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Flower choice by honey bees (*Apis mellifera* L.): sex-phase of flowers and preferences among nectar and pollen foragers

Abstract Bees foraging for nectar should choose different inflorescences from those foraging for both pollen and nectar, if inflorescences consist of differing proportions of male and female flowers, particularly if the sex phases of the flowers differ in nectar content as well as the occurrence of pollen. This study tested this prediction using worker honey bees (*Apis mellifera* L.) foraging on inflorescences of *Lavandula stoechas*. Female flowers contained about twice the volume of nectar of male flowers. As one would predict, bees foraging for nectar only chose inflorescences with disproportionately more female flowers: time spent on the inflorescence was correlated with the number of female flowers, but not with the number of male flowers. Inflorescence size was inversely correlated with the number of female flowers, and could be used as a morphological cue by these bees. Also as predicted, workers foraging for both pollen and nectar chose inflorescences with relatively greater numbers of both male and female flowers: time spent on these inflorescences was correlated with the number of male flowers, but not with the number of females flowers. A morphological cue inversely associated with such inflorescences is the size of the bract display. Choice of flowers within inflorescences was also influenced predictably, but preferences appeared to be based upon corolla size rather than directly on sex phase.

Key words *Apis mellifera* · *Lavandula stoechas* · Pollen content · Nectar content · Foraging preference

Introduction

Heterogeneity in resource availability is a major problem for foraging animals: the problem has been much studied in flower-visiting insects, particularly bees. In the face of

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this heterogeneity, bees can enhance their foraging returns by taking advantage of inflorescence or floral cues that signal resource availability, or by adopting behavioural mechanisms that manipulate resources, such as traplining (Corbet et al. 1984). This paper addresses the use of plant cues, and how this is affected by what resource the bee is collecting.

Several studies have suggested that bees can choose flowers by assessing nectar content directly (Cameron 1981; Bell et al. 1984; Marden 1984a), or by using the odour of previous visiting workers to avoid depleted flowers (e.g. Schmitt and Bertsch 1990, Giurfa and Nuñez 1992, 1993). Other analyses indicate that morphological cues rather than nectar content influence preferences for inflorescences, and imply that such cues could provide the basis for preferences in the absence of recently deposited odour cues (Barrow and Pickard 1984; Galen and Newport 1987; Harder 1988; Duffield et al. 1993): bees can be attracted to plants on the basis of morphology, for instance preferring larger plants with more flowers (e.g. Geber 1985; Primack and Kang 1989; Ohara and Higashi 1994). Plant and/or flower morphology has occasionally been correlated with nectar production (e.g. Marden 1984b; Zimmerman and Pyke 1986; Harder and Cruzan 1990), indicating an adaptive reason for choice based on morphology.

Recently, Duffield et al. (1993) presented evidence that worker honey bees foraging on French lavender (*Lavandula stoechas*) used morphological characteristics of inflorescences and individual flowers within inflorescences in deciding where to forage. The characteristics that these bees apparently preferred enabled selection of flowers with a greater than average nectar volume and sugar mass. The main feature affecting choice of inflorescence was the number of open flowers on the head. Although the number of open flowers correlated positively with measures of nectar content per flower (i.e. flowers in large inflorescences had a disproportionately high mean nectar content), nectar content varied considerably.

One obvious potential factor contributing to variance in nectar content is the sex of flowers, well known to in-

fluence nectar production (e.g. Thomson et al. 1982; Bell et al. 1984, Willson and Agren 1990); bees might benefit by choosing flowers of one sex rather than another. The sex of flowers within inflorescences also influences other resources available to bees, since female-phase flowers offer no pollen (see Thomson et al. 1982; Seeley 1985). Consequently, workers foraging for nectar, which may be produced in profitable quantities by both sexes of flower, are likely to differ in their preferences from those foraging for pollen (e.g. Galen and Plowright 1985). The association between the number of open flowers on an inflorescence and choice by bees might thus conceal more complex influences of floral characteristics on preference.

In this study we looked for evidence of choice, based on flower sex, by bees foraging on *L. stoechas*, following on from our previous study (Duffield et al. 1993). The flowers of *L. stoechas* are hermaphroditic and strongly protandrous (Devesa et al. 1985, Muñoz and Devesa 1987). Inflorescences are almost cylindrical aggregations of dichasia at the top of a long peduncle and are terminated by several showy, sterile, purple bracts that vary in number and size between heads (Herrera 1991). Dichasia are arranged in varying numbers into vertical columns, with each dichasium bearing five flowers (Herrera 1991). Anthesis of the first flower within dichasia ("central" flowers; Herrera 1991) is synchronous and occurs over the first 10 days of the 40–50 day blooming period of an inflorescence. Within inflorescences, anthesis of central flowers does not overlap that of the four remaining ("lateral"; Herrera 1991) flowers in a dichasium (Herrera 1991). During the blooming period, therefore, inflorescences bear varying numbers of open flowers at different stages of bloom and thus of each sexual function. Sex-phase differences in nectar content (e.g. Thomson et al. 1982; Bell et al. 1984) and variation in the number of flowers of each sex-phase could thus lead to considerable variation in the profitability of inflorescences with any given number of open flowers.

Here, we examine whether the sex-phase of flowers does indeed influence choice of inflorescences, and possibly individual flowers within inflorescences, in bees foraging for nectar only, or for pollen and nectar. We asked the following questions:

1. Does the sex-phase of flowers at the time of sampling influence their resource value to foraging bees?
2. Does (a) the choice of inflorescence, and (b) the time spent on an inflorescence by bees depend on the number of flowers of each sex-phase as expected in bees foraging for nectar and for both nectar and pollen?
3. Does the choice of flowers within inflorescences depend on sex-phase as expected in bees foraging for nectar and for both nectar and pollen?

Methods

Observations were made during 10 days in April 1993 in the 16×16 m area of shrubland in Portugal (Quinta de Sao Pedro field station, Sobreda de Caparica; 38°39′ N, 9°11′ W) studied by Duf-

field et al. (1993). *L. stoechas* was the dominant shrub within the area and was visited predominantly by bees from the same two nearby hives as in the study of Duffield et al. (1993). Bees were observed foraging on inflorescences of *L. stoechas* between 0800 and 1630 hours, depending on the start of foraging activity on different days and the difficulty of collecting nectar samples later in the day when nectar volumes had been depleted by harvesting and/or evaporation.

Sex-phase of flowers and nectar availability

Flowers could be sexed easily in the field, since the anthers of male-phase flowers bore variable quantities of easily visible, bright yellow pollen, whereas the anthers of female-phase flowers were withered and white. Flowers that could not be sexed immediately on superficial inspection were examined under a handlens at ×10 magnification and classified as male if anthers appeared functional and/or bore any pollen. We could thus assign all flowers studied to one sex-phase or the other.

To determine sex differences in nectar content, 21 randomly-chosen inflorescences distributed across five randomly chosen bushes were bagged with muslin between 1700 and 1900 hours on 2 days to prevent harvesting. Before bagging, a number of morphological and other measures associated with nectar content (Duffield et al. 1993) were taken for each inflorescence (Table 1). The following morning, each bagged inflorescence was removed in turn and its flowers sampled for nectar content. Individual flowers were sexed, removed gently from the inflorescence, and the nectar extracted from the open posterior end of the corolla using a 1-μl Camlab disposable microcapillary tube. Nectar volume was measured as the length (mm) of capillary uptake and concentration as g sucrose/100 g solution using Bellingham and Stanley handheld refractometers calibrated between 0–50% and 40–85%. Based on nectar volume and concentration we then calculated the mass (μg) of sugar in each flower using the equation of Búrquez and Corbet (1991; see Duffield et al. 1993). Because it was not possible to measure concentration accurately for small nectar volumes, there are no estimates of concentration and sugar mass for some samples (see below and Duffield et al. 1993) and these are omitted from the analysis.

Choice of inflorescence by bees

We selected individual bees foraging on *L. stoechas* flowers opportunistically. Once selected, focal bees were classified as either (1) foraging for pollen (or pollen and nectar) (pollen/nectar foragers) or (2) foraging only for nectar (nectar-only foragers) based on the presence or absence respectively of conspicuous yellow pollen in the corbiculae. Any bee that could not be classified unambiguously was ignored. Of course, some bees may have been misclassified because, for example, a pollen/nectar forager might have collected little or no pollen at the time of observation; however,

Table 1 The morphological and other variables measured for each inflorescence

1	Time of day (hour+minutes)
2	Ambient temperature (°C) at the inflorescence, using a hand-held RS-Components digital thermometer held within 2 mm of the inflorescence
3	Height (cm) of the inflorescence base above the ground
4	Inflorescence length (mm) from its base to the base of the terminal bracts
5	Inflorescence width (mm) at its centre
6	Total number of open flowers on the inflorescence
7	Total number of female flowers
8	Total number of male flowers
9	Number of terminal bracts
10	Length (mm) of the longest terminal bract

given the large number of flowers visited by individual bees, such misclassification probably involved few if any bees, and thus has little influence on the results. As in the study of Duffield et al. (1993), we watched each focal bee until it responded to an inflorescence in one of three ways, which identified the inflorescence as:

1. *Visited (V)* – the bee alighted and probed at least one flower with the proboscis before departing;
2. *Rejected (R)* – the bee inspected flowers in flight (one or more flowers were touched with the antennae or legs) but did not alight; or
3. *Ignored (I)* – the bee approached the inflorescence but then avoided it by changing course without pausing or contacting flowers.

We then measured the characteristics in Table 1 for each inflorescence.

Time spent on inflorescences by bees

Focal bees were selected and classified as above and followed until they alighted on an inflorescence (therefore type V above). We timed the period between the bee alighting on and leaving the inflorescence to the nearest 0.01s using a digital stopwatch, and then measured the characteristics in Table 1 for the visited inflorescence.

Choice of flowers within inflorescences

Focal bees were selected, classified and followed to a V inflorescence as above. Once the bee alighted, we recorded the sequence of flowers probed ("sampled" flowers) and passed over without probing ("ignored" flowers) by marking the appropriate flowers with a small dot of enamel paint as the bee moved around the inflorescence. The time bees spent on each flower was obtained by transcribing real-time commentary on magnetic tape. When the bee departed, we measured for each sampled and ignored flower the maximum diameter of the corolla of each open flower on the inflorescence (see also Duffield et al. 1993), and characteristics 3–10 in Table 1 were recorded for each inflorescence.

Statistical analysis

We used a variety of parametric and non-parametric tests, the latter where data were distributed non-normally. We used principal components analysis (PCA) on inflorescence morphology as a data-reduction technique, to reduce the data to its main uncorrelated axes of variation. In this we used two variables (number of male and number of female flowers) that were probably not normally distributed: although PCA is a parametric technique, it is sufficiently robust to withstand departures from normality (Reyment 1971), and is here not being used for statistical testing, for which the assumption of normality is more critical (Manly 1986). Our other multivariate technique, discriminant function analysis (DFA), was used on the scores of the principal component axes, which are normally distributed.

Results

The distribution and nectar content of male- and female-phase flowers

Inflorescences varied considerably in the number, ratio and spatial distribution of male- and female-phase flowers. Female flowers predominated, with inflorescences bearing on average over 5 times more female flowers (mean ± SE per inflorescence = 11.59 ± 0.69, n = 145) than male (2.24 ± 0.18, n = 145) at the time of sampling

Table 2 The influence of floral sex phase on nectar characteristics in 21 heads on five bushes of *Lavandula stoechas*. The smaller sample sizes in the actual tests result from some heads being unisexual, and in some we had too small volumes to be able to measure concentrations

	Female	Males	Paired t	df	P
Volume (μl$\times 10^{-3}$)	93±20	47±10	2.15	14	<0.05
(subset of volumes where concentrations could be measured:			0.16	7	ns)
Concentration (%)	44±4	51±4	0.63	7	ns
Sugar mass (μg)	2.4±0.3	2.6±0.3	0.98	7	ns

(large-sample Mann-Whitney z = 11.47, n = 290, $P \ll 0.001$). Of the inflorescences sampled 23% bore no male flowers at all at the time of sampling. The spatial arrangement of male and female flowers on the head showed little consistency. Although male flowers tended to occur higher on the head, there was no significant difference between the sexes in either their relative (number in vertical sequence) or absolute (distance in mm from the base of the inflorescence) position on the vertical axis of the inflorescence.

Paired t-tests comparing floral sex-phase within inflorescences (and thus controlling for differences in nectar production between heads – Duffield et al. 1993) revealed a significant difference in nectar volume, with females yielding twice the volume of males, but no differences in concentration or sugar mass (Table 2). This apparent contradiction arises because of the smaller sample sizes for the latter, caused by the very small volumes of nectar present in many flowers, particularly males: in the subset of heads where concentrations could be measured in both male and female flowers, there was no difference in nectar volume (Table 2).

Sex-phase of flowers and choice of inflorescence by bees

Based on the difference in nectar content between male and female flowers and the finding of Duffield et al. (1993) that foraging preferences by honey bees on *L. stoechas* vary with nectar volume, but not concentration, we would expect nectar-only foragers to prefer inflorescences with more female flowers, but pollen/nectar foragers to favour inflorescences with more flowers of both sexes.

Several morphological characteristics of inflorescences could be used by bees to indicate, directly or indirectly, the number of each sex-phase of flower and/or one or more measures of nectar content per flower. Since preferences by bees might be based directly on the number of flowers of either sex or on other characteristics of inflorescences that correlate with the number of flowers, we included inflorescence length, width, height above the ground, terminal bract conspicuousness (number of bracts, maximum length) and the number of open flowers of each sex-phase in analyses.

Table 3 Principal components analysis of morphological variables of inflorescences

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	2.3	1.2	1.1	1.0
% Variance	33.1	16.8	15.5	14.7
Cumulative %	33.1	49.8	65.3	80.0
		— loadings —		
Original variables				
Number of male flowers	0.04	−0.62	−0.16	0.58
Number of female flowers	0.28	−0.16	−0.70	0.10
Height of inflorescence	0.30	−0.10	−0.44	−0.62
Inflorescence length	0.53	−0.18	0.31	−0.15
Inflorescence width	0.43	−0.41	0.44	−0.11
Number of bracts	0.43	0.48	−0.04	0.15
Length of longest bract	0.44	0.38	−0.00	0.45

Table 4 Results of discriminant function analyses of the scores on the principal components of Table 2, using data for bees foraging on nectar only, and on both nectar and pollen. The analysis attempts to discriminate between data for "visited", "rejected", and "ignored" inflorescence

	Pollen/nectar bees		Nectar-only bees	
	DFA 1	DFA 2	DFA 1	DFA 2
Eigenvalue	0.35	0.05	0.14	0.12
χ^2 (see note 1)	19.4	2.7	20.4	2.4
df	8	3	8	3
Significance	<0.02	ns	<0.01	ns
Original variables	Standardized coefficients			
PCA 1	−0.22	0.55	0.17	0.95
PCA 2	0.84	0.25	0.21	0.10
PCA 3	0.77	−0.49	0.92	−0.15
PCA 4	−0.06	0.93	−0.35	−0.12
Group centroids				
Visited	−0.83	−0.07	−0.38	0.08
Rejected	0.24	0.28	0.49	0.08
Ignored	0.54	−0.23	0.02	−0.21
% Correctly classified	55		46	

[1] Based on Wilks' λ

These variables are intercorrelated, making interpretation of the results complicated. We therefore used a PCA of the (standardized) variables to generate a set of uncorrelated composite variables. As Table 3 demonstrates, the main axis of variation, axis 1, accounting for 33% of the variation, is mostly a general size axis: this interpretation is based upon the loadings, which are of the same sign and, apart from the loading on the number of male flowers, the same approximate magnitude (see Blackith et al. 1979). The second and fourth axes contrast the number of male flowers with bract display and inflorescence height respectively, whereas the third axis contrasts the number of female flowers against inflorescence size. The first four axes together account for 80% of the variation.

We wanted to discriminate between inflorescences visited and those rejected or ignored by bees; this was done by DFA, to identify variables associated with choice of inflorescences by our focal bees. We split the data into nectar/pollen and nectar-only bees, and performed separate analyses on each. The prediction was that choice of inflorescences in nectar-only bees would be associated with axis 3 (with a high positive loading on the number of female flowers, which contain more nectar), whereas choice in pollen/nectar bees would be associated with both male and female flowers, i.e. axes 2 and/or 3 (and possibly also axis 4, which like axis 2 also has high loadings on the number of male flowers).

In the results of both discriminant function analyses, the first axis was significant (see Table 4). For nectar-only bees, as predicted, the difference between inflorescences visited and those not visited lay in those characteristics associated with axis 3, i.e. related to the number of female flowers: because axis 3 is also associated with inflorescence size, the latter could be used by bees as a more readily identifiable morphological indicator of the number of female flowers. The coefficient for axis 3 on the first discriminant function is positive (Table 4), and axis 3 is negatively associated with the number of female flowers (Table 3). Visited inflorescences are at the negative end of the discriminant function (Table 4), implying that visited inflorescences have *more* female flowers;

similar reasoning shows that visited inflorescences are relatively small.

Also as predicted, choice of inflorescences for pollen/nectar bees is associated with axis 2 and, to a lesser extent, axis 3: again, axis 2 is a composite of the number of male flowers and more readily usable morphological indicators, namely the bract display and inflorescence height. The coefficients of the discriminant function and the principal component axes, together with the mean position of visited inflorescences on the discriminant function, show that visited inflorescences have relatively more (female and male) flowers than either Rejected or Ignored inflorescences, and have a relatively small bract display.

The DFAs thus imply that the two types of forager select inflorescences on different criteria. Figure 1a shows that inflorescences visited by nectar-only foragers contained significantly more female flowers than on either rejected or ignored inflorescences, but the number of male flowers did not differ. On the other hand, inflorescences visited by pollen/nectar foragers had significantly more flowers of both sexes (Fig. 1b).

Sex-phase of flowers and time spent on inflorescences

Floral sex also affected time spent by the two types of bee on inflorescences (Fig. 2). For nectar-only bees, the time spent on an inflorescence increased significantly with the number of female flowers (Fig. 2a) but not with the number of male flowers (Fig. 2b). In contrast, for pollen/nectar bees, residence time increased with the number of male flowers (Fig. 2c) but not female flowers (Fig. 2d). The relationship between residence time and
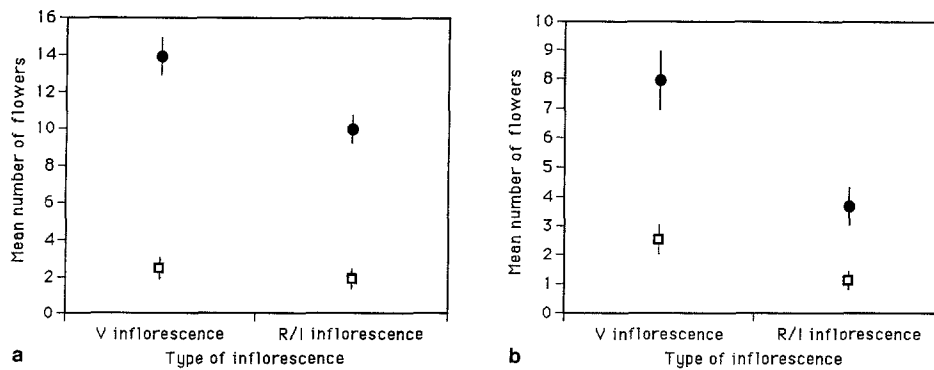
Fig. 1 The mean (± SE) number of female (*filled circles*) and male flowers (*open squares*) on the three categories of inflorescence (*V* visited, *R,I* rejected or ignored). The prediction is that nectar foragers should visit inflorescences with more females but should not respond to the number of males; pollen/nectar foragers should visit inflorescences with more flowers of either sex: these specific hypotheses were tested using non-parametric anova (see Meddis 1984) for: **a** nectar-only foragers (females, $z = 3.00$, $P < 0.01$; males, $H = 2.53$, 2 *df*, ns); **b** pollen/nectar foragers (females, $z = 2.28$, $P < 0.05$; males, $z = 3.44$, $P < 0.001$)

the number of flowers of each sex was thus consistent with the availability of the resources gathered by the two types of bee.

Sex-phase and choice of flowers within inflorescences

Surprisingly, there was no direct evidence of bias towards flowers of a given sex within inflorescences. Nei-

Fig. 2a–d The relationship between residence time (s) and the numbers of flowers on inflorescences among: nectar-only foragers for **a** female flowers (test of regression slope, $t = 3.76$, $df = 59$, $P < 0.005$), **b** male flowers ($t = 0.12$, $df = 59$, ns); pollen/nectar foragers for **c** female flowers ($t = 0.91$, $df = 39$, ns) **d** male flowers ($t = 2.08$, $df = 39$, $P < 0.05$)

ther type of bee probed flowers of one sex more than the other since there were no rank correlations between the proportion of flowers probed and the proportion of male flowers (nectar-only, $r_s = 0.19$, $n = 25$, ns; pollen/nectar, $r_s = -0.20$, $n = 10$, ns), and probing time did not differ between sexes (Kruskal-Wallis test: nectar-only $H = 0.98$, $n = 84$, ns; pollen/nectar $H = 0.01$, $n = 45$, ns).

However, relationships between bee response and flower morphology imply an indirect bias in the expected direction, at least by pollen/nectar foragers. Male flowers (mean ± SE = $3.04 ± 0.10$ mm, $n = 30$) had significantly broader corollas than female flowers ($2.77 ± 0.04$ mm, $n = 128$: 1-way ANOVA for the difference, $F_{1,156} = 7.1$, $P < 0.01$). When the tendency to probe and time spent on probed flowers were analysed with respect to corolla diameter rather than flower sex, differences between bee types emerged which were consistent with expectation. We used a multifactor ANOVA on corolla diameter, with factors of floral sex (male, female), bee type (nectar-only, pollen/nectar), and choice (probed, ignored). The data came from bees foraging on 34 inflorescences: since the three-way interaction of the full factorial model was not significant, we used a model with only two-way interactions. For pollen/nectar foragers, the corolla diameter of sampled flowers ($3.3 ± 0.1$, $n = 46$) exceeded that of ignored flowers ($2.6 ± 0.2$, $n = 7$), but this was not the case for nectar-only foragers ($2.9 ± 0.1$ and $2.8 ± 0.1$ respectively) (interaction $F_{1,151} = 4.6$, $P < 0.05$). Similarly probing time varied positively with corolla diameter for pollen/nectar foragers (Fig. 3a) but not for nectar-only foragers (Fig. 3b).

Interestingly, for all foragers together, visited female flowers had larger corolla widths (mean $2.83 ± 0.05$) than ignored ones ($2.50 ± 0.10$) (1-way ANOVA for the difference, $F_{1,126} = 8.4$, $P < 0.01$), and in females corolla width varied positively with nectar volume ($r_s = 0.19$, $n = 184$, $P < 0.01$) but not with sugar weight ($r_s = 0.08$, $n = 88$, ns). There were no such relationships for male flowers ($F_{1,28} = 1.8$, ns; $r_s = 0.10$, $n = 86$, ns, and $r_s = -0.38$, $n = 25$, ns respectively).
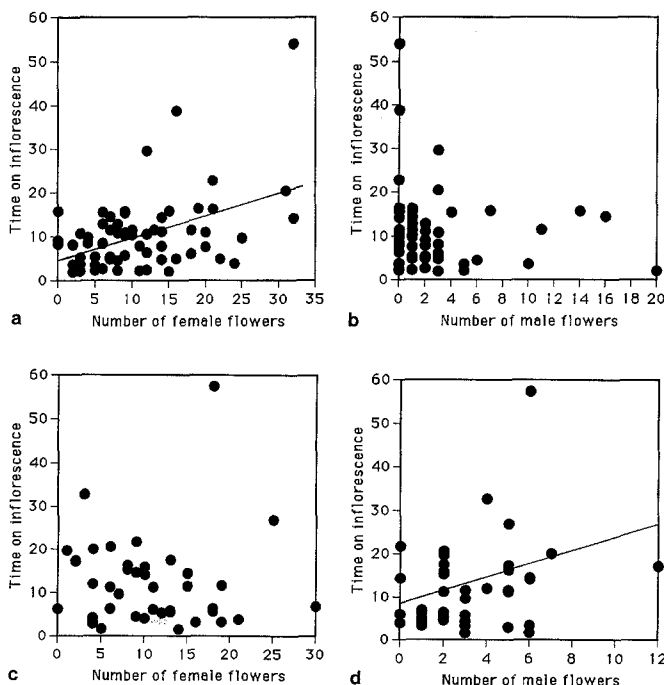
Discussion

In *L. stoechas* flowers in the female phase contain a greater volume of nectar than those in the male phase, and because there were many more females than males during the study, it is probable that the female phase is
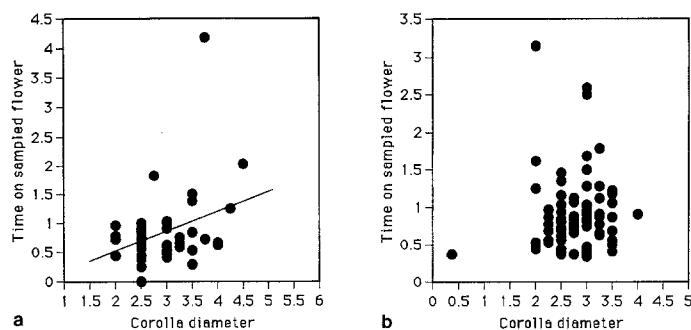
Fig. 3 The relationship between corolla diameter (mm) and probing time (s) for **a** pollen/nectar foragers (test of regression slope, $t = 3.47$, $df = 50$, $P < 0.01$) **b** nectar-only foragers ($t = 0.88$, $df = 103$, ns)

longer. The tendency for heads to comprise predominantly flowers of one sex-phase is probably a function of age. During the first and second weeks of flowering, there is a high degree of synchrony among inflorescences which can bear flowers that are all male-phase or all female-phase at a given time. Older heads are less synchronous and can bear a variety of combinations of male-phase and female-phase flowers (J. Herrera, personal communication to C.J.B.; see also Muñoz and Devesa 1987). Many authors have found differences in nectar standing crop with age and/or gender in cosexual flowers (e.g. Thomson et al. 1982; Bell et al. 1984; Zimmerman and Pyke 1986; Delph and Lively 1989; Klinkhamer and de Jong 1990): Willson and Agren (1990) reviewed gender differences in monoecious and dioecious plants. Females do not always have more nectar than males, however. In our case it is probable that females actually contain more nectar sugar also, but the small volumes made this difficult to show. We conclude that in *L. stoechas* females have more nectar than males, while lacking pollen as a resource for foraging bees. What are the consequences for bees of these differences?

We have previously shown that in this system worker honey bees are influenced in their choice of *L. stoechas* inflorescences by the number of open flowers on the head (Duffield et al. 1993). The present results reveal more subtle influences based on the resources for which bees were foraging and sex-phase differences in the rewards of flowers. Nectar-only foragers preferred the higher volume female flowers, and spent longer foraging on heads with more female-phase flowers, while being uninfluenced by the number of male-phase flowers. In contrast, pollen/nectar foragers preferred heads with more male and female flowers, and foraging time on inflorescences increased with the number of male-phase flowers but was unaffected by the number of females. Bumblebees are known to behave very differently when foraging for nectar as against when foraging for pollen: for example, they differ in visit frequencies to different flower types in the gynodioecious *Phacelia* (Eckhart 1991, 1992), revisitation frequencies and distances moved (Zimmerman 1982), and their arrival positions on an inflorescence match differing reward distributions

(Galen and Plowright 1985). In the experimental study of Thomson (1988), bumblebees responded to manipulated nectar distributions, but not to manipulated pollen rewards. Here we have demonstrated that honey bees foraging for different rewards respond to the appropriate sex-phase flowers.

How do they do this? It is likely that they cue in to morphological features associated with sex phases, since it is difficult to believe that they can distinguish and count the rather inconspicuous flowers at a distance. Bumblebees are known to prefer visiting larger plants or plants with more flowers (Thomson 1988; Klinkhamer et al. 1989; Klinkhamer and de Jong 1990; Eckhart 1992) [although this poses a problem of geitonogamy (Klinkhamer and de Jong 1993)], and also to prefer larger flowers (e.g. Bell 1985; Galen and Newport 1987); their choice of individual flowers or inflorescences is usually interpreted in terms of maximizing rewards (Galen and Plowright 1985; Harder 1988). Our previous study showed that honey bees choose inflorescences of *L. stoechas* with relatively high numbers of open flowers and relatively few bracts (Duffield et al. 1993). In this work we suggest that honey bees foraging for nectar only, or for both pollen and nectar, are choosing the appropriate inflorescences by using morphological indicators, bract display to indicate the presence of male flowers, and inflorescence size to indicate female flowers. This may well set up selection pressures on plants, since nectar-only and pollen/nectar foragers are expected to have different abilities to transfer pollen: Mitchell (1994) has tested a path model of the way in which plant traits influence reproductive success by influencing pollinator behaviour in *Ipomopsis aggregata*, and such a model may well be useful for *L. stoechas*.

The response of bees to individual flowers within inflorescences provided only indirect evidence for resource-related discrimination by sex-phase. Bumblebees match their arrival on inflorescences to the positions where resource density is greatest, different for nectar-collecting and pollen-collecting individuals (Galen and Plowright 1985). Pollen/nectar honeybee foragers in our system appeared to select and spend more time sampling flowers with wider corollas, which tended to be male, while nectar-only foragers showed no clear preference with respect to corolla diameter. The positive correlation between corolla diameter and nectar volume found previously (Duffield et al. 1993) was corroborated for female-phase flowers, and bees foraging on female-phase flow-

ers were more likely to sample those with larger corollas. The fact that there was not a significant distinction in this tendency between nectar-only and pollen/nectar foragers is consistent with the fact that both were collecting nectar.

The results may also be interesting in the context of our growing understanding of the dynamics of memory in honey bees. Honey bees appear to have both long- and short-term memories (Greggers and Menzel 1993); the long-term memory is affected by experience of different rates of reward over a period of time, and potentially could become entrained by association with morphological cues. Short-term memory in honey bees (Greggers and Menzel 1993) and bumble bees (Real 1992; Cresswell 1990) appears responsive only to the last flower visited, and affects departure decisions on the current inflorescence. Differences in criteria used within and between inflorescences may thus relate to interactions between the bees' experience and long- and short-term memories (Greggers and Menzel 1993).

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