Are insects flower constant because they use search images to find flowers?

Dave Goulson

Goulson, D. 2000. Are insects flower constant because they use search images to find flowers? – Oikos 88: 547–552.

Many insects which gather nectar or pollen exhibit flower constancy, a learned fidelity to a particular species of plant. Recent studies suggest that foraging insects may use a perceptual mechanism akin to a search image to detect flowers, in a manner analogous to the way that predators search for prey. This has emerged as an alternative (but not mutually exclusive) explanation for flower constancy to that proposed by Darwin, who suggested that it may result from a limited ability to learning or remember the handling skills appropriate for particular flowers. However, search images are thought to be a mechanism for locating cryptic prey. 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. One possible explanation for this apparent contradiction is that flowers are effectively cryptic when viewed against a background which contains many other flowers of similar colour. I present experimental evidence which suggests that a background of flowers of similar colour does reduce foraging efficiency of bumblebees, but that a background of dissimilarly coloured flowers has no effect. This I interpret as evidence that flowers may be cryptic, suggesting that pollinators may indeed use a search image in location of flowers. However, the relative importance of constraints on foragers' abilities to locate flowers versus their abilities to handle them as causes of flower constancy remain to be elucidated.

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

Many of the most familiar insect groups, including most bees, butterflies and moths, and also some flies and beetles, depend for their sustenance upon pollen or nectar rewards provided by flowers. It is generally only adult, winged insects that specialise in visiting flowers; immature stages do not have the mobility necessary to gather such sparsely scattered resources. Even for flighted insects, 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. 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. 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, and learning to handle such flowers takes time. It is perhaps not surprising that the foraging behaviours which have evolved to combat these problems have been the focus of numerous studies. One characteristic strategy of insects visiting flowers is known as flower constancy.

Flower constancy

Insects foraging for nectar or pollen have long been known to exhibit a learned fidelity to flowers of a

particular plant species which has previously provided a reward. In doing so they ignore many other suitable and rewarding flowers which they pass, but of course they also avoid visiting unsuitable flowers. This behaviour was first described by Aristotle in the honeybee, *Apis mellifera* (Grant 1950), and subsequently attracted the attention of Darwin (1876). More recently it became known as flower constancy (a term perhaps first coined by Plateau 1901 and defined by Waser 1986) and has been identified in the foraging regimes of other pollinators too. The preference shown by an individual insect is not fixed, and varies between individual foragers of the same species (Heinrich 1979, Barth 1985). It has long been apparent that the terms 'constancy' and 'fidelity' are slightly misleading in this context since some foragers will sample other flowers to keep track of changing rewards over time (known as minoring in bumblebees), and may also change their preference over time in response to a sequence of low rewards or reduced availability of their preferred flower (Heinrich 1979, Chittka et al. 1997, Goulson et al. 1997a).

Flower constancy is intriguing from a behavioural viewpoint and is of crucial importance to plant reproductive biology (it influences the outcome of interspecific competition for pollination services and has been implicated as a contributory factor in sympatric speciation by reducing inter-morph pollen transfer, Grant 1952, 1992, 1994, Goulson 1994, Goulson and Jerrim 1997). Studies of flower constancy have continued to focus primarily on Hymenoptera, principally honeybees and bumblebees, but in the last ten years it has become clear that flower constancy is more widespread. It has recently been identified in butterflies (Lewis 1989, Goulson and Cory 1993, Goulson et al. 1997a, b) and hoverflies (Syrphidae; Diptera) (Goulson and Wright 1998), and circumstantial evidence from analysis of gut contents in pollen feeding beetles suggests that they may also exhibit constancy (De Los Mozos Pascual and Domingo 1991). It thus seems probable that flower constancy is a general phenomenon amongst foragers which gather nectar and/or pollen.

Several explanations for flower constancy have been proposed; perhaps the most favoured theory is based on an idea proposed by Darwin (1876) which has become known as Darwin's interference hypothesis (Lewis 1986, Waser 1986, Woodward and Laverty 1992). However, this has not stood up well to empirical evaluation (Woodward and Laverty 1992, Laverty 1994a, Gegear and Laverty 1995, Goulson et al. 1997b). Recent experimental studies suggest that additional explanations for flower constancy may be required, and one possibility is that pollinators use a search image to find flowers. However, the search image concept is generally associated with foragers searching for cryptic prey.

Darwin's interference hypothesis

This argues 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 which differ in floral structure. Learning to extract rewards 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 (Laverty 1980, Lewis 1986, Laverty and Plowright 1988). Knowledge of how to handle one flower species can be lost when it is replaced by information about handling a different species, or retrieval of memories may be hampered by switching between species of flower differing in floral morphology (interference effects) (Heinrich et al. 1977, Lewis 1986, Woodward and Laverty 1992). 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 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 and Laverty 1992, Laverty 1994a, Gegear and Laverty 1995, Goulson et al. 1997b). Switching between simple flowers of different species does not induce interference effects (Laverty 1994a), and with experience bumblebees can learn to switch between different tasks without interference effects (Dukas 1995). In any case 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). Experience with other species of broadly similar flower morphology may actually increase learning rates (Laverty 1994b). Lastly, 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 and Wright 1998). Thus Darwin's interference hypothesis does not appear to be sufficient to explain flower constancy.

The search image hypothesis

Tinbergen (1960) introduced the search image as an explanation for prey selection patterns of great tits (*Parus major*) foraging under natural conditions in woodland. He noted that individual birds tended to collect sequences of the same prey species, and that

548

they exhibited positive frequency-dependent selection. Although an intuitively appealing concept, search images have proved difficult to demonstrate convincingly, and it remains unclear how frequently they occur in natural situations (Guilford and Dawkins 1987, Allen 1989). Also, the cognitive mechanisms which give rise to the use of a search image are poorly understood. Almost all definitions of search images specify that they apply to cryptic prey (although Tinbergen himself 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 and Allen 1983). This assumption now appears to be valid: experiments using pigeons (*Columba livia*) have found that search image effects are only evident when prey are cryptic (Bond 1983, Bond and Riley 1991, Reid and Shettleworth 1992). Adoption of a search image for a particular prey's visual characteristics enhances its detectability and interferes with incoming perceptual information regarding alternative prey types (Bond 1983). 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 (Langley 1996). Both honeybees and bumblebees are able to use selective attention when distinguishing among flower types (Klosterhalfen et al. 1978, Dukas and 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, Eysenck and Keane 1990, Posner and Peterson 1990). Dukas and Ellner (1993) predicted that if predators have a limited attention 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 both a limited ability to process information simultaneously and from selective attention to cues associated with particular prey types.

The mechanism involved may apply equally to 'prey' such as flowers, which far from being cryptic have evolved to be conspicuous. Studies of pollinator behaviour (either in the laboratory or field) almost invariably focus on situations where the pollinator is presented with many flowers. Often several plant species have flowers of very similar colour to the insect eye (Kevan 1978, 1983, Chittka et al. 1994, Waser et al. 1996). When viewed against a backdrop of other floral displays (either of the same or different plant species) all of which are vying for the attention of pollinators then any particular flower may be effectively cryptic (Fig. 1) (Endler 1981). There is evidence that flower constancy declines as flower density (and thus crypsis) declines (Kunin 1993, Goulson et al. 1997a), in accordance with the predictions of Dukas and Ellner (1993). 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. Dukas and Real (1993) demonstrate that bumblebee foraging efficiency is limited in part by their ability to recognise rewarding flower types, and that they make fewer errors in identification when visiting only one rewarding flower type (even when the flower types differ markedly in colour). Thus 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, Laverty 1994a, Chittka et al. 1997), even when these flowers have very different structures (Wilson and Stine 1996). Conversely, pollinators rarely switch between flower species of similar structure but of different colour (Wilson and Stine 1996). Darwin's interference hypothesis predicts precisely the reverse, but this is consistent with the hypothesis that search images are used by foragers.

Can flowers be cryptic? An experimental test

So are flowers really hard to find when viewed against a background of similarly coloured flowers of other species? To test this, I quantified the flight times of wild bumblebees, *Bombus pascuorum*, foraging among grids of flowers of *Lotus corniculatus* (Leguminosae) or *Vicia cracca* (Leguminosae), two species which are favoured by *B. pascuorum*. Flowers of *L. corniculatus* are yellow and those of *V. cracca* are purple. These grids were presented either with or without a background of yellow flowers of species not generally visited by *B. pascuorum*. If yellow flowers are harder to locate when viewed with many other yellow flowers, then search times should be longer than when locating yellow flowers against a green background, or when locating purple flowers against either a green or green and yellow background.

Experiments were carried out in a flower rich meadow at Chilworth, Hampshire during July 1998. Freshly picked inflorescences of *L. corniculatus* or *V. cracca* were placed in pots of water sunk into the ground on a 3×3 grid with 1 m between inflorescences. The sward was naturally rich in yellow flowers of various *Hieracium* sp. (Compositae), *Senecio jacobaea*

(Compositae) and *Hypericum perforatum* (Guttiferae), none of which were visited by *B. pascuorum*. To the human eye these flowers are of very similar colour. Areas were chosen which did not naturally contain any purple flowers. In half of the experimental grids all naturally occurring yellow flowers within the grid or within 1 m of it were cut off and discarded. Thus there were four treatments; *L. corniculatus* with and without a background of yellow flowers, and *V. cracca* with and without a background of yellow flowers. Each treatment was replicated four times (16 grids in total). Each grid was observed sequentially in random order until a *B. pascuorum* worker visited it. The flight time between inflorescences in the grid was recorded onto a dictaphone and subsequently transcribed. Where more than two flowers were visited within the grid, a mean flight time was calculated. Each bee was then caught, marked with Tipp-Ex® (Tipp-Ex Ltd., Camberley, Surrey), and not used in any further observations. Observations were repeated on five successive days. Thus for each replicate grid flight times between inflorescences were available from five bees. These were used to calculate a single grand mean flight time for each replicate grid, and only the grand means were used in the analysis to avoid psuedoreplication. Data were analysed by two-way analysis of variance.

Mean flight times between inflorescences were longer when bees were foraging on *L. corniculatus* than on *V. cracca* ($F_{1,12} = 33.8$, $p < 0.001$) and were longer when yellow flowers were present as a background than when they were not ($F_{1,12} = 26.8$, $p < 0.001$). More interestingly, there was a significant interaction between the two; a background of yellow flowers greatly increased flight times when foraging on the yellow-flowered *L. corniculatus*, but had no effect when foraging on *V. cracca* ($F_{1,12} = 19.6$, $p < 0.001$) (Fig. 2). Bees took on average twice as long to locate *L. corniculatus* flowers when they were presented against a background of other yellow flowers compared to when they were on their own. Frequently bees were observed to approach to within 1–2 cm of yellow flowers other than *L. corniculatus*, most often *Hieracium* sp., but then rejected them after close inspection. This is not really surprising since small flowers of different species but with similar colour are likely to be indistinguishable to a bee until it is at very close range. In fact *L. corniculatus* inflorescences are hard for human observers to find when mixed with other yellow flowers (see Fig. 1). Of course, bee vision is different to our own, and it is likely that some of the flower species present were, to a bee, markedly different in colour or brightness to *L. cornic-*

Fig. 1. Can flowers be cryptic? The vegetation shown is typical of temperate semi-natural grassland, in that it contains a diverse array of plants many of which flower at the same time. Flowers of at least ten different species of insect-pollinated plant are visible. Many flowers which commonly occur together have colours which are extremely similar to insect colour vision systems (Kevan 1978, 1983, Chittka et al. 1994, Waser et al. 1996), and to the human eye. In this example there is a predominance of yellow-flowered plants (six species). Flowers of different plant species have different structures and require different handling skills. A great diversity of bumblebees, honeybees, flies and butterflies forage among such flowers for nectar or pollen. Each insect has to make foraging decisions while on the wing as to which flowers to visit. Due to constraints of morphology and experience a particular insect will probably only be able to quickly access just one or two of the available plant species, so that mistakes in flower choice will be costly in terms of time wasted. How apparent is the birds-foot trefoil (*Lotus corniculatus*) (bottom right and elsewhere)? When viewed against a background mosaic of yellow, purple and green, a small yellow flower is cryptic although it is brightly coloured.
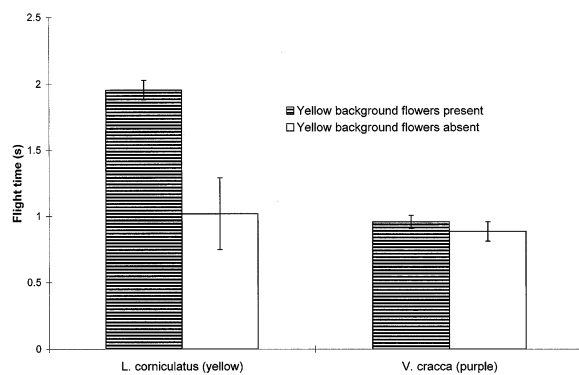
Fig. 2. Flight times (mean (s) $\pm$ SE) of *B. pascuorum* when moving between inflorescences arranged in a regular grid with 1-m spacing, with and without a natural background of yellow flowers. Times are grand means of individual means from each bee, based on five bees per grid and four replicate grids.

ulatus. However, the results suggest that at least some of the species had a similar spectral reflectance since their presence appeared to increase bee foraging time.

Conclusions

The weight of evidence suggests that foragers looking for flowers use search images, i.e. they have a limited ability to process visual information from many floral displays simultaneously, and so selectively attend to particular visual features of their preferred flowers. Of course, this does not rule out the possibility that Darwin's interference hypothesis may also be valid since the two hypotheses are not mutually exclusive (Wilson and Stine 1996). A perceptual mechanism 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.

References

Allen, J. A. 1989. Searching for search image. – Trend Ecol. Evol. 4: 361.

Barth, F. G. 1985. Insects and flowers, the biology of a partnership. – George Allen and Unwin, London.

Blough, D. S. 1979. Effects of the number and form of stimuli on visual search in the pigeon. – J. Exp. Psychol. Anim. Behav. Processes 5: 211–223.

Bond, A. B. 1983. Visual-search and selection of natural stimuli in the pigeon-the attention threshold hypothesis. – J. Exp. Psychol. 9: 292–306.

Bond, A. B. and Riley, D. A. 1991. Searching image in the pigeon: a test of three hypothetical mechanisms. – Ethology 87: 203–224.

Chittka, L., Shmida, A., Troje, N. and Menzel, R. 1994. Ultraviolet as a component of flower reflections, and the colour perception of Hymenoptera. – Vision Res. 34: 1489–1508.

Chittka, L., Gumbert, A. and Kunze, J. 1997. Foraging dynamics of bumblebees: correlates of movements within and between plant species. – Behav. Ecol. 8: 239–249.

Corbetta, M., Miezin, F. M., Dobmeyer, S. et al. 1990. Attentional modulation of neural processing of shape, colour, and velocity in humans. – Science 248: 1556–1559.

Darwin, C. 1876. The effects of cross- and self-fertilization in the animal kingdom. – Murray, London.

De Los Mozos Pascual, M. and Domingo, L. M. 1991. Flower constancy in *Heliotaurus ruficollis* (Fabricius 1781, Coleoptera: Alleculidae). – Elytron (Barc) 5: 9–12.

Dukas, R. 1995. Transfer and interference in bumblebee learning. – Anim. Behav. 49: 1481–1490.

Dukas, R. and Ellner, S. 1993. Information processing and prey detection. – Ecology 74: 1337–1346.

Dukas, R. and Real, L. A. 1993. Learning constraints and floral choice behaviour in bumblebees. – Anim. Behav. 46: 637–644.

Dukas, R. and Waser, N. M. 1994. Categorization of food types enhances foraging performance of bumblebees. – Anim. Behav. 48: 1001–1006.

Endler, J. A. 1981. An overview of the relationships between mimicry and crypsis. – Biol. J. Linn. Soc. 16: 25–31.

Eysenck, M. W. and Keane, M. T. 1990. Cognitive psychology. – Lawrence Erlbaum, London.

Gegear, R. J. and Laverty, T. M. 1995. Effect of flower complexity on relearning flower-handling skills in bumble bees. – Can. J. Zool. 73: 2052–2055.

Goulson, D. 1994. A model to predict the role of flower constancy in inter-specific competition between insect pollinated flowers. – J. Theor. Biol. 168: 309–314.

Goulson, D. and Cory, J. S. 1993. Flower constancy and learning in the foraging behaviour of the green-veined white butterfly, *Pieris napi*. – Ecol. Entomol. 18: 315–320.

Goulson, D. and Jerrim, K. 1997. Maintenance of the species boundary between *Silene dioica* and *S. latifolia* (red and white campion). – Oikos 78: 254–266.

Goulson, D. and Wright, N. P. 1998. Flower constancy in the hoverflies *Episyrphus balteatus* (Degeer) and *Syrphus ribesii* (L.) (Syrphidae). – Behav. Ecol. 9: 213–219.

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

Goulson, D., Stout, J. C. and Hawson, S. A. 1997b. Can flower constancy in nectaring butterflies be explained by Darwin's interference hypothesis? – Oecologia 112: 225–231.

Grant, V. 1950. The flower constancy of bees. – Bot. Rev. 3: 82–97.

Grant, V. 1952. Isolation and hybridization between *Aquilegia formosa* and *A. pubescens*. – Aliso 2: 341–360.

Grant, V. 1992. Floral isolation between ornithophilous and sphingophilous species of *Ipomopsis* and *Aquilegia*. – Proc. Natl. Acad. Sci. USA 89: 11828–11831.

Grant, V. 1994. Modes and origins of mechanical and ethological isolation in angiosperms. – Proc. Natl. Acad. Sci. USA 91: 3–10.

Guilford, T. and Dawkins, M. S. 1987. Search images not proven: a reappraisal of recent evidence. – Anim. Behav. 35: 1838–1845.

Heinrich, B. 1979. "Majoring" and "minoring" by foraging bumblebees, *Bombus vagans*: an experimental analysis. – Ecology 60: 245–255.

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.

Kevan, P. G. 1978. Floral coloration, its colormetric analysis and significance in anthecology. – In: Richards, A. J. (ed.), The pollination of flowers by insects. Academic Press, London, pp. 51–78.

Kevan, P. G. 1983. Floral colours through the insect eye: what they are and what they mean. – In: Jones, C. E. and Little R. J. (eds), Handbook of experimental pollination ecology. Van Nostrand Reinhold, New York.

Klosterhalfen, S., Fischer, W. and Bitterman, M. E. 1978. Modification of attention in honey bees. – Science 201: 1241–1243.

Kunin, W. R. 1993. Sex and the single mustard: population density and pollinator behavior effect on seed-set. – Ecology 74: 2145–2160.

Langley, C. M. 1996. Search images: selective attention to specific visual features of prey. – J. Exp. Psychol. 22: 152–163.

Laverty, T. M. 1980. Bumble bee foraging: floral complexity and learning. – Can. J. Zool. 58: 1324–1335.

Laverty, T. M. 1994a. Costs to foraging bumblebees of switching plant species. – Can. J. Zool. 72: 43–47.

Laverty, T. M. 1994b. Bumblebee learning and flower morphology. – Anim. Behav. 47: 531–545.

Laverty, T. M. and Plowright, R. C. 1988. Flower handling by bumblebees-a comparison of specialists and generalists. – Anim. Behav. 36: 733–740.

Lawrence, E. S. and Allen, J. A. 1983. On the term 'search image'. – Oikos 40: 313–314.

Levin, D. A. 1978. Pollinator behaviour and the breeding structure of plant populations. – In: Richards, A. J. (ed.), The pollination of flowers by insects. Academic Press, London, pp. 133–150.

Lewis, A. C. 1986. Memory constraints and flower choice in *Pieris rapae*. – Science 232: 863–865.

Lewis, A. C. 1989. Flower visit consistency in *Pieris rapae*, the cabbage butterfly. – J. Anim. Ecol. 58: 1–13.

Plateau, F. 1901. Observations sur le phénomène de la constance chez quelques hyménoptères. – Ann. Soc. Entomol. Belg. 45: 56–83.

Posner, M. I. and Peterson, S. E. 1990. The attention system of the human brain. – Ann. Rev. Neurosci. 13: 25–42.

Reid, P. J. and Shettleworth, S. J. 1992. Detection of cryptic prey: search image or search rate? – J. Exp. Psychol. 18: 273–286.

Tinbergen, L. 1960. The natural control of insects in pine woods. 1. Factors influencing the intensity of predation by songbirds. – Arch. Neerl. Zool. 13: 265–343.

Waser, N. M. 1986. Flower constancy: definition, cause and measurement. – Am. Nat. 127: 593–603.

Waser, N. M., Chittka, L., Price, M. V. et al. 1996. Generalization in pollination systems, and why it matters. – Ecology 77: 1043–1060.

Wilson, P. and Stine, M. 1996. Floral constancy in bumble bees-handling efficiency or perceptual conditioning. – Oecologia 106: 493–499.

Woodward, G. L. and Laverty, T. M. 1992. Recall of flower handling skills by bumblebees: a test of Darwin's interference hypothesis. – Anim. Behav. 44: 1045–1051.