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Visit larger displays but probe proportionally fewer flowers: counterintuitive behaviour of nectar-collecting bumble bees achieves an ideal free distribution

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Summary
1. Patterns of pollinator responses to variation in floral display size have significance for pollen flow among plants. Here we test a theoretical model for explaining such patterns by simultaneously assessing bumble bee behaviour and nectar availability in two native stands of *Cirsium purpuratum* with different spatial densities.

2. A bumble bee (*Bombus diversus*) foraging on a plant remembered and avoided only one or two flower heads that it had probed before, so that the flower-head revisitation rate increased as it stayed longer on a plant. Moreover, the revisitation rate increased less rapidly on larger displays.

3. The number of heads probed per plant increased less than proportionally with display size, and this increase was smaller at higher plant density. This pattern is consistent with our expectation that a bee leaves a plant when the cost of flower-head revisitation exceeds that of interplant movement. However, bees left plants slightly earlier than predicted.

4. As predicted, the visitation rate of bees per plant showed a decelerated increase with floral display size, and this increase was greater at higher plant density.

5. As a result of these complementary changes in the number of heads probed per plant and visitation rate per plant across plant densities, nectar rewards per head were equalized among displays (an ideal free distribution was achieved).

Key-words: *Bombus*, floral display size, foraging behaviour, flower revisitation, ideal free distribution, plant–pollinator interaction

Introduction

Plants within a population often vary considerably in the numbers of open flowers (Wilson & Price 1977; Pleasants & Zimmerman 1990). Variation in floral display size causes two types of pollinator response which can influence pollen dispersal. First, larger floral displays attract more pollinators per unit time (Dreisig 1995; Klinkhamer & de Jong 1990; Klinkhamer, de Jong & Bruyn 1989; Ohara & Higashi 1994; Ohashi & Yahara 1998; Robertson & Macnair 1995; Thomson 1988). This increased attractiveness promotes increased pollen receipt or removal, or potential mate diversity (Harder & Barrett 1996). Second, the number of flowers that individual pollinators probe per plant within a foraging bout also increases with floral display size (Geber 1985; Harder & Barrett 1995; Klinkhamer et al. 1989; Robertson 1992), which increases self-pollination among flowers on the same plant (geitonogamy; de Jong, Waser & Klinkhamer 1993; Richards 1986). Thus the relation of plant fitness to floral display size depends on the details of the two types of pollinator responses.

In order to predict how pollinators respond to variation in floral display size, we developed a theoretical model based on considerations of optimal foraging (Ohashi & Yahara 1999). First, we considered a situation in which a pollinator foraging on a plant is increasingly likely to revisit previously probed flowers until the cost of flower revisitation exceeds that of moving to another plant. Such behaviour results in the number of flowers probed per plant increasing less than proportionally with the size of floral display. Next, based on previous empirical studies (Dreisig 1995; Robertson & Macnair 1995), we assumed that pollinators distribute themselves on displays of different size according to an ideal free distribution so that they can gain equal nectar rewards per flower. Given this behaviour, the rate at which individual plants receive pollinator visits...
increases in a decelerating manner with the size of their floral display.

Our model (Ohashi & Yahara 1999; Ohashi & Yahara 2001) made unique predictions concerning the effects of plant density on the two types of pollinator response to variation in floral display size. First, the number of flowers probed per plant should increase less strongly with floral display size at higher plant density. Although some authors have argued that a pollinator probes a smaller proportion of flowers as plant density increases (e.g. Cibula & Zimmerman 1984; Cresswell 1997; Heinrich 1979; Klinkhamer & de Jong 1990; Zimmerman 1981), they did not address the effect of plant density on the functional relation between the number of flowers probed per plant and floral display size. Second, visitation rate per plant should increase more strongly with display size at higher plant density. Although we found that a few previous observations on changes in pollinator behaviour across plant densities were consistent with our predictions (Klinkhamer & de Jong 1990; Klinkhamer et al. 1989), these studies did not test their findings statistically, nor did they investigate whether gain per flower was equalized among different-sized displays.

In this paper we assess the effects of plant density on the responses of bumble bee behaviour in two native stands of Cirsium purpuratum (Maxim.) Matsum. First, we quantified the revisitation rate of bees to flower heads as a function of the number of previously probed flower heads on a plant, and the relative cost of interplant movement at each density. Incorporating these estimates into the model, we predicted the number of flower heads probed per plant in relation to floral display size, and compared it with observed behaviour. Second, we compared the relations between floral display size and the number of flower heads probed per plant, the visitation rate per plant, and the visitation rate per head in high- and low-density areas. Finally, we quantified nectar productivity and standing crops per head at each density to assess whether bees gain equal average nectar rewards per head regardless of variation in flower heads probed per plant with floral display size smaller at higher plant density? (iii) Is the increase in visitation rate per plant with floral display size greater at higher plant density? (iv) Is the average visitation rate per head on each plant balanced by the per-head nectar productivity of the plant, irrespective of its floral display size? (v) Can the relationship between the number of flower heads probed by a bumble bee per plant and floral display size (number of flower heads per plant) be quantitatively predicted by the model?

In addition, we assumed that a pollinator remembers probing a maximum of \( m \) flowers on a plant and avoids revisiting them, but arbitrarily chooses among the remaining \( (F - m) \) flowers where \( F \) is the size of floral display. Hence the flower revisitation rate \( (r) \) will increase linearly with the position of the flower in a visit sequence \( (t) \) (Fig. 1a). That is,

\[
r = (t - m - 1)(F - m) \quad (t > m)
\]

\[
r = 0 \quad (t \leq m)
\]

Because revisited flowers yield little or no nectar, this will cause a gradual decrease in the rate of energy gain per flower with increasing \( r \). We refer to such a decrease in the rate of energy gain as 'patch depression' (originally termed 'depression' by Charnov, Orians & Hyatt 1976). Assuming that nectar productivity per flower is constant, we predicted the number of flowers that a pollinator will probe before leaving a plant as

\[
t = (1 - k)F + mk \quad (F > m)
\]

\[
t = F \quad (F \leq m)
\]

where \( t \) is the number of flowers probed per plant (for further details see Ohashi & Yahara 1999; Ohashi & Yahara 2001). The predicted pattern is shown in Fig. 1(b). The number of flowers probed per plant \( (t) \) increases with floral display size \( (F) \). When \( k < 1 \), the increase in \( t \) is slower than the increase in \( F \). At higher plant density, the increase in \( t \) with increasing \( F \) is smaller.

Next, we expanded the model for variable display sizes by considering visitation rate per plant as a combined response of many pollinators (Ohashi & Yahara 1999; Ohashi & Yahara 2001). We assumed that pollinators
Relationship between pollinator visitation rate per plant \((V_p)\) and floral display size \((F)\) was predicted as

\[
V_p = \frac{V_f}{F} \left(1 - k \frac{F}{F + m k} \right) \quad (F > m)
\]

\[
V_p = \frac{V_f}{F} \quad (F \leq m)
\]

where \(V_f\) is constant (for further details see Ohashi & Yahara 1999, Ohashi & Yahara 2001). The predicted pattern is shown in Fig. 1(c). Pollinator visitation rate per plant \((V_p)\) increases in a decelerating manner with floral display size \((F)\), which counterbalances the decline in \(1/F\) on larger displays. At higher plant density, the increase in \(V_p\) with increasing \(F\) is greater.

These predictions largely depend on the assumptions that the pollinator’s ‘memory size’ is a constant that is smaller than display size, that nectar productivity per flower is equal among displays, and that pollinators distribute themselves on plants according to an IFD. To test our model, therefore, the assumptions and the predicted patterns should be supported empirically. Therefore we investigated the foraging behaviour of bumble bees and nectar distribution among plants in dense and sparse stands of \(C.\) purpuratum.

Materials and methods

ORGANISMS AND STUDY SITE

\(C.\) purpuratum is a herbaceous perennial that inhabits flood plains or volcanic barrens in the Kanto and Central Districts of mainland Japan. It produces large, purple, nodding flower heads (400–700 florets per head) on several erect flowering stalks that elongate from a basal rosette. All florets within a flower head are hermaphrodite and protandrous. The number of flowering heads provides a practical measure of floral display size for a \(C.\) purpuratum plant (Ohashi & Yahara 1998).

We studied \(C.\) purpuratum on a floodplain along the Kinu River \((\approx 800\) m), Tochigi Prefecture, Japan. During 1997 and 1998, main blooming occurred from September to October. Floral display size varied from one to 35 heads per plant, and 78.5% of plants had fewer than five flower heads. The most frequent pollinators were the bumble bee, \(B.\) diversus Smith. In addition, \(B.\) honsbuenstis Tkalcu, \(B.\) consobrinus wittenburgi Vogt and \(B.\) hypocrita Perez also visited \(C.\) purpuratum, but only rarely. The other rare visitors of \(C.\) purpuratum have been described elsewhere (Ohashi & Yahara 1998). \(C.\) cirsium flowers offer nectar and pollen, but most bees do not actively collect pollen in the sense of manipulating the anthers. Thus we considered nectar to be the primary reward.

For several reasons, the \(C.\) cirsium–\(B.\) bombus system seems particularly appropriate for testing our model. (i) Flower heads are irregularly distributed in three-dimensional space within a plant, so that flower-head revisitation by bees is more likely than if heads had a regular distribution. (ii) Individual plants are dispersed so that each plant represents a distinct patch. (iii) Plants receive frequent visits by bees, so we could record numerous sequences of flower-head visitation on each plant. (iv) Bumble bees appear to compete extensively for nectar, and the visitation rate per head is almost equal among different-sized displays, suggesting an IFD (Ohashi & Yahara 1998).

BUMBLE-BEE RESPONSES TO FLORAL DISPLAY SIZE

During early September 1997 and 1998, we selected two areas with different spatial densities at our site. In the high-density area, mean distance to the nearest two neighbours was \(1.48\) m \((n = 18, SE = 0.11)\) in 1997 and
1.31 m (n = 22, SE = 0.13) in 1998, and in the low-density area, 1.0–2.0 m (n = 18, SE = 0.82) in 1997 and 0.8–1.5 m (n = 22, SE = 0.50) in 1998. These areas were separated by >50 m, so that few bees foraged in both areas.

During each daily observation in 1997, we selected one or two pairs of one large plant (six to 16 flowering heads) and one small plant (one to three flowering heads) in each density area. For each plant we numbered flowering heads consecutively and observed them for 80 min, either directly or indirectly with 8 mm video cameras (Handycam CCD-TR250, Sony). For each plant we recorded the number of bees that visited, the number of flower heads probed per visit, and the sequence of flower heads probed during each visit. We repeated these 80 min observations three times a day for six focal plants, separated by 30 min intervals (0700–0820, 0830–1010 and 1040–1200), so that each focal plant was observed for 4 h. These daily observations were conducted at three separate times during the flowering season in 1997 (6–7, 13–14 and 19–20 September). We also recorded the date of anthesis of each head on 12 plants to describe flower-head age distribution within plants.

In 1998 we conducted similar observations on 7–12, 14, 17–18, 20–22, 24, 26–27, 29–30 September, and 2 October. For each daily observation we selected one or two plants in each density area and monitored their bee visits continuously for 6 h (0830–1430). Because we primarily sought to collect data on flower-head revisitation during 1998, we did not always include large and small displays in pairs. Display size of focal plants ranged from eight to 18 heads.

**TIME COST OF FLIGHT WITHIN AND BETWEEN PLANTS**

To estimate the discounting rate for interplant movement (€), we timed inter- and intraplant bee flights, and the probing time of individual heads (time from landing until leaving a head) to 0.01 s with a digital stopwatch (ATC-1100, CASIO) in the high- and low-density areas. These measurements were repeated during the peak of pollinator activity (1100–1400) on 24–25 September 1997.

**STANDING CROP OF NECTAR SUGAR PER HEAD**

In parallel with monitoring bee visitation in 1997 (6–7, 9, 13–14, 16 and 19–21 September), we selected a pair of displays (large, six to 13; small, two or three heads per plant) in each density area, and measured nectar standing crop in all flower heads on them. On each observation day we sampled nectar at 06.30, 08.20, 10.10 and 12.00 h. We roughly divided each head into inner, middle and outer florets, then picked five middle florets from each head with forceps. This influenced neither nectar productivity of other florets, nor bee visits to the head (K.O., unpublished results). Sampled florets were placed in 1.5 ml microcentrifuge tubes and taken to the laboratory in a chilled airtight container. We also sampled five middle florets from each of 20 flower heads just after they had been probed by bees.

In the laboratory, we collected floral nectar by inserting a 1–10 µl GELoader Tip (Eppendorf, Germany) into a flower and sucking up the nectar with a 5 µl syringe. We then flushed the tip with 3–5 µl distilled water and soaked it up with a rounded wick (6 mm diameter) of chromatography paper (Whatman 3MM Chtr). We thus soaked up nectar from five florets with a wick and dried it at 37 °C.

Nectar of *C. purpuratum* primarily contains sucrose (>90% of solutes), so we measured the sucrose content of each sample. We dissolved the sugar in each wick in 20 µl distilled water, and quantified sucrose content with an automated enzyme electrode analyser (Biotec Analyzer M-110, Sakura Seiki Co. Ltd, Japan). Preliminary analysis showed that sucrose content in five middle florets correlated strongly with that in 25 randomly picked florets from the same head (n = 19, r = 0.91, P < 0.0001).

**NECTAR PRODUCTIVITY PER HEAD**

On 17 September 1997, we examined nectar sugar (sucrose) production rate of flower heads on different-sized displays of *C. purpuratum*. In the high- and low-density areas we selected 18 and 20 plants, respectively, with 1–19 flowering heads per plant. Nectar sugar production rate is highest when the flower is in the male phase, which does not vary among the locations within a head (Tables 1 and 2). To control for this effect of sexual stage, we selected one flower head on each plant which had just passed 3–4 days after anthesis.
and collected five middle, male-phase florets. After the first sampling at 1100 h, each focal head was bagged (2 mm mesh, vinylon 35%, polyester 65%) to allow nectar to accumulate until we sampled five additional florets at 1500 h. Sugar production rate was then determined as the difference between nectar contents before and after bagging. Nectar production over 4 h was much less than the maximum nectar capacity of florets (K.O., unpublished results).

We also checked whether floret number per head varied with head size per plant. We randomly selected one flower head for each of 20 plants with different sizes of floral display (1–29 flowering heads per plant) and counted the total number of florets.

### DATA ANALYSIS

#### Bumble bee behaviour within plants

From observations of sequences of flower-head visits, we determined the extent to which bumble bees revisited flower heads as a function of the number of flower heads available on a plant and the number already visited by the bee during one visit. For each plant, we calculated the flower-head revisitation rate as

\[ r = \frac{R}{R + N} \]

where \( R \) and \( N \) is the number of visit sequences in which the \( r \)th probing was a revisit and a non-revisit, respectively. We then estimated 'memory size' (\( m \)) for each plant by fitting a linear function, \( r = \beta t - (m + 1) \), to the observed relationship between the revisitation rate (\( t \)) and the position of a head in a sequence (\( t \)), where \( \beta \) and \( m \) are constants. Because the number of heads probed before leaving (the maximum \( t \)) varied among visit sequences, even on the same plant, the number of sequences including the \( r \)th probing \( (R + N) \) decreased with increasing \( t \). This would increase the variance of the calculated \( r \) with increasing \( t \). Therefore, to estimate \( \beta \) and \( m \) as accurately as possible, we used the weighted least-squares method with \( 1/(R + N) \) as the weight (Draper & Smith 1998). We also calculated the overall rate of flower-head revisitation for each plant as a ratio of the sum of the number of revisits to the sum of the number of visits over all flower heads on the plant: \( r_\text{overall} = \frac{\sum R}{\sum (R + N)} (t = 3, 4, \ldots) \). Data on plants with fewer than three flower heads were omitted from these analyses.

We estimated the discounting rate for interplant movement (\( k \)) using the observed values of time per head, flight time between heads, and flight time between plants. From the observed distribution of each parameter, we randomly selected one value and calculated the discounting rate (\( k \)) based on equation 1. We repeated this procedure 10 000 times for each density area to estimate the mean \( k \) and its 95% confidence limits.

We adopted such a Monte Carlo procedure because the average of a non-linear function of random variables differs from the function's value for averages of these variables (so-called 'fallacy of the averages'; Wagner 1969).

We calculated the optimal number of flower heads probed per plant per bee (\( t^\ast \)) based on equation 3. Again, we carried out a Monte Carlo procedure involving 10 000 randomly drawn input variables for each size of floral display. Values of \( m \) were drawn randomly from a truncated normal distribution (1 ≤ \( m \) ≤ \( k \)) with the parametric mean and standard deviation based on observed values (see above), and \( k \) was calculated as described above (but 0 ≤ \( k \) ≤ 1). For both high- and low-density areas, the predicted \( t^\ast \) with its 95% confidence limits was compared to the observed \( t \) for each display size.

#### Bumble bee revisitation rate per plant/head

We previously found that the per-head and per-plant revisitation rate on a given size of display fluctuated substantially from day to day (Ohashi & Yahara 1998). Therefore we calculated relative revisitation rate per plant as (number of bee visits to focal plant)/(sum of number of bee visits to all observed plants on the same day) for each plant observed during 1997 and 1998. With regard to the number of flower heads probed per plant, we used mean data for each plant to avoid pseudoreplication due to repeated measurements on the same plant. For similar reasons, we calculated relative mean visitation rate per head for each plant as (mean number of bee visits per head on focal plant)/(sum of mean number of bee visits per head over all observed plants). We then related these three measures of bee behaviour with floral display size using linear or non-linear least-squares regressions with the polytope (simplex) method - a numerical procedure that can be used to minimize a function with respect to a set of parameters (Nelder & Mead 1965; for a basic procedure see Nash & Walker-Smith 1987). Further, we performed ANCOVAs with either of the three measures of bee behaviour as the dependent variable, plant density (high or low) as the independent variable, and display size as the covariate. Prior to analyses, we logarithmically transformed the relative visitation rate per plant and the relative mean visitation rate per head to correct for lack of normality and/or inequality of variances (Sokal & Rohlf 1995).

When the slopes of regression lines were not significant, we performed simple comparisons between the high- and low-density area using Mann–Whitney U tests (we did not use log-transformed variables in such cases). When variances significantly differed between areas, we alternatively used tests for equality of medians (Sokal & Rohlf 1995) to avoid a type I and/or type II error due to heterogeneity of variances (Kasuya 2001).

#### Nectar

We performed an ANCOVA on sugar production rate with plant density (high or low) as the independent variable and display size as the covariate. We also performed a model 1 × 3 factorial ANOVA with nectar standing crop as the dependent variable, floral...
display size and plant density as the independent variables. Prior to these analyses, we logistically transformed the dependent variables to correct for lack of normality.

Results

Bumble Bee Behaviour

The overall rate of flower-head revisitation by bumble bees on a plant (r) averaged 0.025 (n = 24, SE = 0.002) at high density and 0.074 (n = 27, SE = 0.009) at low density. At both densities, overall revisitation rate (r) increased with the size of floral display (F) (high density: \( r = 0.11 + 0.001 F, n = 24, R^2 = 0.21, P = 0.024 \); low density: \( r = 0.005 + 0.007 F, n = 27, R^2 = 0.26, P = 0.0069 \)), with a stronger increase at low density than high density (df = 1, 43, \( F = 5.43, P = 0.024 \)). For each plant, the likelihood of revisitation (r) increased linearly with the position of a head in a visit sequence after probing a few non revisited heads (Fig. 2). The transition from no revisits to increasing revisits (\( r = m + 1 \)) occurred after an average (±SE) of 3.0 ± 0.26 heads or 2.3 ± 0.23 heads in the high- and low-density areas, respectively. The risk of revisitation increased less rapidly with successive probings on large displays than on small displays (Fig. 2). The estimated slope of the regression line was negatively correlated with display size (Fig. 3). The slope of this relation in the low-density area was 2.3 (1997) or 3.0 times (1998) greater than in the high-density area (df = 1, 32, \( F = 23.0, P < 0.0001 \); df = 1, 38, \( F = 18.5, P = 0.0053 \) in 1998).

Flight time between plants varied significantly between high and low densities (high density: \( n = 60, \text{mean} \pm \text{SE} = 4.21 \pm 0.28 \) s; low density: \( n = 49, \text{mean} \pm \text{SE} = 7.43 \pm 0.41 \) s; \( U = 522.5, P < 0.0001 \), Mann–Whitney U-test). On the other hand, the estimated memory size did not vary significantly with floral display size (high density: \( n = 24, r = 0.13, P = 0.55 \); low density: \( n = 27, r = 0.095, P = 0.64 \)).

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Bumble bees probed fewer heads per plant than expected, although the observed means always fell within the 95% confidence limits of the predictions (Fig. 3). Bees usually left a plant spontaneously, but interference by other pollinators (including bumble bees and other visitors) or vespid wasps caused about 12% of departures (data on 17 plants in 1998).

The number of flower heads that bees probed per plant (\( t_r \)) increased linearly with, but less rapidly than, floral display size (Fig. 3). The slope of this relation in the low-density area was 2.3 (1997) or 3.0 times (1998) greater than in the high-density area (df = 1, 32, \( F = 23.0, P < 0.0001 \) in 1997; df = 1, 38, \( F = 18.5, P = 0.0053 \) in 1998).

The relative visitation rate per plant increased in a decelerating manner with floral display size during 1997 (Fig. 4), but this pattern was not evident during 1998, when we observed few small displays. Visitation rate per plant increased more rapidly in both years and reached a higher maximum in the high- than in the low-density area (intercept: \( df = 1.33, F = 18.5, P = 0.0001 \) in 1997; \( df = 1.13, F = 34.4, P < 0.0001 \) in 1998; slope: \( df = 1.32, F = 0.55, P = 0.47 \) in 1997; \( df = 1.12, F = 0.044, P = 0.84 \) in 1998, ANCOVA for log-transformed dependent variable).

During 1997, the average visitation rate per head per hour varied among plants from 0.84 to 14.4. The relative mean visitation rates per head (\( V_r \)) at both densities did not vary significantly with floral display size (Fig. 5a); high density: \( n = 16, F = 2.00, P = 0.18 \);
low density: \(n = 20, F = 0.51, P = 0.49\). We detected no significant difference in \(V_f\) between the high- and the low-density area (\(U = 121, 0, P = 0.21\), Mann–Whitney \(U\)-test). During 1998 the average visitation rate per head per hour varied among plants from 2.42 to 16.8. The relative mean visitation rate per head \(\bar{V}_f\) did not vary with floral display size (Fig. 5b; high density: \(n = 8, F = 0.30, F = 0.60, P = 0.039, P = 0.85\), nor between the two areas (\(U = 31, 0, P = 0.92\), Mann–Whitney \(U\)-test). Thus bumble bees utilized large and small displays equally in terms of average visitation rate per head. Within each plant, however, variation in visitation rate differed greatly among flower heads (CV = 0–77.3%, data on 21 plants in 1997).

**Mean nectar sugar production rate of a flowering head** \(\left(\mu g\mbox{ sucrose floret}^{-1}h^{-1}\right)\) did not vary with floral display size (Fig. 6). Furthermore, plants in the high- and low-density area produced equivalent amounts of nectar sugar (high density: \(n = 18, \bar{V}_f = 16.7 \pm 2.1 \mu g\mbox{ floret}^{-1}h^{-1}\), low density: \(n = 20, \bar{V}_f = 16.0 \pm 1.5 \mu g\mbox{ floret}^{-1}h^{-1}\); Fisher’s exact probability = 0.63, test for equality of medians). In addition, the number of florets per head did not vary with floral display size (\(n = 20, r = 0.12, P = 0.63\)). Thus, irrespective of floral display size, *C. purpuratum* provided similar nectar rewards per head for pollinators. On each plant, however, there seemed to be some variation in nectar productivity among heads, derived from their asynchronous flowering (CV of flower-head age within a plant per day = 0–47.1%, data on 12 plants in 1997).

Standing crop of nectar in flowering heads \((n = 144\) heads, mean \(\pm SE = 16.9 \pm 1.8 \mu g\mbox{ floret}^{-1})\) varied neither with display size (df = 1.140, \(F = 0.60, P = 0.44\))

**NECTAR AVAILABILITY**

Mean nectar sugar production rate of a flowering head (\(\mu g\mbox{ sucrose floret}^{-1}h^{-1}\)) did not vary with floral display size (Fig. 6). Furthermore, plants in the high- and low-density area produced equivalent amounts of nectar sugar (high density: \(n = 18, \bar{V}_f = 16.7 \pm 2.1 \mu g\mbox{ floret}^{-1}h^{-1}\), low density: \(n = 20, \bar{V}_f = 16.0 \pm 1.5 \mu g\mbox{ floret}^{-1}h^{-1}\); Fisher’s exact probability = 0.63, test for equality of medians). In addition, the number of florets per head did not vary with floral display size (\(n = 20, r = 0.12, P = 0.63\)). Thus, irrespective of floral display size, *C. purpuratum* provided similar nectar rewards per head for pollinators. On each plant, however, there seemed to be some variation in nectar productivity among heads, derived from their asynchronous flowering (CV of flower-head age within a plant per day = 0–47.1%, data on 12 plants in 1997).

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Relative mean visitation rate per head

Fig. 5. Observed relationships between relative mean visitation rate per head (V) and floral display size (number of flowering heads per plant, F). Data in (a) 1997, (b) 1998. During both years and in both areas these variables were not significantly correlated with each other (see text).

Fig. 6. Relationships between nectar productivity of a flowering head and floral display size (number of flowering heads per plant, F). In both areas these variables were not significantly correlated with each other (see text).

The estimated memory size of bumble bees was between one and two heads (Fig. 2). This suggests that bumble bees store spatial information on previously probed flower heads in spatial working memory (or short-term memory) with limited capacity and persistence. This appears to contradict the fact that bees often exhibit large long-term memory capacity for spatial information, such as the location of the nest and flower patches (Menzel et al. 1996). In nature, however, bees often probe hundreds of flowers successively during one foraging trip, in which case spatial working memory may be more efficient than long-term memory in terms of processing speed and flexibility. Honeybees also use spatial working memory to avoid flower revisitation instead of long-term memory (Brown & Demas 1994; Brown et al. 1997). It is unclear why bumble bees began revisiting previously probed heads slightly later on a plant in the high-density than in the low-density area. This may reflect some flexibility in bees’ foraging strategy in response to plant density. Otherwise, bees might use neighbouring plants as temporal signposts or landmarks in the high-density area. For example, Redmond & Plowright (1996) have reported that bumble bees avoid flower revisitation more efficiently when landmarks are available.

As a consequence of this small memory size, the risk of flower-head revisitation increased linearly with the position of a head in a visit sequence after just two or three heads had been probed (Fig. 2). Because bees depleted the nectar in heads to 20% of the initial crop, our result indicates that increasing risk of flower-head revisitation caused a gradual decrease in the rate of gain per head (patch depression). This role of flower revisitation in patch depression has been poorly appreciated because bees seldom revisit flowers: 2.9% (Pyke 1979); 3.5% (Pyke 1982); 0.2 and 3.0% (Galen & Plowright 1985). However, we observed patch depression even though bees revisited 5.1% of the heads they probed. Several previous studies have also found that a pollinator is increasingly likely to revisit flowers as it stays longer on a plant or inflorescence (Pyke 1978, Pyke 1981, Pyke 1982, Redmond & Plowright 1996).

Flower-head revisitation rate increased more slowly on larger displays (Fig. 2). This is simply because larger displays offer more flower heads from which to choose and relieve the risk of flower-head revisitation, as predicted in equation 2 and Fig. 1(a). Pyke (1982) also reported a similar result in bumble bees foraging on Aconitum columbianum (Table 14 of Pyke 1982). Previous authors have often considered the spatial gradient of nectar crops per flower as the cause of patch depression (Best & Bierzychudek 1982; Hodges 1981; Hodges 1985). However, as Pyke (1982) pointed out, spatial structuring of nectar crops alone cannot explain why pollinators...
tend to be more tenacious on larger displays, because flowers on large displays often contain the same nectar distribution as those on small displays (Pyke 1978, Pyke 1982; Wolf & Hansworth 1986; this study, but see Hodges 1985). We suggest therefore that the risk of flower revisitation, as well as nectar distribution pattern, is important in understanding pollinator behaviour on plants.

RESPONSES TO VARIATION IN FLORAL DISPLAY SIZE AND PLANT DENSITY

As has been observed repeatedly for other species (reviewed by Goulson 2000; Ohashi & Yahara 2001), the number of heads that bumble bees probed per plant increased less than proportionally with floral display size, so that the proportion of flower heads probed per bee \( (r/F) \) declined with display size (Fig. 3). This increase in the number of heads probed per plant was significantly slower in the high- than in the low-density area (Fig. 3). Ohashi & Yahara (1999) (see Fig. 1b) proposed that this change would result because bees decrease the marginal level of revisitation for leaving a plant (dashed line, Fig. 1a) at higher plant density, which reduces the difference in number of flower heads probed per plant between large and small displays \( (t_i - t_o) \).

We also found that visitation rate per plant increased at a decelerating rate with floral display size (Fig. 4). A decelerating increase of visitation rate per plant with increasing display size has been reported in previous studies (reviewed by Iwasa, de Jong & Klinkhamer 1995; but see Anderson 1988; Ohara & Higashi 1994; Sih & Baltus 1987). As predicted, visitation rate per plant increased more strongly with increasing display sizes at higher plant density (Fig. 4).

The preference for visiting larger displays counter-balanced the decline in the proportion of flower heads probed by a bee on larger displays, so that the average visitation rate received per head did not vary with display size, irrespective of plant density (Figs 3 – 5). This strongly suggests that bees preferred to visit large displays because a decline in the proportion of heads probed per plant reduced the competition among bees on these plants. Because neither nectar production rate per head, nor head size (floret number per head), varied with floral display size of the plant, an equalization of the visitation rate per head means that bumble bees gained equal nectar rewards per head on all sizes of display – they achieved an IFD. As a result of this, flower heads on large and small displays contained the same amounts of nectar crop. Dreissig (1993) found that foraging bumble bees achieved an IFD by visiting individual Anchusa officinalis and Viscaria vulgaris according to its nectar productivity and the proportion of flowers that a bee probed on that plant. Similarly, with regard to pollen foragers Robertson et al. (1999) reported that bumble bees responded to genetic variation in pollen quality (proportion of inviable pollen grains) among Mimulus guttatus plants by visiting the high-quality patch more often and by visiting more flowers within the patch.

We do not emphasize that the distribution of bumble bees conformed strictly to an IFD. Some authors have noticed that the restrictive assumptions for the continuous input IFD model (see above) are often violated under natural conditions (Kennedy & Gray 1993; Mlmkisi 1994). In addition, we found that the overall rate of flower-head revisitation \( (r_c) \) increased with display size, especially at low plant density. Ohashi & Yahara (1999) predicted that this would result because the ratio of \( m \) to \( t \) declines with display size and plant density. If bees could detect these subtle differences in the rate of energy gain among plants and adjust their distributions to a complete IFD, the average visitation rate per head might have varied with display size. However, such effects seemed too small to affect actual bees’ visitation. Thus an equalization of the visitation rate per head among plants observed here can be regarded as a quasi-IFD.

The strategies that individual bumble bees might use to achieve an IFD are still open to question. As Dreissig (1995) suggested, bees’ preferences for visiting large floral displays may partly explain the IFD. It should be noted, however, that the observed visitation rates per plant cannot be viewed simply as an amplified pattern of ‘individual bees’ choice in relation to floral display size. Individual bumble bees frequently confine their foraging to small areas within a larger plant population, and they appear to overlap their foraging areas (Williams & Thomson 1998). Therefore a bee has to adjust the degree of overlap in its foraging area with others, while deciding how often it should visit each size of display. It has been suggested that bumble bees have some abilities needed for such complicated adjustments. For example, bees are known to fly longer distances after encountering lower rewards (area-restricted searching; reviewed by Motro & Shmida 1995). By adopting this rule while foraging along its own foraging route (trapline; Thomson 1996 and references therein), bees may efficiently reduce the spatio-temporal bias in nectar distribution. To clarify how these foraging patterns contribute to an IFD, a detailed description is required of individual bees’ behaviour and their use of space.

QUANTITATIVE PREDICTIONS OF NUMBER OF FLOWER HEADS PROBED PER PLANT

The predicted optimal number of flower heads probed per plant was generally larger than that observed.
Another possibility is the assumption of our model that the bees have ‘complete information’ on nectar distributions within plants – that information obtained while foraging on a plant is of no value for their decision-making. In nature, pollinators rarely have complete information and their environment is usually stochastic, so that they appear to use full or partial information gained at each flower to decide when to leave a plant; pollinators often leave a plant just after probing one or two flowers with little or no nectar (Hodges 1985; Pyke 1978; Pyke 1982; Thomson, Maddison & Flowlright 1982).

Such simple probabilistic rules may provide a practical method to approach a mathematical optimum in nature (see also Iwasa, Higashi & Yamamura 1981; McNamara & Houston 1980). We assumed complete information because our aim was simply to find an optimum plant departure, rather than patch-leaving rules that visitors actually follow. However, this difference might result in a quantitative discrepancy between expectation and observation.

Conclusions

Recent empirical research on plant–pollinator interactions has identified a puzzling feature of pollinator foraging behaviour in response to the decrease in plant density. First, pollinators may be attracted less strongly to plants growing at lower densities (Kunin 1997). Second, nectar-collecting bumble bees achieve an ideal free distribution.

(Prob. 3) The most probable reason for this discrepancy is the variation in nectar productivity among heads within a plant. All available flower heads on a plant were used to quantify the size of floral display. However, flower age varied greatly among heads within a plant, so that this might result in a substantial variation in nectar productivity among heads. If bees probed older and less rewarding heads infrequently, as has been reported in other systems (Cruzan, Neal & Willson 1988; Gori 1983; Oberschall & Bohning-Gaese 1999), the realized mean number of heads probed per plant would be fewer than that predicted.

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Nectar-collecting bumble bees achieve an ideal free distribution


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