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Habitat assessment ability of bumble-bees implies frequency-dependent selection on floral rewards and display size

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Foraging pollinators could visit hundreds of flowers in succession on mass-flowering plants, yet they often visit only a small number—potentially saving the plant from much self-pollination among its own flowers (geitonogamy). This study tests the hypothesis that bumble-bee (*Bombus impatiens*) residence on a particular plant depends on an assessment of that plant's reward value relative to the overall quality experienced in the habitat. In a controlled environment, naive bees were given experience in a particular habitat (all plants having equal nectar quality or number of rewarding flowers), and we tested whether they learn about and adaptively exploit a new habitat type. Bees' residence on a plant (number of flowers probed per visit) was eventually invariant to a doubling of absolute nectar quality and increased only slightly with a doubling of absolute flower number in the habitat. These results help to explain why pollinators are quick to leave highly rewarding plants and suggest that the fitness of rewarding plant traits will often be frequency dependent. One implication is that geitonogamy may be a less significant constraint on the evolution of rewarding traits than generally supposed.

Keywords: Bayesian foraging; floral evolution; frequency dependence; geitonogamy; marginal value theorem; nectar production

1. INTRODUCTION

The type of selection acting on the reproductive traits of animal-pollinated plants will often depend on the details of pollinator foraging behaviour. Behaviour plays a major role, for instance, in the conflict between not only attracting many visitors to a plant but also minimizing self-pollination among its flowers (geitonogamy)—a central theme in the evolutionary ecology of plant reproduction (recent reviews by Barrett (2003), Harder *et al.* (2004) and de Jong & Klinkhamer (2005)). A conflict can arise if the same traits that increase a plant's attractiveness to pollinators also increase the number of flowers probed per visit ('residence' on the plant; Charlesworth & Charlesworth 1987; Klinkhamer & de Jong 1993). Plants that display more rewarding flowers than competing conspecifics, for example, not only attract more pollinators but can also encourage longer residence and more geitonogamy (e.g. Harder & Barrett 1995; Eckert 2000; Karron *et al.* 2004). Given these results and the expected costs of geitonogamy (e.g. pollen discounting, inbreeding depression in selfed seeds; see Harder *et al.* (2004)), many authors have supposed that selection sets an upper limit on plants' investment in rewarding traits (e.g. Wyatt 1980; Klinkhamer & de Jong 1993). The existence of mass-flowering displays can therefore seem contradictory (de Jong *et al.* 1993; Harder *et al.* 2004), and by the same logic, so might the staggering cumulative nectar production of such displays (see Dupont *et al.* 2004).

This logic, however, implies that pollinator residence on a plant simply increases with the plant's absolute reward value, and in some cases (e.g. de Jong *et al.* 1992), models of reproductive investment have assumed that pollinators probe every flower per visit to a plant. In reality, pollinators of mass-flowering species probe only a tiny proportion of flowers per visit (reviewed by Robertson (1992) and Harder *et al.* (2004)). Furthermore (and perhaps consistent with this observation), foraging theory suggests that pollinator residence on a plant should depend on the relative advantage of leaving to forage elsewhere. The marginal value theorem (MVT; Charnov 1976) suggests that if foraging gains decelerate with further residence on a plant ('depression', e.g. due to increasing risk of revisiting flowers; Ohashi & Yahara 2001), then pollinators would do best by leaving when the rate of reward intake falls to the maximum possible rate in the habitat (assuming complete knowledge of that habitat). Hence, on a plant with a particular reward value, optimal foragers should probe fewer flowers (and transfer less self pollen) as the reward quality of the habitat increases. From the plant's perspective, this means that the fitness of rewarding traits may often depend on the frequency of other rewarding traits in the population or community (Pyke 1980; Cresswell & Galen 1991; Biernaskie & Elle 2007).

The predicted evolutionary dynamics of rewarding traits can be altered significantly by a geitonogamy cost that is frequency dependent. If, for instance, pollinator residence increases only with a plant's relative (but not absolute) reward value (Biernaskie & Elle 2007), then a relatively rewarding mutant can invade a resident

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population when the benefit of attracting pollinators initially outweighs the geitonogamy cost. But once the mutant trait value becomes common, pollinators probe the same number of flowers per plant as in the former resident population, thus 'resetting' the cost and potentially favouring even further investment in rewarding traits. Still, the extent to which pollinator residence on a plant actually varies with the relative and absolute value of traits such as nectar quality and floral display size has not been studied in detail.

If pollinators are to behave according to the MVT, they must first use a learning rule that assesses the quality of their current habitat and adjusts their departure threshold towards the optimal value (cf. McNamara & Houston 1985). Here, we report a controlled experiment that tests whether bumble-bees (*Bombus impatiens*) with prior experience in a particular habitat (all plants having equal nectar quality or number of rewarding flowers) can learn about and adaptively exploit a new habitat type (with different nectar quality or display size). Evidence from field experiments suggests that bees may in fact adjust plant residence to the mean quality of a population (Hodges 1985; Cibula & Zimmerman 1987; Harder & Barrett 1995), but in these cases it was impossible to fully control the prior experience of individual foragers or to independently vary display size and floral rewards. Furthermore, the current study isolates the effects of prior information and learning by comparing the behaviour of naive and experienced bees in the same habitat type. If bees use the proposed learning rule, we predict the following results.

- Bees should initially probe more flowers on plants that are nectar rich relative to prior experience (when 'rich' plants are perceived as rare), but eventually treat both habitat types equally. This follows the MVT when all patches are of a single type: varying the absolute resource density of patches alone has no effect on optimal residence time (e.g. Charnov & Parker 1995).
- Bees should initially probe more flowers on plants with relatively large floral displays (all else equal), but this should change with further experience in a large-display habitat. The risk of revisiting flowers probably increases more slowly on large displays than on smaller ones (Ohashi & Yahara 2002), meaning that bees can probe more flowers at each plant (and in this sense, large-display habitats are 'richer'). But residence should be longer when large displays are perceived as rare than when perceived as common.

2. MATERIAL AND METHODS

(a) *Bees, artificial plants and general methods*

Worker bumble-bees (*B. impatiens* Cresson; supplied by Biobest Biological Systems, Canada) were trained to collect sucrose solution (herein 'nectar') from artificial flowers within a large screened enclosure ($3.4 \times 2.0 \times 4.6\ m^3$). Bees entered the enclosure through a gated tunnel connected to their nest box. The 'flowers' were clear, 1.5 ml polypropylene microcentrifuge tubes with the cap removed and a circular collar (6.5 cm in diameter) of blue cardboard fixed around the tube's entrance. Flowers were grouped into inflorescences (herein 'plants') along a green Styrofoam tube (length 75 cm; circumference 6.5 cm) in two staggered columns, with flower openings spaced 5.5 cm apart. Each plant could hold up to 16 flowers (i.e. two columns of eight flowers). Bees were initially trained to collect nectar from four flowers arranged haphazardly on a single plant that rested horizontally in the enclosure. When tests were not in progress, these flowers were filled as necessary to provide the colony with nectar, and this was the only foraging experience that bees had before an experimental trial. The concentration of floral nectar in the training flowers depended on the experiment being performed (details below).

Experimental trials consisted of two phases, during which a single marked bee made numerous consecutive foraging bouts from its colony to the enclosure. During all trials, 12 identical plants were presented in a linear array of two staggered columns, with plants spaced 60 cm apart. All flowers contained a 3 μl nectar reward, placed near the bottom of the tube. Depleted flowers were recorded and manually replenished after a bee's departure from a plant; hence, the only empty flowers encountered were those revisited during a single plant visit (bees completely emptied all probed flowers). The first phase ended when the bee reached a specified number of total plant visits (excluding the last visit of every bout) and later returned to the colony to unload its crop. Before the next foraging bout, we replaced all plants with a new set for phase two. The flowers on these new plants were always made with washed centrifuge tubes and fresh cardboard collars. Throughout all experimental trials, we recorded the number of flowers probed per plant (including revisits) before departure to visit another plant in the array. Individual bees were tested only once and then removed from the colony.

(b) *Experiment 1: manipulation of nectar quality*

This experiment used 16-flowered plants and two treatment levels that individual bees experienced in one of two orders: 20% (w/w) sucrose solution in all flowers ('nectar-poor' habitat) for phase one and 40% sucrose in all flowers ('nectar-rich' habitat) for phase two or vice versa. Phase one lasted for 50 plant visits and phase two lasted for at least another 50 visits (we sometimes recorded two extra foraging bouts to increase the likelihood of observing learned behaviour). The goal of the nectar manipulation was to alter the rate of energy gain per flower without varying any other aspects of foraging economics. Sucrose concentration (as opposed to volume) was manipulated because the ingestion rate of a given volume of sucrose by *B. impatiens* is constant up to a concentration of 40–50% (Harder 1986). Hence, it is probable that our manipulation increased the energy gain per flower without affecting floral handling time.

The order of treatment levels (poor ⇒ rich, rich ⇒ poor) was assigned to individual bees from two different colonies. Bees that were assigned to begin with a particular treatment level were trained with that concentration of nectar. We could not randomly assign the order of treatment levels to individual bees within a colony, however, because it was only possible to train bees collectively. Instead, the first four bees tested from a colony were given one order (e.g. poor ⇒ rich, trained on 20% sucrose only) and the next four bees were given the opposite order (rich ⇒ poor, trained on 40% sucrose). We did the same with eight bees from the second colony but reversed the order of treatment levels.

Table 1. ANOVA results from (*a*) experiment 1 (manipulation of nectar quality) and (*b*) experiment 2 (manipulation of display size). (In all models, there were two response variables for each bee (a mean residence behaviour for each treatment level). For the poor ⇒ rich and small ⇒ large orders, model 1 uses the mean initial behaviour in phase two (first 10 plant visits of phase two) and model 2 uses the mean learned behaviour in phase two (last 25 visits for (*a*) and last 50 visits for (*b*)). For all other orders, the mean residence is an average from all of phase one or two, or an average of the entire trial (for the mixed order in (*b*)). Each model also included the term 'Bee [Order]', but tests were not performed on this random factor. Least-squares mean values from the interaction plots of each model are presented in figure 2.)

	model 1		model 2	
(*a*) nectar quality	$F_{1,13}$	*p*-value	$F_{1,13}$	*p*-value
order	26.5	0.0002	1.23	0.29
treatment level	38.5	<0.0001	0.33	0.57
order × treatment level	65.2	<0.0001	5.15	0.041
(*b*) display size	*F* (d.f.)	*p*-value	*F* (d.f.)	*p*-value
order	0.70 (2,23)	0.50	6.31 (2,23)	0.0065
treatment level	240 (1,23)	<0.0001	154 (1,23)	<0.0001
order × treatment level	0.20 (2,23)	0.82	7.64 (2,23)	0.0029

(c) *Experiment 2: manipulation of floral display size*

This experiment also had two treatment levels, but individual bees experienced them in one of three orders: all plants having 8 flowers in phase one ('small-display' habitat) and then 16 flowers in phase two ('large-display' habitat); all plants having 16 flowers in phase one and 8 flowers in phase two; or a random spatial distribution of six 8-flowered plants and six 16-flowered plants in both phases. The randomly mixed habitat was included as a type with intermediate frequency of large displays. All flowers in this experiment had 3 μl of 30% sucrose solution (and bees were trained only with 30% sucrose). Both phases lasted for 100 plant visits, but as above, phase two sometimes went slightly beyond 100 visits. In mixed arrays, a new random distribution of display sizes was presented every five foraging bouts, and, as always, plants were replaced in between phases.

Initially, the order of treatment levels (small ⇒ large, large ⇒ small or mixed) was assigned to individual bees from two different colonies in a completely randomized design. This yielded six bees per treatment level order. Later, to increase our ability to detect differences between the small ⇒ large and the mixed orders in particular, we randomly assigned four additional bees to each of these orders, using a third colony.

(d) *Data analysis*

Because each bee experienced both treatment levels in a particular experiment, the factor 'Bee' (identifying individual subjects) is used as a random blocking factor throughout. The dynamics of bee behaviour as a function of experience in experimental trials is presented in leverage plots (JMP Start Statistics, SAS Institute, Inc.) of the mean number of flowers probed per plant at intervals of 5 (experiment 1) or 10 (experiment 2) plant visits. These plots are interpreted in the same way as simple regression plots, but they describe the marginal contribution of 'Experience' after adjusting for variation due to Bee. We summarize the relationships in leverage plots by calculating a linear regression slope for each bee and then estimating the mean slope and 95% confidence interval (CI) for a particular habitat type.

For each experiment, two split-plot ANOVA models were used to estimate the mean plant residence for particular order–treatment level combinations. All models included the factors 'Order of treatment levels' (acting at the level of individual bees) and 'Treatment level' (acting within each bee), their interaction, plus the random factor 'Bee (nested within Order)' to identify bees as the experimental units. Two response variables were associated with each bee: a mean plant residence for each treatment level. For the poor ⇒ rich and small ⇒ large orders (where we predicted a change in behaviour with experience in phase two), the response variable for 'rich' and 'large' was either a mean of the initial response in phase two (defined as the first 10 plant visits; see model 1 in table 1) or a mean of the 'learned' behaviour in phase two (defined as the last 25 visits in experiment 1 and last 50 visits in experiment 2; see model 2 in table 1). For all other treatment level orders, the mean residence was from all of phase one and all of phase two, and in the mixed display size habitat, from the entire trial. From these analyses, we report least-squares (LS) means for every order–treatment level combination, and the differences between LS means, as estimated by Tukey's HSD comparisons. Models were estimated with the REML method, using JMP v. 5.01. Throughout the paper, means and 95% CIs are presented as mean (lower limit, upper limit).

3. RESULTS

Details of the ANOVA models are given in table 1. In §3*a*,*b*, we focus on the estimates of the effect sizes from those models and on the dynamics of bee behaviour with experience.

(a) *Experiment 1: manipulation of nectar quality*

We first used this experiment to confirm that the probability of revisiting at least one flower on a 16-flowered plant increased with the total number of flowers probed on the plant (repeated measures logistic regression, using Bee as the subject variable; $G=11.13$; $p<0.0008$; $n=16$ bees). For example, during visits of 8, 10 and 14 flowers per plant, the probability of including at least one revisit was estimated as 0.12 (0.06,0.18), 0.27 (0.19,0.35) and 0.53 (0.42,0.64), respectively. This increasing probability of flower revisitation may be the primary reason that bees leave our artificial plants before probing every flower.

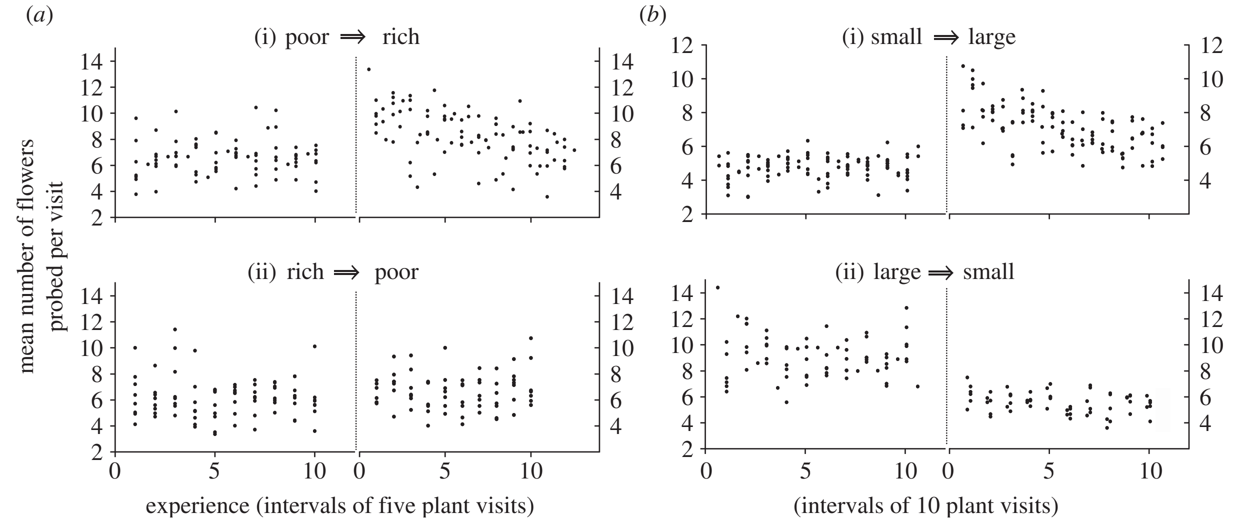

Figure 1. Leverage plots of the relationship between the number of flowers probed per plant and experience in (*a*) experiment 1 or (*b*) experiment 2, where the dotted line separates phases one and two. A mean is given for each bee at each interval of experience. (*a*) The mean regression slope across bees in phase two of the poor⇒rich order was −0.28 (95% CI −0.41, −0.15; $n=8$ bees), but otherwise, the mean slope was not significantly different from zero in any other habitat type. (*b*) The mean regression slope in phase two of the small⇒large order was −0.25 (95% CI −0.42, −0.14; $n=10$ bees), but the mean slope was not significantly different from zero in any other habitat type.

When habitat types were presented in the poor⇒rich order, the initial response of bees in phase two was to probe an average of 3.48 (2.50,4.50) more flowers per plant than in phase one (figures 1*a*(i) and 2*a*). Average plant residence gradually declined with experience in the rich habitat, however (figure 1*a*(i)), and by the end of phase two, the mean residence did not differ significantly from the poor habitat in phase one (figure 2*a*; mean difference = 0.76 (−0.31,1.85)). Concurrent with this declining mean residence in the rich habitat was an increase in foraging efficiency: in the first 10 plant visits, bees revisited an average proportion of 0.059 (0.048,0.069; $n=8$ bees) flowers per plant; by the last 10 visits, a significantly smaller proportion of flower probes were revisits (0.019 (0.008,0.029) flowers per plant).

The mean residence of naive bees in phase one of the rich⇒poor order did not vary with experience (figure 1*a*(ii)), and was not detectably different from the learned response at the end of phase two of the poor⇒rich order (figure 2*a*). With prior experience in the rich habitat, bees initially rejected all flowers in phase two (poor habitat), and in fact one bee stopped foraging altogether. When the others resumed normal foraging, however (usually after approx. 5 min of searching the habitat), mean plant residence in the nectar-poor habitat did not differ significantly from the rich habitat in phase one (figure 2*a*; mean difference = −0.46 (−1.50,0.59)).

(b) *Experiment 2: manipulation of floral display size*

Bees in the small⇒large order initially probed an average of 4.04 (2.84,5.24) more flowers per plant on large displays than on the small displays in phase one (figures 1*b*(i) and 2*b*). But as above, plant residence in the large-display habitat gradually declined with experience in phase two (figure 1*b*(i)), so that the mean difference between phase one (small displays) and the learned behaviour in phase two (large displays) was only 1.80 (0.59,3.00) flowers probed per plant (figure 2*b*). The LS mean residence on large displays by the end of the small⇒large order was

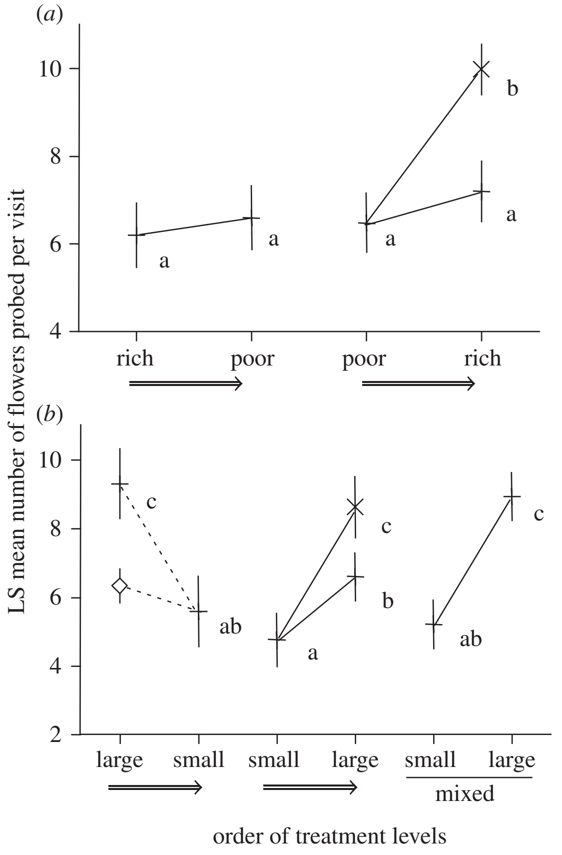

Figure 2. Least-squares mean number of flowers probed in the habitat types of (*a*) experiment 1 and (*b*) experiment 2. The mean initial response of bees in phase two of the poor⇒rich and small⇒large orders is denoted by the diagonal cross symbol; otherwise, the mean value in phase two of these orders represents the learned behaviour. The mean values for the mixed order in (*b*) were taken over the entire trial (the mean difference in residence on large and small plants did not differ significantly between phases one and two). The mean shown by the diamond symbol in (*b*) is of the bees in experiment 1 that were also naive to the large floral display habitat (details in text). Error bars give the 95% CI, and means labelled with different letters are significantly different by a Tukey HSD comparison.

significantly less than the mean residence on large displays in the mixed display habitat (mean difference: 2.41 (0.64,4.18) flowers per plant; see figure 2*b*). Incidentally, we note that bees in our mixed habitat encountered large and small plants completely randomly, rather than showing a preference for visiting large displays: bees visited large displays at a mean frequency of 50.6% (48.3,52.9; $n=10$ bees). This was true even though bees had the ability to discriminate between our small- and large-display sizes in the experimental arrays (data not shown).

The mean residence of naive bees in phase one of the large⇒small order did not vary with experience (figure 1*b*(ii)), but the mean number was surprisingly large and significantly greater than the learned response of bees in phase two of the small⇒large order (figure 2*b*). Unfortunately, the average behaviour of naive bees in this large-display habitat was skewed by two bees (out of a sample of six) that were particularly persistent on large displays. Note, however, that all plants in experiment 1 also had 16 flowers and that bees in phase one of this experiment can also be considered as naive to the large-display habitat. The LS mean number of flowers probed per plant by these naive bees (shown by the diamond symbol in figure 2*b*) was similar to the learned response of bees in phase two of the small⇒large order.

4. DISCUSSION

Our results demonstrate that bumble-bee residence on a particular plant depends not only on the reward quality of that plant but also on the expected foraging gain elsewhere, which is learned through experience. Bees initially stayed much longer on plants in a habitat that was more rewarding than their previous experience. But given further experience with rewarding types, the average plant residence was nearly invariant to absolute nectar quality and increased only slightly with the number of rewarding flowers per plant in the habitat. We discuss these results in relation to foraging theory below. Our second objective is to emphasize how the foraging behaviour observed here can translate into frequency-dependent selection on floral rewards and display, which has been largely overlooked (but see discussions by Pyke (1980), Harder & Barrett (1996), Morgan (2000), Ferdy & Smithson (2002) and Biernaskie & Elle (2007)). Our study suggests that to fully appreciate the adaptive evolution of rewarding traits, it is necessary to consider not only how selection acts on a rare, relatively rewarding trait value but also how selection changes if that trait value were to become common.

(**a**) ***Contribution to foraging theory***

The experimental environment of the current study was very similar to the assumptions of the MVT in its simplest form (i.e. most habitats of a single patch type, constant travel time within and between patches, rewards available at every flower). The MVT gives the optimal behaviour when foragers have complete information about such an environment. In reality, foragers might use simple rules to learn the environmental parameters and the appropriate patch residence time as specified by the MVT (McNamara & Houston 1985). Our study suggests that bumble-bee residence depends on initial estimates of habitat quality (which we imposed experimentally) and that bees can learn to adjust plant residence towards a seemingly adaptive value. We did not directly measure whether bees maximized the long-term rate of reward intake ('optimality' *per se*). However, bees did stay longer on a relatively rewarding plant when the estimate of average intake rate should have been low, and mean residence gradually declined as experience was swamped with the more rewarding habitat type. This behaviour seems adaptive in the sense that the decline in mean residence was associated with improved foraging efficiency (fewer flower revisits). Furthermore, if we assume that the mean residence adopted by naive bees in the richer habitat types is adaptive, then it is important to note that most experienced bees in the richer habitats eventually converged to that same average behaviour.

The use of information from prior foraging experience and current sampling in a patch is an example of Bayesian updating (recently reviewed by McNamara *et al.* (2006) and Valone (2006)). Few studies have provided convincing evidence of Bayesian foraging, but our design is particularly valuable because it allowed us to manipulate prior information but hold current sampling experience fixed (as advocated by Valone (2006)). Naive bees acted as a 'no prior information' control, and we found that their behaviour in the richer habitat types did not vary over time. The fact that bees with experience in a less rewarding habitat did alter their behaviour over time in the richer habitats is strong evidence that prior information and learning altered these bees' decisions. Given that bees had to learn only a uniform habitat quality, these results provide the most basic evidence for Bayesian foraging (McNamara *et al.* 2006). A test of whether bumble-bees can also learn the distribution of patch types in an environment (the more difficult task) will be presented in a forthcoming study.

Our experiments suggest that the plant residence behaviour of bees depends on the mean reward value in a monomorphic habitat. Real populations, on the other hand, are often characterized by wide variation around the mean (e.g. Biernaskie & Cartar 2004; Biernaskie & Elle 2005). Hence, it may be necessary to ask whether such variation hinders pollinators' ability to learn the mean quality of a habitat and behave accordingly. Bees also seemed to maintain a long 'memory window' of at least 20 or more plants in our experimental conditions, yet it would be interesting to know how much of their recent experience pollinators remember when foraging in a more variable or structured population (see Cibula & Zimmerman 1987). Despite these caveats, our results may have important implications for selection on rewarding plant traits.

(**b**) ***Implications for selection on floral display size***

It is well known that, within populations, pollinator residence on a plant increases with floral display size at a decelerating rate (reviewed by Ohashi & Yahara (2001)). This was evident in our mixed display habitat, where bee residence did not increase in proportion with the doubling of display size (figure 2*b*). We also showed, however, that the increase in residence on large displays is even smaller when they are common in the habitat. The effect known within populations is unlikely to fully explain the sharp decline in the proportion of flowers probed per visit with increasing mean display size among species (see Harder *et al.* 2004). Consider, for example, that bee pollinators probe only approximately 9–12 flowers, on average, in populations of *Hybanthus prunifolius* (mean display size of 226 flowers; Augspurger 1980) and *Echium wildpretii* (mean display size of approx. 1800 flowers; introduced honeybees probe approx. 35 flowers per plant; Dupont *et al.* 2004). Given our results, the fact that mass-flowering plants typically compete with many other mass-flowering individuals in the population (or community) may help to explain why pollinators are quick to leave such large displays. An additional hypothesis which deserves attention is that mass-flowering plants may be visited so frequently that pollinators often find empty flowers, encouraging early departure (Harder *et al.* 2004). Yet in our experiments, where flowers were always rewarding (save revisits), it is unclear why both naive and experienced bees should visit so few flowers in our large-display habitats. Revisits were generally rare (approx. 3% of all flower visits), meaning that bees usually left a plant after probing a rewarding flower and suggesting that the *perceived* risk of revisitation may be a key determinant of plant departure (see also Ohashi & Yahara 2001, 2002).

For selection to favour further investment in floral display size, some benefit of relatively large displays must outweigh the potential cost of longer residence and increased geitonogamy. If a benefit exists, however, the behaviour observed in our study suggests that this initial cost should lessen as larger displays become common, potentially favouring even further investment in display size. One probable benefit of relatively large displays is that they attract more visitors (reviewed by Ohashi & Yahara (2001)). Furthermore, it seems plausible that the attractiveness of a particular display size declines as the mean display size of the population increases, ensuring that relatively large displays have a competitive advantage (‘asymmetric competition’; cf. Biernaskie & Elle 2007). This form of competition for pollinator visits can favour escalating investment in display size, even if pollinator residence and geitonogamy increase with the mean display size of the population (Biernaskie & Elle 2007; see also Morgan 2000). In some species, mass flowering is in fact maintained despite the occurrence of significant geitonogamy costs (e.g. Eckert 2000; Dorken *et al.* 2002).

(c) *Implications for selection on floral rewards*

We found that bees’ residence on a plant is eventually independent of the absolute quality of nectar per flower in a habitat, and we suggest that this result might extend to floral rewards in general (e.g. nectar volume, pollen availability: any trait that increases the per flower net intake rate). In some cases, plants with a relatively rapid rate of nectar production can encourage frequent pollinator visitation to the plant and also promote longer residence per visit (e.g. Cartar 2004). When this is true, further investment in nectar production may be favoured if a benefit of attracting frequent visitors outweighs the potential geitonogamy cost associated with a relatively high rate of nectar production. Our results suggest that this initial cost may be effectively ‘reset’ once any particular investment in nectar production becomes common in the population. On the other hand, if pollinator visitation rate can eventually match plants’ rate of nectar secretion, then pollinators will not actually encounter larger nectar rewards per visit, and residence on a plant should not depend on the rate of nectar production (de Jong & Klinkhamer 2005).

In contrast to our emphasis so far, floral rewards may sometimes function to encourage pollinator residence on a plant when geitonogamy is not of great consequence. Encouraging longer residence may be adaptive if plants already have effective mechanisms to minimize geitonogamy (e.g. herkogamy and dichogamy; reviewed by Barrett (2003)) or if pollinator visitation in the habitat is so scarce that the main problem for a plant is to attract at least some visitors (Iwasa *et al.* 1995). In the latter case, large floral displays may be used to attract pollinators to the plant, while floral rewards ensure that pollinators stay long enough to engage most of the plant’s pollen in dispersal and to import enough pollen to fertilize its ovules. In this context, geitonogamy can evolve as a by-product of selection for attraction and longer residence and, in some cases, may even act as a form of reproductive assurance (Lloyd 1992; Harder & Johnson 2005). The intriguing implication of our results is that further investment in floral rewards may be continually favoured (checked only by rising energetic costs or other constraints) because longer pollinator residence (a benefit, in this case) is a consequence of increasing the relative, but not absolute, value of rewards. Although previously overlooked, this would be another example of the type of selection on floral traits that is strictly analogous to sexual selection in animal populations (cf. Biernaskie & Elle (2007)). Some plant species do in fact seem to produce an abundance of rewards (see Schemske 1980; Harder & Barrett 1992; Dupont *et al.* 2004), and it would be interesting to know if a frequency-dependent competition accounts for this apparent extravagance.

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