Why do pollinators visit proportionally fewer flowers in large patches?

D. Goulson

Goulson, D. 2000. Why do pollinators visit proportionally fewer flowers in large patches? – Oikos 91: 485–492.

Pollinators collect resources that are patchy, since flowers are usually aggregated on several spatial scales. Empirical studies have established that pollinators almost invariably visit a smaller proportion of flowers as patch size increases. This has not been adequately explained. Here I present data on the payoff curve achieved by bumblebees, *Bombus lapidarius*, when visiting patches containing different numbers of inflorescences, and use the marginal value theorem to predict the optimum duration of stay within patches. The data demonstrate that visiting a declining proportion of inflorescences as patch size increases is an optimal strategy, if we assume that bees are attempting to maximise their rate of reward acquisition. I argue that this occurs because searching for the remaining unvisited inflorescences is easier in a small patch. On large patches, bees visited more inflorescences per patch than predicted (although still visiting a declining proportion). I suggest that this may occur because bees are using simple departure rules which result in near-optimal behaviour. I show that a departure rule based on two successive encounters with empty inflorescences closely predicts observed behaviour.

D. Goulson, Biodiversity and Ecology Div., School of Biological Sciences, Univ. of Southampton, Biomedical Sciences Building, Bassett Crescent East, Southampton, UK SO16 7PX (dg3@soton.ac.uk).

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. Flower visitors must make decisions concerning how best to exploit this patchy distribution. Studies of the response of pollinators to varying patch sizes have found that foragers spend longer and visit more flowers in large patches, as one would intuitively expect (Schmitt 1983, Geber 1985, Andersson 1988, Schmid-Hempel and Speiser 1988, Klinkhamer et al. 1989, Klinkhamer and de Jong 1990, Eckhart 1991, Dreisig 1995, Robertson and Macnair 1995, Brody and Mitchell 1997). More interestingly, studies of a diverse range of plant – pollinator systems have also found that the pollinators visit a smaller proportion of the available flowers in larger patches (Beattie 1976, Heinrich 1979, Zimmerman 1981,

Schmitt 1983, Geber 1985, Morse 1986, Andersson 1988, Schmid-Hempel and Speiser 1988, Thomson 1988, Klinkhamer et al. 1989, Klinkhamer and de Jong 1990, Pleasants and Zimmerman 1990, Dreisig 1995, Harder and Barrett 1995, Robertson and Macnair 1995, Brody and Mitchell 1997, Goulson et al. 1998a, Ohashi and Yahara 1998) (although Sih and Baltus 1987 found that bumblebees visited a higher proportion of flowers in large patches of *Nepeta cataria*). The explanation for this pattern is not obvious.

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 received criticism (e.g. Pierce and Ollason 1987), they remain a valuable starting point for generating hypotheses to explain behaviour. Optimal foraging models assume that foragers maximize their rate of resource acquisition (Charnov 1976). This is a reasonable as-

sumption 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 perhaps less reasonable for insects such as butterflies which intersperse nectaring with activities such as searching for mates or oviposition sites, and so regularly indulge in longer flights than do most foraging bees (Schmitt 1980, Waser 1982, Goulson et al. 1997).

The marginal value theorem is an optimality model for examining the behaviour of foragers exploiting patchy resources (Charnov 1976). The theorem 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 payoff curve for staying within a patch and the mean travel time between patches are known. Can the marginal value theorem explain why pollinators visit a decreasing proportion of flowers in a patch as patch size increases? Several researchers have applied the marginal value theorem to pollinators foraging on flowers held in vertical racemes (Pyke 1978b, 1981, 1984, Hodges 1981, Zimmerman 1981, Best and Bierzychudek 1982, Pleasants 1989). The aim of these studies was to predict when the insect should move to a new inflorescence, and to examine what departure rules might be used to achieve the most efficient strategy. However, this is a rather special case. Vertical racemes are easy to search systematically (insects typically start at the bottom and work upwards, Heinrich 1975, 1979), and usually have a predictable, declining reward in successively higher florets (Pyke 1978c). More commonly, a pollinator has to search amongst loose aggregations of flowers or inflorescences with no clear spatial structuring. Here the search strategy employed by the pollinator will largely determine the shape of the payoff curve that it gains from visiting a patch of flowers. If we can ascertain the shape of the payoff curve in different patch sizes, then it will be possible to predict the optimal duration of stay (sometimes known as the "give up time", Charnov 1976).

Two models have been developed applying the marginal value theorem to pollinators exploiting patches within which flowers were haphazardly arranged (Goulson 1999, Ohashi and Yahara 1999). Both models predict that pollinators should visit a greater proportion of flowers in small patches if they forage systematically and so are able to avoid flowers that they have just depleted. However, quantification of the relevant parameters had not been made, so only qualitative predictions were possible.

The assumption of non-random foraging within a patch is a reasonable one. Both bees 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 and Heinrich 1981,

Pyke 1983, 1984, Schmid-Hempel 1984, 1985, 1986, Cheverton et al. 1985, Dreisig 1985, Ginsberg 1985, 1986, Ott et al. 1985, Plowright and Galen 1985, Schmid-Hempel and Schmid-Hempel 1986, Soltz 1986, Kipp 1987, Kipp et al. 1989, Pyke and Cartar 1992). 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 areas with few flowers or unrewarding flowers, and remain for longer in patches which provide a high reward or where flowers are dense (Pyke 1978a, Heinrich 1979, Pleasants and Zimmerman 1979, Thomson et al. 1982, Rathcke 1983, Real 1983, Cibula and Zimmerman 1987, Kato 1988, Cresswell 1997). If they encounter flowers that they have already emptied, bumblebees and honeybees are able to avoid entering them using the presence of repellent scent marks placed on their previous visit, although they still incur a small time penalty due to the time it takes to detect the scent mark (Núñez 1967, Wetherwax 1986, Giurfa and Núñez 1992a, Giurfa 1993, Giurfa et al. 1994, Goulson et al. 1998b, Stout et al. 1998).

It seems probable that 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. Thus we would expect the rate of reward acquisition to begin to decline after a period of time spent within the patch. If travel time between patches is short, then an insect should depart soon after this decline begins (Goulson 1999). We do not know what proportion of flowers on a patch an insect can visit before it begins to have difficulty locating new flowers without making mistakes. And we do not know how this proportion changes with patch size. Once these relationships are known, we will be able to make testable predictions as to when a bee should depart from a patch.

Here I describe an empirical study intended to test whether visiting a declining proportion of flowers as patch size increases is the optimal strategy. I quantify the travel time between patches and the shape of the payoff curve for bees foraging in a range of patch sizes. These parameters are then used to predict the optimum duration of stay within patches, and these values are compared to observed durations. Departure rules are considered which may explain the observed behaviour.

Methods

Experiments were conducted during July 1998. Patches of inflorescences of white clover, *Trifolium repens*, were created by mowing a sward of flowers in a meadow in Warwickshire, UK. Patches were circular, contained an approximately even density of inflorescences, and were

situated a minimum of 2 m apart. All flowers were removed from areas between patches, and any other flower species present in the experimental area were removed. The patches contained 5, 10, 20 or 50 inflorescences.

The vast majority of visits to *T. repens* at the study site were by *Bombus lapidarius* (L.) (Hymenoptera; Apidae); all experimental observations were of this species. To exclude insects, patches were covered with ventilated plastic sheeting for one hour before observations. Once the sheeting was removed, the first naturally foraging bee to visit the patch was observed. A dictaphone was used to record events, and subsequently transcribed using a stopwatch to record times. The time taken to locate and to handle each successive inflorescence was recorded, and also the number of inflorescences visited before departure. If a bee returned to an inflorescence that it had already visited, this was recorded separately. If any other bee approached the patch during recording, it was guided away as unobtrusively as possible (following Inouye 1978). Five bees were observed foraging on each patch, with the patches being covered with sheeting for 1 h before each visit. Each patch size was replicated five times (five separate patches were created of each size). Travel times between patches were recorded for 40 bees that departed one patch and then visited another within the experimental array (these observations were made when the sheeting was not in place on any patch). It is possible that some bees were observed on more than one occasion, but this was unavoidable as marking them may have influenced their behaviour. Since the local population was large, it is unlikely that this occurred often.

Analysis

The five bees that visited each replicate patch cannot be considered independent replicates, since attributes of the patch may have influenced behaviour. Hence data from all five bees was combined as means for subsequent analysis, leaving five true replicates per patch size. The search time to find each consecutive new inflorescence was analysed in GLIM (Crawley 1991) according to patch size and the proportion of inflorescences already visited, to determine whether search times increased as the number of unvisited inflorescences remaining declined, and whether this relationship differed between patch sizes. Handling times of inflorescences were subjected to the same analysis.

Having quantified search and handling times, we can construct payoff curves for bees visiting each patch size, assigning a reward value of one for each inflorescence handled. This assumes that rewards per inflorescence are independent of patch size. Line of best fits for curves were explored in SPSS 8.0. These were then used to calculate the optimum duration of stay within

patches in relation to patch size, and compared to observed durations.

Results

The mean travel time between patches was 2.29 ± 0.63 s. Predictably, search time within patches increased as the proportion of inflorescences visited increased ($F_{1,271} = 47.1$, $p < 0.001$). For patch sizes of greater than five inflorescences, this increase in search rate is not apparent until more than half of the inflorescences have been visited (Fig. 1). Interestingly, there was also a significant overall difference in the search rate according to patch size ($F_{1,271} = 3.88$, $p < 0.05$). Search times were shorter by an average of approximately 0.6 s in the smallest patch size (five inflorescences), compared to the larger patches all of which were approximately similar with a mean search time of about 1.6 s (Table 1). There was no significant interaction between the
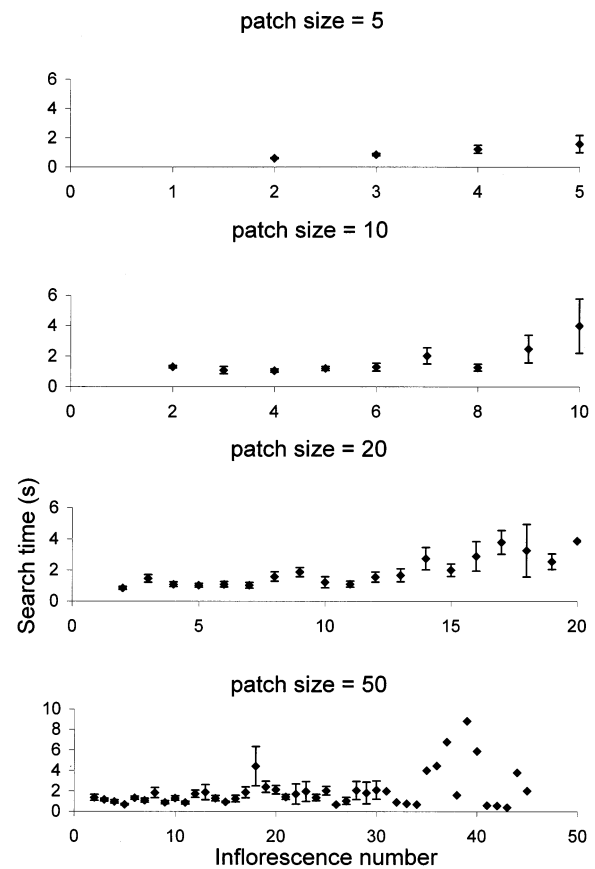

Fig. 1. Search times for successive inflorescences within patches ($\pm$ SE). Values shown were calculated by taking the means for five bees that visited each patch, and using these means from five replicate patches to calculate a grand mean and standard error. The bees' arrival at the first inflorescence in a patch was deemed to be the time of arrival in the patch, so there is no search time for the first inflorescence.

Table 1. Mean search times for inflorescences in patches of different sizes with SE and sample sizes.

Patch size	Search time	SE	N
5	1.03	0.16	19
10	1.60	0.22	39
20	1.71	0.14	81
50	1.69	0.13	140

effects of patch size and the proportion of inflorescences visited on search times ($F_{3,271} = 0.21$, $p > 0.05$).

The mean handling time (all patches combined) was 9.79 s per inflorescence (S.E. = 0.35, $n = 320$). Patch size had no effect on handling time ($F_{3,315} = 0.82$, $p > 0.05$), and handling time did not change as the proportion of inflorescences visited in a patch increased ($F_{1,315} = 0.50$, $p > 0.05$). There was no significant interaction between the two ($F_{3,315} = 0.27$, $p > 0.05$). As handling time is independent of patch size, the assumption that reward per inflorescence is equal across patch sizes appears to be valid, since inflorescence handling time is closely correlated to reward received (Harder 1986, Kato 1988). Thus we can construct payoff curves for each patch size, allocating an equal reward per inflorescence handled (Fig. 2). All four of these curves are very closely described by quadratic equations, with each linear and quadratic term significantly improving the fit of the line (Table 2). From these equations we can calculate the predicted optimum duration of stay in each patch, by calculating the point of contact between the curve and a tangential straight line plotted through coordinate (-2.29, 0) (following Charnov 1976) (Appendix 1). The optimum duration of stay increases with patch size, but is less than proportional so that to achieve a maximal rate of reward per time bees should visit a smaller proportion of inflorescences in larger patches (Table 3). For the smallest patch size, the

Table 2. Equations best describing payoff curves of reward received against time for bees foraging in four different sizes of patch. All equations are quadratic (reward $= at + bt^2$), and necessarily pass through the origin. The SE of each term is given below in brackets. It should be noted that the high values of r^2 result from use of a constant handling time in constructing the payoff curve.

Patch size	a	b	r^2
5	0.10145	-0.00015	1.0
	(0.00038)	(8.50×10^{-5})	
10	0.09726	-8.20×10^{-5}	0.99998
	(0.00068)	(7.39×10^{-6})	
20	0.09631	-4.56×10^{-5}	0.99998
	(0.00032)	(1.75×10^{-6})	
50	0.09317	-1.70×10^{-5}	0.99994
	(0.00040)	(9.72×10^{-7})	

predicted optimum duration of stay is close to the observed value, but as patch size increases, observed and predicted values diverge. Bees remain in large patches for longer than predicted, although they still visit a declining proportion of inflorescences as patch size increases (Table 3). The maximum rate of reward acquisition varies little with patch size; including travel time to reach the patch, it is predicted to be 0.089, 0.088, 0.090 and 0.089 inflorescences s^{-1} for patch sizes of 5, 10, 20 and 50, respectively. The actual mean rates of reward acquisition were 0.095, 0.078, 0.074 and 0.083 inflorescences s^{-1}.

Discussion

As has been found in the vast majority of previous studies, the proportion of inflorescences visited within a patch declined with increasing patch size. Bees visited on average 75% of inflorescences in small patches compared to 33% in the largest patches. Does this follow
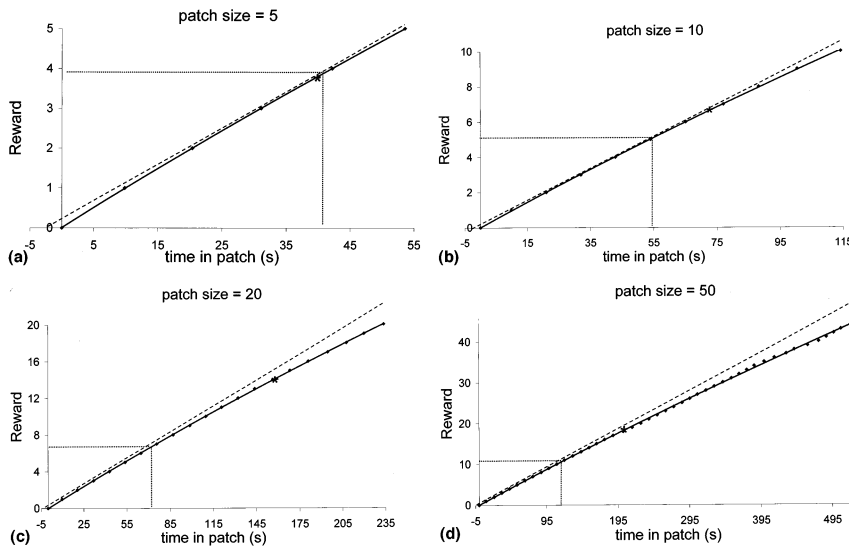

Fig. 2. Payoff curves for bees visiting patches of different sizes. Curves are constructed from measured search times, which increase as the proportion of inflorescences within the patch that have already been visited increases. Handling time is independent of patch size with a mean of 9.79 s per inflorescence; this value is used for constructing curves. Reward is measured as number of inflorescences handled. The optimum duration of stay and number of inflorescences handled in each patch size is marked (dotted lines). ★ = observed duration of stay within patches.

the predictions of the marginal value theorem? To my knowledge this is the first attempt to quantify payoff curves for pollinators foraging within patches of inflorescences. Search times for each successive inflorescence increased in all patch sizes as the duration of stay increased. This is what one would expect for any forager exploiting a patch of resources; as resource densities are depressed, it becomes increasingly hard to locate them. Since handling times were not affected by patch size or duration of stay, it is this increasing search time that results in the typical payoff curve with a declining slope (Charnov 1976). It is the shape of the curve (and the travel time between patches) that determines the optimal duration of stay. Travel time between patches was short (2.27 s), as is generally the case in studies of pollinators (Dreisig 1995). The predicted optimum duration of stay is close to the observed value for the smallest patch size, but the predicted values become less than those observed as patch size increases. However, even in the largest patch size where the discrepancy between observed duration of stay and the predicted optimum is greatest, the bees are still achieving a rate of reward acquisition very close to the optimum due to the shape of the payoff curve (Fig. 2d). So although bees are apparently behaving in a sub-optimal way in larger patches (assuming that calculation of the payoff curves is accurate and that the assumptions of the model are met), they are only very slightly sub-optimal.

Both observed and predicted durations of stay result in a declining proportion of inflorescences being visited as patch size increases. It appears that visiting a declining proportion is optimal, but why is it optimal? The answer must lie in the changing patterns in search time. I have previously argued that, in small patches, use of a systematic search pattern could enable pollinators to visit all of the inflorescences without mistakes, and thus without an increase in search time (the payoff curve would be a straight line) (Goulson 1999). Similarly, Ohashi and Yahara (1999) suggest that pollinators are able to memorize and avoid the last few flowers that they visited, so that when the number of flowers in the patch is less than or equal to the number that can be

memorized, the pollinator should visit every flower in the patch. Clearly if pollinators can memorize the positions of flowers that they have visited, they can do so for only a very few (less than four). Even in patches containing just five inflorescences, search time exhibited a marked increase with the fifth inflorescence taking on average 2.5 times as long to locate as the second. However, the mean search time in small patches was lower than that in large patches, even though bees were visiting a larger proportion of the inflorescences present. Why might this be? Presumably searching for the remaining unvisited inflorescences is simpler in a small patch than in a large one. In this respect pollinators visiting flowers represents a rather different situation to that for which the marginal value theorem was originally developed (predators searching for prey) because the flowers remain after they have been visited. By doing so they render locating the remaining unvisited flowers more difficult. The explanation as to why search times overall are longer in bigger patches may be illustrated by a simple numerical example. Consider a bee foraging in a patch of five inflorescences, that has already visited three of them. If it visits the next inflorescence at random, it has a 2/5 chance of locating one of the unvisited ones on its first attempt. However, the simple movement rules of bees render it unlikely that it will visit the inflorescence it has just left, so it actually has a chance of 2/4 of locating an unvisited flower on the first attempt. In contrast, consider a bee in a patch of 50 flowers, of which it has visited 30 (the same proportion). When it departs from the 30th flower it has a 20/49 chance of striking an unvisited flower on its first attempt, a value substantially less than 2/4. Finding the fourth flower of five, and so achieving an 80% visitation rate (as most bees did), is substantially easier than locating the 31st, 32nd, … 40th flower in a patch of 50 (and very few bees did so). This argument does not require the pollinator to memorize the positions of flowers that it has recently visited, only that it does not immediately visit the flower that it just departed from.

Another way of considering this is to examine what cues stimulate departure from a patch. Factors trigger-

Table 3. Estimated optimums and observed values for the duration of stay in each patch (s) and the number of inflorescences visited before departure. Error are given as (± SE) or if the errors were asymmetrical, as a range.

	Patch size			
	5	10	20	50
Optimum duration of stay (s)	41.20 (40.09–42.38)	54.46 (52.09–57.17)	71.88 (70.47–73.39)	114.3 (111–117.9)
Observed duration of stay	37.4 (± 7.78)	73.3 (± 14.6)	155.1 (± 40.2)	194.6 (± 69.9)
Optimum no. inflorescences visited per patch	3.92 (3.83–4.03)	5.05 (4.84–5.29)	6.69 (6.56–6.82)	10.4 (10.1–10.7)
Observed no. inflo./patch	3.76 (± 0.21)	5.92 (± 0.89)	11.68 (± 1.45)	16.40 (± 2.65)

ing departure from inflorescences or patches of flowers have been studied in some detail. In both bumblebees and solitary bees, low rewards promote movement among inflorescences (Cresswell 1990, Kadmon and 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 and Real 1993a, Giurfa and Núñez 1992b). 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 and 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 and Real 1993a). 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 and Plowright 1978, Waddington 1980, Cibula and Zimmerman 1987, Kadmon and Shmida 1992, Dukas and Real 1993a, b).

For simplicity, let us suppose that a bee departs from a patch if it encounters two inflorescences in a row that it has already visited (and which are thus more-or-less empty). If we assume, as above, that the bee is equally likely to encounter any inflorescence (excluding the one that it just left), then it is simple to calculate the probability that this inflorescence has already been visited, and to square this to obtain the probability of this happening twice and the bee departing from the patch. We can thus calculate the probability of a bee departing after one visit, two visits, and so on, and use this to calculate the expected mean number of inflorescences visited per patch for bees using this departure rule. For the patch sizes used in this study, we would predict mean numbers of inflorescences visited per patch to be 3.95, 6.06, 9.88 and 18.48. These values are remarkably close to those observed (Table 3). Whether this is coincidence is hard to say without explicitly studying the departure rules used in this system, but nonetheless this example illustrates an important point; that a simple departure rule can result in pollinators visiting more inflorescences per patch but a declining proportion of inflorescences per patch, exactly as is observed in nature.

Although it seems that we can explain the declining proportion of inflorescences visited by pollinators in larger patches, this does not explain the discrepancy between our observed duration of stay and that predicted by the marginal value theorem. There are several possible explanations. Implicit in the model used is the assumption that energy expenditure is constant. If flight between patches were more costly than foraging within patches, this may result in bees spending longer in each

patch. Secondly, since bees had been excluded from the patches for 1 h, the rate of reward was presumably high. Thus the bee may perceive the experimental patch to be more rewarding than the average patch based on its previous experience; this too could lead to an extended duration of stay. It may simply be that there is not a simple departure rule that bees can use to achieve an optimal strategy. Since whatever rule they are using at present achieves something close to the predicted optimum, selection pressure to improve will be weak.

To summarise, I demonstrate that pollinators spend proportionally less time in larger patches, a familiar result. I show that this broad pattern is predicted by the marginal value theorem, and argue that this occurs because searching for unvisited inflorescences is easier in a small patch. A simple departure rule based on two successive encounters with inflorescences that have already been visited closely predicts observed behaviour.

References

Andersson, S. 1988. Size-dependent pollination efficiency in *Anchusa officinalis* (Boraginaceae): causes and consequences. – Oecologia 76: 125–130.

Beattie, A. J. 1976. Plant dispersion, pollination and gene flow in *Viola*. – Oecologia 25: 291–300.

Best, L. S. and Bierzychudek, P. 1982. Pollinator foraging on foxglove (*Digitalis purpurea*): a test of a new model. – Evolution 36: 70–79.

Brody, A. K. and Mitchell, R. J. 1997. Effects of experimental manipulation of inflorescence size on pollination and pre-dispersal seed predation in the hummingbird-pollinated plant *Ipomopsis aggregata*. – Oecologia 110: 86–93.

Charnov, E. L. 1976. Optimal foraging: the marginal value theorem. – Theor. Popul. Biol. 9: 129–136.

Cheverton, J., Kacelnik, A. and Krebs, J. R. 1985. Optimal foraging: constraints and currencies. – In: Hölldobler, B. and Lindauer, M. (eds), Experimental behavioural ecology and sociobiology. Sinauer, pp. 109–126.

Cibula, D. A. and Zimmerman, M. 1987. Bumblebee foraging behaviour: changes in departure decisions as a function of experimental manipulations. – Am. Midl. Nat. 117: 386–394.

Crawley, M. J. 1991. GLIM for ecologists. – Blackwell.

Cresswell, J. E. 1990. How and why do nectar-foraging bumblebees initiate movements between inflorescences of wild bergamot *Monarda fistulosa* (Lamiaceae). – Oecologia 82: 450–460.

Cresswell, J. E. 1997. Spatial heterogeneity, pollinator behaviour and pollinator-mediated gene-flow: bumblebee movements in variously aggregated rows of oil-seed rape. – Oikos 78: 546–556.

Dreisig, H. 1985. Movement patterns of a clear-wing hawk-moth, *Hemaris fuciformis*, foraging at red catchfly, *Viscaria vulgaris*. – Oecologia 67: 360–366.

Dreisig, H. 1995. Ideal free distributions of nectar foraging bumblebees. – Oikos 72: 161–172.

Dukas, R. and Real, L. A. 1993a. Effects of recent experience on foraging decisions by bumblebees. – Oecologia 94: 244–246.

Dukas, R. and Real, L. A. 1993b. Effects of nectar variance on learning by bumblebees. – Anim. Behav. 45: 37–41.

Eckhart, V. M. 1991. The effects of floral display on pollinator visitation vary among populations of *Phacelia linearis* (Hydrophyllaceae). – Evol. Ecol. 5: 370–384.

Geber, M. A. 1985. The relationship of plant size to self-pollination in *Mertensia ciliata*. – Ecology 66: 762–772.

Ginsberg, H. S. 1985. Foraging movements of *Halictus ligatus* (Hymenoptera: Halictidae) and *Ceratina calcarata* (Hymenoptera: Anthophoridae) on *Chrysanthemum leucanthemum* and *Erigeron annuus* (Asteraceae). – J. Kans. Entomol. Soc. 58: 19–26.

Ginsberg, H. S. 1986. Honey bee orientation behaviour and the influence of flower distribution on foraging movements. – Ecol. Entomol. 11: 173–179.

Giurfa, M. 1993. The repellent scent-mark of the honeybee *Apis mellifera ligustica* and its role as a communication cue during foraging. – Insectes Soc. 40: 59–67.

Giurfa, M. and Núñez, J. A. 1992a. Honeybees mark with scent and reject recently visited flowers. – Oecologia 89: 113–117.

Giurfa, M. and Núñez, J. A. 1992b. Foraging by honeybees on *Carduus acanthoides* – pattern and efficiency. – Ecol. Entomol. 17: 326–330.

Giurfa, M., Núñez, J. A. and Backhaus, W. 1994. Odour and colour information in the foraging choice behavior of the honeybee. – J. Comp. Physiol. 175: 773–779.

Goulson, D. 1999. Foraging strategies for gathering nectar and pollen in insects. – Persp. Plant Ecol. Evol. Syst. 2: 185–209.

Goulson, D., Ollerton, J. and Sluman, C. 1997. Foraging strategies in the small skipper butterfly, *Thymelicus flavus*: when to switch? – Anim. Behav. 53: 1009–1016.

Goulson, D., Stout, J. C., Hawson, S. A. and Allen, J. A. 1998a. The effects of floral display size and colour on recruitment of three bumblebee species to comfrey, *Symphytum officinale* L. (Boraginaceae), and subsequent seed set. – Oecologia 113: 502–508.

Goulson, D., Hawson, S. A. and Stout, J. C. 1998b. Foraging bumblebees avoid flowers already visited by conspecifics or by other bumblebee species. – Anim. Behav. 55: 199–206.

Harder, L. D. 1986. Effects of nectar concentration and flower depth on handling efficiency of bumblebees. – Oecologia 69: 309–315.

Harder, L. D. and Barrett, S. C. H. 1995. Mating cost of large floral displays in hermaphrodite plants. – Nature 373: 512–515.

Hartling, L. K. and Plowright, R. C. 1978. Foraging by bumblebees on artificial flowers: a laboratory study. – Can. J. Bot. 63: 488–491.

Heinrich, B. 1975. Energetics of pollination. – Annu. Rev. Ecol. Syst. 6: 139–170.

Heinrich, B. 1979. Resource heterogeneity and patterns of movement in foraging bumblebees. – Oecologia 40: 235–245.

Heinrich, B., Mudge, P. R. and Deringis, P. G. 1977. Laboratory analysis of flower constancy in foraging bumblebees: *Bombus ternarius* and *B. terricola*. – Behav. Ecol. Sociobiol. 2: 247–265.

Hodges, C. M. 1981. Optimal foraging in bumblebees: hunting by expectation. – Anim. Behav. 29: 1166–1171.

Hodges, C. M. 1985. Bumblebees foraging: the threshold departure rule. – Ecology 66: 179–187.

Inouye, D. W. 1978. Resource partitioning in bumblebees: experimental studies of foraging behavior. – Ecology 59: 672–678.

Kadmon, R. and Shmida, A. 1992. Departure rules used by bees foraging for nectar: a field test. – Evol. Ecol. 6: 142–151.

Kato, M. 1988. Bumble bee visits to *Impatiens* spp.: pattern and efficiency. – Oecologia 76: 364–370.

Kipp, L. R. 1987. The flight directionality of honeybees foraging on real and artificial inflorescences. – Can. J. Zool. 65: 587–593.

Kipp, L. R., Knight, W. and Kipp, E. R. 1989. Influence of resource topography on pollinator flight directionality of two species of bees. – J. Insect Behav. 2: 453–472.

Klinkhamer, P. G. L. and de Jong, T. L. 1990. Effects of plant density and sex differential reward visitation in the protandrous *Echium vulgare* (Boraginaceae). – Oikos 57: 399–405.

Klinkhamer, P. G. L., de Jong, T. L. and de Bruyn, G. J. 1989. Plant size and pollinator visitation in *Cynoglossum officinale*. – Oikos 54: 201–204.

Morse, D. 1986. Inflorescence choice and time allocation by insects foraging on milkweed. – Oikos 46: 229–236.

Núñez, J. A. 1967. Sammelbienen markieren versiegte Futterquellen durch Duft. – Naturwissenschaften 54: 322–323.

Ohashi, K. and Yahara, T. 1998. Effects of variation in flower number on pollinator visits in *Cirsium purpuratum* (Asteraceae). – Am. J. Bot. 85: 219–224.

Ohashi, K. and Yahara, T. 1999. How long to stay on, and how often to visit a flowering plant? – a model for foraging strategy when floral displays vary in size. – Oikos 86: 386–392.

Ott, J. R., Real, L. A. and Silverfine, E. M. 1985. The effect of nectar variance on bumblebee patterns of movement and potential gene dispersal. – Oikos 45: 333–340.

Pierce, G. J. and Ollason, J. G. 1987. 8 reasons why optimal foraging theory is a complete waste of time. – Oikos 49: 111–118.

Pleasants, J. M. 1989. Optimal foraging by nectarivores: a test of the marginal-value theorem. – Am. Nat. 134: 51–71.

Pleasants, J. M. and Zimmerman, M. 1979. Patchiness in the dispersion of nectar resources: evidence for hot and cold spots. – Oecologia 41: 283–288.

Pleasants, J.M. and Zimmerman, M. 1990. The effect of inflorescence size on pollinator visitation of *Delphinium nelsonii* and *Aconitum columbianum*. – Collect. Bot. 19: 21–39.

Plowright, R. C. and Galen, C. 1985. Landmarks or obstacles: the effects of spatial heterogeneity on bumble bee foraging behaviour. – Oikos 44: 459–464.

Pyke, G. H. 1978a. Optimal foraging: movement patterns of bumblebees between inflorescences. – Theor. Popul. Biol. 13: 72–98.

Pyke, G. H. 1978b. Optimal foraging in hummingbirds: testing the marginal value theorem. – Am. Zool. 18: 739–752.

Pyke, G. H. 1978c. Optimal foraging in bumblebees and coevolution with their plants. – Oecologia 36: 281–293.

Pyke, G. H. 1981. Honeyeater foraging: a test of optimal foraging theory. – Anim. Behav. 29: 878–888.

Pyke, G. H. 1983. Animal movements: An optimal foraging approach. – In: Swingland, I. R. and Greenwood, P. J. (eds), The ecology of animal movement. Clarendon, pp. 7–31.

Pyke, G. H. 1984. Optimal foraging: a critical review. – Annu. Rev. Ecol. Syst. 15: 523–575.

Pyke, G. H. and Cartar, R. V. 1992. The flight directionality of bumblebees: do they remember where they came from. – Oikos 65: 321–327.

Rathcke, B. 1983. Competition and facilitation among plants for pollination. – In: Real, L. (ed.), Pollination ecology. Academic Press, pp. 305–325.

Real, L. 1983. Microbehavior and macrostructure in pollinator plant interactions. – In: Real, L. (ed.), Pollination ecology. Academic Press, pp. 287–302.

Robertson, A. W. and Macnair, M. R. 1995. The effects of floral display size on pollinator service to individual flowers of *Myosotis* and *Mimulus*. – Oikos 72: 106–114.

Schmid-Hempel, P. 1984. The importance of handling time for the flight directionality in bees. – Behav. Ecol. Sociobiol. 15: 303–309.

Schmid-Hempel, P. 1985. How do bees choose flight direction while foraging? – Physiol. Entomol. 10: 439–442.

Schmid-Hempel, P. 1986. The influence of reward sequence on flight directionality in bees. – Anim. Behav. 34: 831–837.

Schmid-Hempel, P. and Schmid-Hempel, R. 1986. Nectar-collecting bees use distance-sensitive movement rules. – Anim. Behav. 34: 605–607.

Schmid-Hempel, P. and Speiser, B. 1988. Effects of inflorescence size on pollination in *Epilobium angustifolium*. – Oikos 53: 98–104.

Schmitt, J. 1980. Pollinator foraging behaviour and gene dispersal in *Senecio* (Compositae). – Evolution 34: 934–943.

Schmitt, J. 1983. Flowering plant density and pollinator visitation in *Senecio*. – Oecologia 60: 97–102.

Sih, A. and Baltus, M. S. 1987. Patch size, pollinator behaviour and pollinator limitation in catnip. – Ecology 68: 1679–1690.

Soltz, R. L. 1986. Foraging path selection in bumblebees: hindsight or foresight? – Behaviour 99: 1–21.

Stout, J. C., Goulson, D. and Allen, J. A. 1998. Repellent scent marking of flowers by a guild of foraging bumblebees (*Bombus* spp.). – Behav. Ecol. Sociobiol. 43: 317–326.

Thomson, J. D. 1988. Effects of variation in inflorescence size and floral rewards on the visitation rates of trap lining pollinators of *Aralia hispida*. – Evol. Ecol. 2: 65–76.

Thomson, J. D., Maddison, W. P. and Plowright, R. C. 1982. Behaviour of bumblebee pollinators on *Aralia hispida* Vent. (Araliaceae). – Oecologia 54: 326–336.

Waddington, K. D. 1980. Flight patterns of foraging bees relative to density of artificial flowers and distribution of nectar. – Oecologia 44: 199–204.

Waddington, K. D. and Heinrich, B. 1981. Patterns of movement and floral choice by foraging bees. – In: Kamil, A. and Sargent, T. (eds), Foraging behavior: ecological, ethological, and psychological approaches. Garland STPM Press, pp. 215–230.

Waser, N. M. 1982. A comparison of distances flown by different visitors to flowers of the same species. – Oecologia 55: 251–257.

Wetherwax, P. B. 1986. Why do honeybees reject certain flowers? – Oecologia 69: 567–570.

Zimmerman, M. L. 1981. Optimal foraging, plant density and the marginal value theorem. – Oecologia 49: 148–153.

Zimmerman, M. L. 1983. Plant reproduction and optimal foraging: experimental nectar manipulations in *Delphinium nelsonii*. – Oikos 41: 57–63.

Appendix 1. Calculating the optimum duration of stay within patches.

The pay-off curve is described by a curve of the form: $r = ct + dt^2$ (1)

where r is the reward (number of inflorescences visited), t is the time elapsed in the patch, and c and d are constants.

This curve has a slope of $c + 2dt$ (2)

The equation of the tangential line to this curve is: (3)
$r = at + b$

Where a and b are constants

Let travel time between patches $= v$. Eq. 3 must pass through $(-v, 0)$.

Hence $b = va$ (4)

Thus the equation of the straight line is: $r = at + va$ (5)

This line forms a tangent to the curve when the slopes of the curve and line are equal, when

$a = c + 2dt$ (6)

And when line and curve intercept at

$At + va = ct + dt^2$ (7)

Substituting in value for a from eq. 6:

$t(c + 2dt) + v(c + 2dt) = ct + dt^2$ (8)

Rearranging:

$Tc + 2dtt + vc + 2vdt = ct + dtt$ (9)

$Dtt + vc + 2vdt = 0$ (10)

Since v, c and d have been estimated, we can calculate t.