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Can flower constancy in nectaring butterflies be explained by Darwin's interference hypothesis?

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Abstract When foraging for nectar many insects exhibit flower constancy (a preference for flower species which they have previously visited) and frequently ignore rewarding flowers of other species. Darwin proposed the favoured explanation for this behaviour, hypothesizing that learning of handling skills for one flower species interferes with the ability to recall handling skills for previously learned species. A crucial element of this hypothesis is that savings in handling time resulting from constancy must exceed increases in travelling time necessitated by ignoring other suitable species. A convincing quantification of this trade-off has not been achieved and tests to date on bumblebees indicate that savings in handling time are too small to offset an increase in travelling time. To assess further the validity of Darwin's hypothesis, handling and flight times of the butterfly, *Thymelicus flavus,* were measured under natural conditions, and the abundance and reward provided by the available flower species quantified to enable estimation of foraging efficiency. Butterflies exhibited a mean increase in handling time of 0.85 s per flower associated with switching between flower species, although the magnitude of this difference varied greatly among flower species. Switching was not associated with a decrease in travelling time, contrary to expectation. Switching was more frequent following a lower than average reward from the last flower visited. In butterflies, flights serve functions other than movement between nectar sources, such as mate location (unlike worker bees). Hence constancy may be a viable strategy to reduce time spent in handling flowers and increase time available for other activities. Although savings in handling time may be small, Darwin's interference hypothesis remains a valid explanation for flower constancy in foraging butterflies.

Key words Foraging efficiency · Majoring · Butterfly · Reward · Learning

Introduction

Honeybees are proverbially industrious yet appear to be inefficient. The phenomenon of flower constancy (exhibited by honeybees, bumblebees and butterflies) seems to represent a sub-optimal pattern of foraging that attracted the interest of Aristotle (Grant 1950) and Darwin (1876), and continues to provoke empirical and theoretical studies (Lewis 1986, 1989; Possingham et al. 1990; Real et al. 1990; Woodward and Lavert 1992; Goulson and Cory 1993; Goulson 1994; Laverty 1994a,b; Goulson et al. 1997). Individual insects learn to associate a particular colour, shape or scent with reward and visit a particular flower species more frequently than would be expected by chance. In doing so they are presumed to incur a penalty of increased travelling time in comparison to a generalist strategy of visiting all suitable flowers, and may also ignore more rewarding alternative "prey" types (Wells and Wells 1983, 1986).

Several explanations for flower constancy have been proposed (Darwin 1876; Proctor and Yeo 1976; Real 1981; Barth 1985; Waser 1986; Dukas and Real 1993a), but the consensus at present is that constancy is a result of restricted knowledge and learning constraints. Insects may be flower-constant because they do not have information on rewards available from alternative sources (Wells and Wells 1986). Also, foragers may be constrained by their ability to learn, retain and retrieve motor skills for handling several prey types (flower species) (Hughes 1979). Learning to extract nectar or pollen 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 (e.g. Laverty and Plowright 1988; Lewis 1986, 1993). 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

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species of flower differing in floral morphology (interference effects) (Heinrich et al. 1977; Stanton 1984; Gould 1985; Lewis 1986; Woodward and Laverty 1992). Hence after the initial learning process a flower-constant forager maintains a low handling time, while a labile forager may incur a penalty of an increased handling time following switches between flower species. This is essentially an amplification of the hypothesis first proposed by Darwin (1876) (Waser 1983).

Despite the proliferation of literature discussing the causes of flower constancy few tests have been attempted, and there is little empirical evidence to support Darwin's explanation for flower constancy. Tests to date (on bumblebees) found that increases in handling time following switching were too small to compensate for savings in travelling time (Woodward and Laverty 1992; Laverty 1994a; Gegear and Laverty 1995). Woodward and Laverty (1992) found small interference effects (0.8–2.0 s) when caged bees were forced to switch between two flower species. Laverty (1994a) found no interference effects when bees foraged naturally among four plant species with simple flower structure, and small effects when switching between two complex flower species ($\cong$ 1 s). Similarly, Gegear and Laverty (1995) found that interference effects were linked to morphological complexity: there were no interference effects following learning of a second flower species with simple morphology, but an increase in handling time of 2.2 s resulted from learning to handle a complex flower. Also, experience with other species of broadly similar flower morphology may actually increase learning rates (Laverty 1994b).

We attempt to test Darwin's interference hypothesis in the small skipper butterfly, *Thymelicus flavus* (Lepidoptera: Hesperiidae). *T. flavus* exhibit a significant "history effect" (*sensu* Lewis 1989), in that they are more likely to visit flowers of the same species as that last visited, after taking into account spatial effects (i.e. they exhibit a degree of constancy) (Goulson et al. 1997). However, switching between flower species is common (Goulson et al. 1997). We test whether butterflies do incur a penalty of increased handling time when switching between species under natural conditions. Secondly, we test whether flight times are shorter when butterflies switch between flower species. By quantifying time budgets and nectar rewards we estimate the relative efficiencies of constancy to particular flower species and switching. Lastly, we examine factors triggering switching behaviour.

Materials and methods

Field-work was carried out in July and August 1996 at Yew Hill Nature Reserve (near Compton, south of Winchester, Hampshire, NGR 455265) in southern England. Yew Hill is a flower-rich grassland on chalk soils with a north-easterly aspect, and supports a large population of *T. flavus*.

Flower species and nectar reward

Including casual observations, we noted *T. flavus* visiting flowers of nine plant species (although some of them were visited very rarely): *Vicia cracca, Lathyrus pratensis, Trifolium pratense* (Fabaceae), *Achillea millefolium* (Compositae), *Centaurea scabiosa, Leontodon autumnalis* (Asteraceae), *Knautia arvensis* (Dipsacaceae), *Rhinanthus minor* (Scrophulariaceae) and *Anacamptis pyramidalis* (Orchidaceae). We estimated the abundance of flowers of these nine species using a 182-m transect across the study site taken on 25 July, recording all fully open (but not senescent) inflorescences within 1 m either side of the transect. The transect was chosed to lie across the centre of the area used for behavioural observations.

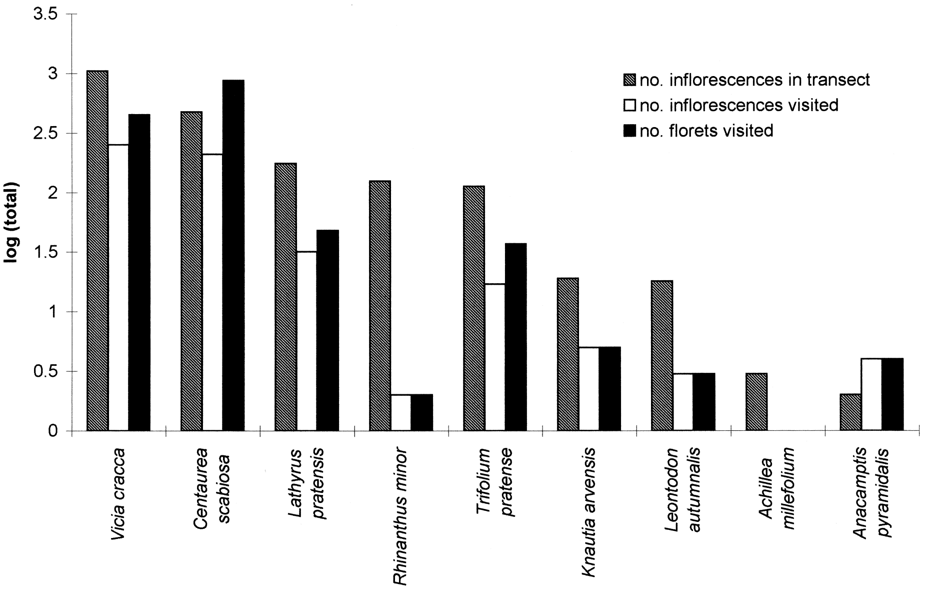
T. flavus primarily visited flowers of four species of plant: *C. scabiosa*, *Lathyrus pratensis*, *Trifolium pratense* and *V. cracca*. Flowers of the three legume species are all similar in structure, although they differ markedly in colour (to the human eye) and the number of open flowers per inflorescence. *T. pratense* frequently has >20 red flowers per inflorescence, *V. cracca* 4–8 purple flowers and *L. pratensis* 1–5 yellow flowers. *C. scabiosa* is a typical composite with many small purple flowers. We measured corolla depths for 30 flowers of each of these four most frequently visited plant species. The volume of nectar was also recorded for these plant species to ascertain any differences in nectar availability. We measured the volume of nectar available both in flowers which had been covered by a paper bag for at least 90 min, and in flowers which had not been covered. We removed nectar from five flowers on each of ten inflorescences from different plants for each of the four species, both covered and uncovered. Samples were taken on two consecutive days (22–23 July) between 10 a.m. and 3 p.m., during which time the weather was approximately uniform and sunny and *T. flavus* and other insects were active. Nectar was extracted using a drawn-out glass microcapillary tube, and the drop of nectar blotted onto filter paper (Whatman Type 1 Qualitative). A calibration curve was constructed using known volumes of sucrose solution pipetted onto filter paper. The resulting linear regression line fitted through the origin (area=2675.1×volume, r^2=0.98) was then used to convert the diameter of each circle on the filter paper into a volume.

During the same period we measured nectar concentrations using a refractometer (Bellingham and Stanley Ltd., London, UK) powered by a portable generator. To obtain sufficient volumes ten inflorescences on different plants of each species were covered with fine netting for 4 h before extracting nectar as above. Nectar from ten flowers from each inflorescence was combined to provide sufficient volumes for accurate measurement of concentration.

Butterfly foraging behaviour

To quantify flight and handling times we recorded the sequence of visits of individual *T. flavus* foraging under natural conditions among flowers onto a dictaphone, and subsequently transcribed timings from the audio tapes using the behavioural analysis software package *Observer* (Noldus Information Technology, Wageningen, The Netherlands). All recordings were made between 10 a.m. and 3 p.m. Flight times between flowers and handling time on each flower were recorded. *T. flavus* is unusual in its tolerance of very close observation while foraging, so that the time taken from landing to location of the nectaries could be observed (during which the proboscis is maneuvered into position) henceforth called probing time. Once the nectary was located the proboscis became still or pulsed rhythmically as the butterfly imbibed nectar (henceforth called feeding time). We followed each butterfly until it was lost from sight, engaged in a swirl with a conspecific or ceased to visit flowers. In total 121 individuals were followed while visiting 1408 flowers (the range of flowers visited per butterfly was 3–36). None of the butterflies oviposited during observation.

Fig. 1 Numbers of inflorescences of each of the ten plant species visited by *Thymelicus flavus* in an 182 m×2 m transect across the study site, and the total numbers of individual flowers and inflorescences actually visited by 121 foraging *T. flavus*



Analysis

Probing, feeding and flying times were analysed using ANOVA to partition differences between plant species and according to whether the butterfly arrived from a different flower species or the same species. Mean times were used per each individual for each of the flower species visited. Probing times did not approximate to a normal distribution, and so a Box-Cox procedure was used to estimate the appropriate transformation ($Y'=Y^{0.175}$) (Sokal and Rohlf 1981). Similarly feeding times and flying times were log-transformed to achieve approximation to normality. Flights were excluded from the analysis when the butterfly returned to the same inflorescence. Plant species and previous experience (same flower, different flower or unknown) were initially included as factors, and all two-way interactions, with sequential removal of factors which did not contribute significantly to the model.

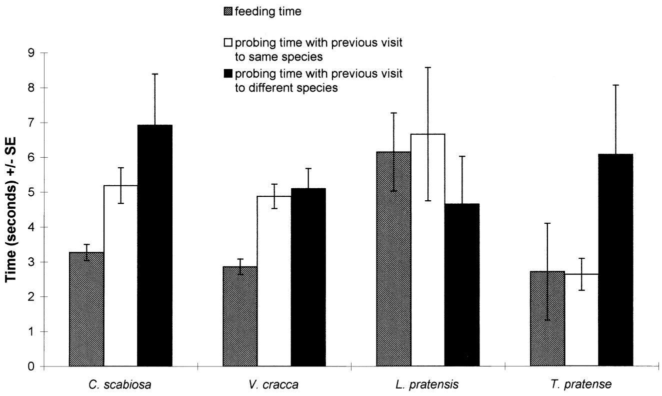


Fig. 2 Feeding and probing times (mean±SE) of 121 *T. flavus* visiting flowers of four species. Probing times are separated according to whether the flower that the butterfly previously fed upon was of the same or of a different species. Sample sizes for feeding time, probing time (previous visit to same species) and probing time (previous visit to different species) were 869, 790 and 26 for *Centaurea scabiosa*, 453, 376 and 28 for *Vicia cracca*, 49, 30 and 10 for *Lathyrus pratensis* and 37, 26 and 9 for *Trifolium pratense*, respectively

Results

The abundance of the nine species of flower seen to be visited by *T. flavus* matches approximately with the number of inflorescences of each which were actually visited by the 121 foraging butterflies (linear regression: $r^2=0.89$, $F_{1,7}=54.9$, $P<0.001$) (Fig. 1). Since visits were scarce to all but four flower species (*C. scabiosa*, *V. cracca*, *L. pratensis* and *Trifolium pratense*) analysis of time budgets during foraging was confined to these species. Overall, differences in probing time for each flower species were not significant ($F_{3,306}=1.17$, n.s.), with means of 5.3, 4.6, 6.2 and 2.8 s for *C. scabiosa*, *V. cracca*, *L. pratensis* and *T. pratense* (Fig. 2). There is no obvious relationship between probing time and corolla depth (5.1±0.13, 7.3±0.09, 9.0±0.22 and 10.5±0.14, mm±SE for *C. scabiosa*, *V. cracca*, *L. pratensis* and *T. pratense*, respectively). Notably, *T. pratense* has the deepest flowers yet the shortest mean probing time.

Overall there was no significant difference in probing time following a switch in plant species visited compared to butterflies which had previously visited the same flower species (means 5.10 and 5.76 s, $F_{2,306}=0.35$, n.s.) (Fig. 2). However, although probing time did not differ significantly according to either plant species or switching/constancy in isolation, there was a significant interaction between the two ($F_{6,\ 306}=2.72$, $P=0.014$) (Fig. 2). Probing times differed markedly according to previous experience in only one flower species, *T. pratense*, (means 6.07 and 2.63 s, respectively). For *L. pratensis* the mean probing time is actually higher following a recent visit to the same species (Fig. 2). There is no obvious relationship between morphological complexity and the effects of experience on handling time (for example, the probing times for the three legumes exhibit quite different patterns).

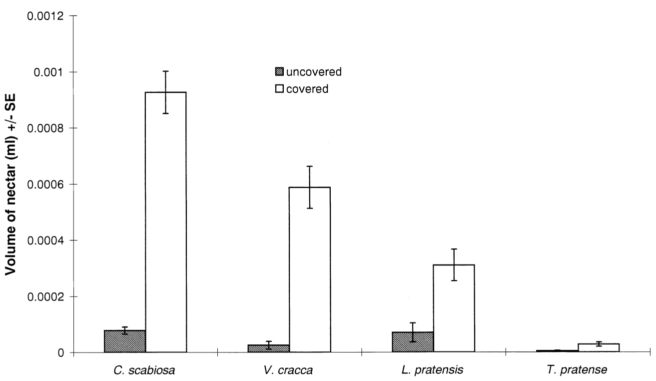


Fig. 3 Nectar volumes (±SE) in flowers of the four plant species most commonly visited by *T. flavus*. Flowers were either uncovered, and thus exposed to depletion of nectar levels by visiting insects, or covered in paper bags for 90 min to exclude insects. For each species five flowers were sampled from ten inflorescences on separate plants

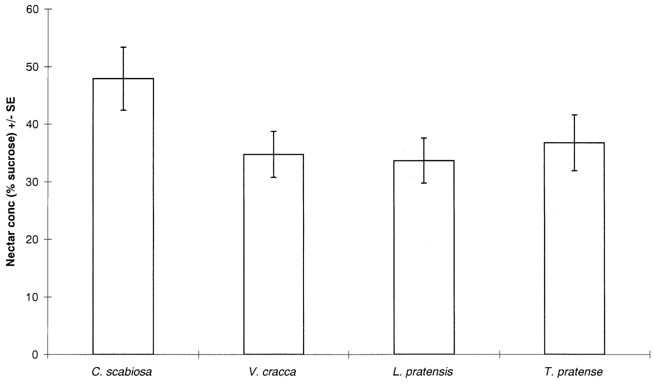


Fig. 4 Nectar concentrations (±SE) in flowers of the four plant species most commonly visited by *T. flavus*. Nectar was pooled from ten inflorescences, and five samples taken per species. Refractometer readings were calibrated against known concentrations of sucrose solution

As might be expected, feeding time was not affected by switching/constancy ($F_{2,224}$=1.81, n.s.), but differed between plant species ($F_{3,224}$=4.31, P=0.006). The primary cause of this difference is the greater feeding time on *L. pratensis* compared to other species (Fig. 2). Contrary to expectation, there is little apparent relationship between mean feeding time and the mean levels of nectar available in the four species, although *T. pratense* has both the lowest nectar volume in uncovered flowers and the shortest feeding time (Fig. 3). The nectar volume present differed significantly among species when both uncovered and covered (Kruskal-Wallis test, χ^2_3=45.1, P<0.001, and χ^2_3=155.4, P<0.001, respectively). However, nectar volumes when covered versus uncovered were not closely linked: in particular, *L. pratensis* contained approximately 3 times more nectar than *V. cracca* under natural conditions, but when insects were excluded *L. pratensis* accumulated about half of the nectar volume found in *V. cracca* (Fig. 3). *C. scabiosa* produced the highest volume of nectar under both conditions, and also the highest concentration of nectar, although differences between species in nectar concentration were not statistically significant (Kruskal-Wallis test, χ^2_3=4.16, P=0.24) (Fig. 4).

Feeding times have been shown to be indicative of the volume of reward obtained (Harder 1986, Kato 1988). Thus we can examine whether butterflies were more likely to switch species following a lower than average reward (as indicated by a feeding time below the average for each flower species). Of 405 flights between inflorescences, 348 were between the same flower species and 57 involved a switch (14%). Switching was less common following an above-average reward; switching occurred in 9 out of 117 flights (7.7%) compared to 48 out of 288 flights (16.7%) when the last reward received was low (χ^2_1=4.8, P<0.05).

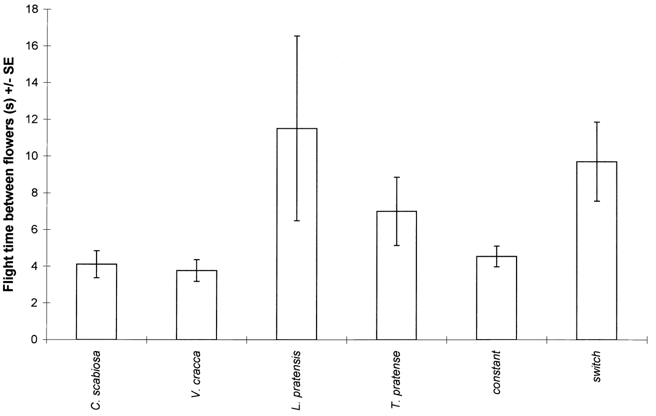


Fig. 5 Flight times of foraging butterflies. The *first four columns* indicate flight times of butterflies which visited the same flower species successively (they were flower-constant). The mean for all four plant species (*column 5*) does not differ significantly from that for flight times when switching between flower species (*column 6*). Based on 418 flights by 121 butterflies

The mean flight time between inflorescences for foraging butterflies was 5.70 s (±0.68 SE). When insects visited successive flowers of the same species, the flight time between flowers differed significantly according to the plant species visited ($F_{3,115}$=4.24, P=0.007). This difference is primarily attributable to the greater flight time when foraging among *L. pratensis* compared to the other species (Fig. 5). Overall there was no difference in the flight time when butterflies were constant compared to when they switched between flower species ($F_{1,115}$=2.69, P=0.104), although on average insects flew for longer when switching between flower species (Fig. 5). There was no relationship between feeding time and subsequent flight time ($F_{1,309}$=0.017, n.s.).

Expected rewards for strategies of constancy to each of the four plant species can be calculated from the mean reward per inflorescence (nectar concentration×volume×no. flowers visited) divided by the total of mean observed flight, probing and feeding times (Table 1). This calculation assumes that the nectar reward in randomly selected inflorescences is representative of those

Table 1 Calculation of expected rewards per time for constancy to each of four flower species versus switching between species. Expected reward from a strategy of switching assumes that inflorescences are visited in proportion to their abundance, and uses observed flight times

	Centaurea scabiosa	*Vicia cracca*	*Lathyrus pratensis*	*Trifolium pratense*	Switching
a) Observed flying time	4.10	3.77	11.5	7.00	9.72
b) Handling time per flower (probing+feeding)	8.46	7.74	12.8	5.34	9.08
c) Mean no. Flowers visited per inflorescence	4.16	1.78	1.50	2.18	2.41
d) Handling time per inflorescence ($b\times c$)	35.2	13.8	19.2	11.6	21.9
e) Reward per flower (µg sucrose)	3.73	0.86	2.37	0.16	1.72
f) Reward per inflorescence (µg sucrose) ($c\times e$)	15.5	1.54	3.55	0.35	5.34
Reward per time (µg s^{-1}) ($f/(a+d)$)	**0.39**	**0.09**	**0.12**	**0.02**	**0.17**

actually visited; there is evidence that bees may be able to detect and avoid inflorescences which contain little reward (Corbet et al. 1984; Wetherwax 1986; Kato 1988; Duffield et al. 1993; Guirfa 1993). The calculation does not take into account differences in energetic costs of different foraging strategies which may relate to the proportion of time spent in flight. The expected reward for *C. scabiosa* is markedly higher than for the other species, with *T. pratense* the least efficient choice. The expected reward from a strategy of switching can similarly be approximated by using the mean reward per flower weighted according to frequency of each flower species (i.e. assuming that the butterfly visits flowers as it encounters them), and using actual mean flight time for butterflies switching between flower species. Visiting each of the four flower species as they are encountered results in a lower reward per time than constancy to *C. scabiosa*, but a higher reward than constancy to the other three flower species despite the small increase in probing time.

Discussion

Differences in the proportions of inflorescences of plant species visited by *Thymelicus flavus* can be attributed largely to differences in abundance, with common species visited more than scarce species. Despite the great differences in mean nectar volume between flower species, no clear preferences for the more rewarding species are apparent in terms of overall visitation.

We demonstrate that, for butterflies foraging under natural conditions, recent experience of a particular flower species may reduce the time required to locate the nectaries on subsequent visits (although this difference was marked only for *Trifolium pratense*). It is worth noting that for one plant species (*L. pratensis*) there was actually a non-significant decrease in handling time following switching. The overall decrease in handling time with experience is in accordance with Darwin's interference hypothesis (Darwin 1876), and with laboratory studies of butterfly behaviour (Lewis 1986). It is also in agreement with studies of bumblebee foraging under caged and field conditions (Woodward and Laverty 1992; Laverty 1994a), both in that there is a saving in handling time associated with constancy, and that this saving is small. The mean increase in handling time found here (0.85 s) is similar to that found for caged bumblebees switching between two plant species (0.8–2.0 s) (Woodward and Laverty 1992) and for bumblebees foraging naturally among four plant species (≅1 s) (Laverty 1994a). The increase in handling time is considerably less than that found for the butterfly, *Pieris rapae* (7 s) (Lewis 1986), but in the latter study effects of switching were quantified after long periods of enforced constancy under laboratory conditions.

Laverty (1994a) argues that the small saving in handling time he observed is insufficient to account for constancy, since Darwin's hypothesis depends upon the avoidance of interference effects resulting in a time saving in excess of the increased travelling time required by constancy (compared to visiting all available flowers). Our estimates of reward per time indicate that constancy to *C. scabiosa* is the most profitable strategy, with switching more profitable than constancy to the other three species. Contrary to naive expectation the observed flight time for movements between different flower species (9.72 s) is greater than the mean flight times for constancy to three of the four plant species. Switching is not associated with a saving in travelling time. This finding is in accordance with previous studies of *Thymelicus flavus* which suggest that switching is associated with longer flights (Goulson et al. 1997). In bees, constancy to an artificial flower has been found to decline with increasing flight time between visits (Greggers and Menzel 1993), while a low reward may actually trigger longer flights (Dukas and Real 1993b). We may expect switching to occur when an individual finds itself in an area in which the preferred food source is absent or scarce. Alternatively switching may be triggered by a low or zero reward in recently visited flowers. Using the feeding time per flower as an indication of reward received, we found evidence for the former. Switching occurred more frequently following a lower than average feeding time. In bees, low rewards from individual flowers are known to promote movement among inflorescences of the same flower species (Cresswell 1990; Kadmon and Shmida 1992) and have been found to promote switching between different coloured artificial feeders in laboratory studies (Greggers and Menzel 1993). To our knowledge ours are the first field data suggesting switching among flower species as a result of receiving a low reward.

In *T. flavus* the flowers encountered during flights ending in a switch tended to include low frequencies of the flower species previously visited (Goulson et al. 1997). Hence it seems probable that both low rewards per flower and a low abundance of the prefered flower may trigger switching behaviour, foraging decisions which clearly make economic sense.

An ideal test of Darwin's interference hypothesis would compare strictly constant individuals with butterflies which exhibited no constancy. Instead, we suggest that the butterflies are facultatively constant, moving between flowers of the same species when that species is abundant and rewarding, but switching if they cannot find it. By exploiting the patchy nature of flower distributions and foraging largely within clumps of each plant species nectarivores can keep both flight and handling times to a minimum.

Previous studies suggest that, in butterflies, flights between flowers are longer than those made by bees and are often longer than is necessary simply to find another flower (Schmitt 1980; Waser 1982; Goulson et al. 1997). A probable explanation for this is that, in butterflies, flights may serve several purposes including mate location, territory defence and larval foodplant location (activities not carried out by bees) (Waser 1982; Goulson et al. 1997). If this is so then Darwin's interference hypothesis does not require savings in handling time to exceed increases in travelling time. Savings in handling time may allow more time for these other activities, so that any saving is advantageous.

A definitive test of Darwin's interference hypothesis remains elusive. If butterflies are not constrained by travelling time (since this may serve other functions) then constancy may be a mechanism for minimising time spent on flowers. However it remains to be demonstrated that Darwin's hypothesis provides a valid explanation for flower constancy in worker bees which are largely freed from activities other than foraging.

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