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Foraging dynamics of bumble bees: correlates of movements within and between plant species

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What rules determine whether bumble bees continue exploiting plants of the species just visited or switch to another species? To tackle this question, we recorded handling times and flight times from bees foraging in a natural meadow containing five plant species. Inter- and intra-specific plant distances were quantified. The bee-subjective colors of the five species were determined; two of these species had similar colors and structures, while three species were distinct from all others. The following rules were identified: (1) The decision to switch species was correlated with previous flower handling time, which we assume is a function of the reward amount received at the flower. After short handling times, the probability of switching to another species increased, whereas it decreased after long handling times. This difference became even greater if the bee had had a run of several short or several long handling times. (2) Constant flights (those between flowers of the same species) and transition flights (those between flowers of different species) followed stereotyped temporal patterns independent of the distances between flowers. Constant flights within five plant species consistently had median durations of about 2 seconds, whereas median transition times between species took 3–6 seconds. (3) This temporal rule broke down, however, if the flowers of two species had similar colors, in which case transition flights had equal dynamics as constant flights. (4) Bees switched more frequently from rare than from common species but even more frequently between similar species. We conclude that the bees' choices were determined by a set of rules that guided them to stay with the current plant species as long as flowers were rewarding *and* available within close distance but to switch to another species if flowers offered low rewards *or* were not encountered at close range. *Key words:* bumble bees, *Bombus,* flower color, flower constancy, foraging, pollination ecology, switching. *[Behav Ecol 8:239–249 (1997)]*

Foraging bees have to make economic choices among a multitude of different flower species with different signals and rewards (Giurfa et al., 1995; Greggers and Menzel, 1993; Waddington and Heinrich, 1981; Waser, 1983). The principles by which bees forage among plants of a single species have been the subjects of numerous studies. A well-established rule is, for example, that bees leave patches or individual plants and tend to fly longer distances when several of the previous rewards were low (Dukas and Real, 1993; Giurfa and Núñez, 1992; Pyke, 1978; Thomson et al., 1982; Zimmerman, 1983). Bumble bees, however, often visit several distinct flower types during single foraging flights (Bennett, 1883; Clements and Long, 1923; Grant, 1950; Waser, 1986). Bees' decisions to stay constant on their current plant species or switch to another are not well understood.

According to Heinrich (1979), visitation of different flower species can be categorized into two types: majoring (systematic exploitation of flowers of only a single type) and minoring (exploratory visits to other types). A minor can become a major when the bee finds its flowers more rewarding than its current specialty. However, bumble bees are often observed to forage systematically from flowers of several species during single bouts (Bennett, 1883; Free, 1970; Grant, 1950; Thomson, 1981; Waddington, 1983), and so the majoring-minoring dichotomy cannot fully explain how bees make choices in a mixed floral array.

Laboratory studies using artificial flowers have primarily investigated the overall distribution of choices between targets of different color (e.g., Chittka et al., 1992; Waser, 1986), or different nectar amounts and variances (e.g., Banschbach and Waddington 1994; Heinrich, 1976; Real, 1991; Thomson et al., 1982), but not the question of what induces a switch between floral types. Only a few studies have analyzed the sequential dynamics of choices made by bees foraging from mixed food-source types (e.g., Greggers and Menzel, 1993), although the importance of considering visitation sequences in addition to frequencies was recognized long ago (e.g., Waddington, 1983).

Here we relate a real-time sequential analysis of bees' choices to the spatial distribution of five plant species on which the bees forage. We ask which events along a foraging bout trigger a transition from one species to another, and under which circumstances bees stay flower constant. In detail, we attempt to answer the following questions:

1. Does recent foraging history, as assessed by measuring flower handling times (which possibly is a function of the nectar amount in the flowers) correlate with the frequency of transitions between species? In other words, is a transition from one species to another more likely after the bee has encountered one or several flowers with low rewards on its current specialty?

2. Is travel time between flowers related to the probability of leaving the plant species on which the bees currently collect food? Foraging pigeons, for example, become less selective the longer they spend searching for potential food sources. As travel time increases, the birds are more likely to accept a less-preferred prey type (Fantino and Abarca, 1985). This makes sense because a forager that spends excessive time in searching for a food type that has become less available or more difficult to locate will waste energy and time. Another

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reason why travel time might be positively correlated with transition probability is mechanistic. There may be interference effects when different foraging tasks are executed at short time intervals (Greggers and Menzel, 1993; Menzel, 1979), which may favor *not* switching to another plant species when it is encountered at close range. Are bees more likely to switch between plant species when travel times between potential food sources are increased?

3. What is the role of the similarity between floral signals in relation to transition frequency and travel time (Waser, 1986)? This question is tied into the above two, because all rules predicting a transition between plant species may break down if two species are indistinguishable and may apply only partially when species are distinguishable but similar. A forager that has decided to leave its current specialty because of low yields will not switch to a species that appears indistinguishable from that specialty. If a bee searching for another flower of the species just visited encounters a flower of a different, but indistinguishable species, it should be ready to accept this flower even in a short time window after the last visit. Thus, questions 1 and 2 cannot be answered without taking into account the bee-subjective similarity of the flowers of the species in question.

4. Finally, we ask how the foraging rules established in an attempt to answer questions 1–3 influence transition frequencies in relation to flower density and similarity, which we hope will ultimately allow us to extrapolate from those rules to implications for plant reproductive success.

METHODS

A meadow was selected with five plant species in bloom in a nature reserve near Berlin (Naturschutzgebiet Lange Dammwiesen, Strausberg, Brandenburg, Germany). The species were *Lotus corniculatus* L., *Lathyrus pratensis* L., *Vicia cracca* L., Fabaceae; *Cirsium oleraceum* (L.) Scop., Asteraceae, and *Lythrum salicaria* L., Lythracaceae. *Vicia, Lotus,* and *Lathyrus* have zygomorphic flowers of relatively low complexity; all of them are fabaceous and therefore similar in handling. *Lythrum* has radially symmetric open flowers presented vertically on an elongated inflorescence. *Cirsium* is a long-tubed thistle whose inflorescence faces upward.

We chose an area of 8 m × 20 m within which the distributions of inflorescences of all five species appeared maximally homogeneous. All observations of bumble bee choices were made within this plot, which contained 777 inflorescences (henceforth "flowers") of *Vicia*, 642 of *Lotus*, 253 of *Lathyrus*, 153 of *Cirsium* and 120 of *Lythrum*.

Four species of bumble bees foraged in the meadow: *Bombus pascuorum, B. veteranus, B. terrestris,* and *B. lapidarius.* Observers recorded the choices of individual bees on tape by announcing (a) the species of a flower at the moment a bee landed on it, and (b) the moment of departure from this flower. The tapes thus contained the sequence of flower choices, the flight times between all flowers, and the time spent on each flower. Choice recordings were stopped when a bee left the 8 m × 20 m plot or was lost by the experimenter. All data were recorded during five days in July 1993 between 1100 and 1400 h. During 11 hours of choice sequences recorded during this period, a total of 4464 visits to flowers (and flight times between these) was accumulated (*B. pascuorum* 2368 visits; *B. veteranus* 1122; *B. terrestris* 107, and *B. lapidarius* 867).

Does the reward sequence influence transition frequencies?

It is likely that the reward sequence influences the bee's decision to stay constant on one species or to switch to another. To test this possibility, we used the handling time as an indirect measure of the reward received at an individual flower. The rationale is that extracting a larger amount of nectar takes a longer time (see Discussion for references and caveats).

Handling times as well as interflower distances and flight times, here (Figure 5) as elsewhere (e.g., Brown and Clegg, 1984; Kunze, 1995; Levin and Kerster, 1969) are skewed toward longer values; thus the median, rather than the mean, will be used as a measure of descriptive statistics. Handling times differed strongly among plant species, with medians (N of observations) as follows: *Cirsium* 9.4 (288), *Lythrum* 5.9 (578), *Vicia* 4.1 (2205), *Lotus* 3.5 (880), and *Lathyrus* 2.7 (512) seconds. They also differed widely among individual bees. For example, one individual of *Bombus pascuorum* had a median handling time of 7.3 seconds ($n = 30$) on *Vicia*, while another individual of the same species took a median of 2.2 seconds ($n = 34$). Thus, to test whether handling times could be pooled across bees, we used the Kruskal-Wallis test (Sachs, 1984: 238). Twenty tests were performed (i.e., for all four species of bumble bees and all five species of plants). Handling times differed significantly ($p < .05$) between individuals in 11 of these 20 tests. An overall p value was then determined using Fisher's test for combining probabilities ($p < .001$; Sokal and Rohlf, 1981: 780). To cope with this heterogeneity, handling times were related to each individual bee's median handling time on the plant species in question. To this end we evaluated an individual bee's handling time on a single flower relative to the distribution of all that bee's handling times on the flower species, not relative to the distribution of handling times of all bees on that species. Only bees that had visited a given flower species at least five times were included in the analysis of handling times. Medians, lower and upper quartiles of the handling time distributions were determined for each individual bee. This procedure was repeated for each flower species visited by that bee. Subsequently, the following quantities were determined: n, number of times a handling time *below* the median (lower quartile) were followed by a transition; m, number of times such handling times were followed by a constant flight; p, number of times a handling time *above* the median (upper quartile) were followed by a transition; q, number of times such handling times were followed by a constant flight.

The probability that a bee switches after a short (< median) handling time is defined as $n / (n+m)$, whereas the probability that it switches after a long (> median) handling time is $p / (p+q)$. To test whether the two pairs of values were significantly different, n and m vs. p and q were evaluated by means of the chi-squared goodness-of-fit test (Sachs, 1984: 251). To determine whether only extremely long or short handling times were likely to result in increased or reduced probabilities of switching species, the same procedure was repeated, taking into account only handling times that fell above the upper or below the lower quartile of each individual bee's handling times. We also tested whether the transition probability might significantly change after two or three consecutively visited flowers above or below the individual medians (upper or lower quartiles).

Can flight times be predicted from interflower distances, or by a choice rule applied by the bees?

We examined whether the flight time distributions for the 25 possible flower combinations differed significantly among bee species. Each species was tested against all other species by means of the Mann-Whitney U test. There were six pairwise bumble bee species comparisons for 25 plant combinations, a total of 6 × 25 = 150 tests. Fifty-one of these possible combinations could not be tested because bees of one or both species compared never moved between flowers of two species in question in the direction required. This means that 99 tests were performed. Fisher's combined probability value for these tests is $p = .426$ (n.s.); thus, we pooled the flight time distributions for the four bumble bee species.

We then tested whether flight time distributions between all flower species can be pooled across individual bees. We started by testing individuals of each bumble bee species by means of the Kruskal-Wallis test. All 25 possible combinations of the five plant species were tested. An overall probability value was determined using Fisher's test for combining probabilities ($p = .325$, n.s.). We thus conclude that the flight time distributions may be pooled within species.

The distances between flowers of all pairs of species must be quantified to interpret the flight times of bees between these species. The species *from* which distances (or flight times) were measured is termed the *reference species*. The species *to* which distances (or flight times) were measured is called the *target species*. To quantify distances, a flower of the *reference species* was randomly selected out of the meadow. The distance to the nearest flower of the same species was determined, as was the distance to the nearest flower of another species. In some cases, only the distance to the nearest flower of a different species was determined. This procedure was repeated several times for each pair of species (see Figure 2a for numbers of measurements). Note that the distance distributions are not necessarily reciprocal for a given pair of species; for example, distances from the most common species to the least common species may be greater than those in the opposite direction. Hence, distances were measured from every *reference species* to every *target species*.

For each *reference species*, we compared the flight time distributions of constant flights and transition flights that originated on this species, using the Mann-Whitney *U* test. We then asked whether the flight times observed could be predicted from the interflower distances as measured (which would be the null expectation predicted from random movements), or whether an additional choice rule applied by the bees is necessary to explain the flight times of the bees. Specifically, we asked if bees generally spend a set time searching for flowers of the species just visited, before their readiness to accept flowers of a different species increases.

What are the effects of flower signal similarity and density on transition times and frequencies?

To assess the similarity of flower signals and its effects on bee movements, it is necessary to quantify the bee-subjective properties of these signals. For this purpose, the reflectance spectra of the five plant species were measured by means of a photodiode-array-spectrophotometer (for details, see Chittka and Menzel, 1992. The formulas for converting flower spectral reflectance into bee-subjective colors can be found in that paper as well). The spectral sensitivity curves of *Bombus terrestris* as electrophysiologically determined by Peitsch et al. (1992) were used to calculate color loci. It is appropriate to use these functions to predict color appearance for the other *Bombus* species, since photoreceptor spectral sensitivity is conservative in the Apoidea (Chittka, 1996).

We looked specifically for pairs of flowers that differed strongly in their similarity. We then asked whether transition times between more similar species differed from those between plants whose signals are clearly distinguishable. Finally, we asked whether transitions were more frequent between similar species and whether transition frequencies also depended on the relative densities of the five species present in the array.

RESULTS

Handling times are negatively correlated with transition frequencies

No significant differences were found between the transition probabilities following flower handling times that fell above or below the individual bee's median handling time of that flower species ($p > 0.1$ for all plant species), nor even after two or three consecutive visits with handling times all above or below the median ($p > .5$ for all plant species).

The transition probabilities for 1–3 consecutively visited flowers of each of the extreme categories (i.e., below the individual bee's lower quartile of handling times for that plant species, or above the upper quartile) are given in Figure 1. The transition probability increased with the number of previously visited flowers whose handling times fell below the lower quartile and decreased with the number of previously visited flowers with handling times above the upper quartile. In *Lythrum* and *Cirsium*, the difference was significant when the previous visit only was evaluated. In *Vicia* and *Lotus*, the difference became significant after two consecutively visited flowers of these handling time categories (Figure 1). The deviation became even stronger at three consecutively visited flowers in most species; however, since the number of cases to be evaluated declines rapidly as one proceeds to longer sequences, this difference was no longer significant. In summary, extremely short handling times were associated with a higher probability to switch species, while this probability became progressively lower with increasing numbers of consecutively visited flowers with extremely long handling times.

Transitions between species are longer than constant flights, independently of the spatial distribution of flowers

With very few exceptions, transitions were significantly longer than constant flights (Figure 2b). Since plants are often patchily distributed, this result may be an artifact generated by the fact that distances between flowers of the same species are usually smaller than those to flowers of any other species. To exclude this possibility, it must be demonstrated that, at least for some species, heterospecific distances are not longer than distances between plants of the same species. If there are such pairs of species, and if transitions between such species are still longer than constant flights within each species, we can assume that flight times are not simply a function of distances between plant species. To this end, descriptive statistics of distance distributions of nearest neighbors between all pairs of species can be compared with flight times between these species in Figure 2.

We started by inspecting flights originating on (and distances measured from) the most common species, *Vicia* and *Lotus*. Heterospecific distances from these two species to all others were significantly longer than those from *Vicia* to *Vicia* or from *Lotus* to *Lotus*. Correspondingly, as one might expect, flights from *Vicia* to all other species took significantly longer than those from *Vicia* to *Vicia* (Figure 2b). The same was the case for *Lotus* (with the exception of flights from *Lotus* to the similar *Lathyrus*; see subsequent section). Clearly, for *Vicia* and *Lotus*, the observation that transitions took longer than constant flights can simply be explained by the distances between plants.

Does this also apply in the rare species, *Cirsium* and *Lythrum*? In both of these, distances to all other species were *not* significantly longer than intraspecific distances. Thus, here are two interesting cases where we would expect *equal* times for constant and transition flights, if flight times were a simple function of distances. They were not; all the transition time distributions originating on *Cirsium* and *Lythrum* were signif-

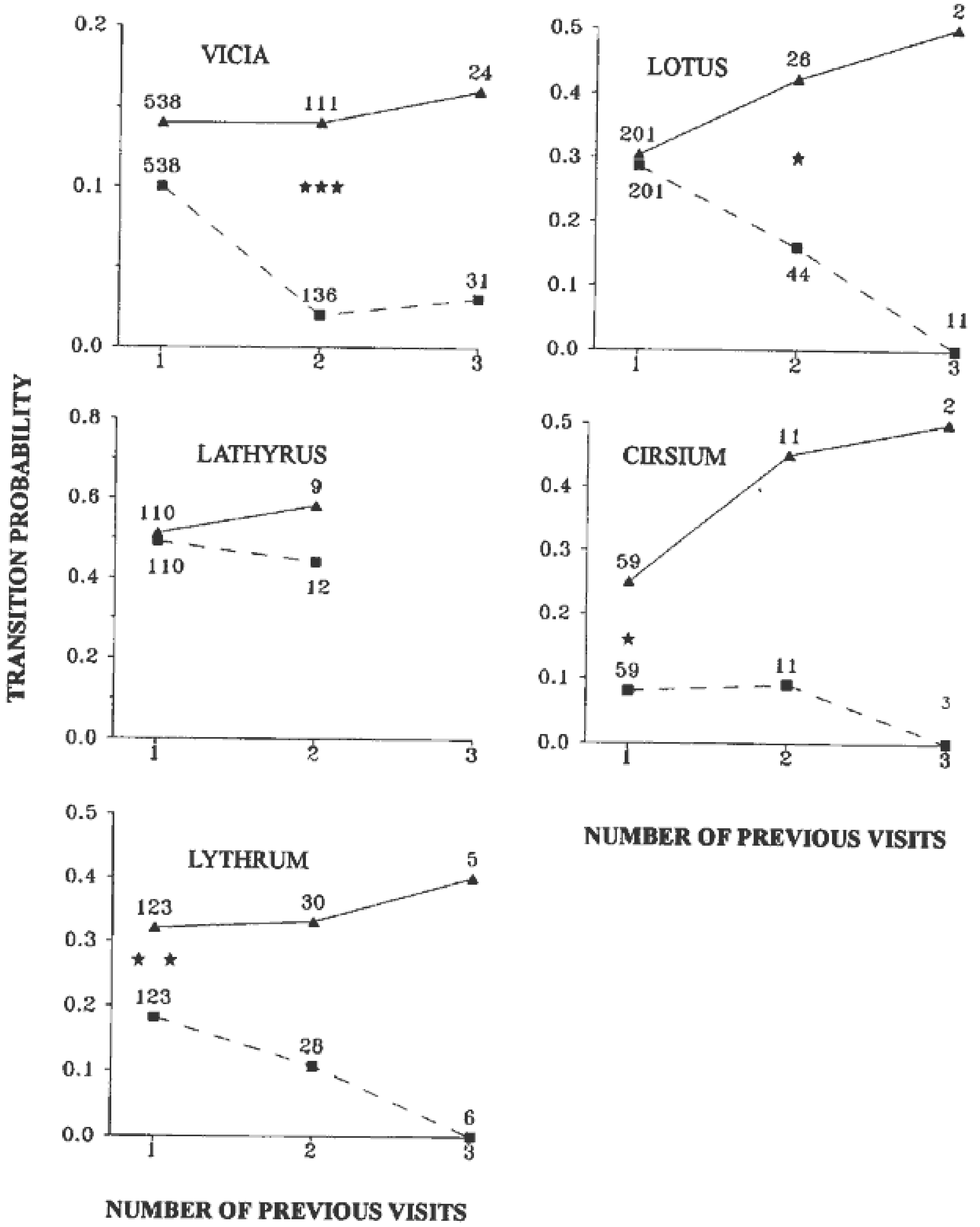

Figure 1

The probability of leaving a plant species is related to the handling times of the last visited flowers. The continuous line denotes the transition probability after 1–3 consecutively visited flowers with extremely short handling times (those that fell below the lower quartile of the handling time distributions of each individual bee for that plant species). The probability was determined as the number of cases a switch occurred after short handling times, divided by the total number of such handling times. Numbers of observations are given next to each data point. In the lower right graph (*Cirsium*), for example, the uppermost point indicates the following: there were two cases in which a bumble bee had a run of 3 consecutive visits to *Cirsium* with handling times that all were shorter than that bee's lower quartile of all its handling times on *Cirsium*. In one of these two cases, this run was followed by a switch to another species; hence, the transition probability is .5. The dashed line indicates the transition probability after 1–3 flowers with extremely long handling times (above the lower quartile of each bee), calculated in the same fashion. Asterisks indicate significance differences between the two curves (*$p < .05$; **$p < .01$; ***$p < .001$).

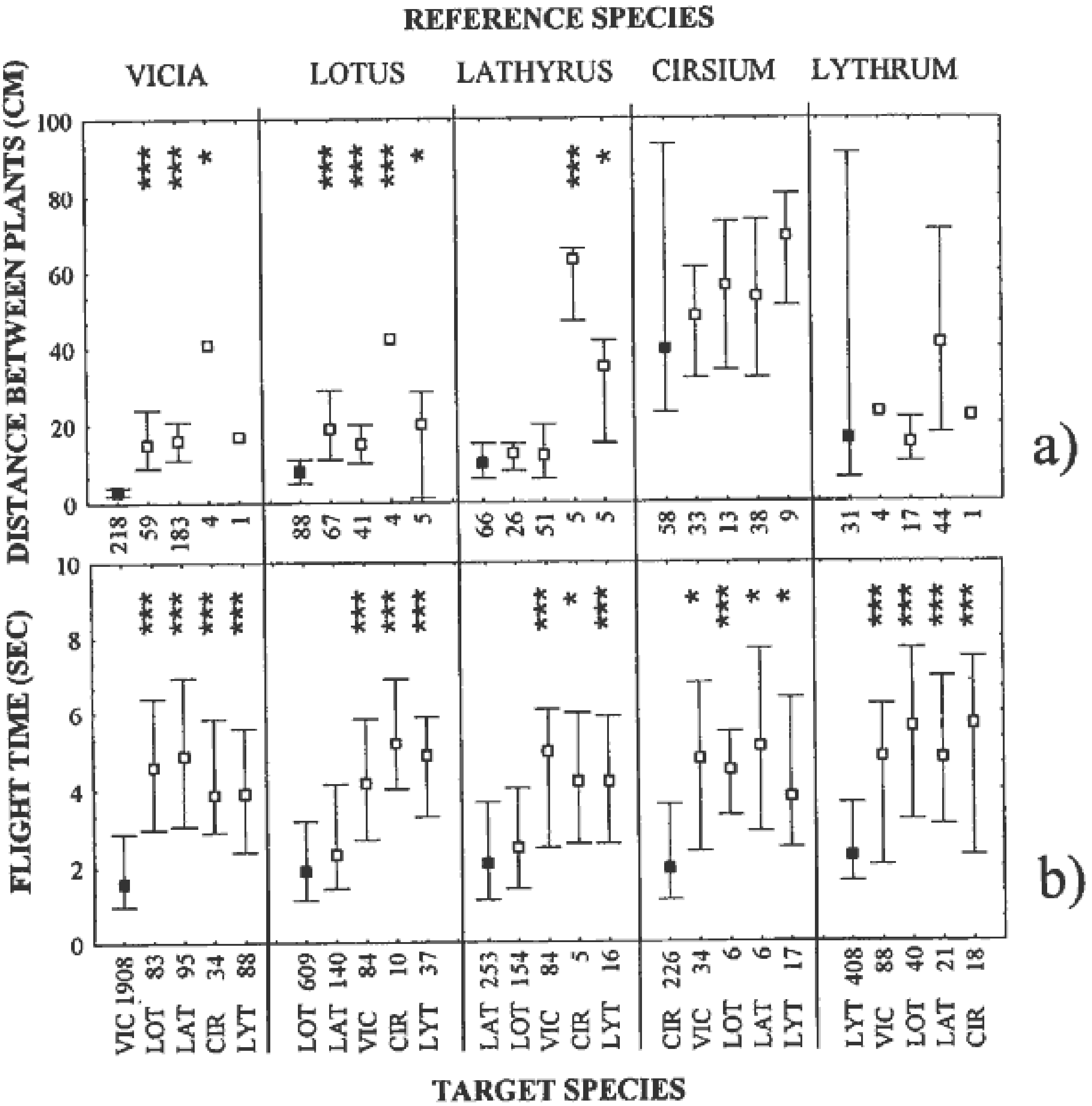

Figure 2
Descriptive statistics for the distance distributions (Figure 2a) and flight time distributions (Figure 2b) for all 25 pairs of plant species. The *reference species* (*from* which distances are measured, or from which bee flights originate) is given above each of the five vertical sections of the graphs. The *target species* (*to* which distances are measured, or where bee flights terminate) are listed below Figure 2b, followed by the number of observations of flight times. Species are sorted from left to right in the order of their densities. Numbers of distance measurements are given below Figure 2a. Squares indicate medians, whiskers denote upper and lower quartiles. For each *reference species*, distance distributions within the *reference species* (left in each of the five section, black squares for medians) are compared with distances to the four other *target species* (white squares for medians) by the Mann-Whitney *U* test (Figure 2a). The same comparisons are performed for the flight time distributions. Asterisks indicate significant differences (see legend Figure 1).

icantly longer than the constant flights (Figure 2b, Figure 5a). Thus, the flight time distributions cannot simply be explained by the spacing of nearest-neighbor flowers for the two rare species.

This picture is confirmed when one looks at the species that grew at an intermediate density (*Lathyrus*). The distances to less-common species (*Cirsium, Lythrum*) were significantly longer than to other *Lathyrus* flowers, whereas distances to more common species (*Vicia, Lotus*) were not. However, with the exception of flights from *Lathyrus* to the most similar species (*Lotus*, see subsequent section), *all* transitions were significantly longer than the constant flights starting from *Lathyrus* (Figure 2b, Figure 5b) In summary, there were several cases where interspecific distances were not significantly longer than intraspecific ones. Nevertheless, transition times *were* longer than constant flights, and thus flight times do not appear to be a simple function of flight distance.

To test whether there was an overall correlation between distances and flight times for all pairs of species, we plotted the median flight times over the median distances for all 25 combinations of plant species (Figure 3). The correlation was not significant (r_s = .289; n = 25; p = .159). Some of the distance measurements are supported by only very few data points (Figure 2a). We thus recalculated the correlation for those data points, which were supported by more than 10 distance measurements. Again, the correlation was not signifi-

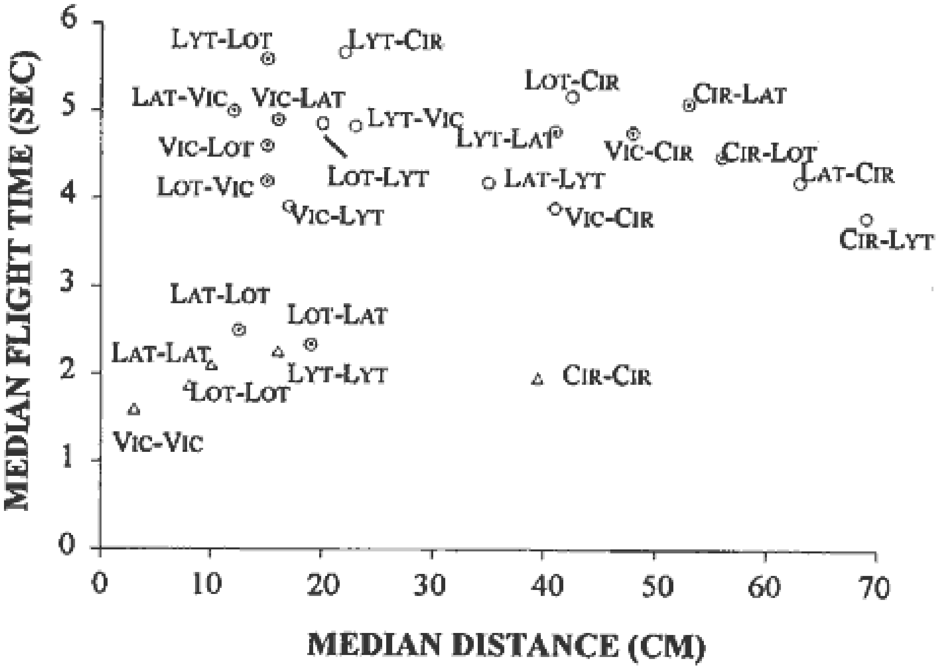

Figure 3
Median flight times as a function of median distances for all 25 pairs of species. Triangles indicate constant flights, circles denote transitions. Circles with a central dot are supported by more than 10 distance measurements. Each data point is labeled with the first three letters of the *reference species* (left) and the *target species* (right). Where this label cannot be placed directly next to the point (in the case of Lotus-Lythrum flights), label and point are connected by a line. The correlation is not significant (see text).

cant ($r_s = 0.419$; $n = 16$; $p = .106$). Since bees might only fly to flowers of a given species when these are close to a particular starting point, they might predominantly fly distances at the lower margin of each distance distribution. In this case, the median distance might not be an appropriate measure when distributions have identical medians, but different variances and minima. Thus, we also calculated the correlation between median flight times and (a) the minimal distances of each combination of plant species and (b) the lower quartile of the distance distributions. Again, we used only the 16 sets of distance measurement supported by $n > 10$. Both correlations were not significant (a: $r_s = .332$; $p = 0.21$; b: $r_s = .419$; $p = 0.106$).

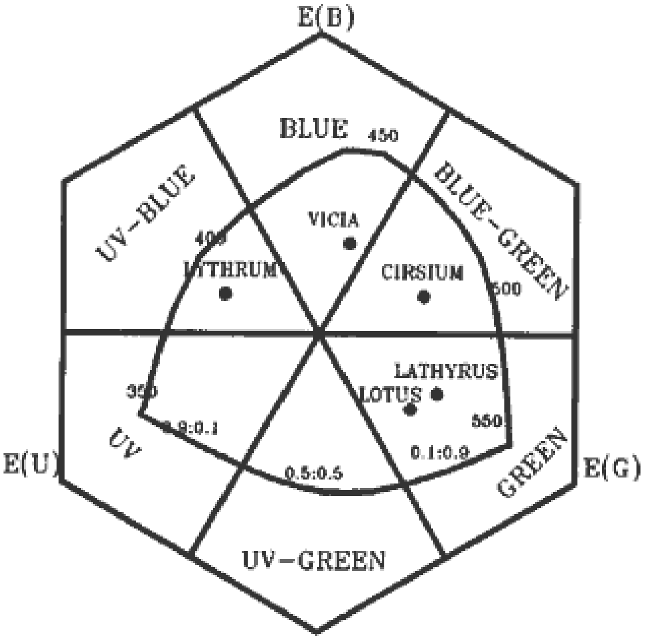

Figure 4
The color loci of the five species plant present in the investigation in the color hexagon (Chittka, 1992; Chittka et al., 1994). The continuous curve denotes the spectrum locus, in 10 nm steps from 300 to 540 nm. The bottom segment of the spectrum locus connects the loci of 300 and 540 nm in nine mixtures of the two lights in ratios of 0.9:01; 0.8:0.2, etc. (see Chittka, 1992, for details). Distances in the color hexagon are correlated with color differences as perceived by a bee.

Rather than being correlated with median distances, median flight times fell into two distinct clusters along the time axis (Figure 3), those generated by constant flights (about 2 sec) and those produced by transitions (about 5 sec). The former cluster, however, also contains two heterospecific flight time medians that belong to the species with similar signals, i.e., *Lotus* and *Lathyrus* (see subsequent section).

In conclusion, assuming that our samples of inter-flower distances yield unbiased estimates of the distances encountered by the bees (see Discussion for potential problems), the temporal dynamics of flights between the plant species in our study cannot be explained by the spatial arrangement of flowers in a straightforward way. Constant flights and transitions follow stereotyped temporal patterns clearly distinguishable from one another. Thus we conjecture that flight dynamics are actually governed by a fixed choice rule of the bees rather than by the spatial distribution of flowers directly. Using such a rule, bees might choose to stay faithful to the species just visited whenever a novel flower of that species is encountered in the immediate time interval after the last visit. On the other hand, they might switch preferably when flowers of the same species have not been encountered for more than 3 sec of flight.

Flower signal similarity affects the dynamics of transitions between species

The flower colors of the five species tested here are depicted in a hexagonal space that indicates how a bee will perceive color (Figure 4). *Lotus* and *Lathyrus* have bee green colors that lie extremely close to each other in this color space. Additionally, their sizes and shapes are practically identical. The experimenters, who had to identify the plants quickly when recording insect choices, were only able to tell these two species apart by their leaves and the presence of tendrils on *Lathyrus* only. Visually, they should be hardly distinguishable for a bee. All other species are distinct in both color and shape.

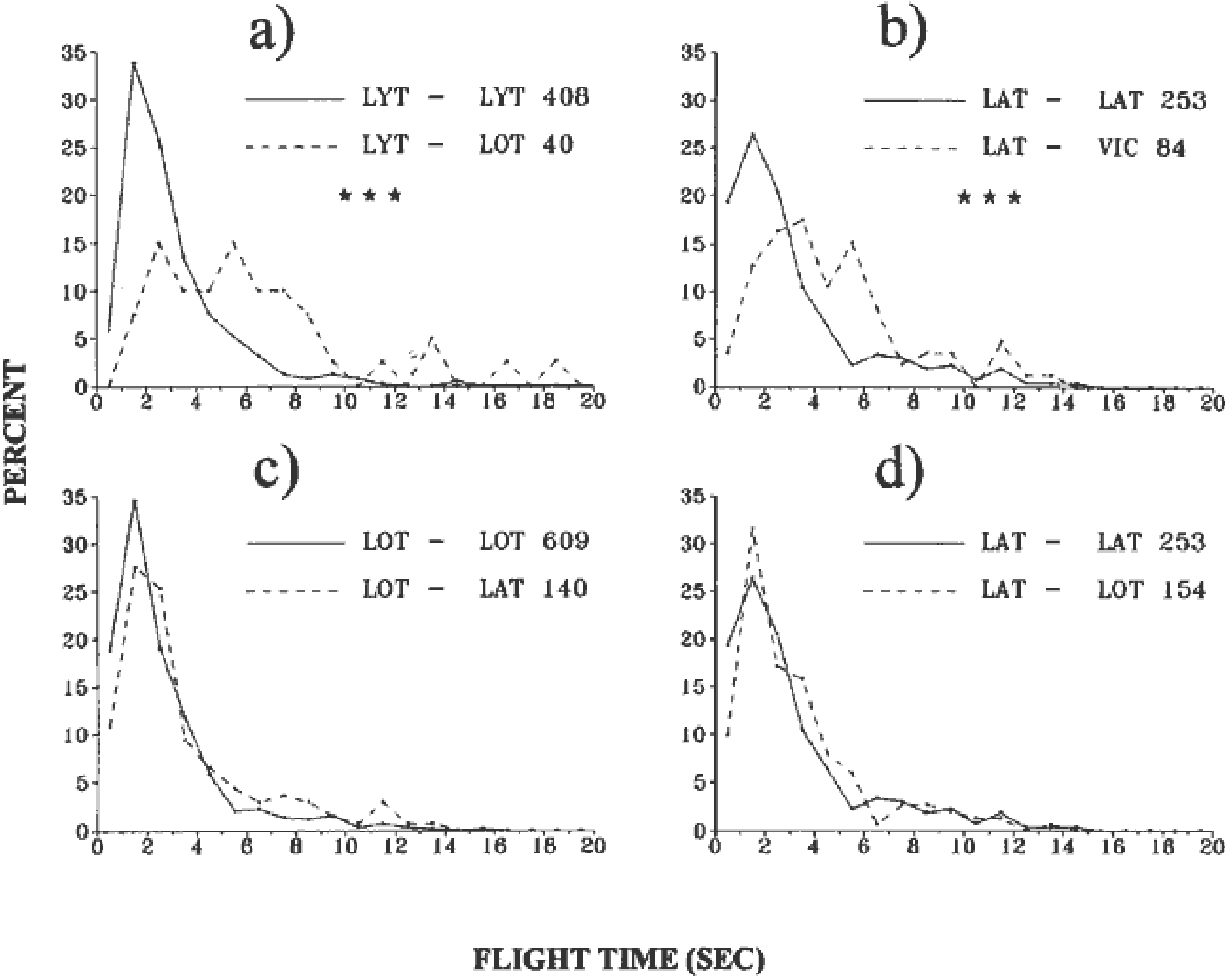

Figure 5
Frequency distributions of representative flight time distributions for flower constant flights (continuous lines) and transitions (dashed lines), given as percentages calculated for each 1-s interval. Numbers behind species abbreviations indicate how many flights were evaluated. Abbreviations indicate the two species that were connected by the respective flights. Each transition time distribution is compared with the constant flight times that originate on the same *reference species* by the Mann-Whitney *U* test; asterisks indicate significant differences.

Cirsium is bee blue-green, *Vicia* is bee blue, and *Lythrum* is UV-blue (color terminology, see Chittka et al., 1994). Are these similarities apparent in the flight time distributions?

Of the 25 combinations tested, there were only two exceptions to the rule that constant flights took shorter times than transitions. These were (1) the flights from *Lotus* to *Lathyrus* (whose distribution forms an almost perfect match with that of the *Lotus* to *Lotus* flights, Figure 5c) and (2) the flights from *Lathyrus* to *Lotus* (which matches the *Lathyrus* to *Lathyrus* flights equally well, Figure 5d). This is remarkable since these are the only two species that are similar in color and pattern. Is it possible, then, that bees treated flowers of both species as members of a single one? To examine this possibility, it is necessary to test whether the dynamics of flight between and within these two species might simply be a function of their distance distributions.

This may indeed be true in one of the cases. Distances from *Lathyrus* to *Lotus* were, in fact, not longer than intraspecific distance among *Lathyrus* flowers (Figure 2a). Correspondingly, the flight times among *Lathyrus* flowers and those from *Lathyrus* to *Lotus* were statistically indistinguishable. Note, however, that this was the *only* pair of species where transitions from a rare to a common species did *not* take longer than constant flights within the rare species, as one would expect from the distance distributions.

We then asked whether bees switching from *Lathyrus* to a more common species generally exhibited this pattern. To this end, we evaluated the flights from *Lathyrus* to *Vicia*. Distances from *Lathyrus* to *Vicia* were not statistically different from intraspecific distances between *Lathyrus* flowers, and so the situation is directly comparable to the *Lathyrus* to *Lotus* transitions above. We would expect no difference between the flight times for the two pairs of species, if these times were simply a function of distance. However, this expectation is not met; transitions to *Vicia* were significantly longer than for flights between *Lathyrus* flowers (Figure 2b, 5b). Thus, the difference between the transitions originating on *Lathyrus* and ending on either *Vicia* or *Lotus* can be likely explained by the observation that *Lotus* matches *Lathyrus* in signal, whereas *Vicia* does not. Turning to *Lotus* as a *reference species*, the flight time distributions are even more surprising. As predicted from the distances (Figure 2a) all transitions starting on flowers of this species should be longer than the constant flights. However, this was not the case for the *Lotus*-*Lathyrus*

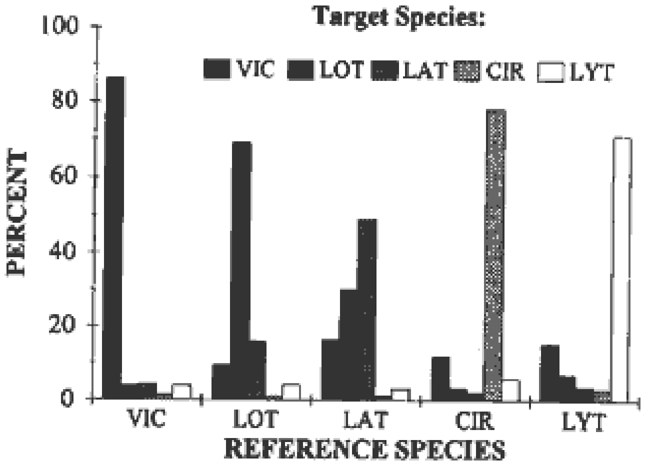

Figure 6
Percentages of constant flights (e.g., *Vicia* → *Vicia*) and all possible combinations of transitions (e.g., *Vicia* → *Lotus*). For each *reference species*, the five columns (denoting one *target species* each) add up to 100%. Number of flights evaluated for each *reference species*: *Vicia* 2208, *Lotus* 880, *Lathyrus* 512, *Cirsium* 289, *Lythrum* 575.

flights, which showed the same dynamics as the constant flights from *Lotus* (Figure 5c).

Thus, in the case of *Lotus* and *Lathyrus*, the general rule that transitions between different species took longer than constant flights did not apply. Since this observation could not be related to the spatial arrangement of flowers, we conjecture that it is based on the strong similarity of the two species. Because of this similarity, bees were more prone to switch between these two species in the first few seconds of a flight than to switch to a species with well-distinguishable signals.

Flower similarity and density together influence transition frequencies

Bumble bees switched between species frequently, on average eight times per minute or 18 times per 100 flower visits. However, from every reference plant species (except *Lathyrus*), the frequency of constant flights was significantly higher (for all species $\chi^2 > 49$; df = 1; $p < .001$) than the frequency of transitions between species (Figure 6). This was true for the more common species *Vicia* (86% constant flights) and *Lotus* (69% constant flights) as well as for the locally rare species *Cirsium* (78% constant flights) and *Lythrum* (71% constant flights). This result may be produced by the fact that flowers of each species are aggregated in space, although in *Cirsium* and *Lythrum*, flowers of other species are generally available at equal distance as conspecific flowers (Figure 2a). The present data do not allow us to test rigorously whether bees are actually more constant than would be expected by the spatial arrangement of plants, but they do permit us to test whether transition frequencies are influenced by relative flower density and similarity. The null expectation is that switches from less common species to more common species are more frequent than vice versa. To test this possibility, we compared the numbers of constant and transition flights that originated on *Vicia* with the numbers of constant and transition flights that started on *Lythrum*.

The frequency of transitions relative to constant flights was significantly higher when these flights originated on the less common species (*Lythrum*) than when bees came from a more common species (*Vicia*); $\chi2 = 78$, df = 1, $p < .001$). The same is true if one compares *Vicia* and the second least common species, *Cirsium* ($\chi2 = 14$, df = 1, $p < .001$). Thus, bees did indeed switch more frequently between species when their flights originated on rare species than when they started off a common species. This result fits the null expectation; these transition frequencies might be explainable by random movements.

This relationship becomes less clear if one looks at *Lotus* and *Lathyrus*. Likewise, one would expect a higher frequency of transitions to the most common species, *Vicia*, and a low frequency of flights to the less common species. Indeed, the percentage of transitions to *Vicia* from these two plant species (10% of all flights from *Lotus*; 16% from *Lathyrus*) was higher than to *Cirsium* (1% from *Lotus*; 1% from *Lathyrus*) or *Lythrum* (4% from *Lotus*; 3% from *Lathyrus*; Figure 6). Again, this observation might be explained by random movements. However, transitions from *Lathyrus* to the most similar species, *Lotus* (30%) were even more frequent than those to *Vicia* (16%), even though *Vicia* was the more common species. The same was the case for *Lotus* (to *Lathyrus* 16%; to *Vicia* 10%). These differences were significant when tested against random (*Lotus-Vicia* vs. *Lotus-Lathyrus*: $\chi2 = 7.1$; df = 1; $p < .01$; *Lathyrus-Vicia* vs. *Lathyrus-Lotus*: $\chi2 = 10.6$; df = 1; $p < .005$). Note that a test against random is conservative here because the null expectation from the relative densities of flowers is that switches to the more common species are more frequent than vice versa. Thus, the effect of flower similarity on transition frequency was even greater than that of relative densities. The percentage of flower constant flights originating on *Lathyrus* (a species intermediate in density *and* similar to a more common species) was only 49% - the lowest of all plant species in the present investigation. Constant flights and transitions from Lathyrus were not significantly different from random ($\chi2 = 0.04$; df=1; p> 0.5).

In summary, while durations of transitions between species cannot be explained with the spatial arrangement of flowers, the frequency of transitions can, at least where flower signals are clearly distinguishable. Switches from rare species are indeed more frequent than from common species. Moreover, signal similarity strongly affects transition frequency. Transitions to a similar species are even more frequent than to a more common species.

DISCUSSION

In this study we present a real-time sequential analysis of handling times and flight durations in a mixed array of natural flower species. The goal was to determine which events trigger a transition from one species to another. The following components of the bees' foraging bouts were investigated.

Handling times, flower rewards, and transition frequencies

We found that bees were more likely to leave a plant species when the time spent on the previous flowers was extremely short. The reverse was found for sequences of visits with outstandingly long handling times. When other influences are kept equal, handling time is a correlate of the reward (Bertsch, 1987; Greggers and Menzel, 1993; Kunze, 1995; Pyke, 1978; Schmid-Hempel, 1984; Taneyhill, 1994;). From this perspective, the observed behavior makes sense, in that bees leave a species when the last rewards indicate that flowers of this species are depleted in the immediate neighborhood; thus it may be more favorable to switch to a different species. However, since handling time is potentially correlated with several other parameters, it is critical that these other influences be eliminated before correlation with nectar amount is discussed.

(a) Handling times are a function of individual handling skills (Laverty, 1980, 1994a). We circumvented this difficulty by relating the handling times to the median handling time of individual bees throughout their foraging bout. In theory, it is also possible that handling skills improved during our observation of a single bout. This is unlikely because learning to handle flowers of relatively low complexity takes up only a small fraction of the bee's lifetime. For example, Laverty (1994a) showed that the time required by naive bees to reach the handling efficiency of experienced bees on flowers of *Vicia cracca* (one of the species used in our study) is less than 5 min (60 visits), which appears to be a negligible portion of a bee's foraging career of several weeks. Hence, we consider it unlikely that novices starting to forage in our meadow might have distorted the data in a noticeable fashion. (b) Handling times are different for different plant species, because these differ in morphological complexity and the way in which nectar must be extracted (Laverty, 1994a; Schmid-Hempel, 1984; Waser, 1983). This difficulty was overcome in our study by evaluating the handling times of each plant species separately. (c) Finally, handling time can be an indicator of cost, rather than reward; for example, handling times maybe increased immediately after a transition between species (Heinrich, 1976; Laverty, 1994b). This problem is not relevant in our study, because we looked at handling times before (not after) transitions.

Thus, we assume that time spent on flowers is indeed a correlate of the reward received. From this viewpoint, we conjecture that the decision to continue visiting flowers of the same species or to switch is based on an estimation of the reward from the previously visited flowers. This is not surprising, given that several studies have shown that bees assess the reward levels of individual flowers relative to an expectation for mean rewards at the species in question, leave flower patches and tend to fly longer distances after encountering several depleted flowers (Dukas and Real, 1993; Giurfa and Núñez, 1992; Heinrich et al., 1977; Pyke, 1978; Schmid-Hempel, 1984; Taneyhill, 1994). Our findings are consistent with those of Dukas and Real (1993) and Taneyhill (1994) in that more than a single previous visit is evaluated for comparison with the average reward to be expected at the respective flower species. However, to the best of our knowledge, this is the first study that relates transition frequencies in a mixed species array to estimated reward levels.

The observed behavior makes sense if nectar is patchily distributed in flowers of a given species (Pyke, 1978). Such distributions are reasonable, but have seldom been demonstrated, except at very small spatial scales (Pleasants and Zimmerman, 1979; Thomson et al., 1982; Waser and Mitchell, 1990). If the last several rewards were low in a patch of flowers, the probability is high that the next one is likewise low. If patchiness in flower rewards is primarily determined by flower constant nearest neighbor movements by pollinators, then flowers of one species in a patch may have been recently depleted, whereas those of another species still offer a high reward. Thus, in a mixed species array, it may be adaptive to switch to another species rather than fly a large distance to another patch, whose conditions may be equally unpredictable.

Flight times, distances between flowers, and a temporal rule for switching species

Flights between flowers of different species take consistently longer than those between flowers of the same species. Constant flights peaked at 1–2 s, whereas transitions of all kinds were most frequent at 4–5 s. Several observations suggest that this difference cannot be explained simply by interflower distances. (a) The distances from flowers of the low density species to flowers of another species were often not larger than to flowers of the same species. (b) Flight times were poorly correlated with nearest-neighbor distances between species (Figure 3). Rather, flight times fell into two clusters, which appeared to be independent of distance. Membership in the clusters was determined by whether the flights link pairs of flowers of the same or of different species. (c) The velocity of bumble bees flying between flowers of a patch can be as low as 35–50 cm/s (Kunze and Chittka, 1996), but even most of the heterospecific distances between flowers were considerably below 50 cm (Figure 2a). Thus, it is unlikely that distances alone set the limit for the drastically longer transition flights.

These analyses assume that our samples of inter-flower distances yield unbiased estimates of the distribution of distances actually experienced by foragers. This may not necessarily be the case at each given point of a foraging trajectory. Ideally, it would be desirable to know the bee's options at each particular point of a bout and to evaluate which option is chosen among the available ones. In a natural flower array, this would imply mapping the complete three-dimensional arrangement of flowers and monitoring the entire flight trajectory of the bee among individually labeled flowers. Since this is hardly practicable in arrays with large numbers of flowers, we chose to compare median flight times to the medians, lower quartiles, and minima of nearest neighbor distance distributions. While individual distances may certainly deviate from these estimates, it is hard to see how this bias would produce a pattern in which all median transition times are longer than median constant flights, with the two exceptions that involve the species whose signals are similar.

Thus, we conjecture that flight durations between species are determined by a choice rule applied by foraging bees rather than directly by distance. This rule might guide the bees to move preferentially to flowers of equal signal when these are encountered in the first few seconds of flight but favor switching after more than 3–4 seconds have passed without finding another flower of the same species. A related strategy has been described in foraging pigeons, which become less selective in their food type preference the longer they spend traveling between potential food sources (Fantino and Abarca, 1985). This makes sense because a forager that persists in searching for a food type that has become less available will waste precious time and energy. However, in bees foraging on several species of flowers, the explanation is not quite so straightforward. There is no reason to assume that the flower type last visited is implicitly the most preferable one, nor is it necessarily the type most familiar to the bees, unless one, or both, of the following conditions are true: (a) there is a limitation of memory which does not allow retrieval of more remote memories with equal ease as those for the previous visits, or (b) rewards across species are so unpredictably distributed that it is generally preferable to stay with the current species so long as it yields acceptable rewards. While our data do not allow us to distinguish between these explanations, the following studies on honey bees are of relevance to this problem.

Marden and Waddington (1981) tested bees in arrays of equally rewarding yellow and blue artificial flowers. They found that when bees were given the choice between a yellow and a blue flower equidistant from the current flower, they predominantly chose a target with the same color as the one just visited. However, when distances were unequal, bees mostly chose the nearest flower irrespective of color. While the latter is clearly advantageous, the former finding is difficult to understand by adaptive reasoning. When flowers are equally rewarding, and both types familiar to the tested bees, there is no adaptive reason to move preferentially between flowers of equal color. Do these results mean that bees only remember the last food source that they have visited? No. Menzel et al. (1993) review several experiments to show that long-term memory capacity in bees is large and holds accurate records of signals and reward probabilities over long periods of time. However, more relevant to the present discussion, Greggers and Menzel (1993) showed that there may be *short-term* interferences when different memories are retrieved at short-time intervals. Data on bumble bees concerning such constraints are not available, but the above studies hint that, in general, there may be limitations that favor executing equal tasks (visiting flowers of the same species) repetitively, rather than alternating randomly between familiar tasks.

Such a retrieval constraint is clearly maladaptive when flower rewards are predictable and similar across species. To avoid bypassing rewarding flowers, memories of familiar flowers should be available at any time (Waser, 1986). This limitation, however, may possibly be turned to advantage in natural conditions, where rewards are variable (Heinrich, 1979; Kunze, 1995; Thomson et al., 1982; Waser, 1983) and less predictable for the individual foraging bee (Mangel, 1990). In nature, numbers of flowers are large compared to the experimental arrays in the above studies (Greggers and Menzel, 1993; Marden and Waddington, 1981), and the foraging activities of other visitors make rewards to be expected at individual flowers less reliable (Mangel, 1990; Waser and Mitchell, 1990). Under such conditions, it may be useful to apply a win-stay, lose-shift strategy: stay with the current plant species as long as flowers are rewarding *and* available within close distance; shift if flowers offer low rewards *or* are not encountered at close range. While our data are consistent with this interpretation, further experiments are necessary to test this hypothesis rigorously. Such experiments should control for the spatial arrangement of food source types, and possibly the timing of the onset of the stimuli marking the next targets after each visit.

Effects of flower density and signal similarity

Unsurprisingly, bees in our study switched more frequently from the locally rare species than from common species. It has been observed that pollinator constancy decreases as distances between plants increase (Brown and Clegg, 1984; Grant, 1949; Levin and Anderson, 1970). Such behavior does not require a rule applied by the bees; it would be expected even from a forager who moves randomly to nearest neighbor plants.

More interestingly, however, bees are more likely to leave a species when encountering flowers of another species similar in visual display signal. Most likely, this is a consequence of the temporal foraging rule discussed in the preceding section. If it is true that bees search predominantly for flowers of the species just visited in the first few seconds of flight, then the prediction is that flowers of other species are bypassed even if they are available at equal (or possibly, closer) distance. Correspondingly, transition frequencies are depressed in the first few seconds of each flight, so long as visual signals are clearly distinguishable. If, however, the searching bee encounters a flower of a different species that closely matches the current search image during the first few seconds, it may be more ready to switch. As a result, bees would switch even more frequently between similar species than to a more common species found at close distance. This is precisely the result found in the present investigation. That flower similarity influences transition frequencies between species has been suspected before (Brown and Clegg, 1984; Chittka and Menzel, 1992; Waddington and Heinrich, 1981; Waser, 1986), but is shown here for the first time in relation to quantified, bee-subjective similarity of flower color. For the set of plants used here, judgments of color identity and discriminability would have produced similar results if human observers had assessed the results. However, this was not predictable. There are numerous pairs of plant species whose colors are indistinguishable for humans but distinct for a bee, or plants that look identical to a bee but distinct for humans (Chittka et al., 1994). Thus, biological color signals must be interpreted using an appropriate model of color perception for the receiver of these signals.

Plants obviously profit from pollinators that move predominantly between flowers of the same species, because a directed and efficient pollen transfer will be facilitated (Darwin, 1876; Grant, 1949; Waser, 1986). It has been conjectured that species that bloom simultaneously and sympatrically should diverge in signal (Chittka and Menzel, 1992; Kevan, 1978; Waser, 1983). It is interesting, then, to speculate about the conditions under which divergence in signals will actually be favored. In our study, the species with the lowest potential to keep pollinators constant was *Lathyrus*, a species that was intermediate in density and similar in color to a more common species, *Lotus*. Maximal constancy was exhibited by bees foraging on *Vicia*, which was the most common species and whose signal was well-distinguishable from all other species in the array. However, flowers blooming at low density may actually profit from having signals that converge on those of other species. While this may be a poor strategy to keep pollinators constant, it may be a way to entice bees to switch to a low-density species, which otherwise might not receive any visits at all (Chittka, 1993; Feinsinger, 1983; Heinrich, 1976; Rathcke, 1983; Thomson, 1981).

Conclusion

This field study was conducted to identify the rules that determine the sequence of choices of bees foraging among plants of different species. Some of the results confirm earlier observations (i.e., the dependence of transition frequency on relative plant density; e.g., Grant, 1949); others had been anticipated (i.e., relationship of transition frequency and signal similarity; e.g., Waser, 1983). For the first time, we show that bees are more prone to switch species when rewards of their current specialty are low. This result is attractive; however, we measured handling time rather than reward itself. Thus, even though we have good reasons to believe that the two are correlated, tests in which rewards are controlled are desirable. The most intriguing result is at the same time the one that clearly needs further examination: the temporal choice rule we have proposed here should be tested in laboratory setups where timing and spacing of distinct signals are tightly controlled. Data from such tests should allow a more precise identification of choice rules, their relationship to memory dynamics, and the implications for plant reproductive success in relation to spatial arrangement and similarity of plants.

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