Choosing rewarding flowers; perceptual limitations and innate preferences influence decision making in bumblebees and honeybees

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Abstract Flowers exhibit great intra-specific variation in the rewards they offer. At any one time, a significant proportion of flowers often contain little or no reward. Hence, foraging profitably for floral rewards is problematic and any ability to discriminate between flowers and avoid those that are less rewarding will confer great advantages. In this study, we examine discrimination by foraging bees among flowers of nasturtium, *Tropaeolum majus*. Bee visitors included carpenter bees, *Xylocopa violacea*, which were primary nectar robbers; honeybees, *Apis mellifera*, which either acted as secondary nectar robbers or gathered pollen legitimately and bumblebees, *Bombus hortorum*, which were the only bees able to gather nectar legitimately. Many flowers were damaged by phytophagous insects. Nectar volume was markedly lower in flowers with damaged petals (which were also likely to be older) and in flowers that had nectar-robbing holes. We test whether bees exhibit selectivity with regards to the individual flowers, which they approach and enter, and whether this selectivity enhances foraging efficiency. The flowers approached (within 2 cm) by *A. mellifera* and *B. hortorum* were non-random when compared to the floral population; both species selectively approached un-blemished flowers. They both approached more yellow flowers than would be expected by chance, presumably a reflection of innate colour preferences, for nectar standing crop did not vary according to flower colour. Bees were also more likely to accept (land on) un-blemished flowers. *A. mellifera* gathering nectar exhibited selectivity with regards to the presence of robbing holes, being more likely to land on robbed flowers (they are not able to feed on un-robbed flowers). That they frequently approached un-robbed flowers suggests that they are not able to detect robbing holes at long-range, so that foraging efficiency may be limited by visual acuity. Nevertheless, by using a combination of long-range and short-range selectivity, nectar-gathering *A. mellifera* and *B. hortorum* greatly increased the average reward from the flowers on which they landed (by 68% and 48%, respectively) compared to the average standing crop in the flower population. Overall, our results demonstrate that bees use obvious floral cues (colour and petal blemishes) at long-range, but can switch to using more subtle cues (robbing holes) at close range. They also make many mistakes and some cues used do not correlate with floral rewards.

Introduction

Efficiently gathering floral rewards is problematic as the reward per flower varies greatly between plants of a single species and between flowers on a single plant. Variation may be due to micro-environmental influences, genetic variation, age of the plant or age of the flower and also a result of the pattern of depletion of rewards by previous visitors (reviewed in Goulson 1999). At any one time, many flowers may be empty (Wetherwax 1986; Real and Rathcke 1988; Cresswell 1990; Waser and Mitchell 1990).

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If foragers can distinguish between more and less rewarding flowers of their preferred species, they can enhance their foraging success (reviewed in Goulson 1999, 2003). The time it takes for a bumblebee forager to handle a flower varies greatly according to floral morphology, from as little as 1 s for simple flowers to up to 10 s for complex flowers (e.g. Heinrich 1979b; Pyke 1979; Hodges 1981; Best and Bierzychudek 1982; Osborne 1994; Cresswell 1999). If the flower contains little or no reward, this time is wasted and because foraging in larger bee species such as bumblebees requires considerable expenditure of energy, visiting flowers with little or no reward is costly (Ellington et al. 1990). Hence, there is strong selection pressure on bees to evolve efficient means of choosing the more rewarding flowers.

Both bumblebees and honeybees are often seen to hover in front of a flower, sometimes briefly touching the corolla and then depart without probing into the flower structure. These rejected flowers contain, on average, less nectar than flowers, which are probed (Heinrich 1979a; Corbet et al. 1984; Wetherwax 1986; Kato 1988; Duffield et al. 1993). Several mechanisms may be in operation. Where the flower structure is open and the anthers are clearly visible, bumblebees are able to directly assess the pollen content of open flowers visually (Zimmerman 1982; Cresswell and Robertson 1994). It has been suggested that they may be able to determine the nectar content of some flower species in the same way (Thorp et al. 1975, 1976; Kevan 1976). It has also been proposed that they may be able to assess nectar volumes from the scent of the nectar itself or the scent of fermentation products from yeasts in the nectar (Crane 1975; Williams et al. 1981; Heinrich 1979a). They could plausibly detect nectar volumes from humidity gradients surrounding the flower (Corbet et al. 1979). However, apart from visual detection of pollen availability, none of these mechanisms of direct detection of floral rewards have been demonstrated.

It has long been known that bumblebees, honeybees, solitary bees, hover flies and butterflies are able to discriminate between age classes of flowers using visual cues, which correlate with reward (Jones and Buchmann 1974; Kevan 1978; Thomson et al. 1982; Weiss 1995a). Discrimination among flowers according to their age may be facilitated by clear visual cues given by the plant itself, particularly by colour changes, which variously occur in part or all of the flower (Kevan 1983; Gori 1983, 1989; Delph and Lively 1992; Weiss 1995a, b; Weiss and Lamont 1997; Nuttman et al. 2006). For example, flowers of *Pulmonaria* sp. change from red to blue, enabling bumblebees and flower bees (*Anthophora pilipes*) to select the more rewarding red flowers (Oberrath et al. 1995). These age-dependent preferences can be flexible; honeybees select 3-day-old capitula of *Carduus acanthoides* in the early morning, and switch to 2-day-old capitula later in the day. This accurately targets the time of maximum nectar production in capitula, which is from mid-way through their second day until early on their third (Giurfa and Núñez 1992).

Rates of nectar production may vary with flower age, but there is no general pattern to the changes in nectar production with age. Commonly, nectar production declines after the flower opens (Voss et al. 1980) or reaches an early peak and then declines (Bond and Brown 1979; Frost and Frost 1981; Bertin 1982; Pleasants and Chaplin 1983; Southwick and Southwick 1983; Cruzan et al. 1988; Nuttman et al. 2006), but in some species nectar production increases with flower age (Pyke 1978; Brink and De Wet 1980; Corbet and Willmer 1980; Best and Bierzychudek 1982; Robertson and Wyatt 1990).

To date, studies have either examined the relationship between floral cues and insect visitation rates or have studied the close range behaviour of bees with regards to their response to scent marks left on flowers by previous foragers. Few attempts have been made to assess the scale over which discrimination between flowers operates. In this study, we examine the foraging choices of both legitimately foraging bumblebees and nectar-robbing honeybees to floral characteristics, which correlate with reward and test whether foraging decisions result in improved foraging efficiency.

Materials and methods

Experiments were conducted at Quinta de Sao Pedro Field Study Centre in Lisbon, Portugal, during June 2006. The site consists of 4 ha of grassland and open woodland.

Tropaeolum majus L. Tropaeolaceae was one of the most abundant herbaceous plant species within the wooded areas. It is an annual plant, native to South America, but widely naturalised in Europe. It flowers in May and June, producing polymorphic red/orange or yellow flowers. Nectar is located at the end of a deep (~10–12 mm) and narrow tube and so is not readily accessed by most insect species. Within the study site, three bee species commonly visit *T. majus*: honeybees, *Apis mellifera* L.; carpenter bees, *Xylocopa violacea* L. and bumblebees, *Bombus hortorum* L. *X. violacea* is by far the scarcest of the three species and is a primary nectar robber, biting a slit in the nectar tube to gain access to the nectaries. *A. mellifera* are both secondary nectar robbers and also gather pollen by accessing the flower legitimately. *B. hortorum* has a very long tongue (~15 mm) and is the only bee species able to collect nectar legitimately. At the study site, phytophagous insects, notably larvae of *Pieris* spp. (Lepidoptera), damaged many flowers.

To quantify the frequency of nectar-robbed flowers within the population and of the two colour morphs, 200 nasturtium flowers in the study site were randomly selected using random number tables to generate coordinates. Damage to flowers was also recorded on a three point scale: 1=complete and un-blemished; 2=slight damage to petals; 3=heavy damage and/or some petals shrivelled. The volume of nectar in each flower was measured using a micro-capillary tube.

Bee foraging was recorded as follows. For both *A. mellifera* and *B. hortorum*, the flowers that each bee approached were recorded. An approach was defined as flying within 2 cm of a flower. Flowers were scored as rejected if the bee did not land or feed or accepted if the bee landed and attempted to gather pollen or nectar. Each flower that had been approached was then scored as above for colour, damage and nectar robbery. Bees were then caught and marked with a queen marking disc (E.H. Thorne, Wragby, Lincs, UK) to avoid observing the same bee on subsequent occasions. Data were collected for *B. hortorum*, all of which were collecting nectar, and *A. mellifera*, which were either collecting nectar as secondary robbers or collecting only pollen (no bees switched between tasks). Too few *X. violacea* were present to obtain useful data. The probability of bees accepting or rejecting flowers according to floral characteristics was analysed in the generalised linear interactive modelling (GLIM) software using binomial errors, using flower colour, damage category and whether the flower had previously been robbed as potential explanatory factors. Analysis of variance (ANOVA) was used to compare the effects of damage and robbery on nectar levels per flower.

Results

Of the 200 randomly selected flowers, 71% were orange and 29% were yellow. Robbed flowers comprised 42.7% of the population (57.3% un-robbed). There was no association between colour and whether a flower had been robbed ($\chi^2_1 = 1.42$, $p>0.05$). Approximately equal numbers of flowers fell into each damage category (32.1%, 33.2% and 34.7% for damage categories 1, 2 and 3, respectively). There was no association between colour and damage category of a flower ($\chi^2_2 = 1.14$, $p>0.5$). However, there was a strong association between damage category and whether a flower had been robbed; 40.1% of flowers with undamaged petals had been robbed compared to 65.6% and 65.2% for damaged flowers in categories 2 and 3, respectively ($\chi^2_2 = 10.8$, $p<0.01$).

Nectar levels did not differ between orange and yellow flowers ($F_{1,195}=0.014$, $p=0.652$). Nectar levels were significantly lower in robbed flowers compared to un-

robbed ($F_{1,193}=26.7$, $p<0.001$) and were lower in damaged flowers compared to undamaged ($F_{2,195}=35.9$, $p<0.001$; Fig. 1). There was no significant interaction between effects of robbing and petal damage on nectar levels ($F_{2,195}=1.72$, $p=0.141$).

Bee foraging behaviour can be examined at two levels: whether the flowers that they approached were a random sample of the population and whether the decision to land on (accept) a flower after an approach was influenced by floral characteristics. Both *A. mellifera* and *B. hortorum* approached significantly more yellow flowers than would be expected from the frequency (29.0%) of yellow flowers in the population. For *A. mellifera*, 40.8% of 358 approaches were to yellow flowers ($\chi^2_1 = 23.9$, $p<0.001$). For *B. hortorum*, 37.7% of 204 approaches were to yellow flowers ($\chi^2_1 = 7.53$, $p<0.01$).

Approaches to flowers were also not random with regards to petal damage. For *A. mellifera*, 56.4% of approaches were to flowers with un-blemished petals, which comprised just 32.1% of the floral population ($\chi^2_1 = 90.7$, $p<0.001$; Fig. 2). There was no difference in the behaviour of bees collecting pollen vs those collecting nectar in this respect ($\chi^2_2 = 3.55$, $p>0.5$). For *B. hortorum*, 52.5% of visits were to un-blemished flowers, more than would be expected by chance ($\chi^2_1 = 40.1$, $p<0.001$; Fig. 2).

A. mellifera collecting nectar and those collecting pollen did not differ significantly in their likelihood of approaching robbed vs un-robbed flowers ($\chi^2_1 = 2.96$, $p>0.5$) and, overall, the proportion of robbed and un-robbed flowers that were approached did not differ from the proportion of robbed and un-robbed flowers in the random sample of the flower population ($\chi^2_1 = 1.31$, $p>0.5$.; Fig. 3). *B. hortorum* (which were all foraging for nectar) approached
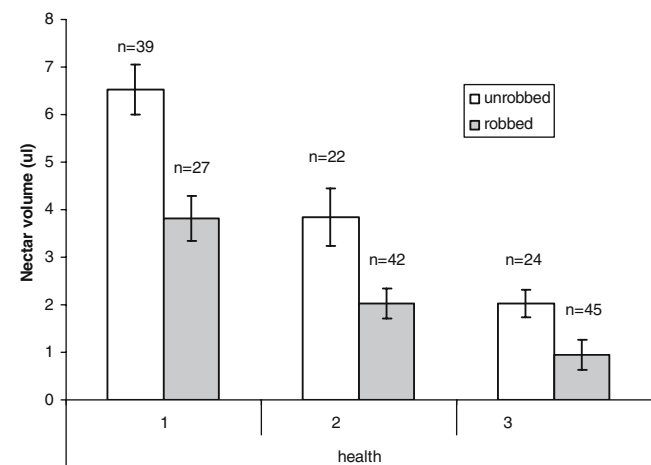

Fig. 1 Nectar volume in flowers according to whether they had previously been robbed by a bee and according to damage category: 1=complete and un-blemished; 2=slight damage to petals; 3=heavy damage and/or some petals shrivelled
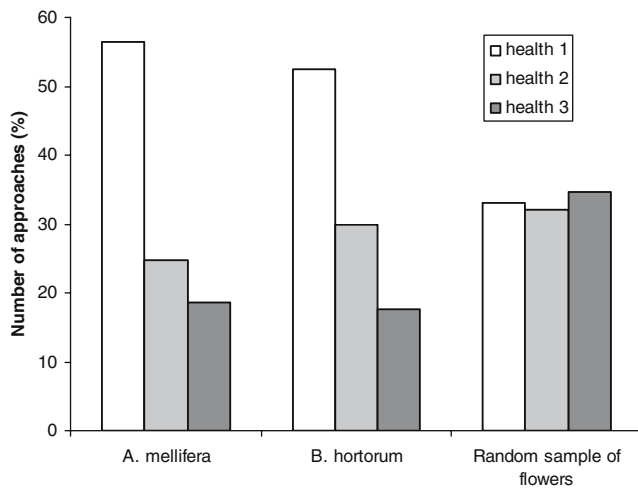
Fig. 2 Numbers of approaches made by foraging *A. mellifera* (*n*= 358) and *B. hortorum* (*n*=204) to flowers according to damage category: 1=complete and un-blemished; 2=slight damage to petals; 3=heavy damage and/or some petals shrivelled. It should be noted that approaches include flowers that were rejected by the bee without landing. Also shown is the frequency of flowers in each category within the population

slightly more un-robbed flowers than would be expected by random foraging ($\chi_1^2 = 4.22$, $p < 0.05$; Fig. 3).

After an approach, *A. mellifera* were more likely to land on un-blemished flowers ($\chi_2^2 = 54.4$, $p < 0.001$), regardless of whether they were foraging for nectar or pollen (proportion of flowers accepted 0.717, 0.517 and 0.239 for flowers in categories 1, 2 and 3, respectively). However, there was a significant interaction between whether bees were collecting nectar or pollen and their response to whether the flower had already been robbed ($\chi_1^2 = 11.4$, $p < 0.01$) (Fig. 4). Nectar foragers were more
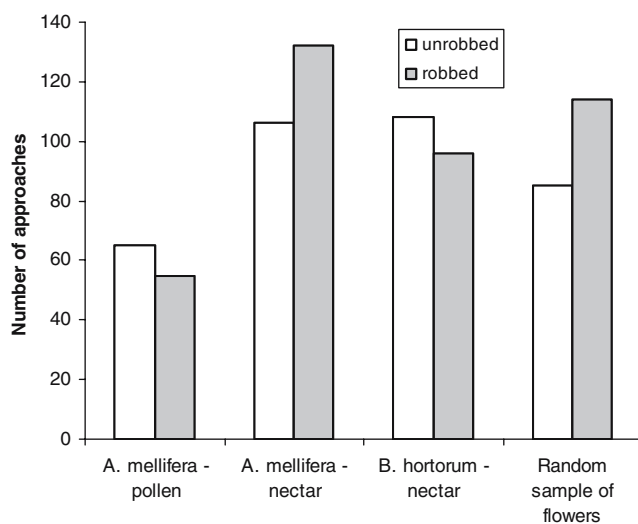
Fig. 3 Numbers of approaches made by *A. mellifera* (collecting either nectar or pollen) and by *B. hortorum* (all collecting nectar) to flowers according to whether they had previously been robbed. Also shown is the frequency of flowers in each category within the population

likely to land on robbed flowers ($\chi_1^2 = 8.71$, $p < 0.05$), but pollen foragers were not influenced by whether the flower had previously been robbed ($\chi_1^2 = 3.43$, $p > 0.5$). Despite discriminating at close range against robbed flowers, 45.3% of *A. mellifera* foraging for nectar still landed on un-robbed flowers from which they were unable to feed.

After an approach, *B. hortorum* (which only collected nectar) behaved similarly to pollen-collecting *A. mellifera*, tending to reject flowers with damaged petals ($\chi_2^2 = 41.8$, $p < 0.001$). They were not significantly more likely to land on un-robbed flowers although there was a weak trend in this direction ($\chi_1^2 = 3.2$, $p > 0.5$; Fig. 4). After an approach, neither *B. hortorum* nor *A. mellifera* were influenced in their decision to land by flower colour ($\chi_1^2 = 0.0$ and $\chi_1^2 = 0.1$, respectively).

Nectar levels varied greatly between *T. majus* flowers in the study area (range 0–14.9 μl) with a mean of 3.11 μl± 0.22 (SE). However, for *A. mellifera*, which are unable to access flowers that have not been robbed, the average accessible reward is much lower at 1.16 μl because the flowers containing the most nectar tend to be those that have not been robbed (i.e. accessible reward is zero). By multiplying the expected reward from flowers in each of the six possible damage/robbing categories by the frequency with which bees approached each category, it is possible to calculate the average reward per flower approached. Similarly, the expected reward in flowers on which the bees actually landed can be calculated. These values can then be compared with the average reward they would obtain by randomly approaching and landing on flowers. The non-random approach of flowers exhibited by both bee species results in an improved average reward per flower approached: 3.99 μl for *B. hortorum* and 1.45 μl for nectar-foraging *A. mellifera* (improvements of 28% and 25%, respectively). The average accessible reward per flower on which the bees actually landed was still higher (4.61 μl for *B. hortorum* and 1.95 μl for *A. mellifera*), representing an increase of 48% and 68%, respectively. However, if bees were able to detect robbery at long-range and approach and visit only the optimal category of flowers (un-robbed un-blemished flowers for *B. hortorum*, robbed un-blemished flowers for *A. mellifera*), then they could obtain an average reward of 6.62 and 3.84 μl per flower, respectively.

Discussion

Our results suggest that bees exhibit both long-range and short-range selectivity among flowers when foraging and that criteria can differ between the two. All bees were more likely to approach flowers with un-blemished petals and were least likely to approach heavily damaged flowers. Because damage is strongly correlated with average nectar

Fig. 4 Proportion of approaches to flowers, which resulted in the bee landing, for *A. mellifera* (collecting either nectar or pollen) and for *B. hortorum* (all collecting nectar)
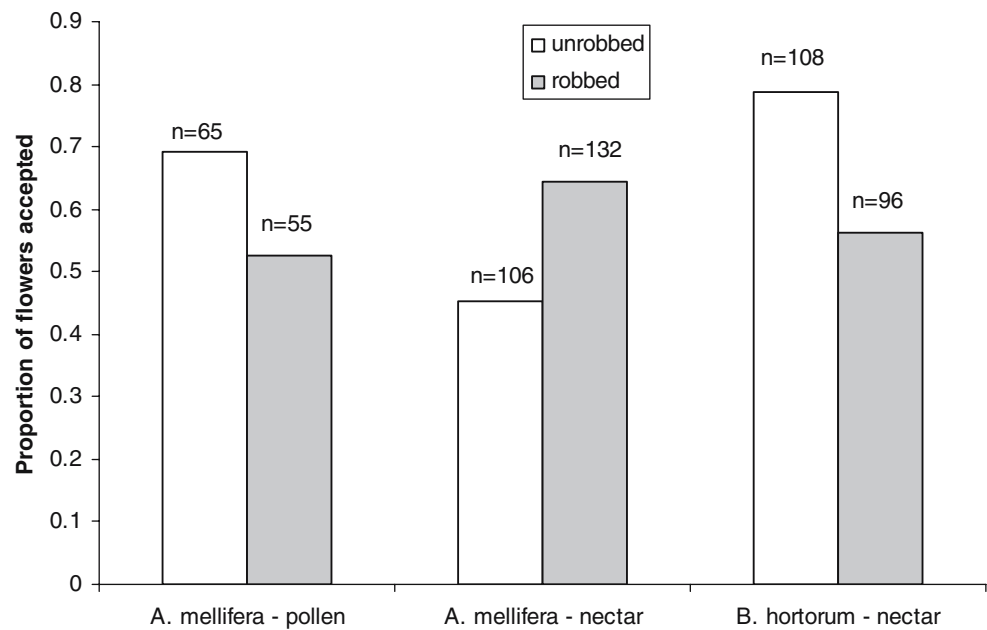
reward, this strategy clearly makes sense for bees collecting nectar. Damaged flowers are more likely to be old, and it seems probable that nectar secretion declines with age in *T. majus*, as occurs in some other plant species (see "Introduction"). For bees collecting pollen, older flowers are presumably also more likely to have had pollen stripped by a previous forager compared to young, un-blemished flowers. This long-range selectivity is almost certainly visual because damaged petals are an obvious signal of probable low reward. Scent cues associated with particular flowers are unlikely to be detectable except at short-range. Visual discrimination against damaged flowers has been described in other pollinators, including various bees and hummingbirds (Krupnick et al. 1999; Pohl et al. 2006). Honeybees and other insects show an innate preference for symmetrical shapes (Möller and Sorci 1998) and this can be reinforced by learning (Giurfa et al. 1996). Because damaged flowers are likely to be asymmetrical and less rewarding, this would readily explain our observations.

It is interesting to note that *A. mellifera* gathering nectar did not selectively approach flowers that had been previously robbed, even though these are the only ones from which they are able to extract rewards. It seems likely that the small hole in the nectar tube made by *X. violacea* is not readily detected from long-range, so that visual acuity limits the ability of bees to make optimal foraging decisions. By favouring un-blemished flowers, *A. mellifera* gathering nectar are increasing their chances of encountering un-robbed flowers that they cannot feed from, for un-blemished flowers are less likely to have been robbed (probably because both robbing and damage are likely to be correlated with age). Nonetheless, this strategy would appear to be worthwhile because un-blemished flowers

have two to three times the reward of blemished flowers. Hence, the average available reward in flowers that *A. mellifera* approach was higher than a random sample.

At short-range (<2 cm), all bees were more likely to reject blemished rather than un-blemished flowers. The end result of both long-range and short-range selectivity is that un-blemished flowers receive 64.7% of all visits by *B. hortorum* and 73.4% of visits by *A. mellifera*, despite comprising only 32.1% of the floral population. *A. mellifera* foraging for nectar were also able to selectively avoid un-robbed flowers at close range, although there were 48 instances in which a nectar-foraging honeybee approached and landed on an un-robbed flower, demonstrating that their ability to detect and avoid un-robbed flowers without landing is far from perfect. *B. hortorum* and pollen-collecting *A. mellifera* exhibited no significant response at either long-range or short-range according to whether flowers had been robbed. When collecting pollen, there is no obvious reason why robbing should influence foraging decisions, but for *B. hortorum* (which were collecting nectar), robbed flowers were less rewarding and should have been avoided if possible. However, both *B. hortorum* and pollen-foraging *A. mellifera* approach flowers from the front, from which angle they would be unable to see damage to the nectar tube.

Both bee species appeared to exhibit a long-range preference for yellow rather than orange flowers, although the standing crop of nectar did not differ between the two colour morphs. This may simply be because bees have an innate preference for particular colours, notably yellow and purple, which reflects the peak sensitivity of their colour receptors (Lunau 1990; Giurfa et al. 1995; Gumbert 2000). Yellow flowers may therefore be easier for them to see in

the shaded woodland in which this study was carried out. This would appear to be an example of floral discrimination driven by perceptual bias rather than being motivated by economic factors and a behaviour, which is selectively neutral to the bee. Form the plant's perspective, this behaviour would be expected to result in long-term selection for yellow flowers over orange in the population (assuming colour has a genetic basis). However, *T. majus* is not a native plant but a garden escape in the study area, so current colour frequencies are likely to have been influenced by artificial selection by man in the recent past.

In addition to visual cues to floral rewards, bees are well-known to use the presence of hydrocarbons left behind by previous insect visitors and so avoid flowers that have been recently visited (Schmitt and Bertsch 1990; Stout et al. 1998; Goulson et al. 1998, 2000, 2001; Goulson and Stout 2001; Stout and Goulson 2002). In this study, we did not have information on the previous visitation history of the flowers, but it is quite probable that the bees were also using scent marks to further improve foraging efficiency. As discussed, un-blemished but previously robbed flowers were scarce, but represented the ideal food source for nectar-foraging *A. mellifera* because they had high average rewards. Of the 62 instances in which a nectar-foraging *A. mellifera* approached such a flower, 54 proceeded to land a feed, but 8 rejected the flower without landing. It seems likely that this may have been a response to the scent of a previous recent visitor.

In summary, both bee species substantially increase the average nectar reward in the flowers that they visited by using a combination of long-range and short-range cues, although their foraging efficiency was limited in part by perceptual constraints. They also exhibit floral selectivity due to innate preferences, which appear to be selectively neutral in terms of foraging efficiency. It would be valuable to investigate how the behaviour of and interactions between primary and secondary nectar robbers and legitimate foragers affects the plant, for the previous studies provide conflicting evidence as to whether nectar robbery has net positive or negative effects on plant reproductive fitness (Morris 1996; Stout et al. 2000; Irwin 2003).

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