Summary

The present dissertation is an integrated study of plant-pollinator interactions, aiming to understand the colouration of flowers from the perspective of the pollinators. To that purpose – and to deepen our understanding of bees' visual and cognitive abilities – bees' foraging behaviour was observed and analysed. Descriptive investigations of flower colour distributions and related rewards in natural plant communities were performed. Behavioural experiments under laboratory conditions were carried out to understand precisely how bees deal with specific colour-reward distributions. During foraging, bees form a reward expectation for a food source. The food source is characterised by its signals. Foraging decisions can therefore be understood as an outcome of interactions between the strength of signal memories and reward estimations. The aim of this work was to evince these kinds of interactions and to characterise the natural conditions under which these abilities of the bees have potentially evolved.

1) The honeybee's dance conveys information concerning the location and profitability of a food source from a foraging bee to its nestmates. It is well known that the forager estimates the profitability of the food sources, i.e. the exploited flower patch, on a subjective scale, which is influenced to a large extent by the energetic value of the obtained reward. But it is unknown how sensory properties of the exploited flower patch are integrated into the estimation of profitability. The dance behaviour was thus used under laboratory conditions to reveal the relationship between the reliability of colours as a visual stimulus that predicts the reward and the forager's subjective evaluation of the offered reward. Signal conditions of different reliabilities were created by distributing a constant reward either on targets of two different colours or on only one of two colours. Bees developed a different search pattern when the reward was only presented on one of the colours, while their general income rate and foraging costs stayed constant. Their subsequent dance probability increased in response to the perceptual changes in the artificial flower patch. These results led to the conclusion that foraging conditions, under which the visual reliability of the food sources increases, enhance the bees subjective estimate of the profitability of the flower patch.
2) Pollinators learn colours as signals for their food sources. Plants evolved floral features, such as colours in competition for efficient pollinators that are able to learn

complex floral traits and to develop flower constancy. Colour and reward distributions were measured in authentic, well-defined plant-pollinator communities to identify whether the selective pressure of pollinators led to characteristic distributions of these flower properties. Floral abundance, functional flower shape, display size and visitation rates were further determined to assess factors which might determine the relative strength of rewards provided within a plant community. Flower colours were quantified using a model for colour vision in honeybees to compare colours on the basis of the pollinator's perception. Flowers of highly rewarding plant species were often visited by bees and often blue-violet (with or without ultraviolet (UV)) in colour, although they rarely matched the colour range that is known to be innately preferred by bees in behavioural experiments. Their colours were not particularly different to less rewarding species' colours and did thus not tend to be easily distinguishable from co-flowering plants. Plant species with open access to their nectar, were mainly best rewarding, but usually less often visited by bees. Species with hidden nectar were usually less rewarding and had fewer, but mainly bee visitors. Species with large single flower displays presented various colours, were not particularly highly rewarding and attracted few bee visitors. Reward distributions were not clustered with respect to chromatic properties of the plant species and differed in every habitat. It is concluded that flowers in specific plant communities both diverge and converge in colour and reward, thereby exploiting the sensory and cognitive abilities of their pollinators.

3) Results of the second chapter indicated that the plant-pollinator system is distinguished by various different and constantly changing conditions with respect to the distribution of flower colours and rewards. Analogue recordings of floral colourations, corresponding rewards and visitation rates were performed in contrasting plant-pollinator communities in North-East Argentina. Similarly to European sites, the investigation of reward properties in relation to chromatic properties indicated a non-clustered distribution of rewards. As opposed to the European results, plant species that were highly rewarding and commonly visited by bees, mostly displayed yellow colours (with and without UV). Colours of highly rewarding or highly visited species tended to be different in appearance from those of less rewarding or less commonly visited species. Further, plant species with hidden nectar were usually more rewarding than those with open access to their nectar, and visits of Apoidea and non-Apoidea occured equally often in all groups of different functional flower shapes. Apoidea

were not the main pollinators of plants with hidden nectar as observed in European sites. Thus, honeybees and bumblebees, which have close phylogenetic origins to the European species and which populated the New World much later, behaved differently in their new environment. They were able to adapt to the new circumstances and were not limited by innate colour preferences. We concluded further, that the composition of the pollinator community in this environment was a selective factor that led to different adaptations in colour-reward distributions of plants.

4) Flowering plants can enlarge their coloured display by either presenting large single flowers or by grouping small single flowers to be more conspicuous to the pollinators. Tests were carried out on honeybees and bumblebees under laboratory conditions to find out how spatial patterning of target and background colours affects the bees' detection of targets. Single target detection depends on the spatial distribution of brightness contrast within the target area coded through a visual system mediated by the long (L) wavelength receptor. Bees were trained to groups of uni-coloured discs and single discs – as a control – with colours either providing or lacking L-receptor contrast to the background. The distance range over which grouped discs were detected exceeded expectations derived from the detection limit of single discs, but only when brightness contrast was present. The result can be explained by a higher density of borders in grouped discs providing input to detector units with centre-surround receptive fields.

5) Mutualistic or Müllerian mimicry involves plant species with similar-looking and rewarding flowers that achieve more effective pollination through their similarity – and thus higher combined flower density. Here, the adaptiveness of such Müllerian mimicry was explored for the first time, demonstrating that *Turnera sidoides* ssp. *pinnatifida* (Turneraceae) – the mimic – achieves a better pollination service and higher reproductive success by sharing pollinators with *Sphaeralcea cordobensis* (Malvaceae) – the magnet species. Since only *T. sidoides* profits from the mimicry, this is a case of one-sided, not mutualistic, mimicry. These two species resemble each other in their uncommon colour, in the eyes of pollinator, and their reward properties. Another geographical colour race of *T. sidoides* also mimics the differently coloured displays of local Malvaceae, proving that convergent similarity is not only the result of similar looking species adapting to the sensorial preferences of shared pollinators.