

## General Conclusions

The dissertation at hand is an attempt to provide a new insight into the bee pollinator's world of perception and consequent implications for choice strategies during foraging. Resulting effects on feature characteristics of flowers are reconsidered from this perspective. The main findings of the five studies are represented and recapitulated in the following.

In Chapter I, I explicate how honeybee foragers are able to evaluate a foraging situation in an artificial flower patch on the basis of their search time for rewarded targets and the number of negative association events experienced during searching. Even if the net energy gain remains constant throughout consecutive foraging bouts, foraging situations can be rated differently by the bee, depending on the reliability of presented targets and the expectations towards the targets based on the learned signal-reward pairings. This evaluation by the bee is expressed in the adjusted communicative behaviour with other nestmates about the food source profitability back in the hive, namely the change in dance probability.

The consequences of these findings are of importance for the understanding of decision making in honeybees during foraging. Until now, analyses of dance communication assumed that honeybees mainly reflect resource profitability on the basis of energy gain and loss in their dance (von Frisch 1965, Heinrich 1975, 1983). The role of the perceptual experience during the foraging trips has been addressed in a few studies which revealed that bees develop a reward expectation connected to a signal memory (Menzel 1985, Menzel und Greggers 1992, Greggers and Mauerlshagen 1997). My study as well as results of De Marco and Farina (2003), provide further evidence that the level of resource uncertainty plays a role in reward evaluation and influences the honeybee's foraging behaviour. A combined analysis has to be considered when analysing factors that may modulate the rate of signal production during recruitment.

The findings of Chapter I have an impact on the discussion about the evolution of floral colouration. My question in Chapter II and III was how the variation of floral colouration within particular plant communities reflects evolutionary trends resulting from the selective pressure exerted by floral visitors. The novelty of this study is the simultaneous recording of floral colours and corresponding reward properties. Colours were characterised from the point of view of the main pollinator group, the bees. The study sites were carefully selected, in intensive collaborations with pollination ecologists, to ensure the use of authentic and well

defined plant communities with an undisturbed plant-pollinator-system. I approached the analyses of this complex data set from the point of view of the foraging needs of animals like bees. Thereby, I took into account their behavioural flexibility made possible through their widely studied learning abilities (Menzel 1985, 1999, Menzel and Giurfa 2001), which exist in contrast to genetically fixed preferences that are hypothesised on the basis of experimental evidence for innate colour and shape preferences (Giurfa *et al.* 1995, Gumbert 2000, Rodriguez *et al.* 2004). Such preferences it has been proposed, are to have co-evolved with floral colouration as adaptations to help young foragers to be successful at their first foraging trips, i.e. to find the most profitable flowers.

Foraging pollinators prefer food sources with an adequate profitability to ensure a positive energy balance. They compare available resources computing supra-threshold differences rather than absolute values (Heinrich 1979, 1883). This is a consequence of a highly spatio-temporally structured environment with an unknown absolute offer of resources and unknown numbers of competitors that exploit the same food sources. Since the reward of different plant species within one community can vary between habitats, it needs to be assessed with relative measures. The selective pressure for adaptations of floral traits, such as colours that serve as advertisements for pollinators, may arise from the frequency and efficiency of the pollinator visits. Thus, the composition of the pollinator community is of large importance. Here, I present evidence for the enhancement of reward quality through the use of particular colours in combination with a suitable functional flower shape (Chapter II). Such adaptations, found in European habitats, lead to the exclusion of inefficient pollinators and targets bees as the main visitor group. Bees are efficient pollinators for entomophilous plants because they learn particular flower features and usually concentrate on a single species during their subsequent flower visits, i.e. they develop flower constancy. The bee pollinator is able to learn and relearn various colour-reward associations during the selection process of the mainly visited plant species. The degree of constancy that bees develop is dependent on various factors, e.g. amount and quality of the reward, abundance, detectability and reliability of the source as well as the conformance of the expectation of the bee with the colour-reward association. The sum of all these factors determine whether a flower is highly rewarding or not. In my field studies I tried to include as many of these factors as possible (Chapter II and III). The first four factors can be directly measured. The factor of reliability can be included by measuring the variability in the quantity and quality of the nectar as well as the occurrence of all other flower visitors. In field studies, one can only speculate whether a bee encounters the expected reward. However, on the basis of these measurements I was able to determine which plant

species belong to the highly or to the low rewarding group of species. To find out whether the selective pressure of bees, induced by the preference of these highly rewarding species, can influence floral colouration, I measured flower colour distributions within highly rewarding bee pollinated plant species and analysed if they possessed bee perceptual differences to the colour distributions of low rewarding species. Additionally, flowers with similar colours for bees were investigated concerning their reward properties. In European sites, no general correlation was found in either of the cases (Chapter II). Hence, pollinators could not rely on large chromatic distance of the flowers of one plant species to another within the patch to ensure a high reward rate. Further, I could not find an indication for Waser's hypothesis (1983) that rare species generally produce a high reward and strongly diverge in signal from co-flowering species to be pollinated effectively. We rather support the hypothesis that rare species try to be as similar as possible in colour to more common and successfully pollinated species to profit from the higher pollinator density (Gumbert and Kunze 2001, Johnson *et al.* 2003a, 2003b, Benitez-Vieyra *et al.* 2006, for a review see Dafni 1984). Therefore I conclude that the selective pressure of bee pollinators did not lead to certain colours that are presented by single or groups of plants in European communities that are generally better rewarding than others.

In Argentinean sites, however, plant species seem to compete for pollinators implementing the strategy to diverge in colour from each other (Chapter III). The majority of them did not particularly specialise their functional flower shape for the use of certain pollinators. The number of species with more complicatedly accessible nectar was relatively low; they presented a great variety of colours and offered a higher reward. These results come closer to suggestions by Waser (1983). Our investigated species with more complicatedly accessible nectar are not rare in all cases; however they do require a higher investment by the pollinator to obtain the nectar. Additionally, flower visits of Apoidea and non-Apoidea occurred to an equal amount in all three groups of plant species with different accessibilities of nectar. We conclude that the composition of the pollinator community with a lower representation of bees in Argentinean sites – as compared to European sites – is a selective factor which leads to different adaptations in colour-reward distributions of plants in natural habitats.

I mentioned previously that the detectability could be measured directly during field studies (Chapter II). These measurements were performed from the honeybee's point of view and were based on the knowledge achieved through different studies, in which the target's detectability varied depending on the target's size and distance, i.e. visual angle to the flower visitor as well as the presence of L-receptor contrast (Giurfa *et al.* 1996, 1997, Giurfa and

Vorobyev 1998, Hempel *et al.* 2001). But displays of natural flowers are often no single or bicoloured discs as they were used in these experiments, but inflorescences that consist of several single flowers that can be differently spaced and form different patterns. It is believed that flowers enhance their detectability for the pollinator by producing these inflorescences instead of a large single flower display. But so far it is not known, how spatial patterning of flower and background colours in complex plant displays affect the insect's perception of targets. Therefore, I performed another behavioural experiment with honeybees and bumblebees under laboratory conditions to find out how the detectability of grouped targets is affected by the size and colour of the single components of the target (Chapter IV). The main finding of this study was that neural mechanisms in the bee's longwave (L-) receptor mediated visual system probably help to enhance important visual object features and thus optimise detection of grouped targets. Since the L-receptor contrast of the target to the background is the only signal needed to achieve target detection at small angular subtenses, it is crucial during approach of the target. Detection of large-sized targets is not influenced by L-receptor contrast (Giurfa and Vorobyev 1998, Niggebrügge and Hempel de Ibarra 2003) but is mediated by the chromatic visual system requiring a large number of excited ommatidia. Target detection at small angular subtenses indicate an L-receptor mediated neural mechanism with an upper and lower limit of sensitivity which is characteristic for smaller antagonistic receptive fields which are sensitive to borders (Kuffler 1953, Fiorentini *et al.* 1999). Thus, the enhancement of important visual object features and the optimisation of the detection of grouped targets seem to be dependent on the density of edges rather than the sum of the areas of the elements. And consequently, measurements of display sizes in Chapter II were performed accordingly. Inflorescences were considered as one display when spaces between single flowers were equal or smaller than the single flowers' displays, and they were regarded as multiple displays when flowers were spaces further apart.

The last chapter concerns a specific phenomenon in plant communities to attract animal pollinators (Chapter V). Plant species sometimes exhibit unique flower displays, but they can also imitate models that are available in their environment. This imitation is known as floral mimicry (Dafni 1984, 1986, Roy and Widmer 1999). The main focus of this study lay on the demonstration that Müllerian flower mimicry is adaptive which has not been explored before (Roy and Widmer 1999). For that reason the two plant species *Turnera sidoides* ssp. *pinnatifida* (Turneraceae) and *Sphaeralcea cordobensis* (Malvaceae) were studied in Córdoba, North Argentina. All necessary requirements for the determination of mimicry, such as similar colours and patterns, sharing of pollinators, and enhanced reproductive success

through combined flower density were fulfilled in this pair. Interestingly, the flower colours of the mimic (*Turnera sidoides* ssp. *pinnatifida*) and the model (*Sphaeralcea cordobensis*) are rare in the studied plant community. They occurred almost alone in one sector of the perceptual colour space of bee vision (Vorobyev *et al.* 2001) and were not superposed with most of the other flowering plants that occupied wide areas of the colour space. This fact also supports my findings in Chapter III. As mentioned before, Waser (1983) postulated that rare flowers should diverge strongly in signal from sympatric species and should additionally be more rewarding. The other possibility would be to be as similar as possible to other flowers, to make use of mimicry. In that case, there would be no need to present any reward to the pollinator (Dafni 1984). Here, the rather rare *Turnera sidoides* ssp. *pinnatifida* mimics the more common *Sphaeralcea cordobensis*, but both species are equally rewarding. The colours of both species are in turn very rare colours. Their flowers do not provide a particularly high reward compared to co-flowering species, but the flowers' reward reliability is not reduced through a food deceptive mimic, as often occurring in mimicry pairs. In contrast, pollinator visitation rates to the mimic and consequential reproductive success is enhanced. This fact is another example of how food certainty may play a role in bee reward evaluation.

The discussed findings provide new insights into the complex interrelations within the plant-pollinator system to advance our understanding of the co-evolution of plants and pollinators. Particularly in such complex systems, generalisations should be handled with care – often they can only explain particular aspects of a few occurrences. It was important for me to integrate classical approaches and methodologies from behavioural, ecological and neurophysiological sciences in order to gain a deeper understanding of this fascinating subject, which is – though for a different, but very beautiful reason – also very present in the perception of humans.

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