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Foraging strategies in the small skipper butterfly, *Thymelicus flavus*: when to switch?

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Abstract. Many insects foraging for nectar or pollen exhibit flower constancy, a learned fidelity to a particular species of plant that previously provided a reward. Constancy may persist even when alternative flowers are available that provide a greater or less variable reward. This strategy entails more travelling time than one of generalization (visiting all suitable flowers as they are encountered). The consensus at present is that this increase in travelling time is offset by decreases in handling time; switching between flower species incurs a cost in time spent learning to 'handle' the new flower species that is avoided by remaining constant. If this is so, then the optimal strategy should depend upon the density of flower species (and thus the travelling time), with switching occurring below a threshold density of the target flower species. This prediction is tested using the butterfly, *Thymelicus flavus*, by analysing foraging patterns under natural conditions. This species exhibited constancy: of 465 visits to flowers 85% were to the same species as last visited. As predicted switches between flower species occurred in response to low encounter rates of the flower species on which the individual had previously fed. However, butterflies ignored the vast majority of suitable flowers that they encountered, even when they were of the species to which they were constant. This casts doubt on explanations for flower constancy as an adaptive strategy that minimizes handling time and maximizes resource acquisition per unit time within learning constraints.

The phenomenon of flower constancy, well documented in honey bees, *Apis mellifera*, seems to represent a sub-optimal pattern of foraging which remains to be explained convincingly (Woodward & Laverty 1992). Honey bees exhibit rapid sensory learning, and can use scent, colour, shape or a combination of all three to identify flower species that previously provided a reward (Koltermann 1969; Menzel & Erber 1978). This learning process takes just three to five consecutive rewards, and can persist for at least 2 weeks (Menzel 1967). Bees can even distinguish between flowers of different ages according to reward (Giurfa & Núñez 1992). When foraging for nectar or pollen, individual honey bees generally exhibit a high degree of flower constancy, fidelity to one particular flower species that has previously provided a reward (93–98% of all visits in a single foraging bout, Grant 1950; Free 1963). Simultaneously other honey bees foraging in the same environment may exhibit constancy to different flower species. Other insect species behave in a similar way, including bumblebees and butterflies (Heinrich 1976; Lewis 1989; Goulson & Cory 1993). By adopting this strategy the insects are bypassing rewarding flowers. If they were not flower constant but visited with equal preference all flower species that provided a reward then they could reduce travelling time. This apparent inefficiency is even more striking when, in two-choice experiments, some bees remain constant to an artificial flower morph which provides a consistently lower reward than the alternative (Wells & Wells 1983, 1986; Wells et al. 1992).

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Several explanations for flower constancy have been proposed (Darwin 1876; Real 1981; Waser 1986), but the one that has been most widely discussed and generally accepted is that flower constancy is a result of restricted knowledge and learning constraints. First, insects that are flower constant are not able to make optimal foraging decisions because they have no experience of rewards available from alternative sources (Wells & Wells 1986). Second, insects may be constrained by their ability to learn, retain and retrieve motor skills for handling more than one flower species. Learning to extract nectar or pollen from within the structure of a flower takes a number of visits to that flower species, so that handling time declines on successive visits (e.g. Laverty & Plowright 1988; Lewis 1993). Knowledge of how to handle one flower species can be lost simply because it is replaced by information about handling a different species, or retrieval of memories may be hampered by switching between species of flower (interference effects; Heinrich et al. 1977; Stanton 1984; Gould 1985; Lewis 1986; Woodward & Laverty 1992). Hence after the initial learning process a flower-constant forager maintains a low handling time, while a labile forager incurs the penalty of an increased handling time following every switch between flower species. However, direct measurement of increases in handling time following a switch suggest that the time penalties incurred by a modest frequency of switching may be too small to account for constancy (Woodward & Laverty 1992; Laverty 1994a). Also, experience with other species of broadly similar flower morphology may actually increase learning rates (Laverty 1994b).

If constancy is the result of this trade-off between handling and travelling time, then the strategy adopted may depend on flower density. Insects should abandon constancy when the preferred flower species falls below a threshold density beyond which the increased travelling time associated with constancy exceeds the saving in handling time (compared with a strategy of generalization). Thus we predict that switching between flowers should occur as a response to a low frequency of encounters with the previously preferred flower species. We test this hypothesis by analysing foraging patterns of the butterfly *Thymelicus flavus* (Brünnich) (Lepidoptera: Hesperiidae) under natural conditions, and in particular by examining whether encounter frequencies of floral types explain the relatively rare switching events.

METHODS

Our experimental methods followed a technique developed by Lewis (1989) from earlier studies on oviposition behaviour in butterflies (e.g. Mackay 1985) and are described here in brief. We observed butterfly behaviour in a rough meadow in east Oxford (U.K.) between 16 July and 5 August 1994 and 18 and 21 July 1995. Ten plant species were visited by *T. flavus*: *Lotus corniculatus, Ononis spinosa, Trifolium pratense, T. repens* (Fabaceae), *Centaurea nigra*, *C. scabiosa*, *Cirsium acaulon*, *C. arvense*, *Leontodon autumnalis* (Asteraceae) and *Rubus fruticosus agg*. (Rosaceae). We followed butterflies while they foraged, maintaining a distance of at least 2 m to avoid disturbance, and marked their path using bamboo canes. We stopped recording when we lost the butterfly or when the butterfly engaged in a swirl with a conspecific. Flowers that fell within 20 cm either side of the path were considered to have been encountered (i.e. detected) by the butterfly (irrespective of their height), and were recorded in sequence (by J.O. to maintain consistency). Recording flowers within an absolute distance of the butterfly (in any plane) would be preferable, but the three-dimensional path cannot easily be recorded. We recorded 56 foraging runs (27 in 1994 and 29 in 1995), composed of 465 visits to flowers and 6004 flowers encountered (Fig. 1). Visits were scored only if we saw the butterfly probe the flower; rarely butterflies would perch on a flower but not attempt to feed, and these events were scored as encounters. No butterflies oviposited while being followed, a behaviour that alters foraging behaviour in *Pieris rapae* (Lewis 1989). We were unable to record the sex of many of the individuals without disrupting natural behaviour, but Lewis (1989) found no difference in the foraging behaviour of male and non-ovipositing female butterflies.

The probability of a butterfly visiting a particular flower that it encountered was estimated using GLIM (McCullagh & Nelder 1989) with binomial errors, with respect to the flower species encountered, and whether this was the same species as that last visited by the insect. The error structure was substantiated during analysis. We used means

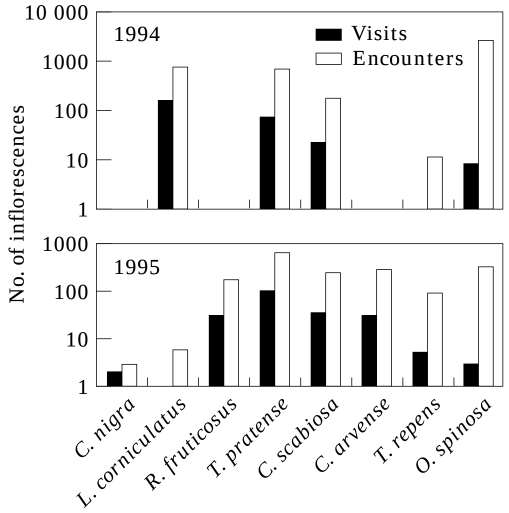

Figure 1. Numbers of flowers encountered, and of those encountered the number that were then visited (fed upon), for each of the eight plant species used by *T. flavus* as a nectar source. *L. autumnalis* and *C. acaulon* are excluded since only one visit was recorded to each.

for each individual butterfly–flower species combination to avoid pseudoreplication. For example the observed probability of butterfly A (Table I) visiting *T. pratense* when the last flower it had visited was *T. pratense* was 2/24, while the probability of it visiting *L. corniculatus* when the last flower visited was not *L. corniculatus* was 0/48. There were no differences found according to year ($F_{1,205}$=3.14), so data were pooled for 1994 and 1995.

To assess which factors may trigger a switch in flower species visited we then examined whether the number of flowers encountered between visits, and the frequency of either the species switched from or the species switched to, affected the likelihood of switching. The foraging bout of each insect was broken down into sequences of flowers encountered (flown over) punctuated by visits to flowers. Each sequence could terminate in a visit to the same flower as that last visited (constancy), or a switch to a different species. For each sequence we calculated the total number of flowers encountered, and the proportion of these flowers that were the same as that previously visited. For sequences ending in a switch we also assessed the proportion of the flowers switched to of those encountered. We then calculated means for each insect, for further analysis. An arcsine transformation of proportions was necessary to give an approximation to normality.

RESULTS

Table I gives sample sequences of flowers encountered and visited by foraging butterflies, one exhibiting constancy and one that switches between flower species. During each flight a butterfly encounters a sequence of flowers each of which it may choose to visit, at which point the flight ends. Flower preferences can be described by the probability of a butterfly visiting each flower as it is encountered (Fig. 2). This probability differed according to flower species ($F_{9,205}$=12.4, P<0.001); for example 21% of the 752 *L. corniculatus* flowers that were encountered were visited compared with only 0.3% of the 2937 flowers of *O. spinosa*. The probability of a visit to a flower when encountered was also determined in part by whether the flower was of the same species as that previously visited (versus a different species; $F_{1,205}$=48.9, P<0.001), termed a history effect (Lewis 1989). There was also a significant

Table I. Sample foraging sequences of flowers encountered for two butterflies, with flowers visited shown in bold

Butterfly	Sequence
A	**Tp** Lc Lc Lc Lc Lc Lc Lc Lc Tp Tp Cs Cs Cs Cs Tp Cs Cs Cs Tp Tp Lc Lc Lc Lc Lc Lc Lc Lc Lc Lc Lc Lc Lc Tp Lc Lc Lc Lc Lc Lc Lc Lc **Tp** Tp Tp Tp Tp Tp Lc Lc Lc Lc Lc Lc Lc Lc Tp Lc Lc Lc Lc Lc Tp Tp Tp Tp Tp Tp Cs Cs Cs Cs Cs Cs Cs Tp Tp Cs Cs Cs Cs Cs Cs Cs Lc Cs Cs Cs Lc Lc Lc Lc Lc Tp Tp **Tp**
B	**Tp** Tp Tp Lc Tp Tp Tp Lc Lc Lc Lc **Tp** Tp Tp Tp Tp Tp Tp Lc Lc Lc Lc Tp Lc Lc Lc Lc Lc Lc Lc Lc Lc Lc Lc Lc Lc Lc Lc Lc Lc Lc Cs Cs Cs Ca Ca Lc Lc Lc **Lc**

Tp=*T. pratense*, Lc=*L. corniculatus*, Cs=*C. scabiosa*, Ca=*C. acaulon*.

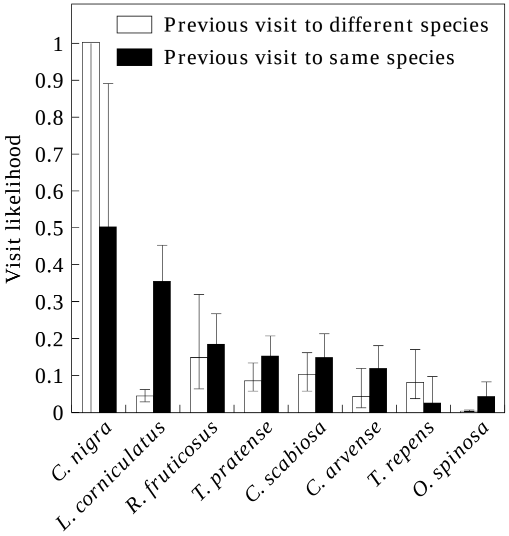

Figure 2. Visit likelihoods (probabilities ± SE) following an encounter for each of the eight flower species commonly visited by *T. flavus*. *L. autumnalis* and *C. acaulon* are excluded since only one visit was recorded to each.

flower species × history effect interaction ($F_{9,205}=3.14$, $P<0.01$). Clearly if flower distributions are clumped then a butterfly is most likely to encounter and therefore to visit the same species as that which it visited last, but this would not result in a 'history effect'. A history effect will occur only if the insect visits a higher (or lower) proportion of flowers of the species it last fed on, than of flowers of a different species. For six out of eight flower species the probability of an insect visiting them was higher if the insect had previously fed on the same species (Fig. 2). For the remaining two species (*T. repens* and *C. nigra*) a visit was less likely when the insect had previously fed upon them, but in both cases the sample size was small (Fig. 1). Overall, the proportion of flowers visited of those encountered was low (7.7%). Even when considering only the flowers encountered that were of the same species as that last visited (i.e. allowing for flower constancy), the proportion that were visited rises to just 17.6%.

Switching between flower species occurred following a low frequency of encounters with the species previously visited, when comparing flights ending in a switch with those when the butterfly remained constant (Fig. 3; mean proportion of flower species previously visited of those encountered in flight ± SE: 0.29 ± 0.06 and 0.57 ± 0.05, respectively, $F_{1,78}=13.2$, $P<0.01$). The flower species switched to comprised a lower proportion of flowers encountered than that of flowers to which a butterfly remained constant ($\bar{X}$ ± SE: 0.25 ± 0.07 and 0.57 ± 0.047, respectively; $F_{1,78}=14.7$, $P<0.01$). A comparison of the frequency distribution of the number of flowers encountered between visits according to whether the flight ended in constancy or switching reveals significant differences ($\chi^2_{11}=42.0$, $P<0.01$), with constant flights more heavily skewed towards a small number of encounters (generally short flights; Fig. 4). The mean number of flowers encountered for flights that terminated in a switch ± SE was 30.0 ± 5.9 compared with 24.0 ± 3.8 for flights ending in constancy. Flights with many encounters typically included many encounters with flowers that were neither of the species visited previously nor of the species that was visited next (Fig. 5). The large number of flights in which fewer than 10 flowers were encountered before one was visited, and that ended in constancy, probably represent short flights within a flower clump dominated by one flower species (Figs 4 and 5).

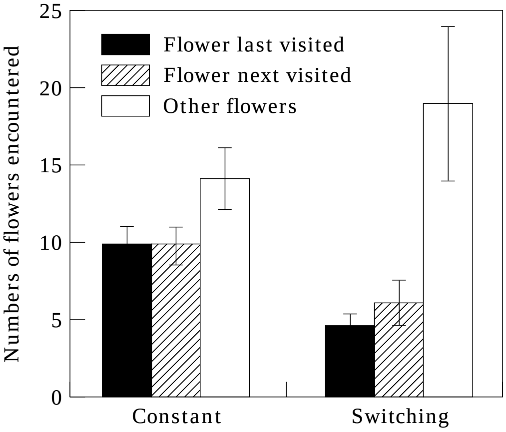

Figure 3. Numbers of flowers ± SE encountered by butterflies during flights between flowers. Each flight ends in either constancy (the butterfly visits the same flower species as last visited) or switching (it visits a different species). Numbers of flowers are divided into those that are the same as that last visited, those that are the same as that next visited (these are the same for constant sequences) and other flowers encountered. Means were used for each insect to avoid pseudoreplication. Based on foraging bouts of 56 insects.

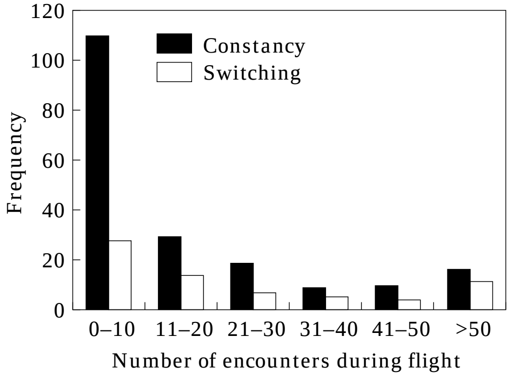

Figure 4. The frequency distribution of foraging flights according to the number of flowers encountered during the flight, based on 262 flights by 56 insects. Flights are divided into those ending in a visit to the same flower species as that last visited (constancy) or to a different species (switching). The number of flowers encountered includes the flower visited at the end of the flight.

DISCUSSION

Thymelicus flavus is clearly able to use a range of flower species, and to adopt different flowers as they become available. Despite repeating field observations at the same site and time of year, there were noticeable differences in the abundance of flower species between 1994 and 1995. For example *R. fruticosus* was abundant and frequently visited in 1995, but in the previous year did not flower during the study period, while conversely the most frequently visited nectar source in 1994 (*L. corniculatus*) was markedly less floriferous in 1995. Clearly the capacity to switch between food sources according to availability is essential given such dramatic between-season fluctuations in flower abundance.

We confirm that *T. flavus* exhibits a significant degree of constancy to flowers previously visited (i.e. there is a history effect sensu Lewis 1989). Flower constancy is well documented for honey bees and bumblebees (e.g. Barth 1985; Waser 1986) but has received comparatively little attention in other insects. In butterflies, constancy has previously been identified in *Pieris rapae* (Lewis 1989) and *Pieris napi* (Goulson & Cory 1993). Confirmation of constancy in a third unrelated butterfly species suggests that it may be a widespread phenomenon among butterflies and perhaps generally among insects that visit flowers.

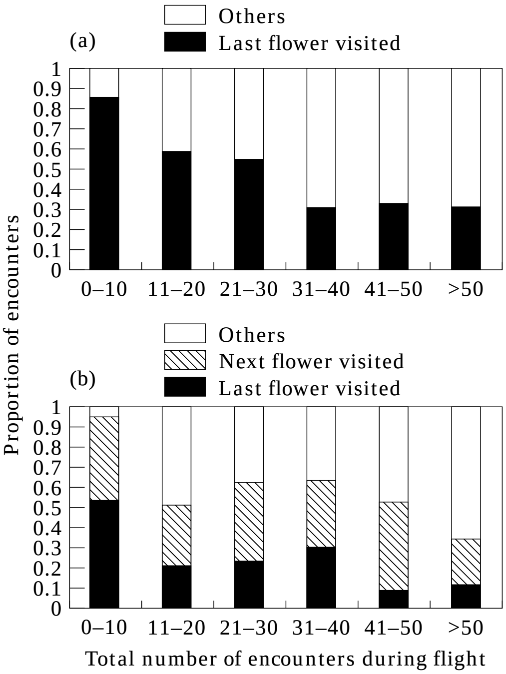

Figure 5. Proportions of different flowers encountered during flights according to the total number of flowers encountered. Flower species are divided into those that are of the same species as that visited at the begining of the flight, the same species as that visited at the end of the flight, and other species. Since there were no significant differences between individuals, data were combined for 56 insects. (a) Flights ending in constancy, $N=193$. (b) Flights ending in a switch between flower species, $N=69$.

Empirical studies of foraging in flower-visiting insects have lagged behind theoretical approaches (with notable exceptions, e.g. Wells & Wells 1983, 1984, 1986; Dukas & Real 1993a, b). At least three alternative hypotheses have been proposed to account for foraging behaviour of nectarivores: maximizing energy gain per unit time (Oster & Heinrich 1976), risk aversion (Caraco 1980; Real 1981) and flower constancy resulting from memory constraints (Darwin 1876; Lewis 1986; Lewis & Lipani 1990; Dukas & Real 1993a). Empirical tests of these hypotheses in honey bees suggest that constancy is the dominant strategy and that bees may remain constant to an artificial flower colour that provides a lower quantity or quality of reward or a more variable reward than alternatives (Wells & Wells 1983, 1986).

If flower constancy is a result of memory constraints and a trade-off between handling time and travelling time (see Introduction), then constancy should be abandoned at low flower densities in favour of switching between flower species as they are encountered. Kunin (1993) described a decline in constancy of both honey bees and syrphids in response to decreasing density of *Brassica kaber*. In *T. flavus* the strategy adopted was correlated with the relative frequency of encounters with the preferred flower species; the likelihood of switching was higher when the frequency of encounters with the previously preferred species was low. A number of alternative explanations are possible. A pattern of random visits would automatically result in switching away from species as they become scarce, but the strong history effect described here suggests that foraging choices are not made at random. Butterflies may perceive how common flower species are as they fly past, so that the foraging decision as to whether to switch or to remain constant is based on short-term sampling of the flower population during at least a portion of the preceding flight. This portion may be small (i.e. the flowers available at the point at which the butterfly decides to feed) since a flower species that is scarce in one portion of the flight path is likely to be scarce elsewhere in the path. If at this point the preferred species is absent or scarce, then the butterfly may switch. Overall, we suggest that butterflies do exhibit preferences based on previous experience, and that they tend to switch from preferred flowers as they decrease in density. However, the causal mechanism involved in this switch is difficult to discern using foraging patterns in natural (rather than experimentally manipulated) distributions of plant species.

One aspect of these data casts doubt on any argument based on foraging efficiency. The majority of flowers encountered were not visited even when the flower was both a favoured species and the previous visit was to the same species. For *L. corniculatus* (one of the most favoured flower species), even when the last flower visited was *L. corniculatus*, the probability of a visit to a flower that was subsequently encountered was only 0.35 (SE: 0.28–0.45). A strikingly similar pattern is evident in the behaviour of the butterfly *P. rapae* (Lewis 1989); in the latter study flowers were scored as encountered if the butterfly passed within 10 cm (rather than 20 cm used in this study). Even so, many suitable flowers were ignored. The probability of any flower being visited when encountered, even when the previous visit was to the same species, was below 0.5 for 10 out of 11 flower species. It is difficult to reconcile these data with existing hypotheses that predict forager behaviour: butterflies simply ignore most of the flowers they encounter, even when they are of the species to which they are constant. We propose three alternative (but not mutually exclusive) explanations.

(1) Many of the flowers recorded as encountered (within 20 cm) may not be seen by the butterfly. The choice of 20 cm was arbitrary, since no information is available as to how far butterflies can see, but we suggest that observing even a small flower at 20 cm is well within the visual acuity of butterflies. If many flowers are not seen then we may expect a relationship between visit rate and flower size: presumably larger flowers are less likely to be overlooked. Although we have only eight flower species to compare, our data do not support this explanation. For example in the ranked order of visit likelihood (Fig. 2) the plant with the largest floral display (*C. scabiosa*) was visited rarely in comparison with the rather small flowers of *L. corniculatus*. However, the size of individual inflorescences may be less important than the degree of aggregation of inflorescences in determining apparency to insects, a factor that we did not quantify.

(2) Many of the flowers encountered may be recognized as unsuitable using criteria beyond our detection (unopened buds and senescent flowers were excluded from our data). Honey bees can distinguish between age classes of flower and avoid less rewarding classes (Giurfa & Núñez 1992), while bumblebees can detect and avoid recently visited flowers (Heinrich 1979; Zimmerman 1982). Given the speed of flight of *T. flavus* and the large numbers of inflorescences ignored we suggest that it is unlikely that the insects have time to assess and reject so many flowers individually. However, this hypothesis could be tested by comparing nectar rewards in visited versus missed flowers.

(3) Gathering nectar may not be the only (or most important) function of activity: the butterflies may also be defending territories, searching for mates or oviposition sites, etc. so that flights are far longer than would be necessary just to travel between flowers. This possibility has been raised previously (Waser 1982), but is difficult to

test. A possible route may be a comparison of the foraging patterns of insects of differing sex and reproductive status. In this respect butterflies are likely to differ from worker bees, which are freed from reproductive activities, and mean distance travelled between flowers tends to be greater in butterflies than in honey bees or bumblebees (Schmitt 1980; Waser 1982).

Despite empirical and theoretical approaches to studying nectarivore foraging, a convincing explanation for flower constancy remains elusive. We provide further evidence that the strategy adopted may vary according to the density of resources, compatible with the hypothesis that constancy maximizes reward per unit time within learning constraints. Paradoxically, however, our data suggest that butterflies do not maximize reward per unit time since they frequently ignore most of the flowers they encounter. A valuable contribution may be made by quantifying travelling and handling times and reward per unit time while manipulating flower density to examine the relative efficiencies of constancy and switching. Clearly further field and laboratory studies are necessary if we are to understand fully why insects forage in the way that they do.

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