There is experimental evidence that rare flowers suffer from a minority disadvantage, receiving proportionately less visits from pollinators than more common species (Levin & Anderson, 1970; Silander, 1978). For example, the number of visits per flower by butterflies to white flowers of *Phlox* sp. was proportional to the relative abundance of white to pink flowers in the population (Levin, 1972). Thus it is predicted here that flower constancy should act to suppress diversity amongst insect pollinated plants by favouring the most abundant species. A simple model is developed which examines the conditions which a scarce plant species must satisfy in order for some insects to develop a preference for them.

2. The Model

Consider a system containing two insect pollinated flowering plant species, A and B, with species A the more common. It is assumed that the plants depend for pollination upon a species or assemblage of insects which exhibit absolute flower constancy, i.e. they visit only one flower species in a foraging bout. Second, it is assumed that the individual insects maximize their foraging efficiency by favouring the plant species which provides the greatest reward per time. For simplicity handling time, and differences in energy consumption between travelling and feeding are ignored.

Let the density of flower A = d_a and the density of flower B = d_b.

Assume that all reward (nectar or pollen) is removed when an insect visits the flower. As time since depletion increases, the reward increases towards a maximum value, r.

The expected reward from visiting a flower of species A is given by

$$R_a = r_a(1 - 1/(L_a + 1)), \quad \text{(Reward/flower)} \quad (1)$$

where L = expected (mean) time since last visit and r = reward per flower when full.

Let the density of insects = d_i, the proportion of insects feeding on flower species A = p and the search rate of insects = q. Then:

$$\text{Rate of location of flower A by an insect} = qd_a. \quad (2)$$

$$\text{Rate of visits to any one flower A by all insects} = pqd_i. \quad (3)$$

$$\text{Rate of visits to all flowers As by all insects} = pqd_a d_i. \quad (4)$$

Mean time between visits to one flower

$$A = L_a = 1/(pqd_i). \quad (5)$$

Expected reward per time when feeding on flower A only:

$$E_a = qd_a r_a(1 - 1/(L_a + 1)) \quad (6)$$

Equations (1–6) are generated similarly for flower B, substituting $(1 - p)$ for p.

The proportion of insects visiting each flower species will reach a stable equilibrium when $E_a = E_b$. By equating eqn (6) for flowers A and B, we derive:

$$P = \frac{d_a r_a(qd_i + 1) - d_b r_b}{qd_i(d_a r_a + d_b r_b)}. \quad (7)$$

$d_a r_a$ and $d_b r_b$ are the densities of each flower species multiplied by the maximum reward available per flower (i.e. when flowers are full). These quantities are henceforth described as the maximum reward densities (M_a and M_b), the reward per area available from each flower species in the absence of nectar depletion by insects.

qd_i is the density of insects multiplied by their individual search rates, and thus represents the rate of searching by all insects per area, a quantity henceforth described as the search density (I).

Equation (7) can now be rewritten as:

$$p = \frac{M_a(I + 1) - M_b}{I(M_a + M_b)}. \quad (8)$$

We can thus now predict the proportion of insects which will feed on each flower species according to three parameters. The maximum reward density which a scarce plant offers in relation to the proportion of pollinators it attracts, for various insect search densities, is shown in Fig. 1. At low values of I, insect visits are strongly biased towards the more common species. For comparison, a line is shown describing the proportion of insects which would feed on the scarce plant if choice were based on the proportion of the total maximum reward density provided by each plant species ($p = M_a/(M_a + M_b)$) (proportional visitation). As I increases, so the model tends towards proportional visitation.

For insect pollination to occur flower B must produce sufficient energy per area to lower p below 1. Marginal values of I and M_b for successful insect pollination of an invading plant species can be obtained by setting p to 1 in eqn (8) (with proportional visitation p is always less than 1). Plant B will only be pollinated if:

$$M_b I > M_a - M_b.$$

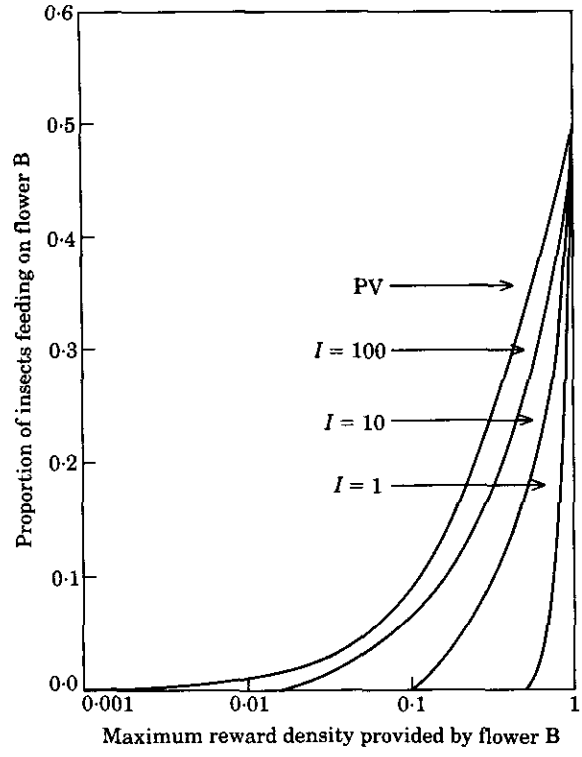

FIG. 1. The proportion of insects visiting a rare flower species with varying values of I (search rate of insects) and M_b (maximum density of reward from scarce flower). M_a (reward from common flower) = 1. For comparison a line of proportional visitation is shown (PV), in which insects are flower constant, but flower choice is determined by the proportion of the total reward density provided by each species ($p = M_a/(M_a + M_b)$).

At low values of M_b and I the invading species will not be pollinated (Fig. 2). Successful invasion becomes more likely when there are large numbers of insect pollinators, and/or when pollinators have a high search rate. To achieve pollination a scarce flower species must provide a relatively large reward per flower (Fig. 3). For example, if we set r_a, d_a (and hence M_a) to 1, and for simplicity assume a search density of 1, and if flower B is 100 times more scarce ($d_b = 0.01$), then the reward provided by each flower of B (r_b) must be more than 50 times that of flower A for any pollinators to visit flower B.

3. Discussion

The model confirms that flower constancy in insects will suppress pollination of scarce species in favour of the most common plant species, and so acts to decrease diversity in plant communities. Scarce species will only be pollinated if they offer a relatively huge reward per flower, which will place them at a competitive disadvantage to the most common species. This situation only breaks down when

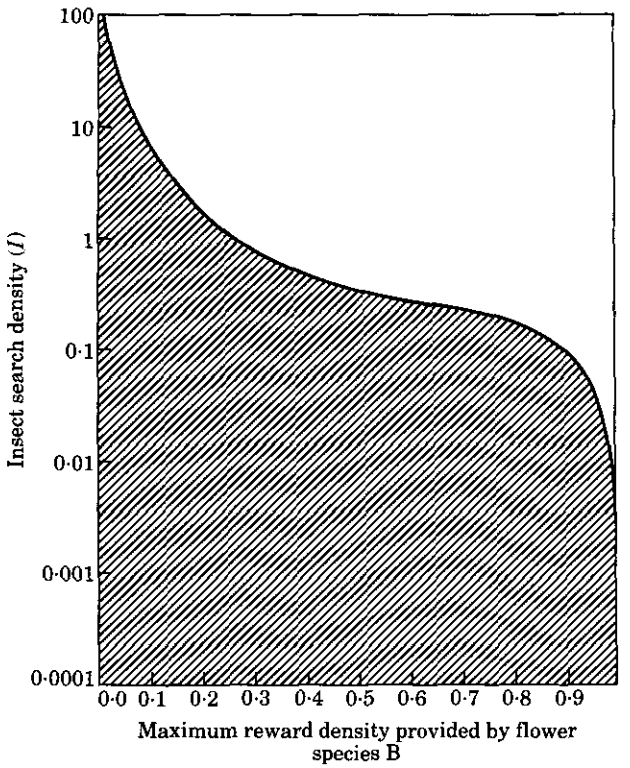

FIG. 2. Marginal values for M_b (maximum density of reward from scarce flower) and I (search rate of insects), below which pollination of the scarce flower will not occur (shaded area). M_a (reward from common flower) = 1. (▨) Pollination of species B will not occur.

insect–insect competition for reward (pollen or nectar) is sufficiently high to deplete the reward offered by the most common species. When this occurs a small number of insects should switch to the rare species, which although encountered less frequently will have flowers which tend to contain more nectar, as they have not been depleted.

The omission of handling time from the model will produce a slight underestimation of the number of pollinators visiting scarce flowers, particularly when the number and search rate of insects is high, for the reward per flower will be reduced in the most common flower species by their more frequent depletion. As there is a decelerating relationship between time spent on the flower and nectar volume (Harder, 1986) uptake of nectar (or pollen) from a few flowers each containing a large volume of nectar requires less handling time than uptake of the same quantity of nectar from many flowers each containing less nectar. Conversely if bees are risk averse (Giurfa & Núñez, 1992) then the model may overestimate visits to scarce flowers, for the mean reward per time when gathering nectar from a few scarce but nectar-rich flowers will have a higher variance than when gathering nectar from an abundant flower species which provides a low reward per flower, regardless of variance in nectar content of each flower species.

Rathcke (1983) suggests that the density of pollinators may be a function of resource density, i.e. as resource density increases so more pollinators are attracted to the area and/or a higher population of pollinators can be maintained. Rathcke suggests that at lower resource densities this may result in facilitation, so that sympatric flower species benefit from the presence of each other, but that at high densities competition for pollinators occurs. In terms of the model given here, for facilitation to occur the search density must increase disproportionately with increasing resource density of flower A, so that the expected reward per time from feeding on A (E_a) is, as a result of depletion, inversely related to the density of flower A (d_a). This is counter-intuitive, for it suggests that insects will be attracted to feed in areas of high flower density in such numbers that they receive less reward per time by doing so, and hence switch to feeding on scarce flowers in that area. Although the presence of sympatric species which flower earlier can increase the density of pollinators available for species which subsequently flower (Waser & Real, 1979) there is

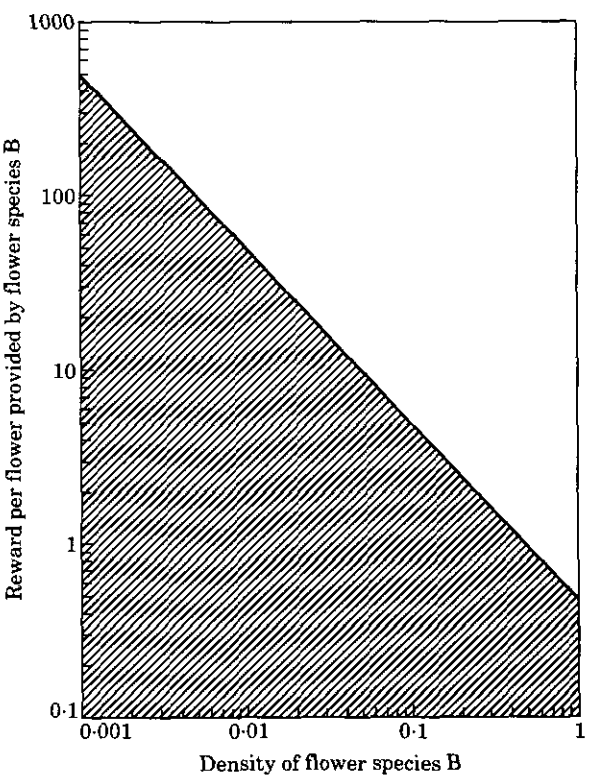

FIG. 3. Reward per scarce flower (r_b) required to reach the pollination threshold with varying densities (d_b) of the scarce flower. r_a, d_a, (and hence M_a) and I are all set to 1, so that r_b and d_b are the relative reward and density, respectively, of flower B compared to flower A. (▨) Pollination of species B will not occur.

little empirical evidence for facilitation between species which flower at the same time (Rathcke, 1983).

Various means are available to scarce plants to achieve insect pollination. Mimicry of the most common species, in terms of flower colour, scent and shape, may increase the number of visits by insects to the rare flower, but may not be advantageous as visiting insects would probably not have come from other members of the same species, and so would not be carrying conspecific pollen. Deposition of foreign pollen on the stigma of a flower may carry the additional disadvantage of lowered seed set due to stigma clogging, chemical or physical interference between pollens, or may result in the production of unviable hybrids (Levin, 1972; Waser, 1978; Thomson *et al.*, 1981). To this author's knowledge, no convincing examples of floral mimicry have yet been described.

Values of I and M_a will vary seasonally, so rare plants can increase their chances of pollination by flowering before or after the most common species, and when a large number of insect pollinators are available. Waser (1982) describes geographic variation in the flowering times of *Ipomopsis aggregata* and *Delphinium nelsoni*, sympatric species which share pollinators, and which strongly suggests that there is selection pressure to minimize flowering overlap. However, he attributes this to avoidance of interspecific pollen transfer rather than competition for pollinators.

Pollination between scarce flowers could be achieved by targeting insect groups which do not exhibit flower constancy, if present, or by using wind pollination. Failing this, reproduction must be achieved by selfing or vegetative reproduction. The model presented here does not consider the role of the spatial distribution of plants in insect foraging behaviour, although this is undoubtedly important. An aggregated distribution, as found in most plants, may increase the number of flower constant insects which visit scarce plants above that predicted by the model, by rendering them locally abundant.

Clearly further research is required to establish the abundance and distribution of flower constancy amongst pollinators, and to measure its importance in field situations.

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