POLLINATORS' STRATEGIES IN FINDING FLOWERS

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ABSTRACT

Two phases of foraging flights of hymenopteran pollinators are discussed: localization of food sources over far distances (hundreds of meters to several kilometers); and spotting of flowers within their visual catchment area. In the first part, evidence from navigational tasks with honeybees is presented which favors the interpretation that bees possess a rich and unique spatial memory of qualified and localized objects. Depending on the motivation, the bee is rather free to navigate with reference to this memory. In particular, bees are guided towards feeding places with specific expectations of their signal and reward properties. In the second part, the processes guiding the bee during its final approach to the flower are analyzed. When arriving in the close vicinity of a rewarding flower, bees first detect and recognize the achromatic green signal and then the chromatic color signal. The dependence on the optical signals of the flowers and the habitat features is studied in a comparison between plants growing in the Israeli Mediterranean and desert habitats. We find that the green contrasts of flowers in desert plants are less prominent than in Mediterranean plants because the green signal of the desert background is more similar to that of flowers, not because the green signals of desert and Mediterranean plants are different. These results are interpreted on the assumption that the green signal of flowers used in further distance detection is an adaptive property of plant species only in the context of all features supporting navigation of insects. The low density growth of desert plants may allow for the possibility that the plants are located by insect pollinators as specified places relative to landmarks. Therefore, further distance visual signals emanating from the flower may be less important in a desert habitat, and reduced green contrast does not become an unfavorable property in desert plants. We conclude that both habitat features and flower signals contribute to the navigational system of insect pollinators, and that the evolutionary development of flower signals needs to be evaluated in the context of the plant species' habitat.

INTRODUCTION

Pollinating insects approach flowers as their food sources often over long distances. Since most of the approach flights are revisits to either the same or to close-by plants, pollinators are guided by their memories of the location of productive flowers and their particular features (signals, manipulatary properties, reward conditions) which the insects have learned during preceding visits. The learning capacity and the richness of memories in insects are usually underestimated, but studies of learning and memory in honeybees both under natural and laboratory conditions document that learning is fast and effective, and memory is rich and long lasting (Menzel, 1985, 1990; Menzel and Müller, 1996). There is no reason to believe that the honeybee is in any way special in its cognitive capacities, rather it appears that honeybees are representative of hymenopteran pollinators (social and solitary bees and wasps). Here, we advocate for a relationship between

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the navigational memories of hymenopteran pollinators for the signals provided by the habitat and the local signals emanating from plants in supporting their relocation. Specifically we argue that the components of the navigational memory of hymenopteran pollinators are so intimately connected that they lead to a unique neural representation of localized and qualified objects (nest site, feeding places with particular properties, landmarks passed by). We shall exemplify this concept using the two extremes of the sequential events during approach flights: far distance navigation in the kilometer range, and the spotting of flowers under visual control in the centimeter range. Our arguments originate from ecological, behavioral, psychophysical, neurophysiological, and modeling studies. We conclude that the components of habitat features and plant signals address a common navigational system of hymenopteran pollinators, and that the evolution of plant signals needs to be understood in the context of the habitat of the particular plant species. As a result, different selective pressures may control the optical signals of flowers in different habitats. Our study case is a comparison between plants growing in the Israeli Mediterranean and in desert habitats. Before we can address this case we need to develop the concept of a navigational system based on a rich spatial memory of localized and qualified objects. Nevertheless, it may be justified to conclude that their search strategy may be based only to a limited degree on learning the location, the signal, and reward properties of flowers, and that therefore these insect groups may not establish such a rich spatial memory of feeding places as bees and wasps appear to do.

Bees differ from other insects in an important aspect. They exploit flowers for the profit of their offspring, not only for their own nutrition. Larvae are usually kept in one nest and fed with a mixture of pollen and nectar. A foraging flight, therefore, always starts and ends at the nest. Since the nest entrance is unobtrusive, usually very small, and its location is unpredictable for the individual animal, the caretaking adult has to learn its location with respect to close and distant landmarks and the locations visual and olfactory signals. The foraging flights carry bees and wasps over long distances (up to several kilometers, depending on the size of the animal), certainly in the range of a million times the size of the particular insect. These long distances are navigated using the sun compass as reference and a distance-measuring device which provides geostable vectors as navigational aids for flight routes between nest site and foraging site (Wehner, 1992; Esch and Burns, 1996; Srinivasan et al., 1996). Plants at the foraging site do not change their position, and since the individual animal exploits the same plant patches at a particular place over a rather long portion of its lifetime, most of the foraging flights are revisitation flights, at least of flower patches. In such flights, food is collected from known places, fixed in space relative to the nest site. Fast and effective learning of geostable vectors through path integration using celestial cues, landmarks, and local features characterizing the goal is a prerequisite for central place foragers, and has been described in detail for the honeybee (Wehner 1992; Wehner and Menzel, 1990; Collett and Baron, 1994; Lehrer and Collett, 1994; Collett, 1995). These spatial learning capacities are used also in spotting flowers.

The scenario of a central place forager exploiting flowers is characterized by highly adaptive navigation systems composed of several subsystems (time compensated sun/polarized light compass, landmark learning en route, image memories in the vicinity of the goals, local feature memories). Most of the data come from honeybees (Collett, 1996; Dyer, 1996; Menzel et al., 1996), but bumblebees and solitary bees and wasps appear to have equally complex navigation systems (Timbergen, 1932; Iersel, 1965; Tengö et al., 1990; Ugolini and Cannici, 1996). In an experiment with bumblebees (Bombus agrorum) we captured individually marked bees at the moment when they left the nest and released each bee separately at a short distance from the nest.
entrance. We found that each bee reliably departed to particular directions on multiple releases (Breyer and Menzel, unpubl.). Most of the bumblebees flew towards one of two directions, some chose one of three directions, and some flew in only one direction. These releases were performed over a period of two weeks, and an individual bee was tested up to 25 times. The directions chosen varied strongly between the individuals but were stable for a particular individual over the testing time. Since we did not see any preference for one particular direction in cases where two or three directions were chosen by an individual, we conclude that each bumblebee had two (or three) potential simultaneous foraging sites and chose among them by consulting its memory of the site before leaving the nest.

A question of debate is the level of integration between the navigational subsystems. Do they act independently and partially as backup systems, or are they integrated into a rich form of unique spatial memory with identified and qualified loci (Menzel et al., 1996)? Three examples will be described here to characterize the level of complexity and integration of the subsystems.

1. DANCE COMMUNICATION IN HONEYBEES

The informational status of location in honeybees can be elucidated by analyzing a communicative process known as the waggle dance (von Frisch, 1967). Bees indicate the location of a feeding place using ritualized movements on the vertical surface of the comb in the dark hive. The speed of the movements codes the distance between hive and feeding place. The direction towards the feeding place relative to the sun’s azimuth (or the polarized light pattern of the blue sky) is transposed into the angle $\alpha$ between the body length axis during the waggle phase and gravity. Since bees are accurately informed about the time of the day and the solar azimuth function (ephemeris function), the angle $\alpha$ changes accordingly during the day (Fig. 1). Sometimes successful foragers continue to dance over many hours even at night, or can be stimulated to dance by blowing the odor of the food sources into the hive ("marathon dancers"). In this way the bees’ memory of food places can be tested at any time of day or night. In a particularly illuminating experiment, Lindauer and von Frisch (cited in von Frisch, 1967, table 37) trained bees to two differ-

![Fig. 1. Dance angles of marathon dancers which were trained to two feeding sites, the morning feeding site (190°) and the afternoon feeding site (100°). The graph gives the solar ephemeris function (sun azimuth vs. time) and the dance angles as arrows riding on the ephemeris function at the time of dance recording. Numbers at the arrows indicate particular individual dance (see text; after von Frisch, 1967, table 37).](image-url)
ent locations at two different times of the day. In the morning (0630 to 0730) bees foraged at a location in the south (190° from the N), and in the afternoon (1600 to 1700) in the east (100° from the N). Their dances at these times indicated precisely the respective directions towards the feeding places. At night, dance directions depended on time. Early at night, the afternoon place was indicated (dances 7.8 in Fig. 1); early in the morning, the morning place (dances 4.5,6) was indicated. In between, they indicated the directions either incorrectly (9.10) or with great scatter (1.2,3). Sometimes they danced in both directions within one dance performance (not shown). A compromise angle was never chosen. Such an angle would indeed be meaningless.

This experiment, as well as many others (Lindauer, 1959; Dyer, 1987; Dyer and Seeley, 1989; Lindauer, 1989; Dyer, 1991; Michelsen et al., 1992), clearly demonstrates that bees establish a memory for food locations to which they can refer even without actually navigating towards or from these locations. Although only the spatial memory of honeybees can be currently determined so precisely due to their particular communicative behavior, there is no reason to believe that other hymenopterans including solitary bees and wasps have a less well-organized representation of food locations.

The memories of these locations are established as geostable vectors in the framework of the sun compass. The origin of the vectors is the nest site, and thus vector memories have a unique and stable reference for all of the many food sites visited during the lifetime of an individual. Memory of vectors becomes activated specifically when the animals are motivated to collect food or during dance communication. Preliminary observations with bumblebees as described above also indicate that more than one food location can be stored in memory and specifically retrieved. The number of food sites kept in memory simultaneously and the precision with which they are stored is still unknown.

2. ROUTE-SPECIFIC MEMORIES OF LANDMARKS

Flight routes along these vectors are embedded in memories about landmarks observed en route. Von Frisch and Lindauer (1954) discovered that extended landmarks like a forest edge or a row of trees can serve as a backup system for the sun-compass-related vector when the sun or blue sky is not visible. This observation was confirmed by Dyer and Gould (1981). Thus, compass vectors and salient landmarks are associatively connected. As a consequence, compass vectors are fixed to the ground and embedded in a geostable reference system. Bees also learn the sequence of localized landmarks along their flight route. Chittka and Geiger (1995a) found that the expected location of the feeding place depends not only on the absolute distance but also on the sequence of landmarks passed by. In the particular experiment, (Fig. 2) bees were trained to a feeding place at a distance of 262.5 m. Their flight path was marked with a row of four yellow 3.50-m-high tents positioned at 75, 150, 225, and 300 m. The feeding site was halfway between the third and the fourth landmark. The experiments were carried out in an otherwise featureless landscape. In the test situation the distance between the landmarks was either stretched (not shown) or compressed (Fig. 2). If bees encountered more landmarks on their way from the hive to the feeder than they had during training, significantly more bees landed at a shorter distance than during control tests with the training landmark arrangement. If they encountered fewer landmarks they flew significantly further. It is interesting to note that this behavior meets the basic criteria in most definitions of counting (Davis and Memmott, 1982; Davis and Pérusse, 1988). The ability to transfer counting to different objects has not been tested, so we do not know yet whether this counting phenomenon is bound to initially learned objects or whether a transfer to equally spaced objects can also be performed. In additional experiments, the authors proved that not only the numbers of landmarks passed by are learned, but also the type of landmark at a particular place (Chittka and Geiger, 1995a; Chittka et al., 1995).

Furthermore, if the direction of the row of landmarks is changed, bees deviate from the compass-directed flight path as long as the angular deviation is not too high. The capacity of the landmarks to guide the bees towards a new compass direction largely depends on whether the sun in a blue sky is visible or not. Under an overcast sky, bees follow the displaced landmarks more strongly (Chittka and Geiger, 1995b).

These results indicate that features of landmarks passed by are learned, not only in direct connection with the nest or feeding site. It is not yet known, however, how these landmarks are seen and whether their color is recognized. Landmarks may be seen in color (Collett et al., 1993), but further evidence is necessary. Since motion cues and other object-related features are seen only with the green receptors (see Lehrer, 1997, this issue) it might well be that objects encountered en route may not appear in color to bees.

Large landmarks close to the feeding place can serve as a beacon (Geiger et al., 1995). Piloting towards a beacon over larger distances (>10 m) is usually of low priority for navigation in bees when compared to sun-compass-related vector orientation but can be demonstrated under particular conditions, e.g., when the sky is overcast for several days. More important for the place-
Fig. 2. The role of sequential landmarks experienced by bees on their flight route between hive and feeding place. The training setup is shown above (a). The positions of the landmarks (tents) are marked by triangles, the test feeders are indicated by circles. H indicates the hive site. The dashed line marks the distance of the training feeder (262.5 m) from the hive. (a) The control test with the unchanged number of landmarks. (b) The test in which the number of landmarks was increased to five. (c) The test in which the number of landmarks was raised to six. (d) Control test for (c) with the original (training) landmark setup, but the test feeder positions as in (c). F2 was placed directly in front of the third tent (after Chittka and Geiger, 1995a).

ment of a feeding place (or the nest entrance) in the vicinity of the target relative to nearby landmarks is the strategy of animals to optimize the match between the currently experienced landmark picture and a memorized landmark picture (Cartwright and Collett, 1983). This important aspect of localizing targets is discussed by Lehrer (1997, this issue), and will not be dealt with here.

3. COMPLEXITY OF NAVIGATIONAL MEMORY

Route-specific memories composed of independent memory items (compass vectors, landmarks along the route, beacons at the goal) are currently considered to fully characterize the structure of long-range navigational memory in bees (Wehner and Menzel, 1990; Wehner, 1992). This may not be fully correct, but a consequence of the methods applied so far, namely training bees to a single feeding site, and thus restricting their knowledge to a single route. Capalidi and Dyer (1995) confirmed observations by Becker cited in von Frisch (1967) under better controlled conditions, and found that bees released in an area which they were likely to have inspected during orientation flights originating at the hive were very well orientated, allowing them to return to the hive quickly. We also observed recently that bees released at distances of 400–500 m from the hive returned quickly to the hive from all directions although they could have established a knowledge of the landscape only during orientation flights and not during food collecting flights (Menzel et al., unpubl.). Such behavior may indicate that bees may have a richer spatial memory than just an association of otherwise independent memories of flight vectors and route-specific memories for landmarks. A richer memory might contain the positions of distributed landmarks relative to a geostable reference system (time-compensated sun compass), and may, therefore, be organized in a geostable rather than in an egocentric fashion. A geostable reference system has the properties of a map although it may not be a metric map. An egocentric reference system, on the other hand, would be devoid of an overall representation of landmarks and their relationships, but would instead memorize the locations of landmarks only with respect to the animal itself. As a consequence, an animal with an egocentric navigation system should not be able to make shortcuts, i.e., to

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choose novel and economic flight routes between two locations (Bennett, 1996).

In order to test whether bees are able to make shortcuts with respect to landmarks it is necessary to establish a memory of the landscape that is richer than route-specific memory (Menzel et al., 1996). To avoid training to a single location, bees were trained to visit two feeding sites, one F1 (115° from the hive) in the morning, and one F2 (40°) in the afternoon. When released at the feeding site not currently visited (F1 in the afternoon, F2 in the morning), the bees flew back to the hive choosing the correct flight direction for the particular release site (Fig. 3). This result indicates that the landmark features at the release site help to retrieve the correct vector memory for the homeward-directed flight. Most importantly, bees never flew directly from F1 to F2 or vice versa, thus indicating that novel shortcuts cannot be performed between known feeding sites, but only between a known feeding site and the hive.

In the critical experiment bees were released at R3, a release site which was never visited by the bees before and which was located halfway between the two feeding sites. Half of the bees chose a flight direction pointing directly to the hive along a flight path which they had never traveled before, neither with respect to the direction of the flight path nor with respect to the landmarks passed by. These data indicate that the particular landmark features at R3 resembling partially those of both feeding sites F1 and F2 retrieve the vector memories for both feeding sites. These two vector memories must then be integrated, leading to a novel flight direction which lies between the two homeward-directed vectors. This behavior was observed only in bees which were trained to both feeding sites. Furthermore, the importance of landmark features in the retrieval of vector memories was confirmed by releasing the bees trained to both feeding sites far away from the training area. In this case they did not show the integrated flight direction displayed at R3.

Our results suggest that bees are capable of vector integration for long distances and for vectors stored separately in memory. Such a capacity would allow for the possibility that novel flight routes towards the hive are taken as the result of a computational process carried out on the contents of separately stored spatial vector memories. We want to stress two points here, first that long-range vector integration was observed only for homeward-directed flights, but not for flights between feeding sites. The finding by Gould (1986) claiming that bees fly shortcuts towards a feeding place is, therefore, not confirmed by our results, and was not replicated either by us or other scientists (see Wehner and Menzel, 1990). This is particularly important in the context of

Fig. 3. Mean vanishing directions of bees released at a place (R3) which they had not visited before and which is positioned between the two feeding sites F1 and F2 (see text). Tests were performed by releasing bees in the morning and in the afternoon at R3 after they were collected at the hive at the moment they departed for the feeding place (HD: hive departing bees), in the morning for F1, in the afternoon for F2. The upper graph gives the location of the hive (H), the two feeding sites (F1, F2), and the release site R3. The vectors 1 to 5 give the directions to and from these sites respectively. The lower graph shows the mean vectors of two distributions of vanishing bearings of bees released at R3. Bees released in the morning were heading towards F1, those released in the afternoon were motivated to fly towards F2. In each case the vanishing bearing distribution fell into two groups, one which indicated compass direction according to the motivation of the bees (vector 2 in the morning, vector 4 in the afternoon), the other a mean direction close to vector 5, which is the direction from R3 to the hive (after Menzel et al., 1995).
the question discussed here on how flowers are localized. It appears that bees visiting different flower locations need first to return home for reorientation. There is no evidence yet that they navigate between far, distant feeding sites, localizing them in a "cognitive map" as a form of spatial representation. The location of the hive, however, may be characterized as a spot in a map-like organized spatial memory, and the locations of feeding sites as perceived from the hive may also be qualified items in such a memory. The lack of the capacity to navigate freely between feeding sites, which were experienced independently from each other in successive foraging bouts, may reflect a motivational limitation rather than a general limitation of spatial memory.

FLOWERS AS UNCOLORED AND COLORED TARGETS

Optical signals emanating from the flowers themselves indicate the precise location of potential food sources and the best position for landing and handling the flower. Thus, optical signals of the target facilitate the discrimination task both at the perceptual and the motor level. Color cues are the most important visual signals that are perceived from some distance (Proctor and Yeo, 1972; Wasner, 1983; Menzel and Shmida, 1993, fig 5; see also in this issue: Chittka, 1997; Giurfa and Vorobyev, 1997; Vorobyev et al., 1997). Bees have the visual apparatus for detection and discrimination of colors and show a high capacity for learning colors (von Frisch, 1967; Menzel, 1985, 1990). Bees perceive colors via the ommatidia of the compound eyes. Most, if not all, ommatidia contain the three spectral receptor types, peaking in the UV, blue, and green part of the spectrum. With such a set of receptor types, bees are capable of trichromatic color vision in most or all visual spots. The composition of ommatidia with spectral receptor types was proven by intercellular recording and marking techniques (Menzel and Blakers, 1976; Menzel and Backhaus, 1991). Behavioral, electrophysiological, and modeling studies have shown that receptor signals are processed in spectral opponent visual pathways (Kien and Menzel, 1977a,b; Menzel and Lieke, 1983; Backhaus, 1991; Chittka et al., 1992).

Visual orientation towards a target is guided not only by color vision but also by achromatic vision (see Giurfa and Vorobyev, 1997, this issue; Lehrer, 1997, this issue), and this achromatic vision may also be responsible for landmark detection en route (see above). The chromatic and achromatic vision in honeybees are used for different purposes. The achromatic system is mediated exclusively by green receptors. In the context of flower localization, it is important to notice that achromatic (= green) signals are detected from a further distance than chromatic (color) signals (Giurfa et al., 1996; Giurfa and Vorobyev, 1997, this issue). Furthermore, the two signals appear mutually exclusive in controlling approach flights because the green signal is learned only from the distance where the color signal is not yet perceived (Giurfa et al., 1997; Giurfa and Vorobyev, 1997 this issue). These perceptual properties, together with the qualities of trichromatic color vision in hymenopteran pollinators, characterize a framework within which the visual signals of flowers are evaluated.

Chromatic and achromatic vision are tuned to different angular sizes of objects. If an object subtends a visual angle larger than 15°, green contrast is not used for detection, and the object is detected on the basis of its chromatic contrast to the background color. Objects subtending visual angles smaller than 15° and down to 5° are detected on the basis of their green contrast. In such an angular range, chromatic contrast does not play a role in the detection task. Finally, reflecting objects like flowers subtending an angle less than 5° cannot be detected, irrespective of the green contrast value (Giurfa et al., 1996; Giurfa and Vorobyev, 1997, this issue). Smaller objects can be detected against the bright sky (e.g., a flying queen by drone bees: Valleri and Coles, 1991, 1993) because of the high quanlantal flux, but this capacity appears not to be related to flower recognition but to mate recognition (van Praag et al., 1980), and may be performed with blue rather than green photoreceptors.

The size of a flower and both its achromatic and chromatic contrasts to the background define the distance over which it can be detected. Since the far distance green signal can be learned by the bee as well as the close-up chromatic signal (Giurfa et al., 1997), both kinds of signals are used in sequence during an approach flight to a particular flower. Because the reproductive success of a plant species is often limited by pollination (Waser, 1983) insects must be able to discriminate between flowers (i.e., insect mediated pollen transfer should be restricted to the same plant species and minimize the transfer of foreign pollen to the stigma). Flower constancy of pollinating insects helps to achieve these goals but requires the ability to detect and discriminate flowers of different species from each other. For this reason flowers should evolve in such a way that they facilitate the discrimination between co-flowering species and also enhance detectability for the pollinating animal (Chittka and Menzel, 1992). Artificial hand pollination often increases seed set in plants (Bierzychudek, 1981), which indicates that seed set is limited by pollinator visitation in these cases. Additionally, paternal success as measured by pollen export from

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the flower also rises with increasing visitation rate (Englund, 1994). A plant’s reproductive success will thus be maximized if the visitation rate of constant pollinators is high. Therefore, a plant has to mark itself in order to be detectable and recognizable by individual pollinators that are not familiar with its location. More insects will visit the plant if it can be seen and recognized from a longer distance. A plant can achieve higher detectability from longer distances by increasing its size and both kinds of visual contrast, green and color contrast.

The size of the flower corolla appears to be the decisive parameter as the following analysis shows. (1) The angular size/detectability functions for both contrasts are very steep (see fig. 3 in Giurfa and Vorobyev, 1997, this issue) and saturate for >5° visual angle for the green contrast and for >15° for chromatic contrast. Thus, the threshold values of angular size of the two visual contrast functions are well defined. (2) The visual contrast/detectability functions are less well defined but reasonable conclusions can be drawn from experimental results and model calculations. With respect to the green contrast, Giurfa et al. (1996) found that a green contrast of 0.3 (positive or negative with respect to the background used) is well above the threshold, and a green contrast of 0.003 is below the threshold (see fig. 3 and table 1 in Giurfa and Vorobyev, 1997, this issue). It can thus be estimated that a green contrast of 0.15 is close to the threshold. We find (Table 1) that only in a few cases, the green contrast of flowers falls into a [-0.3 to 0.3] category, i.e., only a few flower species cannot be detected with the green receptor, achromatic system. This indicates that green contrast values in this range are indeed critical for detectability. Thresholds for chromatic contrast can be estimated on the basis of model calculations which are based on the voltage noise in the photoreceptors (Osorio and Vorobyev, 1996; Vorobyev and Brandt, 1997, this issue).

The detection distance L can be calculated on the basis of these arguments for the green contrast and chromatic contrast. Five representative examples for different corolla sizes of Israeli plant species were examined (Fig. 4). Subtended angle α is related to corolla diameter D and distance L between the target and the detecting animal by the simple equation

\[ \tan \left( \alpha/2 \right) = \frac{D}{2L} \]

Thus, maximal distance from which the flower can be detected is given by

\[ L_{\text{max}} = \frac{D}{2 \tan(\alpha_{\text{min}}/2)} \]

where \( \alpha_{\text{min}} \) is the minimum detection angle, which is

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Bold numbers = only detectable with color contrast  
Italic numbers = not detectable

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equal to $5^\circ$ for flowers whose green contrast exceeds the threshold, and $15^\circ$ for the flowers which lack green contrast, but have supra-threshold chromatic contrast. This simple linear relationship applies for the flowers whose green and/or chromatic contrast exceeds the threshold. If detectability would slowly rise with increasing green or chromatic contrast, conditions would be more complicated, and smaller subtended angles would be compensated for by increased contrast.

A simple way to enlarge the catchment area within which the flower will be detected is to enlarge the signal unit. This can be done by combining flowers in dense inflorescences, enlarging the signaling flower parts (i.e., petals, sepals), or by including non-flower parts of the plant into the signaling unit (i.e., colored leaves). A temporal synchronization of the flowering time at one plant (bushes, trees) also increases detectability. Examples of these strategies are numerous and need not be discussed here.

THE ROLE OF THE BACKGROUND

Detectability of a flower against a particular background obviously depends both on its own intensity and spectral properties and that of the background because contrast results from the reflection of the target against the background. The detectability of the same object may therefore vary if it is contrasted against different backgrounds. A background with a higher reflection in the green part of the spectrum may shift the green contrast of an object below the detection threshold, whereas the same object may be detectable against a background

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which is not as green reflecting. This fact is important in natural situations where flowers may either contrast against soils with different reflections or against its own leaves or those of other plants. In environments that differ in respect to their backgrounds, flowers are expected to adapt their flower signals in a way that fulfills the basic needs of detection and discrimination from each other.

To test whether flower signals are actually adapted to their environment, we analyzed flower colors from 160 flowering plant species growing in 2 different habitats in Israel: the spectral reflection functions of 51 species were measured from the desert in the vicinity of Avdat in the central Negev and Hatzeva in the eastern Negev (Arava), and that of 109 species from the Mediterranean region around Har Gilo (near Bethlehem) and Har Meron (in the North) (see Menzel and Shmida, 1993). The two habitats differ strongly in their prevalent backgrounds, soils and foliage in the Mediterranean region and highly reflecting sand and stones in the desert. The difference in reflection does not cause a chromatic shift because the desert background is higher at all wavelengths (see Chittka, 1997, this issue). Both habitats differ also in species richness and flower density, which are much higher in the Mediterranean region. The colors of plants in the desert and the Mediterranean region have a similar distribution in the color triangle (Fig. 5). The only difference between these habitats is that in the desert, fewer species have UV and UV-blue color (2 × 2 table, \( p = 0.01 \) according to Menzel and Shmida, 1993). Since there is no chromatic shift between the two backgrounds, this effect cannot be an adaptation to increased color contrast but instead may indicate an adaptation of green contrast. To contrast against the highly reflecting desert background, flowers should either have a significantly lower or an even higher green reflectance.

Intuitively, in addition one might expect that detection of flowers in areas with low plant density may depend more strongly on far distance signals because distances between plants are higher. Improved long distance detection in desert plants can be accomplished by higher green contrast and large signaling units (flowers or inflorescences). In the Mediterranean region far distance detection may be less important due to the smaller distances between flowers but a green contrast may be achieved more easily because the background is rather low in the green part of the spectrum. An alternative hypothesis would be that desert flowers growing in distributed micro-patches may depend less on green contrast because their localization can be achieved with the long distance navigational system, and are thus spotted by the pollinators solely with reference to landmarks. The ecological constraints in the desert would certainly not allow an increase of the signaling unit (flower or inflorescence).

The green contrast values of both Mediterranean and desert flowers are calculated by using either a standard background or the respective natural background...
Fig. 6. Green contrast of flower colors for different backgrounds: standard background (green leaves standard) and natural background of the habitat. (a): Plants in the desert and Mediterranean show no differences in green contrast. (b) and (c): Single plant families (Asteraceae and Fabaceae) show lower green contrast value in the desert than in the Mediterranean habitat. Contrast values calculated against standard background tend to be lower in the desert region, but clearly differ from Mediterranean contrast values for the natural backgrounds. Due to the highly reflecting background in the desert, flowers in this habitat generally show a low green contrast.

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No differences are found if the standard background is used. This means that the distribution of the green reflection of Mediterranean and desert flowers is not different. However, if the respective background is used to calculate green contrast, desert flowers show a much lower green contrast than plants in the Mediterranean region. Thus, the first intuitive hypothesis formulated above, suggesting that detection of flowers in areas with low plant density may depend more strongly on far distance signals, can be rejected. The second, alternative hypothesis is supported by the available data; however, the effect is solely due to the different backgrounds because no such effects are found if the same background is used for calculating green contrast.

An analysis of different plant families indicates that species within a family tend to differ less from each other in their reflectances than between different families. We thus analyzed plants of the two families with the most species, Asteraceae and Fabaceae, in order to test if differences between the two habitats occur within a family (Fig. 6b,c). In both families the green contrast values for the standard background tend to be lower for the desert plants than that of their relatives from the Mediterranean region. A significant difference in the
green contrast within a family is found if species are referred to their respective natural backgrounds; plants of the desert show a much lower green contrast than plants from the same family growing in Mediterranean habitats. Thus, flowers in the Mediterranean, but not in the desert habitat, have higher positive green contrast against the natural background.

We next asked whether these differences in green contrast of flowers in the two habitats affect their detectability. We analyzed how many species can be detected against their natural backgrounds by green contrast or chromatic contrast. As pointed out above, the threshold value for detection by means of green contrast is not known exactly. Thus, to provide an estimate of the number of non-detectable species we used two different threshold values: a 0.3 difference between background and object, a contrast sufficient for detection (Giurfa et al., 1996), and a 0.15 difference, which lies between the 0.3 value of perfect detection and the 0.003 value where detection does not occur. Thresholds for chromatic vision are variable (von Helversen, 1972). To account for this variability we performed the calculations for the values of 1, 2 and 3 discrimination steps as predicted by the photoreceptor noise limited model (Vorobyev and Brandt, 1997, this issue, see their eq. 12). Table 1 shows that the result is independent of the threshold values chosen for both visual contrasts. The flowers of all species can be detected by chromatic contrast and the majority of them are detectable by green contrast.

However, in the desert there are more species that do not have a green contrast against the background (13–26 species) than in the Mediterranean region (6–8 species, corresponding to 6–7% of the total species). Of the 8 Mediterranean species that do not have a green contrast, 3 species (Adonis microcarpa, Papaver rhoeas, and Papaver subpratiforme) are visited by beetles. Since these species are also visited by hymenoptera and may even be more effectively pollinated by them, it is unclear whether their color signal (red) and lack of green signal is an adaptation to beetle visitation.

It was observed in behavioral experiments that bees also learn negative contrasts of objects with respect to the background, i.e., situations where the object shows less reflection than the background (Giurfa et al., 1996). This observation shows its importance in the ecological context, especially for habitats with highly reflecting backgrounds. In the Mediterranean species, green contrast differences are mainly positive, while most of the desert species have a negative green contrast (Table 1).

As argued above, the plants which do not have a green contrast can compensate for the impaired detectability by possessing larger flowers. However, we found that in both habitats, flowers without green contrast do not tend to have bigger corollas than those with green contrast (Fig. 7). This result corroborates the effect reported above that desert flowers do not adapt their values of green contrast to compensate for the high reflectance of background.

**DISCUSSION**

We have focused our analysis on hymenopteran pollinators and their capacity to localize flowers by two strategies, applied in temporal sequences when approaching a flower from the nest site. (1) Over large distances, in the range of kilometers, bees and wasps navigate by using the sun compass and relate the path-integrated compass vectors to landmarks both along the flight route and at the goal. (2) At short distances, in the few centimeter range, they use first an achromatic signal (the green signal) and then, at even closer range, a chromatic signal (the color) of the target. We have not considered an important intermediate range, which relates to the capacity of bees and wasps to memorize snapshot views from particular vantage points for localizing a target relative to nearby landmarks in the meter range (Cartwright and Collett, 1983; Collett, 1996; see also Lehrer, 1997, this issue). The memories involved in these three navigational tasks are usually viewed as rather separate entities, but growing evidence indicates that they are intimately connected by associative processes (Menzel et al., 1996). It is therefore likely that the different sets of external stimuli to which these navigational tasks refer are elements of a rich spatial memory with qualified and localized components. The qualification relates to the meaning of these components as extended landmarks and profiles of the horizon for backing up compass directions when the sun or blue sky are invisible, as landmarks passed by en route, as landscape features close to the goal, and as specific features of the goal (e.g., visual and olfactory stimuli, mechanics of the flower, reward properties). The concept of a rich and unique navigational memory composed of interrelated memory items underlying the task of navigation between nest site and feeding sites supports the view that evolution of flower signals should depend on all the other components guiding navigation of pollinators. Our analysis presented here is in line with this view.

Plants are evolutionarily adaptive elements, whereas features of the habitat are constraints. Flowers aim for reliable identification and recognition within the conditions provided by the habitat. If the habitat allows for an easy localization (e.g., in the desert because of the low growth density) the navigational system of the pollinator may need less support by further ranging flower
signals. We, therefore, expect that signal characters displayed by the flower are woven into other components leading to one navigational memory in pollinators. The results of our analysis of green and color signals of flowers in the desert and Mediterranean habitats of Israel can be interpreted along this line of argument, if we assume that these two visual signals are potentially adaptive elements in the coevolutionary relationship between flower and pollinator. Sparingly growing plants in the desert are probably spotted by bees and wasps predominantly by using their spatial memory. Such plants may therefore rely less on their own green contrast signals for the intermediate range of detection than densely blooming plants in the Mediterranean habitat. The color signals of both kinds of plants should depend less on the features of the habitat because this signal may be needed for proper alignment of the flying insect for fast and effective handling, irrespective of how the plant was spotted. The color signal, together with the shape and pattern, may also more reliably indicate the nutritional status of the flower, a feature which should also be independent of the habitat. Mediterranean plants grow in higher densities, they may compete more strongly for pollinators, and the green signal of their flowers appears at a more fluctuating background than that of desert flowers. It may well be that the green signal of flowers under such conditions is more strongly controlled by evolutionary pressure and for that reason stays particularly high.

The arguments presented here need further critical tests. Data from different habitats have to be examined for generality of the effect. Psychophysical studies have to be performed to test whether structured backgrounds obscure flower signals more readily than homogeneous backgrounds. Such experiments also have to study in more detail the combined effects of green contrast and the angular view of the target in determining detectability. Although more data are needed, we believe that our arguments provide a framework for critical testing of the notion that flower parameters are intimately linked to other components of the habitat through their combined effect on the unique navigational memory of pollinators.

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