
Adaptation, constraint, and chance in the evolution of flower color and pollinator color vision

Anciently the teaching was that nothing would have been created that did not have a definite purpose, and more recently it has been that natural selection would eliminate anything that did not serve an equally definite purpose. ... the assumed relation between the colors of flowers and the ... pollinating insects is such a classic ...

Apparently there is something about the internal mechanism ... that makes it difficult for a rose to be blue. ... therefore, the use of the idea of natural selection to explain the absence of blue roses in nature is not only not necessary but it is not justified ... It would be much better for the rose to be blue.

F. E. Lutz (1924)

We commonly think that biological signals and receivers are mutually tuned to one another. Flower colors and pollinator color vision are not exceptions. The diversity of flower colors and the differences in color vision between different classes of pollinators make speculations about their mutual adaptation tempting. Yet close inspection reveals that we know very little about evolutionary changes in flower color induced by selection pressures related to pollination, nor is there much evidence to show that color vision systems of pollinators have been tuned to flower color. We shall review cases where we think such changes have occurred, and other cases where they have not, even where a purely adaptationist scenario would predict evolutionary tuning. In such cases, we suggest alternative explanations, including phylogenetic constraint, exaptation (novel use of traits evolved for other purposes), pleiotropy (selection through correlated characters), and random evolutionary processes such as genetic drift. Because our understanding of these processes in relation

to biological signals and receivers is still in its infancy, our evidence is fragmentary. We hope, however, that it will stimulate future research to add the missing pieces of the puzzle. We shall first discuss possible causes of the diversity of floral color signals and then move on to the evolution of pollinator color-vision systems.

Pollination syndromes and flower colors

One way to explain the diversity of flower colors is to use the concept of pollination syndromes, which holds that particular classes of pollinators are specifically associated with particular floral traits, including floral color (Faegri & van der Pijl 1978). There is current debate on how tight and exclusive these associations are (Waser *et al.* 1996; Johnson & Steiner 2000; Thomson *et al.* 2000; Gegear & Laverly, this volume). One argument involves the significance of red flowers in the context of hummingbird pollination. In the classical view, red flower coloration is a strategy to kill two birds with one stone: such coloration was thought to be invisible for bees and at the same time attractive for hummingbirds (Raven 1972). Therefore, flowers that are morphologically adapted to bird pollination, and on which bees transfer pollen less efficiently than birds do, should be colored red. The premises are flawed, however. Bees do visit red hummingbird flowers, and they can be trained to distinguish red from a green, foliage-like background, as well as from yellow and orange model flowers (Chittka & Waser 1997). Researchers working on hummingbirds have not been able to find a preference for red (Lunau & Maier 1995). Thus, the association between hummingbirds and red flowers is not exclusive.

A recent study by Thomson *et al.* (2000), however, does indicate that the association exists. In seven lineages of the genera *Penstemon* and *Keckiella* (Scrophulariaceae), flowers frequented by hummingbirds are more often orange and red than their bee-visited close relatives. Also, red coloration is strongly associated with other floral traits linked to ornithophily. But what is the significance of such coloration, if it is neither attractive for hummingbirds nor invisible for bees? In our view, there is no necessity for exclusivity: any change in floral trait may be subject to selection if it confers a change in fitness, however small. Red coloration might be an adaptation to facilitate detection by hummingbirds, or to decrease detectability by bees, or both – *even by a few percent*. For flowers that are adapted to hummingbirds, bumble bees may not only transfer pollen less efficiently than birds, thereby acting as pollen thieves

(Thomson *et al.* 2000); they may also rob nectar, further reducing plant fitness (Irwin & Brody 1999). In such circumstances selection would favor any character that diminished visitation by bees.

In many situations, hummingbirds and most bees choose nectar flowers on the basis of their net caloric rewards (Waser *et al.* 1996; Healy & Hurly, this volume; Waddington, this volume). These depend not only on the nectar content of the flowers, but also on the time taken to locate the flowers. Thus, we need to evaluate the *search times* that hummingbirds and bees take for finding red, UV-absorbing flowers, and compare these with times taken to search for flowers of other colors. Data for hummingbirds have yet to be obtained, but results for bumble bees are now available. In a flight arena, we presented *Bombus terrestris* workers with a random arrangement of three identical model flowers, all of which were rewarded. We measured the time taken from entering the arena to landing on the last flower, excluding flower-handling times. Search times strongly depended on color; the larger the color contrast of the flowers with their background, the more rapidly bees would detect the flowers. Red and white (UV-reflecting) model flowers, which make the poorest contrast with their backdrop, took more than twice as long to find than did blue or yellow flowers, for example (Fig. 6.1). Thus, red coloration may indeed be a strategy to reduce visitation by bumble bees to some degree. Another (non-exclusive) possibility is that hummingbird flowers use red color to form a mimicry ring, so that each species will be identifiable as a suitable food source by hummingbirds using experience gained on flowers of different species (Healy & Hurly, this volume).

In general, we expect sharper discontinuities between syndromes where classes of pollinators differ strongly in morphology (so that one type of pollinator transfers pollen substantially better than another) and in sensory system (so that, for example, a particular color is poorly detectable by one type of pollinator, but conspicuous for another). Red hummingbird flowers fit these prerequisites, but we stress that pollinator segregation achieved by red coloration is nowhere near exclusivity. We suspect that this observation extends beyond red flowers. The concept of "private channels" in sensory biology may apply to spectacular specializations such as ultrasonic hearing. However, in many cases, the ranges of sensory systems will overlap, sometimes heavily. In such cases, interactions between signals and signal receivers will not follow a simple crypsis vs. conspicuousness dichotomy. We may have to look for more subtle

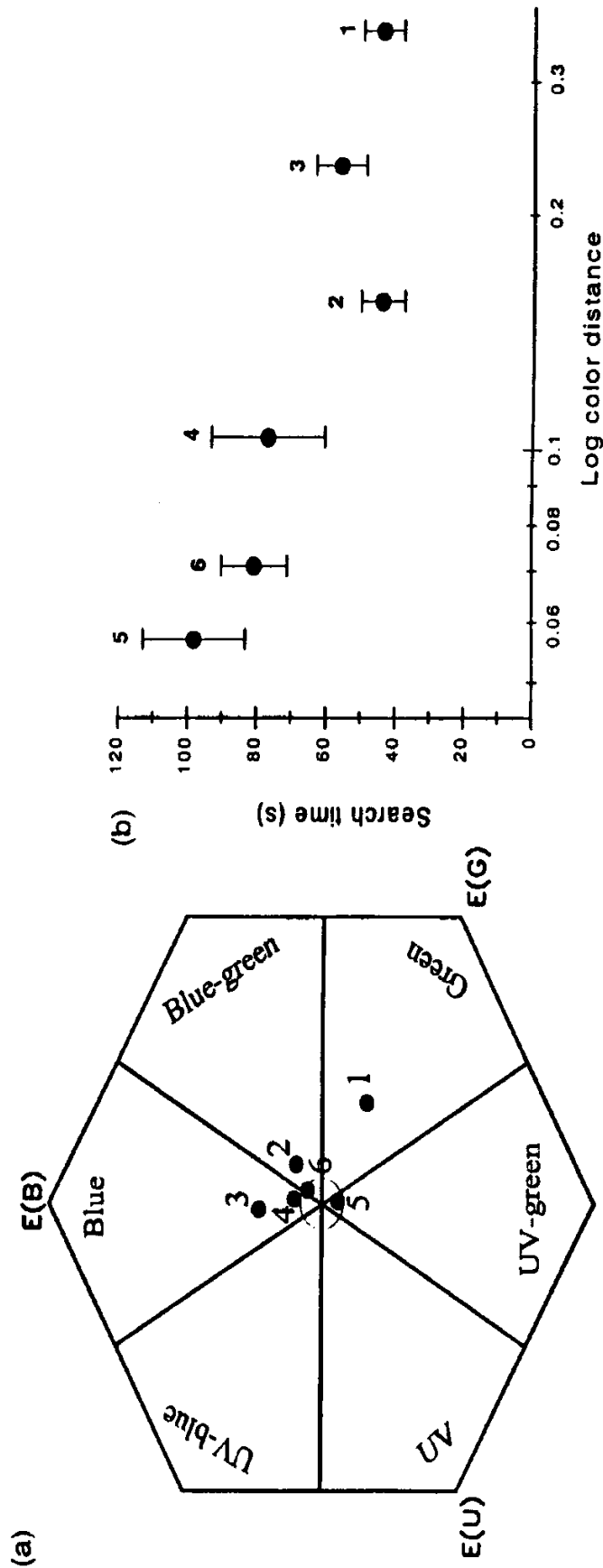


Fig. 6.1. (a) Color loci of targets for bumble bees in the color hexagon. The colors appear to humans as follows: 1—yellow; 2—white (UV absorbing); 3—blue; 4—turquoise; 5—red; 6—white (UV reflecting). The angular position of a color in the color hexagon informs us about the bee-subjective hue. We assume the photoreceptors adapt to the background against which the stimuli are presented; see Chittka (1996) for details. As a consequence of this adaptation process, the background lies in the center of color space. Thus, by definition, the color contrast of a model flower with its background is determined by the distance of its color locus from the center of color space. The distance between the center and each of the hexagon's corners is unity. (b) Correlation between color contrast (target vs. background) and search time ($r_s = -0.83$; $n = 6$; $p < 0.05$). Three colored chips of $\varnothing = 28$ mm were placed in a flight arena at random positions. We measured the time elapsed from entering the arena to landing on the third chip. Note that the correlation of detectability with color contrast is good only for large color targets: for smaller ones, an increasingly strong influence of green contrast is found (see Giurfa & Lehrer, this volume).

differences in effectiveness of different signals for different receivers, and in their actual fitness effects.

There is also the possibility of an evolutionary “arms race”. If, for example, red hummingbird flowers are so profitable that bumble bees might significantly improve their fitness by exploiting them, then bees might be selected to improve their sensory skills to detect such flowers. As we discuss below, this might have happened in *Bombus occidentalis*, a bee species known for extensively robbing hummingbird flowers (Irwin & Brody 1999).

How do we explain the diversity of flower colors whose major reflectance falls within the visual range of practically all pollinators, such as UV, violet, blue, pink, white (typically UV-absorbing), or yellow (with or without UV-reflectance)? Some scientists have extended the syndrome concept to such flowers as well, but if partitioning by syndromes is the major selective pressure that drove floral color diversification, why do we not see stronger segregation? More bluntly, why are not all bumble bee flowers blue, all butterfly flowers orange, and all fly flowers white, for example? In many phylogenetic lineages, switches from one flower color to another occur without an associated morphological adaptation to a different class of pollinator (W.S. Armbruster, unpublished data). In one study on a nature reserve near Berlin, we did not find any differences among the colors of flowers visited by large and small bees, butterflies, flies, and beetles (Waser *et al.* 1996). In a phylogenetic analysis of the distribution of flower colors within two plant genera, Armbruster (unpublished data) found that all the variation occurred in association with bee pollination (see below). Thus, direct selection by pollinators in the sense of an innate affinity (as suggested by some adherents of pollination syndromes) surely cannot explain all the existing variation in floral color (Geegar & Lavery, this volume). In the following paragraphs, we highlight alternative explanations for why floral colors might diverge. Not all of these involve pollinators.

Flower constancy and flower similarity

An alternative view to floral syndromes is that flowers differ in color as a strategy to promote flower constancy. Such fidelity by pollinators favors an efficient and directed pollen transfer between conspecifics (Chittka *et al.* 1999). Conversely, pollinators straying between flowers of different species may lose pollen during interspecific flights (Feinsinger 1987) or even reduce seed set by clogging stigmas with foreign pollen (Waser 1978).

In some closely related species, hybrids may be produced that are sometimes less viable than the parental species, thereby increasing selective pressures to diverge in floral advertising (Levin & Schaal 1970).

To understand the kind of diversity that can be expected to evolve as a strategy to promote constancy, it is critical to know the range over which pollinator-subjective color difference is correlated with flower constancy. For example, if a barely distinguishable contrast between two flower colors can produce 100% constancy, then flower constancy may drive only small-scale color differences, such as between two similar, but just distinguishable, shades of blue. However, character displacement across color categories, such as from blue to yellow, would be harder to explain by pollinator constancy if this were the case. Previous work allows us to predict how color discrimination improves with color distance (Chittka *et al.* 1992), but flower constancy and discrimination are unlikely to increase with color difference in the same way. In measuring flower constancy as a function of floral color difference, we do not ask: "How well can bees distinguish colors?" Instead, the appropriate question is: "How readily do bees retrieve memories for different flower types, depending on how similar they are to the one currently visited?" Discriminability sets the upper limit for constancy, but there is no a priori reason to assume that constancy is directly determined by discriminability.

In order to measure flower constancy as a function of color distance between flower types, we tested six species of apid bees on 15 pairs of plant species or color morphs of the same species, using a paired-flower, bee-interview protocol (Thomson 1981). We did not use the traditional Bateman's Index (Bateman 1951), because this index has a number of complications: it cannot be calculated if animals are completely constant, because the denominator in the formula becomes zero. Additionally, Bateman's Index always yields maximum constancy if the frequency of inconstant transitions from one of the flower types is 0, even if pollinators are inconstant when starting from the other flower type. Therefore, we quantified constancy using a new formula which circumvents these difficulties:

$$\text{cons} = 0.5 \left[(A - B) / (A + B) + (C - D) / (C + D) \right]$$

where *A* represents the number of constant flights from *X* to *X*, *B* the flights from *X* to *Y*, *C* the flights from *Y* to *Y*, and *D* the flights from *Y* to *X*. Constancy calculated in this way can range from 1 (complete constancy) through 0 (random flights between species) to -1 (complete inconstancy).

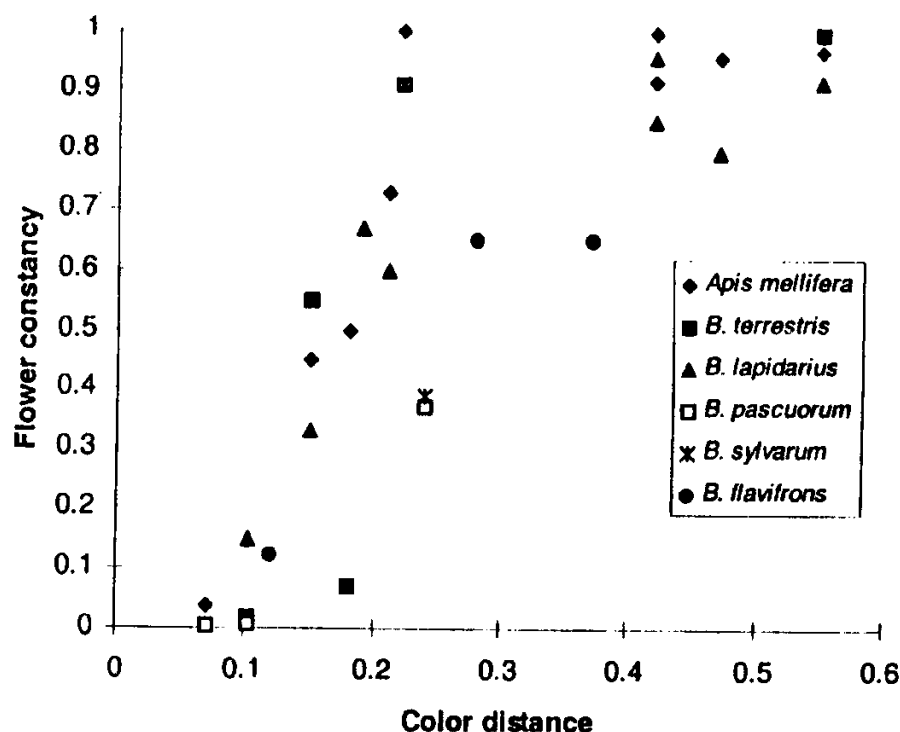


Fig. 6.2. Flower constancy in several species of bees as a function of color distance between pairs of flower types. For each pair of flower types, we recorded at least 80 choices. Flower constancy data are calculated as explained in the text.

This formula can be used only when individuals are coming to the pair of test flowers from both types of flowers.

Even though our analysis ignores differences other than color, there is a clear relationship between bee-subjective color difference and flower constancy (Fig. 6.2). Constancy does not deviate from chance at distances below 0.1 (where discrimination is already 70%; Chittka *et al.* 1992). At distances of about 0.2, constancy levels rise sharply in all pollinator species and above 0.4, constancy is generally above 80%. Thus, flower constancy is negligible at small color differences, even though bees can differentiate these colors well; it is at its maximum only in cases of pronounced differences.

Unfortunately, however, floral divergence due to benefits of constancy is not easily proven. Some authors have taken color diversity of sympatric flowers itself as evidence for character displacement (Menzel & Shmida 1993), but it is critical to test an observed distribution of phenotypes against a null model. Gumbert *et al.* (1999) examined several sets of sympatric and simultaneously flowering plants in a nature reserve near Berlin. A color distance distribution was generated for each set of flower

colors by calculating bee-subjective color distances between all floral color loci in bee-color space. To test whether the flowers differ more strongly in color than would be expected by chance, we compared the real distributions with those produced by a random generator.

When common plants were examined, there were no significant differences between random sets and actual flower color distributions. The only significant deviations were detected in rare plants, and these effects varied with habitat. In one habitat, rare flowers were more similar than expected by chance, in two they were less similar, and in two others, there was no deviation from a random distribution. Thus, flower constancy may have influenced plant community structure in some habitats, but we need more research before concluding that such influences are widespread (Chittka *et al.* 1999).

Finally, pollen flow between populations at different sites may prevent local adaptations to conditions at those sites (Stanton & Galen 1997). In such a situation, plants may gain fitness if gene flow between populations is depressed. Thus, if (and only if) there is a genetic correlation between a trait favoring constancy (such as flower color) and a trait involved in, say, resource acquisition under different ecological conditions, floral signal divergence may indeed be favored (Jones, this volume).

Pleiotropy, exaptation, constraint, and chance in the evolution of flower color

Biologists interested in the evolution of plant and animal signals tend to attribute signal diversity to selective pressures exerted by the signals' receivers (but see Newbigin 1898; Lutz 1924, for early attacks on this view). There are alternative explanations. One is pleiotropy, or indirect selection through genetically correlated characters (Armbruster *et al.* 1997). Carotenoids, responsible for yellow to orange coloration, are essential accessory pigments to chlorophyll in all plants (Scogin 1983). Many other pigment classes involved in floral coloration, or the biochemical pathways leading to the production of such pigments, may also protect against herbivores, UV radiation, and frost, or have unspecified effects on plant vigor (Onslow 1920; Levin & Brack 1995; Armbruster *et al.* 1997; Fineblum & Rausher 1997).

For example, Osche (1979) suggested that the yellow flavonoid coloration of pollen was already present in wind-pollinated ancestors of extant

anthophilous plants and primarily served as protection against mutagenic UV radiation. He suggested that in the early stages of insect pollination, many pollinators might have formed an innate preference for yellow floral signals, and that many plants later evolved large yellow nectar guides as supernormal stimuli to cater to this preference (Osche 1979). This hypothesis remains to be tested by phylogenetic tests, however.

To examine the possibility of pleiotropic effects in floral color evolution, two plant genera with great flower-color variation, *Dalechampia* and *Acer*, were examined using phylogenetically informed analyses (Armbruster *et al.* 1997; Armbruster, unpublished data). In both, flowers shared pigments that were also found in leaves and stems. In *Dalechampia*, similar changes in flower color occurred several times independently in evolutionary history, but these changes were not associated with pollination mode. Instead, in all species with pink or purple flowers, anthocyanins were also expressed in stems and leaves, where they possibly affect plant survival in ways not related to pollination. In *Acer*, the evolution of autumn leaf color actually predates changes in flower color. Again, this suggests that evolutionary changes in flower color may have occurred without any relation to pollination: rather, selective pressures operating on vegetative traits may have first favored the expression of different chemicals (see also Newbigin 1898; Onslow 1920). Then selection to enhance floral detectability may have favored expression of the same compounds in petals. In such cases, the use of particular pigments in the flowers is an exaptation with respect to pollination (Armbruster *et al.* 1997; Armbruster, unpublished data).

Pleiotropy is not the only constraint on flower color. If the flowers of two related species (or populations of the same species) have the same colors, this may not reflect similar selective pressures, be they on floral or vegetative traits. In fact, even if optimality arguments predict different coloration of flowers blooming at two different sites (for example because of the particular competing species in each habitat), they might still have the same color. One type of constraint is ongoing gene flow between populations, which might prevent flowers from local adaptation (Stanton & Galen 1997). Positive frequency-dependent selection by pollinators might also keep floral colors from reaching a local optimum (see Smithson, this volume). In addition, there are phylogenetic constraints on flower color in several plant taxa (Chittka 1997). In many species, a change from one floral color to another may simply require an improbable sequence of mutation events. Finally, genetic drift can act as a kind

of constraint, too: evolutionary chance processes will, with some probability and depending on the size of the population, eliminate intraspecific variance, unless it is continuously added by new mutations or immigration (Adkison 1995).

Conversely, some plants show pronounced variation in flower color among populations (e.g., Beerling & Perrins 1993). These might reflect adaptations to local pollinator preferences, character displacement driven by different competing plants, or, through pleiotropy, adaptations to local selective pressures on vegetative traits. The possibility that simple genetic drift might account for these differences has been left largely unconsidered. To our knowledge, the only exception are the flowers of the *Nigella arvensis* complex, which occur not only in mainland Turkey and Greece, but also on several Aegean islands. There are strong differences in color, pattern, and floral shape among island populations; genetic drift is a likely explanation (Strid 1970). Because these island populations are small, the idea of drift is particularly palatable, but there is no a priori reason to suspect that mainland populations of plants, whose effective population sizes may be as small as those on islands, are immune to chance evolutionary processes.

Has bee color vision adapted to flower color?

The discoveries that bees see ultraviolet and that flowers reflect it were made several decades ago (Kühn 1923; Lutz 1924, and references therein). Ever since, scientists have speculated that UV receptors in bees developed in a coevolutionary process with floral coloration (e.g., Menzel & Backhaus 1991). This notion received recent impetus from computer models showing that bee color vision is indeed the optimal system for detecting and identifying flowers (Chittka 1996). However, to prove that flower signals truly drove the evolution of bee color vision, it must be shown that the ancestors of bees possessed different sets of color receptors prior to the advent of the flowering plants. One must evaluate arthropods whose evolutionary lineages diverged from those of bees before there were flowers. If the color vision of such animals is indistinguishable from that of bees, this implies that it was present in an ancestor of bees that predated the evolution of flower color – and this is exactly what was found (Chittka 1997). The λ_{\max} values (wavelength values of maximum sensitivity) of the Crustacea and Insecta fall into three distinct clusters in the UV (around 350 nm), blue (~440 nm), and green (~520 nm). Red receptors

show up irregularly both in the Crustacea and Insecta; they have evolved several times independently.

Thus, we can infer that insects were well pre-adapted for flower-color coding more than 500 million years ago, about 400 million years before the extensive radiation of the angiosperm plants that started in the middle Cretaceous (100 million years ago). Recent data on the molecular structure of photopigments support the interpretation that the basic types of arthropod visual pigments must be placed at the very roots of arthropod evolution (Chittka & Briscoe 2001). Thus, bee color vision is an exaptation with respect to flower color.

Measured peak sensitivities of receptors vary up to 30 nm across insect species, however (Chittka & Briscoe 2001). Some of this must be measurement error, but we can not exclude the possibility of actual fine-tuning of pigments to particular visuo-ecological tasks. To examine such fine tuning, it is necessary to look at closely related species with known phylogeny and distinct ecological conditions. We mapped the positions of maximum sensitivity of the color receptors of 11 species of bumble bees from five subgenera onto their phylogeny (Fig. 6.3). These species span habitats from European alpine (e.g., *Bombus monticola*) and North American temperate (e.g., *B. impatiens*) to subtropical and tropical South America (*B. morio*), but the λ_{\max} positions are very similar across species. Peitsch *et al.* (1992) claimed that bee species flying in UV-rich environments might have short-wave-shifted UV receptors, while tropical forest-dwelling bees might have long-wave-shifted UV receptors. Our analysis does not support this claim: the alpine *B. monticola* (whose altitude range is 900–2700 m; Hagen 1994) does not differ from *B. terrestris* and *B. lapidarius* (both lowland species that are not found above 1400 m; Hagen 1994). Although the tropical *B. morio* has slightly long-wave-shifted UV receptors compared to the above two, it does not differ from several temperate species.

Several types of molecular constraints, and possibly pleiotropies, that might affect the evolution of color vision have been reviewed in detail elsewhere (Chittka & Briscoe 2001). One source of inertia that is often overlooked in investigations of sensory ecology is simply *chance*. Physiologists often assume that any superior genotype will inevitably be able to spread through a population. Because this assumption is so common, we shall elaborate in some depth why this may not necessarily happen. Imagine that a bumble bee colony produces 100 new queens, one of which carries a new mutation that has a beneficial effect on foraging

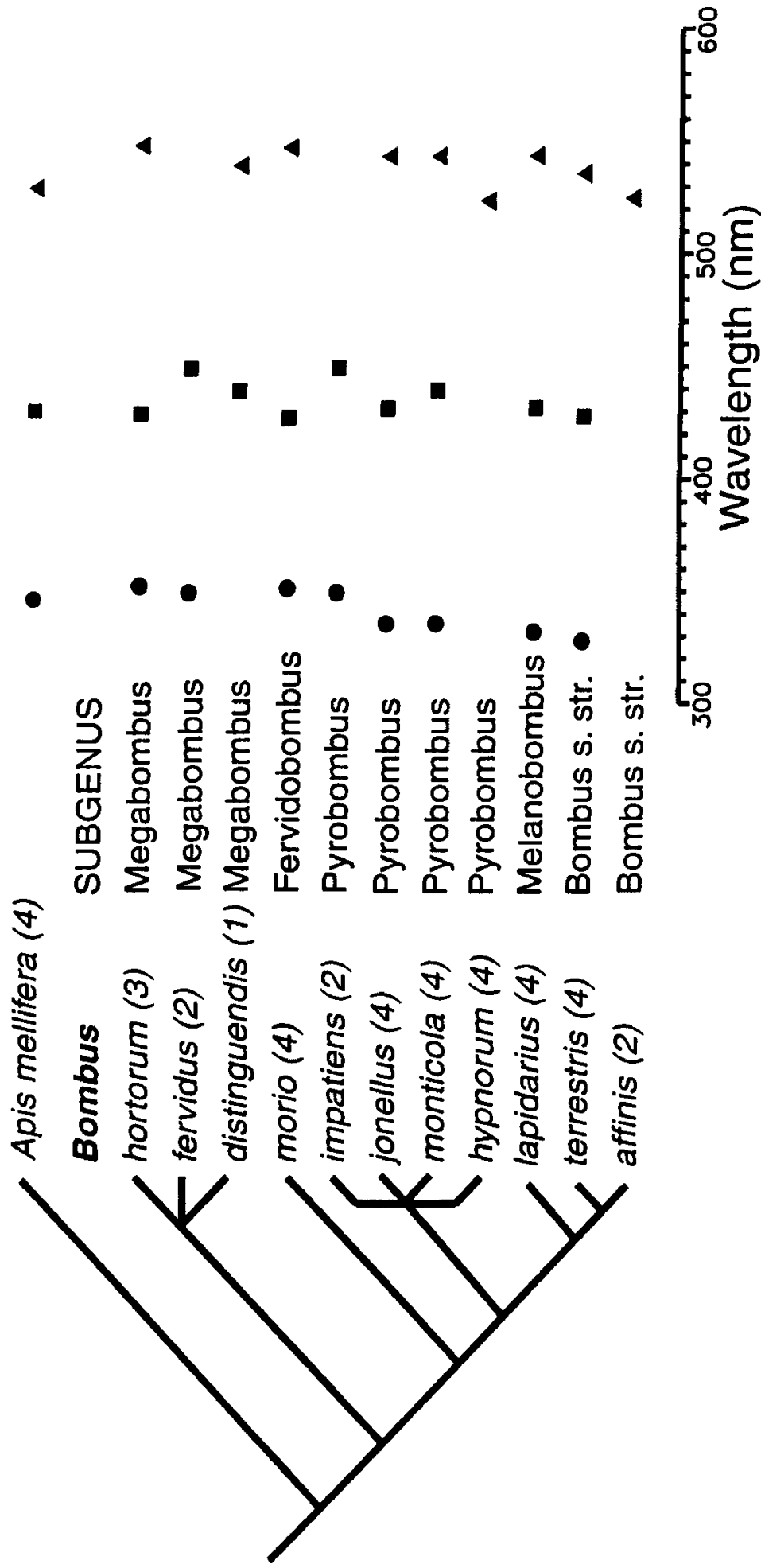


Fig. 6.3. The λ_{max} values of photoreceptors of 11 species of bumble bees superimposed on their phylogenetic tree (according to Scholl *et al.* 1990; Williams 1994), with *Apis mellifera* for outgroup comparison. ●-UV receptors; ■-blue receptors; ▲-green receptors. Note that the absence of some receptor types in some cases does not actually mean that the species is lacking that receptor: in some cases, the authors did not seek to find all the receptors present. References: 1, Mazokhin-Porshnyakov (1969); 2, Bernard & Stavenga (1978); 3, Meyer-Rochow (1980); 4, Peitsch *et al.* (1992).

performance, such as a receptor with an altered spectral sensitivity. In a stable population, only one (or very few) of these queens will survive and again produce fertile offspring. Many will succumb to frost in the winter or bird predators, or their newly founded colonies may be attacked by cuckoo bumble bees or parasites; the question of whether a queen survives all these hardships is entirely unrelated to its foraging ability. Even if the blessed queen successfully starts a colony, and if its worker offspring forage slightly more efficiently, the next generation of queens will be subject to the same unpredictable hazards. Now imagine that the mutation in question is rare and occurs only once in several generations. It is clear, then, that its chances of spreading are very slim. Generally, the probability of the mutation spreading to fixation is correlated with the frequency of the mutation and its relative adaptive advantage and inversely correlated with population size (Ohta 1993). The influence of genetic drift will be further enhanced when reproductive success varies strongly among individuals (Adkison 1995), as is the case in bumble bees (Imhoof & Schmid-Hempel 1999), or when (repeated) bottlenecks occur, such as in Canary Island bumble bees (Widmer *et al.* 1998). The influence of these parameters on the goodness of fit in biological signal–receiver systems has generally been ignored, but should be extremely worthwhile to explore in the future.

The conservation of λ_{\max} values within the bumble bees need not necessarily reflect any kind of constraint, however. If flower-color detection and identification in all these habitats require similar receiver systems, then we would expect conservation even in a world without phylogenetic constraint. Indeed, the estimated optimal color coding systems for Brazilian, Israeli, and German flowers from several habitats were almost identical (Chittka 1996). Be that as it may, the search for sensory adaptations is predictably frustrating if several related species display the same trait. Ideally, we need to study a trait that is variable both within and between closely related species (Chittka & Briscoe 2001). The only striking variation in receptors among the Hymenoptera is the occurrence of red receptors in very few species (Peitsch *et al.* 1992). Why most bee species lack such receptors defies a simple adaptive explanation. Although pure red flowers are rare in many habitats, many flowers do present information in the red part of the spectrum. Bee color-vision systems would, in theory, gain substantially if they had red receptors in addition to UV, blue, and green receptors (Chittka & Menzel 1992).

The evolution of flower-color preference in bumble bees

In an attempt to identify a visual trait that might reveal a more interesting pattern of adaptation to the visual environment, we evaluated the innate floral color preferences of bumble bees. We hypothesized that evolutionary changes of such preferences require changes only in the synaptic efficiency between neurons coding information from the color receptors. Therefore, color preferences might adapt more readily to environmental requirements than do the wavelength sensitivities of color receptors.

In one study, a good correlation was found between the color preferences of naïve honeybees and the nectar offerings of different flowers in a nature reserve near Berlin (Giurfa *et al.* 1995). In brief, honeybees preferred the colors violet (bee UV-blue) and blue (bee blue), which were also the colors most associated with high nectar rewards. This pattern is not unique to the German flora: a similar association of flower color with reward was found in Israel (Menzel & Shmida 1993). However, a correlation never indicates causality. To show that color preferences evolved to match floral offerings, we need to compare a set of closely related bee species (or populations of the same species) that live in habitats in which the association of floral colors with reward is different.

We tested seven species of bumble bees from three subgenera: four from central Europe (*Bombus terrestris terrestris* [229; 8; 4698], *B. lucorum* [39; 2; 547], *B. pratorum* [14; 1; 395], and *B. lapidarius* [83 ;2; 1446]); two from Japan (*B. ignitus* [89; 3; 2782] and *B. hypocrita* [54; 2; 1691]); and one from North America (*B. occidentalis* [122; 4; 3405]). Numbers in brackets give the number of individuals tested, the number of colonies, and the number of choices evaluated. All species preferred the violet–blue range, presumably a phylogenetically ancient preference (Fig. 6.4). In addition, however, *B. occidentalis* had the strongest preference for red of all mainland bumble bee populations examined. This is provocative because this species frequently robs nectar and forages heavily from red flowers apparently adapted for pollination by hummingbirds (Chittka & Waser 1997; Irwin & Brody 1999). Clearly, this preference is derived and therefore might be an adaptation unique to *B. occidentalis*.

We also tested *Bombus terrestris terrestris* from Holland [85; 3; 1670], *B. terrestris terrestris* from Germany [144; 5; 3028], *B. terrestris dalmatinus* from Israel [156; 5; 5731], *B. terrestris dalmatinus* from Rhodes; [150; 5; 5335];

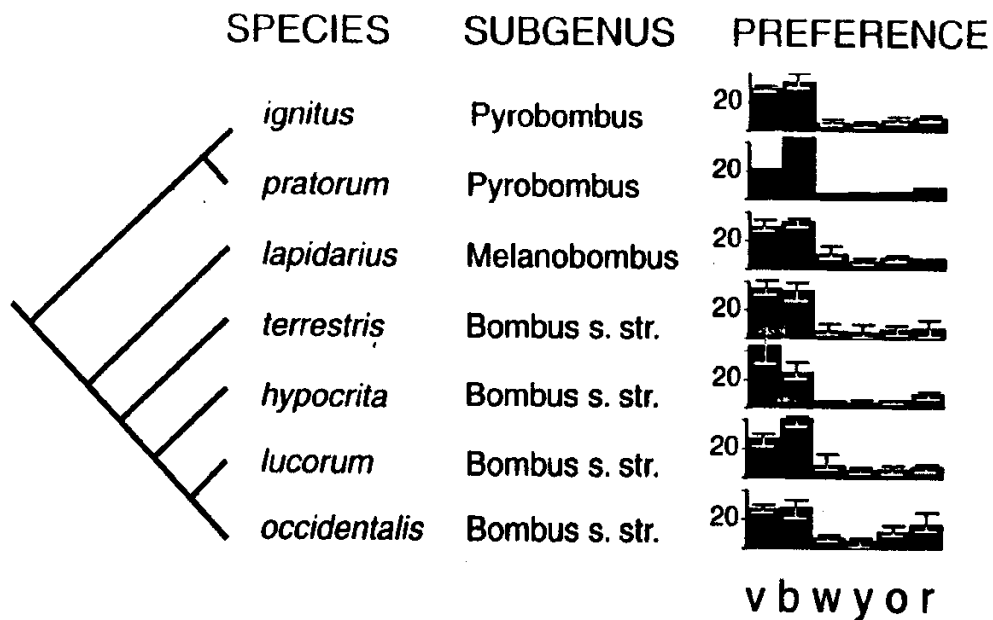


Fig. 6.4. The color preferences of seven species of bumble bees (*Bombus*) superimposed on their phylogeny (Williams 1994). Each bee was experimentally naïve at the start of the experiment, and only the first foraging bout was evaluated. Bees were individually tested in a flight arena; they were offered the colors v–violet (bee UV-blue); b–blue (bee blue); w–white (bee blue–green); y–yellow; o–orange; r–red (the latter three are all bee green). Column height denotes the percentage of cumulative choices of all bees from all colonies. Whiskers show percentages for colonies with extreme values.

B. terrestris sassaricus from Sardinia [133; 4; 4518], *B. terrestris xanthopus* from Corsica [58; 2; 2678], and *B. terrestris canariensis* from the Canary Islands [159; 5; 3904]. The rationale for testing island populations was that evolution often takes a different course there. Generally, the effects of chance, including those of bottleneck events, will be more manifest on islands than in large mainland populations (Adkison 1995; Barton 1998). In addition, small populations might adapt more readily to local conditions, whereas in large populations, gene flow across long distances may prevent local adaptation (Ford 1955; Stanton & Galen 1997). On the other hand, polymorphism, the raw material for evolution, is lost more easily in small populations, and deleterious mutations may spread through island populations more readily. A dramatic example known from the visual system are the totally color-blind people of Pingelap Island (Hussels & Morton 1972; Chittka & Briscoe 2001). The island populations of *B. terrestris* are particularly interesting because they are genetically differentiated from each other and from the mainland population, whereas the entire mainland population, which stretches all through central, southern, and eastern Europe, appears to be genetically more homogenous (Estoup *et al.* 1996; Widmer *et al.* 1998).

Correspondingly, we find no strong differences in color preferences among the mainland *B. terrestris* populations: all showed the same strong preference for violet–blue shades as the other species above. But some island populations show an additional red preference (Fig. 6.5). In *B. t. sarsaricus*, this preference is stronger than that for blue colors in some colonies, and is highly significant in all colonies (significance is determined both by a sign test [number of individuals per colony which prefer red over yellow] and a χ^2 2×2 table [colony choices for red vs. yellow]). In all colonies, both tests yielded similar results). In *B. t. canariensis*, four of five colonies showed a significant preference for red over yellow and orange. The adaptive significance of such red preference is not easy to understand. Some red, UV-absorbing, and pollen-rich flowers exist in the Mediterranean basin, particularly the eastern part, with the highest concentration in Israel (Dafni *et al.* 1990). In Israel, however, bumble bees do not show red preference, and the red flowers there appear to be predominantly visited by beetles (Dafni *et al.* 1990). Some of the red species exist in Sardinia, too, but we do not know to what extent they are exploited by bumble bees. The Canary Islands harbor several orange–red flower species (Vogel *et al.* 1984). These are probably relics of a Tertiary flora, and some seem strongly adapted to bird pollination. In fact, bird visitation has been observed at least in some of these species, but their use by bees is unknown (Vogel *et al.* 1984; Olesen 1985). Thus, we are left with an interesting observation: flower color preferences are clearly variable within *B. terrestris*, but we cannot easily correlate the color preferences in different habitats with differences in local flower colors. The possibility that genetic drift has produced the color preferences in some island populations certainly deserves consideration. To explore this possibility further, it will be necessary to sample the local floral market in more detail (as in Menzel & Shmida 1993; Giurfa *et al.* 1995) and to test whether red preference might simply evolve in some island populations because it is not selected *against*. We hope to measure the impact on foraging performance and fitness of among-colony variation in preference.

Finally, the observed patterns of floral-color preferences within bumble bees suggest that it may be worthwhile to take a closer look at the receptor level. Could some species of bumble bees (such as *B. occidentalis*) or some island populations of *B. terrestris* have actually evolved red receptors? Clearly, the observation of red preference itself cannot be taken as evidence for the existence of red receptors, because detection and identification of red flowers is possible without specific red receptors (Chittka &

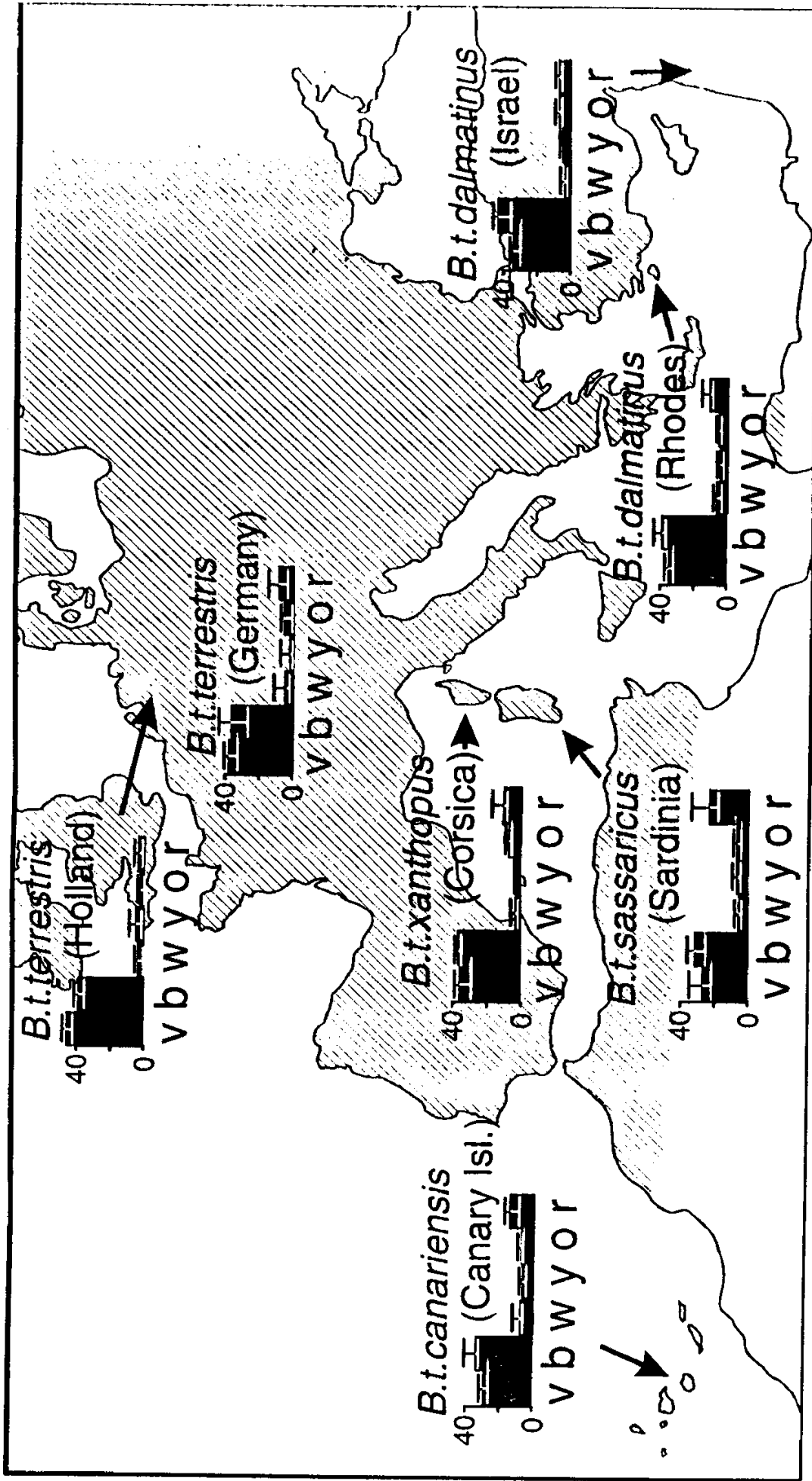


Fig. 6.5. Biogeography of floral color preferences in *Bombus terrestris*. Cross-hatched area: distribution of *B. terrestris* (this range was provided with kind permission by Prof. Pierre Rasmont; the full map will appear in Rasmont *et al.* 2001). For further explanation, see Fig. 6.4.

Waser 1997). Red flowers do take substantially longer to detect (see above), so that the evolution of red receptors might be favored in species whose ranges overlap with that of red flowers. If physiological research does reveal the existence of red receptors in bumble bees with red preference, we envision two possible evolutionary paths towards such receptors in bees. In large populations, red receptors might become fixed only in the case of a strong selective advantage, such as in bees that already exploit red flowers. Conversely, if the fitness advantage conferred by red receptors is comparatively small, new mutants that carry such receptors might be eliminated by genetic drift with very high probability. In the case of such a minor adaptive advantage, red receptors might spread only through relatively small populations, such as those on islands.

Conclusion

We have used flower colors and bee color vision to convey the message that evolutionary matching of signals and receivers will not happen as readily and easily as physiological adaptation of, say, a receptor's sensitivity. In fact, this work contains a number of cases where behavioral, sensory, and floral traits can be better explained by the species' phylogenetic history or constraints than by the assumption that each trait in each species is individually and optimally tailored to its environment. Many paths along the way from genes to traits are intertwined, so that evolutionary changes in one trait may render another trait less efficient or non-functional. Finally, selection acts on individuals, and whether individuals survive and reproduce depends not only on their genetic quality, and certainly not only on the quality of *any* trait in which one happens to be interested. Chance plays an important role, and the role it plays will depend on the strength of selection (or the adaptive value of the trait in question) combined with population size and stability. We encourage readers to consider these ideas when studying the evolutionary tuning of flower signals and insect sensory systems, and to design more studies that specifically test for the above possibilities. If we take alternatives to adaptation seriously, we may ultimately understand adaptation better.

Acknowledgements

This study was supported by DFG grants CH 147/1-2 and CH 147/2-1 to L. Chittka. For discussions or help with the experiments we thank S. Armbruster, A. Gerber-Kurz, P. F. Röseler, J. D. Thomson, and N. M. Waser.

References

- Adkison MD (1995) Population differentiation in Pacific salmon: local adaptation, genetic drift, or the environment. *Can J Fish Aquat Sci* 52:2762–2777
- Armbruster WS, Howard JJ, Clausen TP, Debevec EM, Loquvam JC, Matsuki M, Cerendolo B & Andel F (1997) Do biochemical exaptations link evolution of plant defense and pollination systems? Historical hypotheses and experimental tests with *Dalechampia* vines. *Am Nat* 149:461–484
- Barton NH (1998) Natural selection and random genetic drift as causes of evolution on islands. In: Grant PR (ed) *Evolution on islands*, pp 102–123. Oxford University Press, Oxford
- Bateman AJ (1951) The taxonomic discrimination of bees. *Heredity* 5:271–278
- Beerling DJ & Perrins JM (1993) *Impatiens glandulifera* Royle (*Impatiens roylei* Walp.). *J Ecol* 81:367–382
- Bernard GD & Stavenga DG (1978) Spectral sensitivities of reticular cells measured in intact, living bumblebees by an optical method. *Naturwiss* 65:442–443
- Chittka L (1996) Optimal sets of colour receptors and opponent processes for coding of natural objects in insect vision. *J Theor Biol* 181:179–196
- Chittka L (1997) Bee color vision is optimal for coding flower colors, but flower colors are not optimal for being coded – why? *Israel J Plant Sci* 45:115–127
- Chittka L & Briscoe A (2001) Why sensory ecology needs to become more evolutionary – insect color vision as a case in point. In: Barth FG (ed) *The ecology of sensing*. Springer-Verlag, Berlin
- Chittka L & Menzel R (1992) The evolutionary adaptation of flower colors and the insect pollinators' color vision systems. *J Comp Physiol A* 171:171–181
- Chittka L & Waser NM (1997) Why red flowers are not invisible for bees. *Israel J Plant Sci* 45:169–183
- Chittka L, Beier W, Hertel H, Steinmann E & Menzel R (1992) Opponent colour coding is a universal strategy to evaluate the photoreceptor inputs in hymenoptera. *J Comp Physiol A* 170:545–563
- Chittka L, Thomson JD & Waser NM (1999) Flower constancy, insect psychology, and plant evolution. *Naturwiss* 86:361–377
- Dafni A, Bernhardt P, Shmida A, Ivri Y, Greenbaum S, O'Toole C and Losito L (1990) Beetle pollinated red bowl-shaped flowers – evolutionary convergence in the Mediterranean. *Israel J Bot* 39:81–92
- Estoup A, Solignac M, Cornuet J-M, Goudet J & Scholl A (1996) Genetic differentiation of continental and island populations of *Bombus terrestris* (Hymenoptera: Apidae) in Europe. *Mol Ecol* 5:19–31
- Faegri K & van der Pijl L (1978) *The principles of pollination ecology*, 3rd edn. Pergamon Press, Oxford
- Feinsinger P (1987) Effects of plant species on each other's pollination: is community structure influenced? *Trends Ecol Evol* 2:123–126
- Fineblum WL & Rausher MD (1997) Do floral pigmentation genes also influence resistance to enemies? The *W* locus in *Ipomoea purpurea*. *Ecology* 78:1646–1654
- Ford EB (1955) Rapid evolution and the conditions which make it possible. *Cold Spr Harb Symp* 20:230–238
- Giurfa M, Núñez J, Chittka L & Menzel R (1995) Colour preferences of flower-naive honeybees. *J Comp Physiol A* 177:247–259

- Gumbert A, Kunze J & Chittka L (1999) Floral colour diversity in plant communities, bee colour space and a null model. *Proc R Soc Lond B* 266:1711–1716
- Hagen E von (1994) *Hummeln*. Naturbund Verlag, Augsburg
- Hussels IF & Morton NE (1972) Pingelap and Mokil atolls: achromatopsia. *Am J Hum Genet* 24:304–309
- Imhoof B & Schmid-Hempel P (1999) Colony success of the bumble bee, *Bombus terrestris*, in relation to infections by two protozoan parasites, *Crithidia bombi* and *Nosema bombi*. *Insectes Soc* 46:233–238
- Irwin RE & Brody AK (1999) Nectar-robbing bumble bees reduce the fitness of *Ipomopsis aggregata* (Polemoniaceae). *Ecology* 80:1703–1712
- Johnson SD & Steiner KE (2000) Generalization versus specialization in plant pollination systems. *Trends Ecol Evol* 15:140–143
- Kühn A (1923) Versuche über das Unterscheidungsvermögen der Bienen und Fische für Spektrallichter. *Nachr Ges Wiss, Göttingen, Math-Nat Wiss Kl I*:66–71
- Levin DA & Brack ET (1995) Natural selection against white petals in phlox. *Evolution* 49:1017–1022
- Levin DA & Schaal BA (1970) Corolla color as an inhibitor of interspecific hybridization in *Phlox*. *Am Nat* 104:273–283
- Lunau K & Maier EJ (1995) Innate colour preferences of flower visitors. *J Comp Physiol A* 177:1–19
- Lutz FE (1924) Apparently non-selective characters and combinations of characters including a study of ultraviolet in relation to the flower-visiting habits of insects. *Ann NY Acad Sci* 29:181–283
- Mazokhin-Porshnyakov GA (1969) *Insect vision*. Plenum Press, New York
- Menzel R & Backhaus W (1991) Colour vision in insects. In: Gouras P (ed) *The perception of colour*, vol. 6, pp 262–293. Macmillan, London
- Menzel R & Shmida A (1993) The ecology of flower colours and the natural colour vision of insect pollinators: the Israeli flora as a study case. *Biol Rev* 68:81–120
- Meyer-Rochow VB (1980) Electrophysiologically determined spectral efficiencies of the compound eye and median ocellus in the bumblebee *Bombus hortorum tarhakimalainen* (Hymenoptera, Insecta). *J Comp Physiol A* 139:261–266
- Newbigin MI (1898) *Colour in nature: a study in biology*. John Murray, London
- Ohta T (1993) Interaction of selection and drift in molecular evolution. *Jap J Genet* 68:529–537
- Olesen JM (1985) The Macronesian bird-flower elements and its relation to bird and bee opportunists. *Bot J Linn Soc* 91:395–414
- Onslow MW (1920) *Practical plant biochemistry*. Cambridge University Press, Cambridge
- Osche G (1979) Zur Evolution optischer Signale bei Blütenpflanzen. *Biol unserer Zeit* 9:161–170
- Peitsch D, Fietz A, Hertel H, de Souza J, Ventura DF & Menzel R (1992) The spectral input systems of hymenopteran insects and their receptor-based colour vision. *J Comp Physiol A* 170:23–40
- Rasmont P, Verhaeghe J-C, Rasmont R & Terzo M (2001) *West-Palaeartic bumblebees*. Apollo, Svenstrup (in prep.)
- Raven PH (1972) Why are bird-visited flowers predominantly red? *Evolution* 26:674
- Scholl A, Obrecht E & Owen RE (1990) The genetic relationship between *Bombus moderatus* Cresson and the *Bombus lucorum* auct. species complex (Hymenoptera: Apidae). *Can J Zool* 68:2264–2268

- Scogin R (1983) Visible floral pigments and pollinators. In: Jones CE & Little RJ (eds) *Handbook of experimental pollination biology*, pp 160–172. Scientific & Academic Editions, New York
- Stanton ML & Galen C (1997) Life on the edge: adaptation versus environmentally mediated gene flow in the snow buttercup, *Ranunculus adoneus*. *Am Nat* 150:143–178
- Strid A (1970) Studies in the Aegean flora. XVI. Biosystematics of the *Nigella arvensis* complex. *Opera Bot* 28:1–169
- Thomson JD (1981) Field measures of flower constancy in bumblebees. *Am Midl Nat* 105:377–380
- Thomson JD, Wilson P, Valenzuela M & Malzone M (2000) Pollen presentation and pollination syndromes, with special reference to *Penstemon*. *Plant Sp Biol*, 15:11–29
- Vogel S, Westerkamp C, Thiel B & Gessner K (1984) Ornithophilie auf den Canarischen Inseln. *Plant Syst Evol* 146:225–248
- Waser NM (1978) Interspecific pollen transfer and competition between co-occurring plant species. *Oecologia* 36:223–236
- Waser NM, Chittka L, Price MV, Williams N & Ollerton J (1996) Generalization in pollination systems, and why it matters. *Ecology* 77:1043–1060
- Widmer A, Schmid-Hempel P, Estoup A & Scholl A (1998) Population genetic structure and colonization history of *Bombus terrestris* s. l. (Hymenoptera: Apidae) from the Canary Islands and Madeira. *Heredity* 81:563–572
- Williams PH (1994) Phylogenetic relationships among bumble bees (*Bombus* Latr.): a reappraisal of morphological evidence. *Syst Entomol* 19:327–344