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# Foraging strategies of insects for gathering nectar and pollen, and implications for plant ecology and evolution

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## Abstract

The majority of species of flowering plants rely on pollination by insects, so that their reproductive success and in part their population structure are determined by insect behaviour. The foraging behaviour of insect pollinators is flexible and complex, because efficient collection of nectar or pollen is no simple matter. Each flower provides a variable but generally small reward that is often hidden, flowers are patchily distributed in time and space, and are erratically depleted of rewards by other foragers. Insects that specialise in visiting flowers have evolved an array of foraging strategies that act to improve their efficiency, which in turn determine the reproductive success of the plants that they visit. This review attempts a synthesis of the recent literature on selectivity in pollinator foraging behaviour, in terms of the species, patch and individual flowers that they choose to visit.

The variable nature of floral resources necessitate foraging behaviour based upon flexible learning, so that foragers can respond to the pattern of rewards that they encounter. Fidelity to particular species allows foragers to learn appropriate handling skills and so reduce handling times, but may also be favoured by use of a search image to detect flowers. The rewards received are also used to determine the spatial patterns of searches; distance and direction of flights are adjusted so that foragers tend to remain within rewarding patches and depart swiftly from unrewarding ones. The distribution of foragers among patchy resources generally conforms to the expectations of two simple optimal foraging models, the ideal free distribution and the marginal value theorem.

Insects are able to learn to discriminate among flowers of their preferred species on the basis of subtle differences in floral morphology. They may discriminate upon the basis of flower size, age, sex or symmetry and so choose the more rewarding flowers. Some insects are also able to distinguish and reject depleted flowers on the basis of ephemeral odours left by previous visitors. These odours have recently been implicated as a mechanism involved in interspecific interactions between foragers.

From the point of view of a plant reliant upon insect pollination, the behaviour of its pollinators (and hence its reproductive success) is likely to vary according to the rewards offered, the size and complexity of floral displays used to advertise their location, the distribution of conspecific and of rewards offered by other plant species, and the abundance and behaviour of other flower visitors.

**Key words:** departure rules, flower constancy, ideal free distribution, marginal value theorem, optimal foraging, scent marks, systematic searching

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# Introduction

Pollination biology has generally been studied from either a botanical or a zoological perspective, reflecting the traditional compartmentalisation of research institutions (Waser & Price 1998). It is one of many subject areas in which the ecology of plants and animals is intimately linked, and ideally a pollination biologist should have expertise in both, yet in practice this is rarely the case. Insect foraging behaviour in particular is an area in which knowledge has advanced rapidly in recent years, and the majority of flowering plants rely upon insects to mediate pollen transfer. It is the behaviour of insects which determines which flowers will set seed and which will not, and which governs the pattern of transfer of gametes between plants. This review attempts to synthesize current knowledge of insect pollinator behaviour, particularly with regard to what factors determine which flowers they visit and which ones they ignore.

Many of the most familiar insect groups, including most bees (Hymenoptera: Apoidea), butterflies and moths (Lepidoptera), and also some flies (Diptera) and beetles (Coleoptera), depend for their sustenance upon pollen or nectar rewards provided by flowers. Both nectar and pollen have much to recommend them as food for insects. Nectar provides sugars and water necessary to sustain an active adult insect, while pollen is a rich source of protein. However, it is generally only adult winged insects that specialise in visiting flowers. Immature stages do not have the mobility necessary to gather such carefully rationed and sparsely scattered resources (although of course larvae of bees feed upon pollen collected by adults). Even for insects capable of flight, efficient collection of floral rewards is problematic. The distribution of rewards is unpredictable in time and space; individual plants and plant species open their flowers at different times of the day and flower at different times of the year (Waser 1982b; Zimmerman & Pyke 1986; Real & Rathcke 1988). Flowers are erratically depleted of their rewards by other insects and take varying amounts of time to replace them, so that at any one time many flowers may be empty (Wetherwax 1986; Real & Rathcke 1988; Cresswell 1990; Waser & Mitchell 1990). To add to the difficulties many plant species hide their floral rewards within complex flowers so that only insects with an appropriate morphology can enter them; in particular, efficient nectar extraction necessitates a proboscis which in length roughly matches the depth of the corolla (e.g. Inouye 1978, 1980; Pyke 1982). Thus many of the flowers which a forager encounters may have rewards which are at least partially inaccessible. Even if the forager possesses a suitable morphology, learning to handle flowers with complex structure takes time (Kugler 1943; Schremmer 1955; Weaver 1957, 1965; Macior 1966; Heinrich 1976, 1984; Laverty 1980, 1994a; Waser 1983; Schmid-Hempel 1984; Lewis 1986). Also it seems that insects are unable to retain effective handling skills while foraging among several plant species with different flower structures (Heinrich *et al.* 1977; Lewis 1986; Woodward & Laverty 1992). Thus insects must make economic decisions while faced with a bewildering array of flowers of varying structure, colour and reward. These decisions include choice of flower species, choice of patches within species and choice of individual flowers within patches. Perhaps the most fundamental choice facing a foraging insect is whether to generalise and visit a range of flowers of different species, or to concentrate on just one.

# Choice of flower species

## Specialisation versus generalisation

Although current plant-pollinator mutualisms represent the result of approximately 100 million years of evolution, extreme specialisation is rare (reviewed in Waser *et al.* 1996). There are few examples of plant species which depend on a single or very few pollinator species throughout their range; examples include the Yucca (*Yucca* spp.) (Pellmyr & Thompson 1992; Dodd & Linhart 1994; Bogler *et al.* 1995), Figs (*Ficus* spp.) (e.g. Wiebes 1979; Patel *et al.* 1993; Bronstein & Hossaert-McKey 1996), various orchids such as *Ophrys speculum* (Orchidaceae) (Pouyanne 1917; Nilsson 1992), and a guild of red-flowered plants found in the Fynbos of South Africa which are pollinated by the butterfly *Aeropetes tulbhagia* (Marloth 1895; Johnson & Bond 1994). Examples in which an insect depends exclusively on one plant species for all of its nectar or pollen requirements appear to be even more scarce

(Waser *et al.* 1996), and at present include a handful of species of solitary bee (Westrich 1989). The vast majority of insects visit a range of flowers of different plant species according to availability, and the majority of plants are visited by several or many insect species (Waser *et al.* 1996), although not all may be effective pollinators. Some of these insects exhibit little in the way of specialised adaptations for feeding on nectar or pollen, and are thus only able to exploit simple flowers. For example the inflorescences of many Apiaceae effectively form a platform upon which a range of polyphagous beetles and flies can graze pollen without requiring specialised morphological adaptations or particular handling skills. However, most flower-visiting insects are specialists in that nectar, pollen or both represent their major food source, and in that they do possess appropriate morphological adaptations (typically elongated sucking mouthparts and/or hairs or baskets to trap pollen) (e.g. Thorp 1979; Inouye 1980; Gilbert 1981). This group (which includes, for example, bees and most Lepidoptera) are able to tackle a broad range of flower species, and are responsible for the pollination of many (perhaps most) insect-pollinated plants. Aside from their economic importance as pollinators, this group has become popular for studies of forager behaviour, for examining the assumptions and predictions of foraging models and the interplay between learning, memory constraints and foraging efficiency in a complex and unpredictable environment (e.g. Heinrich 1979a; Wells & Wells 1986; Cresswell 1990; Wells *et al.* 1992; Dukas & Real 1993a, b, c; Dreisig 1995; Menzel & Müller 1996). As these studies have begun to reveal the intricacies of insect foraging behaviour it has become apparent that their behaviour is far more complex than was previously known. In this review I attempt to synthesize our current understanding of the foraging strategies of flower-visiting insects.

## Learning and flower constancy

One striking feature of the behaviour of insects foraging for nectar or pollen is that they often exhibit a learned preference for flowers of a particular plant species which has previously provided a reward. The learning process can be rapid; for example honeybees take just three to five visits to learn to distinguish rewarding and non-rewarding flower morphs (Koltermann 1969; Barth 1985). Both colour, shape, scent, or combinations of these cues may be used to identify rewarding morphs (Wehner 1967; Koltermann 1969; Menzel & Erber 1978). Foragers can learn to selectively attend to particular cues that are associated with reward, and ignore others that are not (Dukas & Waser 1994). Once learned, a preference may persist for minutes, hours or even for days (Menzel 1967; Heinrich *et al.* 1977; Dukas & Real 1991; Keasar *et al.* 1996; Chittka 1998). A forager which exhibits fidelity to a particular flower ignores many other suitable and rewarding flowers which it passes, but it also avoids spending time visiting unsuitable flowers. This behaviour was first described in the honeybee, *Apis mellifera*, in about 350 BC by Aristotle (Grant 1950), and also attracted the attention of Darwin (1876). More recently it became known as flower constancy, a term first coined by Plateau (1901) and defined by Waser (1986), and has been identified in the foraging regimes of a range of other pollinators.

Flower constancy is not simple to explain. It can be an apparently sub-optimal foraging strategy since flower constant foragers ignore many rewarding flowers; in two-choice experiments some honeybees remain constant to artificial flower morphs which provide a consistently lower reward than alternatives (Wells & Wells 1983, 1986; Wells *et al.* 1992; Hill *et al.* 1997). Flower constancy is also of interest since it is of crucial importance in determining reproductive success and patterns of gene flow in plant populations (Levin 1978). From the point of view of the plant, constancy in its pollinators is clearly beneficial since it minimises pollen wastage and stigma clogging with pollen from other species. Thus, flower constancy influences the outcome of interspecific competition for pollination services (Waser 1982b; Rathcke 1983; Kunin 1993). Flower constancy may also reduce intermorph pollen transfer in polymorphic flowers and reduce hybridisation between related species (Grant 1949; Jones 1978; Goulson 1994; Goulson & Jerrim 1997). It has been implicated as a contributory factor in sympatric speciation (Free 1966), although current opinion is that flower constancy alone is unlikely to provide sufficient isolation for speciation to occur (Grant 1992, 1993, 1994; Waser 1998; Chittka *et al.* 1999).

Studies of flower constancy have continued to focus primarily on Hymenoptera, principally honeybees (*Apis mellifera*) and bumblebees (*Bombus* spp.), but in the last ten years it has become clear that flower constancy is much more widespread. It has been identified in butterflies (Lewis 1989; Goulson & Cory 1993; Goulson *et al.* 1997a) and hoverflies (Syrphidae; Diptera) (Kunin 1993; Goulson & Wright 1998), and evidence from analysis of gut contents in pollen feeding beetles suggests that they may also exhibit constancy (De Los Mozos Pascual & Domingo 1991). It seems probable that flower constancy is a general phenomenon amongst insect foragers which gather nectar and/or pollen.

Several explanations for flower constancy have been proposed (for example Real 1981; Waser 1986). For many years the favoured explanation was based on an idea originally outlined by Darwin (1876), which in a more explicit form has become known as *Darwin's interference hypothesis*. Darwin suggested that insects may be constant because they were quicker at repeating the same task (handling a particular type of flower) than they would be if they switched between tasks. More recently this has been interpreted as arguing that constancy is a result of learning and memory constraints; foragers may be limited by their ability to learn, retain and/or retrieve motor skills for handling flowers of several plant species (Proctor & Yeo 1973; Waser 1983, 1986; Lewis 1986, 1989, 1993; Woodward & Laverty 1992). Learning to extract rewards efficiently from within the structure of a flower takes a number of visits to that flower species, resulting in a decline in handling time on successive visits (Lewis 1986; Laverty & Plowright 1988; Keasar *et al.* 1996). Switching between species of flower differing in floral morphology often temporarily increases handling time as Darwin predicted, particularly when the morphology is complex (Heinrich *et al.* 1977; Lewis 1986; Woodward & Laverty 1992; Chittka & Thomson 1997). It has been argued that memories of handling skills for one flower type are replaced if new skills are learned, i.e. insects have a limited memory (Lewis 1986). However, considerable research on insect memory has been carried out in recent years and most researchers now agree that memory capacity is not the limiting factor; bees (and probably related insects) appear to have an accurate and large long-term memory (Menzel *et al.* 1993; Chittka 1998; Menzel 1999). In honeybees and bumblebees, learned handling skills may be retained in long-term memory for weeks even when they are not being used (Menzel *et al.* 1993; Chittka 1998). It appears that bees can learn to suppress associations between sensory inputs and learnt handling skills if they become inappropriate, but that the memories are retained (Chittka 1998). Hence learned motor (handling) skills are probably not lost as new skills are learned, but there is evidence that errors are likely to be made in retrieving the correct memory in the appropriate context if a bee switches between tasks frequently (Greggers & Menzel 1993; Chittka *et al.* 1995, 1997; Chittka 1998). Hence after the initial learning process a flower constant forager maintains a low handling time (but requires longer flight times to locate flowers), while a labile forager may incur a penalty of an increased handling time following switches between flower species (but benefits from a higher density of available resources and so a reduced flight time). Thus Darwin's interference hypothesis requires the trade off between handling and flight times to favour constancy.

Attempts to quantify this trade-off suggest that this may not be so. Studies of bumblebees and butterflies have found that increases in handling time following switching vary greatly between plant species but are generally too small (0–2 s) to compensate for savings in travelling time (Woodward & Laverty 1992; Laverty 1994b; Gegear & Laverty 1995; Goulson *et al.* 1997b). Also, if forced to switch between tasks, bumblebees may eventually be able to eliminate interference effects (Dukas 1995), although probably only when foraging on no more than two types of flower with simple structures (Gegear & Laverty 1998). Indeed bees do switch between simple flowers of different species with minimal interference effects (Laverty & Plowright 1988; Gegear & Laverty 1998; Chittka & Thomson 1997). However, switching between three simple flower types or between two complex flower types does induce substantial handling penalties (Gegear & Laverty 1998). Experience with other species of broadly similar flower morphology may actually increase learning rates (Laverty 1994a). Short-tongued hoverflies which take pollen from anthers extruded beyond the corolla (and thus require little in the way of specialised handling skills) also exhibit constancy (Goulson & Wright 1998). Unexpectedly, switching between plant species tends to be associated with an increase in travelling time (rather than the predicted decrease) (Chittka *et al.* 1997; Goulson *et al.* 1997b). Thus Darwin's interference hypothesis does not in itself appear to provide an entirely adequate explanation for flower constancy.

More recently an additional hypothesis has been put forward; that flower constancy may partly be a result of insect foragers using a search image to locate flowers (Waser 1986; Goulson 1999). Tinbergen (1960) first introduced the search image as an explanation for prey selection patterns of great tits (*Parus major*) foraging under natural conditions in woodland. He found that individual birds tended to collect sequences of the same prey species, and that they exhibited positive frequency-dependent selection. Although they are an intuitively appealing idea, search images have proved difficult to demonstrate convincingly, and it remains unclear how frequently they occur in natural situations (Guilford & Dawkins 1987; Allen 1989). Almost all definitions of search images specify that they apply to cryptic prey (although Tinbergen did not explicitly state this). For example, "as a result of initial chance encounters with cryptic prey, the predator 'learns to see', and selectively attends to those cues that enable it to distinguish the prey from the background" (Lawrence & Allen 1983). This criterion now appears to be valid: experiments using pigeons (*Columba livia*) have found that behaviour consistent with use of a search image is only evident when prey are cryptic (Bond 1983; Bond & Riley 1991; Reid & Shettleworth 1992). Adoption of a search image for a particular prey's visual characteristics appears to enhance its detectability and interferes with incoming perceptual information regarding alternative prey types (Bond 1983; Bond & Riley 1991; Plaisted & MacKintosh 1995). Thus predators tend to discover only one prey type. It has recently become apparent that the search image concept has much in common with a phenomenon known to psychologists as *selective attention*, by which predators learn to detect cryptic prey by selectively attending to particular visual features of the prey which best distinguish them from the background (Bond & Riley 1991; Langley 1996; Langley *et al.* 1996). Both honeybees and bumblebees use selective attention when distinguishing among flower types (Kosterhalfen *et al.* 1978; Dukas & Waser 1994). Psychological studies of humans and various animals have demonstrated that the brain has a limited capacity for processing information simultaneously, i.e. it has a *limited attention* (Blough 1979; Corbetta *et al.* 1990; Posner & Peterson 1990; Eysenck & Keane 1990). An analogous situation has been described in bees; honeybees have a fragile and probably limited short-term memory which is prone to rapid decay and to replacement by new memories (Menzel 1979; Menzel *et al.* 1993; Chittka *et al.* 1999). Dukas & Ellner (1993) predicted that if predators have a limited attention (they are only able to retain identification cues for one preferred prey type in their short-term memory), and prey are cryptic then they should devote all their attention to a single prey type, but that if prey are conspicuous then predators should divide their attention among prey types. Thus search images may result from a limited ability to process information simultaneously or from selective attention to cues associated with particular prey types, or from a combination of the two.

There is an obvious flaw in the reasoning so far, since plants which are pollinated by animals have evolved brightly coloured flowers to attract the attention of their pollinators. It thus seems implausible to argue that flowers may actually be cryptic, yet search images are thought to be a mechanism for locating cryptic prey. However, studies of pollinator fidelity (either in the laboratory or field) almost invariably focus on situations where the pollinator is presented with several flower choices at high densities. When viewed against a background of other floral displays (either of the same or different plant species) all of which are calling for the attention of pollinators then any particular flower may be effectively cryptic since it represents a random sample of the background (Endler 1981). Many flowers which commonly occur together have colours which are extremely similar to insect colour vision systems, and to the human eye (Kevan 1978, 1983; Chittka *et al.* 1994; Waser *et al.* 1996). When an insect flies through a meadow containing several flower species, individual flowers appear in the insect's field of view in very rapidly succession; making some conservative assumptions about flight speed, flower density and size, and the insect's visual resolution, Chittka *et al.* (1999) estimate that a bee encounters a new flower every 0.14 s. Even if the bee had previously encountered all of the flower species, it seems unlikely that in such a short time period the bee would be able to retrieve memories necessary to recognise the flower, recall the likely rewards and the motor skills required to access them, and then make an economic decision as to whether to visit the flower or not.

Levin (1978) was (to my knowledge) the first to suggest that pollinators may develop a search image when foraging for flowers. He argued that frequency dependent selection by pollinators among colour morphs of the same plant species is best explained by use of a search image (constancy to particular colour morphs when all have identical structure cannot be explained by Darwin's interference hypothesis). More recently, this idea has received additional support. There is evidence that flower constancy declines as flower density declines (Kunin 1993; Goulson *et al.* 1997a), in accordance with the predictions of Dukas & Ellner (1993) (although this would also be expected if flower constancy resulted from a trade-off between flight time and handling time). Dukas & Real (1993a) demonstrated that bumblebee foraging efficiency is limited in part by their ability to recognise rewarding flower types. Bees made fewer errors in identification when visiting only one rewarding flower type, even when the flower types differed markedly in colour (although Chittka *et al.* (1999) argue that the experimental design was flawed). It seems that constraints on recognition (rather than handling) may favour constancy. Several studies have demonstrated that pollinators switch readily between plant species which have similarly coloured flowers (Waser 1986; Kunin 1993; Laverty 1994b; Chittka *et al.* 1997), even when these flowers have very different structures (Wilson & Stine 1996). Conversely, pollinators rarely switch between flowers of similar structure but of different colour (Wilson & Stine 1996). Darwin's interference hypothesis predicts precisely the reverse, but this is consistent with the hypothesis that search images are used by foragers. Recent evidence suggests that flowers may indeed be cryptic to foraging bumblebees; search times are longer when the favoured flower species is presented against a background of similarly coloured flowers, compared to when it is presented against a background of green foliage (Goulson 1999). This is hardly surprising since the apparency of flowers is simply a function of the degree of contrast they make with their background (Lunau *et al.* 1996).

The weight of evidence suggests that foragers looking for flowers use search images, or a perceptual mechanism akin to search images such as selective attention to particular visual features of their preferred flowers. Of course, this does not rule out the possibility that Darwin's interference hypothesis may be valid under certain circumstances, since the two hypotheses are not mutually exclusive (Wilson & Stine 1996; Goulson 1999). Use of a search image which renders fidelity a more efficient means of finding flowers (i.e. minimises search time) could act in conjunction with selection for minimised handling times to promote constancy. Carefully executed experimental tests are required to establish the relative importance of these two processes in promoting flower constancy. To do this successfully it would probably be necessary to use arrays of artificial flowers in which both colour and structural complexity could be varied independently. Thus it would be possible to manipulate both apparency (difference in reflectance spectrum compared to background) and handling time, and examine the conditions which promote constancy.

## Switching between plant species

Although flower constancy occurs in a diverse range of insects, it is important to emphasise that constancy is usually far from absolute, and that the terms "constancy" and "fidelity" are slightly misleading in this context. Foragers will sample other flowers to keep track of changing rewards over time (known as "minoring"), and may also change their preference over time in response to a sequence of low rewards or reduced availability of their preferred flower. Minors may be included as a compromise required to track changing rewards through time (Heinrich 1979b). Bumblebees in particular frequently visit flowers of several species during a single foraging bout, and are markedly less constant than honeybees (Bennett 1883; Brittain & Newton 1933; Grant 1950; Free 1970; Thomson 1981; Waddington 1983a). If the favoured flower ceases to be rewarding bees can rapidly replace learned preferences with new ones (Menzel 1969, 1990; Meineke 1978).

Insects may change their foraging preference in response to rewards received or according to changing frequencies of encounter with different flowers. They appear to follow simple rules. When flowers are scarce, theory predicts that foragers should abandon specialisation in favour of generalisation (e.g. Levins & MacArthur 1969; Schoener 1969; Colwell 1973; Kunin & Iwasa 1996). Empirical studies have confirmed that, even given the memory constraints previously discussed which favour constancy, this does indeed occur in insects visiting flowers. Honeybees, bumblebees and hoverflies all abandon constancy when their preferred flower is scarce (Kunin 1993; Chittka *et al.* 1997). For example in honeybees constancy to artificial flowers has been found to decline with increasing flight time between visits (Greggers & Menzel 1993). Kunin (1993) describes a decline in constancy of both honeybees and syrphids in response to decreasing density of *Brassica kaber*. In the butterfly *Thymelicus flavus*, switching tends to occur when an individual finds itself in an area in which the frequency of the preferred nectar source is low compared to other flowers (Goulson *et al.* 1997a). Secondly, foragers tend to switch preference following a low or zero reward from the last flower(s) visited. In honeybees, low rewards from individual flowers have been found to promote switching between different coloured artificial feeders in laboratory studies (Greggers & Menzel 1993). Feeding time is known to be an indicator of the reward received (Pyke 1978a; Schmid-Hempel 1984; Bertsch 1987; Greggers & Menzel 1993), enabling examination of the relationship between reward and subsequent behaviour under natural conditions. Both bumblebees and butterflies exhibit higher rates of switching following low feeding times on individual flowers (Chittka *et al.* 1997; Goulson *et al.* 1997b), although it is as yet unknown whether they integrate information on the rewards received over a number of visits (rather than just the last flower visited). Switching away from a flower species after receiving a low reward may explain apparently risk-averse behaviour which has been recorded in bumblebees and wasps. In experiments where nectar levels were manipulated, these insects preferred floral types which provided a less variable reward over types which provided a more variable reward with the same mean reward per flower (Real 1981; Waddington *et al.* 1981; Real *et al.* 1982; Harder & Real 1987).

Whatever the mechanism involved in switching, having a flexible preference for particular flowers enables insects to adapt their strategy according to changing spatial and temporal patterns of availability of reward in different flower species.

## Search patterns in a patchy environment

Flowers typically exhibit a patchy distribution at a number of levels; flowers are often clustered into inflorescences, several flowers or inflorescences may be clustered on each plant, and the plants themselves are likely to be patchily distributed. Superimposed on this distribution, rewards per flower vary greatly between plants of a single species and between flowers on a single plant due to genetic and environmental influences on reward production rates and also in response to the pattern of depletion of rewards by foragers (e.g. Pleasants & Zimmerman 1979, 1983; Zimmerman 1981a,b; Brink 1982; Thomson *et al.* 1982; Pleasants & Chaplin 1983; Cruden *et al.* 1984; Zimmerman & Pyke 1986; Real & Rathcke 1988; Mangel 1990; Waser & Mitchell 1990; Gilbert *et al.* 1991). Thus in addition to the choice as to which flower species they are to visit, foragers must also make decisions concerning how best to exploit the patchy distribution of their favoured flower(s). One approach to understanding forager behaviour which has proved to be fruitful is the use of optimality models. Although optimality models have in the past been criticized for being unrealistic in several respects (e.g. Pierce & Ollason 1987), they remain a popular and valuable starting point for studying behaviour. Optimal foraging models assume that foragers maximize their rate of resource acquisition. This is a reasonable assumption for workers of social insects since they are freed from many of the constraints which are likely to affect the behaviour of other foragers (Pyke 1978a). However, it is less reasonable for insects such as butterflies which intersperse nectaring with activities such as mate location, and so regularly indulge in longer flights than do most foraging bees (Schmitt 1980; Waser 1982a; Goulson *et al.* 1997a).

Two optimal foraging models are particularly relevant to insects foraging among patches of flowers, the ideal free distribution

(Fretwell & Lucas 1970) and the marginal value theorem (Charnov 1976). I shall examine the predictions of these two models in turn.

## The ideal free distribution

According to the ideal free distribution model, the evolutionary stable strategy for foragers exploiting a patchy resource is to equalize the rate of gain of reward in all patches by matching the proportion of foragers in each patch to the rate of reward production in the patch (Fretwell & Lucas 1970). Although flowers are patchy at a number of spatial scales, most studies of foraging behaviour have used individual plants as the unit of study (the patch), so henceforth the terms patch and plant are used synonymously. Applying the ideal free distribution model, we predict that the ratio of foragers to flowers should be independent of patch size (assuming that reward production per flower does not vary with patch size). If we incorporate travel time between patches, we would expect the proportion of foragers to flowers to increase with patch size, so that foragers in small patches receive a higher reward per time within the patch but spend more time moving between patches. For social organisms the distribution of foragers among patches may also be influenced by the location of nests; if we take into account travel time from the nest then we would predict a higher proportion of foragers close to nests (Dukas & Edelstein Keshet 1998). However, since travel time is often likely to be negligible compared to time spent within patches (Dreisig 1995), the ratio of foragers to flowers should generally remain more or less independent of patch size and nest locations.

So do foragers achieve an ideal free distribution? An ideal free distribution can be achieved by non-random searching or by non-random choice of patches (i.e. a preference for large patches) (Dreisig 1995). Both are exhibited by insects visiting flowers.

### Non-random search patterns

Foragers which adopt a non-random search pattern can achieve a higher reward per time than individuals which are searching randomly, so that non-random searching should predominate where it is possible, although if all foragers have non-random search strategies then rewards per time are the same as when all foraging is random (Possingham 1989). At least two forms of non-random spatial searching have been identified in insects visiting flowers: trap-lining along established routes, and systematic searching (which does not require a prior knowledge of the area). Traplines of various lengths have been identified in butterflies (Gilbert 1975), and in a variety of bees, including euglossines (Janzen 1971; Ackerman *et al.* 1982), flower bees (*Anthophora* spp. – Kadmon 1992), honeybees (Ribbands 1949) and bumblebees (Manning 1956; Heinrich 1976; Thomson *et al.* 1982, 1987, 1997; Thomson 1996; Corbet *et al.* 1984; Williams & Thomson 1998). Bees possess impressive navigational abilities and are able to remember the relative positions of landmarks and rewarding flower patches (Southwick & Buchmann 1995; Menzel *et al.* 1996, 1997) which is no doubt valuable in following traplines. For example honeybees are able to integrate movement vectors; after a series of movements between patches they are able to plot a direct route home, thus avoiding the need to backtrack (Menzel *et al.* 1998). Traplining along a regular route enables the forager to learn which flowers or patches are most rewarding, and also to avoid visiting flowers which it has recently depleted. In addition it may discourage competitors since any new forager attempting to exploit the same flowers may not know which flowers have been most recently depleted and so will initially receive a lower rate of reward than the resident forager (Corbet *et al.* 1984; Possingham 1989).

Even without prior knowledge of the distribution of rewarding flowers, foragers can improve their efficiency compared to a strategy of random searching by using a systematic spatial search pattern so that they avoid encountering areas where they have recently depleted rewards (Bell 1991). For example various bee species and Lepidoptera are able to remember their direction of arrival at a flower, and tend to continue in the same direction when they leave (reviewed in Waddington & Heinrich 1981; Pyke 1983, 1984; Schmid-Hempel 1984, 1985, 1986; Cheverton *et al.* 1985; Dreisig 1985; Ginsberg 1985, 1986; Ott *et al.* 1985; Plowright & Galen 1985; Schmid-Hempel & Schmid-Hempel 1986; Soltz 1986; Kipp 1987; Kipp *et al.* 1989; for exceptions see Zimmerman 1979, 1982). Bumblebees are even able to accomplish this correctly when the flower is rotated while they are feeding on it, provided that there are landmarks available by which they can keep track of their orientation relative to their direction of arrival (Pyke & Cartar 1992). Recent evidence suggests that they also may be able to use the earth's magnetic field to orientate themselves (Chittka *et al.* 1999). Systematic search patterns are also evident in the movements of bees between flowers on the same inflorescence. Many plants present flowers in a vertical raceme, which bees invariably exploit by starting at the bottom and working upwards (Heinrich 1975, 1979a). In some plants the lower flowers in the raceme produce more nectar, so that bees forage upwards until low rewards stimulate departure (Pyke 1978b). However, bumblebees continue to forage upwards even when the distribution of nectar is artificially reversed so that the topmost flowers are most rewarding (Waddington & Heinrich 1979). Whatever the distribution of nectar, this simple foraging rule ensures that bees rarely encounter flowers that they have just visited. From the point of view of the plant, systematic foraging is also beneficial since it is likely to reduce the frequency of selfing.

### Non-random choice of patches

The distribution of foragers among patches depends on the relationships between recruitment rate and patch size, and also how long foragers spend in patches of varying size. In general, insect foragers preferentially visit large patches (plants with many flowers) (Willson & Price 1977; Silander & Primack 1978; Schaffer & Schaffer 1979; Augspurger 1980; Davis 1981; Udovic 1981; Thomson *et al.* 1982; Schmitt 1983; Waser 1983; Bell 1985; Geber 1985; Andersson 1988; Schmid-Hempel & Speiser 1988; Klinkhamer & de Jong 1990; Eckhart 1991; Dreisig 1995; Goulson *et al.* 1998a), although the relationship between recruitment and patch size is often less than proportional (Schmid-Hempel & Speiser 1988; Klinkhamer *et al.* 1989; Dreisig 1995; Goulson *et al.* 1998a).

Several studies have found that this combination of higher recruitment to large patches and systematic searching results in a visitation rate per flower which is independent of plant size (i.e. foragers achieve an ideal free distribution) (Heinrich 1976; Pleasants 1981; Schmitt 1983; Bell 1985; Geber 1985; Schmid-Hempel & Speiser 1988; Thomson 1988; Dreisig 1995; Robertson & Macnair 1995; Kunin 1997). When nectar production rates varied greatly between plants, Dreisig (1995) found that foraging bumblebees achieved an ideal free distribution by preferentially visiting individual *Anchusa officinalis* which had high rates of nectar production, the result of which was that all bees received an approximately equal rate of reward. However, an ideal free distribution was not found in all studies. For example Klinkhamer & de Jong (1990) found that visits per flower by bumblebees declined with plant size in *Echium vulgare*, while Klinkhamer *et al.* (1989) describe the reverse in *Cynoglossum officinale*. The pattern of visitation to patches of a flower may vary between pollinator groups; Sih & Baltus (1987) found that visits per flower in *Nepeta cataria* were higher in large patches for bumblebees and honeybees but lower for solitary bees (Halictidae). The importance of direct physical interference between pollinators has received very little attention, but is one possible cause of such patterns.

The response of pollinators to the spatial distribution of flowers clearly has important consequences for the plant. For example if a plant is pollinated primarily by an insect which prefers to visit small patches of flowers, then it will be disadvantageous for the plants to have an aggregated distribution. This might provide selection for seed dispersal mechanisms. Conversely, if solitary plants are unlikely to be visited because foragers prefer large patches of flowers, then dispersing offspring widely may be a poor strategy. Although only one of many factors which may influence the optimum distribution of plants, the influence of pollinator behaviour has been largely overlooked and deserves attention.

## The marginal value theorem

The marginal value theorem (Charnov 1976) states that a forager should leave a patch when the rate of food intake in the patch falls to that for the habitat as a whole. This can be used to predict the optimal duration of stay of a forager in a patch, if the shape of the pay-off curve for staying within a patch and the mean travel time between patches are known. Several researchers have applied the marginal value theorem to pollinators (Pyke 1978c, 1981, 1984; Hodges 1981; Zimmerman 1981c; Best & Bierzychudek 1982;

Pleasants 1989). I describe a version of this theorem which incorporates our knowledge of the ability of pollinators to carry out systematic searches, and makes qualitative predictions about forager behaviour.

In general, for insects collecting floral rewards the travel time between patches (plants) is usually likely to be small compared to time spent within patches, particularly since most studies focus on areas in which the plants are numerous (Dreisig 1995). For foragers which exhibit a systematic spatial search of the plant, the pay-off curve is likely to be more or less linear on plants with few flowers since most or all of the flowers can be visited in turn without repeat encounters with the same flowers (Fig. 1a). Thus the optimal strategy will be to visit all or nearly all of the flowers on the plant. On a large plant with many flowers the initial rate of return will also be linear (and of approximately the same slope if we assume for simplicity that rewards per flower are independent of plant size). However, a forager will be unable to carry out a systematic search of all the flowers on a large plant without re-encountering flowers that it has depleted. Even if these flowers can be recognized (see below), foraging effi-

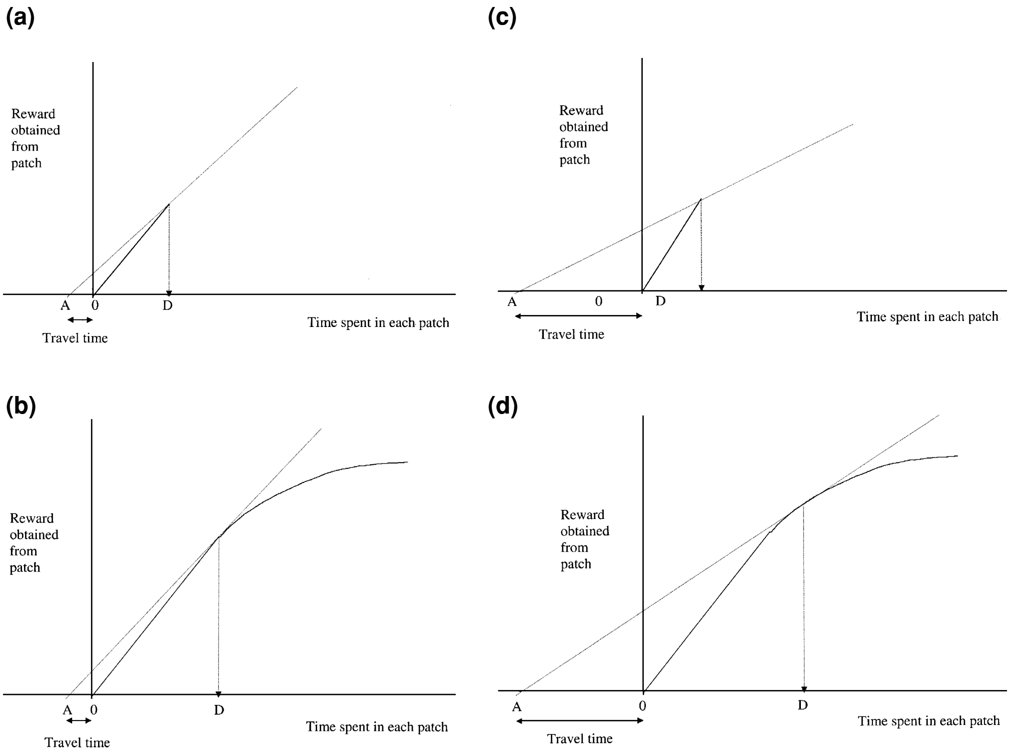

**Fig. 1.** Application of the marginal value theorem to foragers gathering floral rewards. The flowers on a single plant represent a patch. The maximum rate of return per time is given by a line from A which forms a tangent to the pay-off curve for a particular patch. The optimal duration of stay within a patch is then D. Reward per time is the same in a and b, and also in c and d (the foragers follow an ideal free distribution).

a) A small patch with a short travel time between patches. All flowers in the patch are visited using a systematic search

b) A large patch with a short travel time between patches. The forager departs when systematic searching becomes impossible and it begins to revisit flowers.

c) A small patch with a long travel time between patches. As in (a), all flowers in the patch are visited using a systematic search.

d) A large patch with a long travel time between patches.

ciency will drop as time is spent rejecting them. Thus in a large patch the forager should depart when it begins to encounter flowers which it has already depleted (when systematic searching breaks down) (Fig. 1b).

Now let us examine a situation in which travel time is not negligible, where patches are sparsely distributed. Here for foragers to attain an ideal free distribution the ratio of foragers to flowers should increase in large patches. This will lower the slope of the pay-off curve in large patches since each flower will be depleted more regularly, and conversely will increase the slope of the pay-off curve in small patches (Fig. 1c, d).

The model makes specific predictions:

1. When travel time is short the number of visits per flower should be approximately independent of plant size.
2. When travel time is long the visits per flower should increase with plant size (Cowie 1977), and reward per flower decrease on larger plants (or alternatively the forager may switch plant species).
3. Foragers will always visit more flowers on large plants.
4. Foragers will always visit a smaller proportion of the flowers on large plants (unless travel time is very long and the maximum number of flowers small, in which case all flowers should be visited in each patch).

We have already seen that the majority of studies have found prediction (1) to be true. Unfortunately, few studies have examined travel time between patches, or give quantitative data on the distribution of patches. It is probable that most studies have been carried out in situations where plants are abundant so that travel time is small. However, Zimmerman (1981c) found that bumblebees visited a higher proportion of flowers per plant in a low density population of *Polemonium foliosissimum* than in a high density population, in accordance with prediction (2). Further investigations of the relationship between forager behaviour and patch dispersion are clearly required to establish whether this is a general phenomenon.

Prediction (3) holds for all of the systems studied so far; foragers do spend longer and visit more flowers in large patches (Schmitt 1983; Geber 1985; Andersson 1988; Schmid-Hempel & Speiser 1988; Klinkhamer *et al.* 1989; Klinkhamer & de Jong 1990; Eckhart 1991; Dreisig 1995; Robertson & Macnair 1995). Also, they tend to visit a smaller proportion of the available flowers in large patches (Prediction 4) (Beattie 1976; Heinrich 1979a; Zimmerman 1981c; Schmitt 1983; Geber 1985; Andersson 1988; Schmid-Hempel & Speiser 1988; Klinkhamer *et al.* 1989; Dreisig 1995; Robertson & Macnair 1995; Goulson *et al.* 1998a), although Sih & Baltus (1987) found that bumblebees visited a higher proportion of flowers in large patches of *Nepeta cataria*. Hence at least three of the four predictions appear to hold true, with the remaining prediction so far untested. However, no single study has as yet quantified all of the relevant parameters: the costs of travel within and between patches, the distribution of foragers and rewards among patches and the search efficiency of foragers within patches. Until this is carried out over a range of patch distributions a truly convincing test of this model cannot be achieved.

## Decision making underlying forager distributions

The distribution of foragers among patches is determined by the rate at which they are recruited to patches, and how long they stay. It appears that foragers often achieve an approximately ideal free distribution, but how do they do this? What cues are used to determine foraging decisions? Factors governing recruitment rates to patches have received little attention. Greater recruitment to large patches is presumably at least partly because large patches are more apparent or because they are more likely to be encountered, and does not necessarily imply an active preference by the forager. The general finding that increases in recruitment are less than proportional to increases in patch size is less easily explained. It may be because foragers searching for flowers tend to search in two dimensions (they tend to fly at an approximately uniform height) so that the probability of encountering a patch is a function of its diameter rather than its area. Since the number of flowers in a patch is likely to be proportional to its area, this could result in a decelerating relationship between flower number and recruitment. At present there is insufficient information available to determine whether recruitment patterns are the result of passive encounter rates or active choice by foragers.

Departure rules from patches have received more attention. It is clear that the size of rewards recently received and the density of flowers influence the probability of departure. Superimposed on the general tendency for foragers to exhibit directionality, they may also adjust their turning rates and movement distances according to the size of rewards so that they quickly leave unrewarding flower patches and remain for longer in patches which provide a high reward (Pyke 1978a; Heinrich 1979a; Pleasants & Zimmerman 1979; Thomson *et al.* 1982; Cibula & Zimmerman 1987; Kato 1988). They also exhibit higher turning rates in dense patches of flowers (Rathcke 1983; Real 1983; Cresswell 1997). Short flights and frequent turns entails the risk of revisiting flowers, but this is presumably more than offset by the benefits of remaining within a patch containing many or highly rewarding flowers (Zimmerman 1982). In both bumblebees and solitary bees, low rewards promote movement among inflorescences (Cresswell 1990; Kadmon & Shmida 1992). Similarly in bumblebees and honeybees, low rewards trigger longer flights and so often result in departure from the plant or patch (Heinrich *et al.* 1977; Pyke 1978a; Thomson *et al.* 1982; Zimmerman 1983; Kato 1988; Dukas & Real 1993b; Giurfa & Núñez 1992). This has a clear analogy in the triggering of switching between plant species by receipt of low rewards (Greggers & Menzel 1993; Chittka *et al.* 1997; Goulson *et al.* 1997b). There is some disagreement as to the departure rules used by foragers. For some time it was thought that departure from a patch was triggered by the reward from a single flower falling below a threshold (Pyke 1978a; Best & Bierzychudek 1982; Hodges 1981, 1985; Pleasants 1989). It subsequently became apparent that a simple threshold departure rule was not strictly accurate, but rather that the probability of departure increases with decreasing reward (Cresswell 1990; Dukas & Real 1993b). However, any strategy based on only the last visit to a flower seems intuitively likely to be sub-optimal given the high heterogeneity of rewards that is usually found within patches, since it is likely to result in premature departure from highly rewarding patches. In fact recent studies have demonstrated that various bee species are able to integrate information over several flower visits (not just the last one) in making decisions about departure from a patch (Hartling & Plowright 1978; Waddington 1980; Cibula & Zimmerman 1987; Kadmon & Shmida 1992; Dukas & Real 1993b,c).

Of course, departure rules based on rewards received are only effective if there is a positive spatial correlation between rewards in adjacent flowers. Several studies have found similarities in the standing crop of nectar within flowers on the same plant (Pyke 1978c; Hodges 1981; Zimmerman & Pyke 1986, 1988; Real & Rathcke 1988; Waser & Mitchell 1990). Pleasants & Zimmerman (1979) also found spatial autocorrelation in standing crop among neighbouring plants of *Delphinium nelsonii* where bumblebees were the predominant visitors. Conversely, Waser & Mitchell (1990) subsequently found only weak and statistically insignificant spatial autocorrelation in the same species in sites where hummingbirds (which tend to fly further between visits to flowers) were the main visitors. Local “hot” and “cold” reward patches (Pleasants & Zimmerman 1979) are likely since most insect foragers (particularly bees) use localized systematic searches. Hence low rewards may indicate to a forager that either it has visited most of the flowers in the patch, or the patch has recently been depleted by another forager. However, rather more studies of spatial patterns in standing crop are required to be certain that this is the usual pattern.

## Discrimination amongst individual flowers

Individual flowers exhibit considerable variation in the rate at which they produce rewards even within a plant species. This variation may be due to micro-environmental influences, genetic variation, age of the plant or age of the flower. There is good evidence that both bumblebees and honeybees can distinguish between rewarding and non-rewarding flowers without sampling the reward available. They may hover in front of a flower, sometimes briefly touching the corolla, and then depart without probing into the flower structure. These rejected flowers contain, on average, less nectar than flowers which are probed (Heinrich 1979a; Corbet *et al.* 1984; Wetherwax 1986; Kato 1988; Duffield *et al.*

1993). Several mechanisms may be in operation. Bumblebees can assess pollen content of open flowers visually (Zimmerman 1982; Cresswell & Robertson 1994), and may plausibly be able to determine the nectar content of some flower species in the same way (Thorp *et al.* 1975, 1976; Kevan 1976). It has also been suggested that they may be able to assess nectar volumes from the scent of the nectar itself or the scent of fermentation products from yeasts in the nectar (Crane 1975; Williams *et al.* 1981; Heinrich 1979a). They could plausibly detect nectar volumes from humidity gradients surrounding the flower (Corbet *et al.* 1979). However, there is also evidence that insects may discriminate among flowers on the basis of morphological characters which are correlated with reward such as size, age and symmetry, or by using scent marks left by previous visitors. Selection of this sort is likely to have greatly influenced the evolution of floral characters.

## Flower size

A majority of studies have found that insect foragers exhibit higher rates of visitation to larger flowers (usually measured as corolla width) (for example Cresswell & Galen 1991; Galen & Newport 1987; Campbell 1989; Galen 1989; Eckhart 1991; Ohara & Higashi 1994; Conner *et al.* 1996; Shykoff *et al.* 1997), although Cresswell & Robertson (1994) found no relationship between size and visitation. Higher visitation rates may simply be because large flowers are more apparent, but there is some evidence that flower size is correlated with production of pollen or nectar, so that selection of large flowers may be reinforced by learning (Teuber & Barnes 1979; Brink & de Wet 1980; Stanton & Preston 1988; Cresswell & Galen 1991; Duffield *et al.* 1993). Thus, in general it seems that pollinators probably exert directional selection for increasing size of flowers. Presumably there is a trade-off between attracting pollinators and the costs of producing larger flowers. The optimal flower size will presumably vary according to a host of factors, including abundance of pollinators and the abundance of competing flower species.

## Flower age

Rates of production of nectar may vary with flower age (Boetius 1948; Manning 1956). There is no general pattern to changes in nectar production with age. In some plants, nectar production declines after the flower opens (Voss *et al.* 1980) or reaches an early peak and then declines (Carpenter 1976; Bond & Brown 1979; Frost & Frost 1981; Bertin 1982; Pleasants & Chaplin 1983; Southwick & Southwick 1983; Cruzan *et al.* 1988). Conversely, in other species nectar production increases with flower age (Pyke 1978b; Brink & de Wet 1980; Corbet & Willmer 1980; Best & Bierzychudek 1982; Robertson & Wyatt 1990). In some plant species nectar production is independent of flower age (Bertsch 1983; Pleasants 1983; Marden 1984a; Zimmerman & Pyke 1986).

It has long been known that honeybees, bumblebees, solitary bees, hoverflies and butterflies are able to discriminate between age classes of flowers using visual cues, and so preferentially select the more rewarding flowers (Müller 1883; Ludwig 1885, 1887; Kugler 1936, 1950; Jones & Buchmann 1974; Kevan 1978; Lex 1954; Thomson *et al.* 1982; Weiss 1995a). Discrimination among flowers according to their age may be facilitated by clear visual cues given by the plant itself, particularly by colour changes which variously occur in part or all of the flower (Schaal & Leverich 1980; Kevan 1983; Gori 1983, 1989; Delph & Lively 1989; Weiss 1995a). Such changes have been described in 78 families of plant so far (reviewed in Weiss 1995b and Weiss & Lamont 1997). For example flowers of *Pulmonaria* sp. change from red to blue, enabling bumblebees and flower bees (*Anthophora pilipes*) to select the more rewarding red flowers (Müller 1883; Oberrath *et al.* 1995). These age-dependent preferences can be flexible; honeybees select three-day old capitula of *Carduus acanthoides* in the early morning, and switch to two-day old capitula later in the day. This accurately targets the time of maximum nectar production in capitula which is from midway through their second day until early on their third (Giurfa & Núñez 1992a). Although these colour changes are often triggered by pollination and so benefit the plant by directing pollinators to flowers which are as yet unpollinated (Gori 1983; Weiss 1995b), this is not always so. It is unclear why unpollinated older flowers of some species give clear signals that they are producing little reward (Oberrath *et al.* 1995).

## Flower sex

The reproductive success of male flowers (in monoecious and dioecious species) or male-phase flowers (in dichogamous species where male and female function are temporally separated within the same flower) is likely to be more variable than that of female flowers, so that we may expect male flowers to invest more in attracting pollinators. Higher levels of nectar production in male flowers coupled with pollinator preferences for male flowers have been found in a number of systems (Bell *et al.* 1984; Devlin & Stephenson 1985; Delph & Lively 1992; Shykoff & Bucheli 1995). For example, in viper's bugloss (*Echium vulgare*), the protandrous flowers produce more nectar and receive higher rates of visitation during their male phase than during their female phase (Klinkhamer & de Jong 1990). However, male flowers are not always more rewarding (reviewed in Willson & Ågren 1989). For example in *Digitalis purpurea* nectar rewards are higher during the female phase (in this species female phase flowers are at the bottom of vertical racemes and bumblebees forage upwards, so that this arrangement prevents selfing) (Best & Bierzychudek 1982). Also, foragers differ in their requirements; some gather nectar, some pollen, while others may gather both. Those which are collecting pollen clearly benefit from avoiding female flowers, and appear to be able to do so. For example honeybees which are collecting nectar prefer inflorescences of *Lavandula stoechas* with a high proportion of female flowers (which produce more nectar than male flowers), while individuals which are collecting both nectar and pollen choose inflorescences with a greater proportion of male flowers (Gonzalez *et al.* 1995). Similar preferences for pollen or nectar producing flowers according to requirements have been recorded elsewhere, in honeybees (Kay 1982; Greco *et al.* 1996), bumblebees (Alexander 1990; Cresswell & Robertson 1994) and solitary bees (Eckhart 1991). Clearly pollinators are able to distinguish between sexes or sexual phases of the flowers of at least some plant species, and are able to learn which provide the greatest reward.

From the point of view of the plant, forager preferences for flowers of a particular sex clearly threaten efficient pollination; if for example male flowers invest more in attracting visitors so that female flowers are ignored then pollination will be poor. Hence neither sex will benefit if sexual differences are too marked.

## Flower symmetry

All flowers exhibit either radial or bilateral symmetry, although this symmetry is never perfect if measured carefully enough (Neal *et al.* 1998). Recently it has become clear that insects may also use floral symmetry both in floral recognition and in discrimination between more or less rewarding flowers. Honeybees show an innate preference for symmetrical shapes, which can be reinforced by learning (Giurfa *et al.* 1996), although naive bumblebees show no preference for either radial or bilateral symmetry in flowers (West & Laverty 1998). Symmetrical artificial flowers placed in the field attracted more foraging Hymenoptera, Diptera and Coleoptera than less symmetrical flowers (Møller & Sorci 1998). There is a fascinating parallel between the use of fluctuating asymmetry (small random departures from perfect bilateral symmetry) as an indicator of mate quality in animals (reviews in Møller 1993; Møller & Pomiankowski 1993; Watson & Thornhill 1994; Markow 1995, Møller & Thornhill 1998) and these preference by pollinators which also exert sexual selection pressure, but in this situation upon plants. So why might foragers prefer symmetrical flowers? In some systems where pollinators exhibit a preference for symmetrical flowers (for example *Epilobium angustifolium*), floral symmetry appears to be a good indicator of floral reward (Møller 1995; Møller & Eriksson 1995). Also, handling times of bumblebees are lower on symmetrical artificial flowers than on asymmetrical flowers (West & Laverty 1998). Thus there are at least two potential benefits of preferentially visiting symmetrical flowers. If these preferences are widespread, then they should exert strong stabilizing selection upon plants for floral symmetry.

However, it is worth noting that not all studies have found pollinator preferences for symmetrical flowers or a positive relationship between floral symmetry and reward, and more studies are needed before any firm conclusion can be reached (Møller & Eriksson 1995). Studies of fluctuating asymmetry in animals have often suffered from a range of methodological flaws which researchers of floral symmetry would do well to learn from (reviews in Palmer 1994, 1996; Markow 1995).

## Scent marking of flowers

Foragers may be able to avoid visiting flowers which they themselves have recently depleted by use of a systematic search pattern (see above). However, such strategies are of little benefit when intra- and/or interspecific competitors are abundant so that many flowers have been emptied by other individuals. Bumblebees, honeybees and some solitary bees appear to have developed a mechanism to avoid visiting flowers which have recently been depleted by conspecifics by use of scent marks. Scent marks left by the same insect or by conspecifics on previous visits may indicate either that the flower is empty or that it is particularly rewarding, and so influence the decision as to whether to probe the flower for nectar or reject it (Frankie & Vinson 1977; Cameron 1981; Free & Williams 1983; Marden 1984b; Kato 1988; Schmitt & Bertsch 1990; Giurfa 1993). Such markings presumably increase foraging efficiency by reducing time spent handling unrewarding flowers (Kato 1988; Schmitt & Bertsch 1990).

It appears that both attractant and repellent scent-marks may be in operation. Both honeybees and bumblebees leave short-lived repellent marks on recently visited flowers which deter both themselves and individuals from the same colony from probing recently emptied flowers, and thus promote systematic foraging (Núñez 1967; Wetherwax 1986; Giurfa & Núñez 1992b; Giurfa 1993; Giurfa *et al.* 1994; Goulson *et al.* 1998b; Stout *et al.* 1998). These marks may even be used by honeybees to avoid recently visited florets when foraging among the numerous adjacent florets presented in the inflorescences of Asteraceae (Giurfa & Núñez 1993). Similar marks with a repellent action lasting for about 10 min have also been reported in the solitary bee *Xylocopa virginica* (Frankie & Vinson 1977). Recently, it has become apparent that these marks may be detected by other species; four bumblebee species which are sympatric in the UK are all able to detect and reject flowers marked with repellent scent marks left by conspecifics or interspecifics (Goulson *et al.* 1998b; Stout *et al.* 1998). However, there is some evidence that bumblebee and honeybees are unable to use scent marks left by each other (Williams 1998). In addition to repellent marks, both honeybees and bumblebees can also leave scent-marks on rewarding flowers which are attractive to themselves and to conspecifics, and thus concentrate subsequent foraging bouts on rewarding flowers only (Ferguson & Free 1979; Kato 1988; Schmitt & Bertsch 1990). In bumblebees the chemical cue for both attractant and repellent marks appears to be secreted primarily from the tarsi, and tarsal washes in solvent can be used to mimic natural repellency when applied to flowers (Schmitt *et al.* 1991; Stout *et al.* 1998).

Since bees do not forage randomly (see above) they rarely encounter inflorescences which they themselves have just visited, so that the evolutionary benefit gained by leaving scent-marks is not immediately apparent. Presumably they help in avoiding errors in systematic foraging. In social bees the depositors of scent marks may also benefit through improving the foraging efficiency of siblings. However, bumblebee colonies are rather small (compared to honeybees), so that the majority of beneficiaries of marks left by bumblebees are probably not siblings. Competition between bee species is known to occur in some communities (Inouye 1978; Pyke 1982), and thus scent-marking may benefit both siblings and probable competitors. Of course, it is possible that the action of scent-marking did not initially evolve as a benefit to the marker or her siblings. Rather, the ability to detect chemicals accidentally deposited on flowers during foraging is more likely to have been the first (and perhaps only) evolutionary step towards a system of scent marking. Indeed, there is no evidence that repellent scent marks are deliberately deposited. They are comprised of long chain alkanes and alkenes (Schmitt 1990; Schmitt *et al.* 1991) which commonly occur in the cuticles of insects (Lockey 1980; Blum 1981, 1987), and which are bound to be left behind in tiny amounts if any part of the body comes into contact with flower parts.

Plant species vary greatly in the rate at which their flowers secrete nectar. Scent marks which repelled subsequent foragers for a fixed duration of time would be inefficient; optimally, the repellency should cease at the time when nectar levels in the flower have been replenished sufficiently that the flower becomes profitable to visit again. There is some evidence that this occurs; flowers of *Symphytum officinale* are repellent to bees for 20 min following a visit (Stout *et al.* 1998), while flowers of *Borago officinalis* are repellent for only 2 min (Williams 1998). In each species the duration of repellency matched the point at which revisiting became profitable, *B. officinalis* having a higher nectar secretion rate than *S. officinale*. Clearly studies of other systems are necessary before we can safely conclude that bees are able to manipulate the duration of the repellent effect. If they are, it must be either by adjusting the quantity of scent mark deposited, or (perhaps more likely) by adjusting the threshold concentration used for rejection of flowers. Experimental manipulation of scent mark concentrations would enable these alternative hypotheses to be distinguished.

### Other factors

With the exception of studies of scent marking, most work on discrimination among flowers by pollinators has concentrated on visual cues such as size, shape or colour, since these are easily recorded. However, many pollinators undoubtedly also use scents produced by flowers as an important source of sensory information, particularly at close range (reviewed in von Frisch 1967; Williams 1982; Waddington 1983b). The use of modern analytical techniques has revealed that many flowers exhibit intraspecific variation in floral scent quality or quantity (Tollsten & Bergstrom 1993; Knudsen 1994; Olesen & Knudsen 1994; Tollsten & Ovstedal 1994). To my knowledge only two studies have tried to examine whether pollinators discriminate among flowers of the same species using scent. Pellmyr (1986) found that floral scent variation in *Cimicifuga simplex* determined whether bees or butterflies were attracted, while Galen & Newport (1988) found that flowers of *Polemonium viscosum* produce either “skunky” scented flowers which are preferred by flies, and sweet scented flowers which are preferred by bumblebees. It is possible, perhaps likely, that floral scent variation is far more widespread than is currently appreciated, but that it has been largely overlooked due to our own particular sensory biases.

## Conclusions

Overall, the foraging strategies which have been identified tend to increase the expected reward in the next flower visited, by avoiding flowers which have been recently visited, by choosing more rewarding individual plants and individual flowers within each plant, and by choosing more rewarding species (within the constraint of incomplete knowledge of the rewards available). Studies of pollinator foraging have taught us much about their impressive abilities to learn appropriate handling skills and to learn associations between rewards and subtle visual cues. It has recently become apparent that these skills are not confined to the bees, but that other insect groups such as butterflies and hoverflies exhibit comparable learning abilities and forage in similar ways. For example butterflies are now known to learn which flower species have provided them with reward, and can distinguish between differentially rewarding age classes of flowers. They also exhibit flower constancy, flight directionality and some species are known to trapline. Not all of the behavioural mechanisms which underlie observed foraging patterns have been elucidated; for example the cause(s) of flower constancy is still under debate.

One area of pollinator foraging ecology which has, as yet, been largely overlooked is that of interspecific interactions. Although it has rarely been studied, it is clear than foragers occasionally interfere directly with each other while accessing flowers (Johnson & Hubbell 1974; Morse 1981), but perhaps more importantly it has recently been discovered that bumblebees are able to detect and reject flowers which have been visited by other *Bombus* species using scent (Goulson *et al.* 1998b; Stout *et al.* 1998). It is not known how many other pollinators use scent marking, or whether they are involved in other inter-specific interactions. This may prove to be a rewarding area for further study.

To a plant ecologist, many of the processes discussed here may at first glance seem to be of little relevance. Yet every single flower visit made by an insect has important consequences for the plant. When an insect visits a flower, it removes some or all of the rewards present. It may deposit pollen which, depending on the previous behaviour of the insect, may be from another flower on the same plant, from a conspecific which may be nearby or far away, or from a different species, so clogging the stigma. It may leave a scent mark to attract or repel subsequent foragers. Pollen that it carries away may be wasted on the stigma of a different species, or with luck may fertilize a conspecific. The likelihood of each these possible outcomes of an insect visit to a flower is determined by the past, current and future foraging decisions made by the insect. For plants, success in reproduction depends on far more than just attracting insects to their flowers.

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