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Chance and adaptation in the evolution of island bumblebee behaviour

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Abstract We used a population biological approach to assist our understanding of the evolution of behaviour, with island bumblebees as our model system. The widespread European species *Bombus terrestris* occurs on all major Mediterranean, and some Atlantic islands. Bees from different populations differ in a variety of behavioural traits, including floral colour preferences, flower detection, and learning behaviour. We attempted to correlate these behavioural differences with each population's environment, but could not find straightforward adaptive explanations. We also performed reciprocal transplant studies to compare nectar foraging performance of bees from three different populations, but found that non-native bees consistently outcompeted native bees. Thus, we consider genetic drift, exaptation, and pleiotropy as possible alternative explanations to a strictly adaptive explanation for between population behavioural differences in bumblebees.

Keywords Genetic drift · Colour vision · Learning · Body size · Flight speed · Flower colour

Introduction

We introduce island bumblebees (*Bombus terrestris* L.) as a model system to understand the evolution of behaviour. We propose that such a population biological ap-

proach might provide key insights to the relative importance of adaptation, genetic drift and history in shaping behavioural traits (Chittka et al. 2001; Dornhaus and Chittka 2004). 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 and Galen 1997). On the other hand, effects of evolutionary chance processes will be more manifest on islands than in large mainland populations (Adkison 1995; Barton 1998). Bumblebee island populations have probably been exposed to bottlenecks (Widmer et al. 1998). Bottlenecks provide temporary conditions under which genetic drift may "outcompete" selection, so that a deleterious allele may become more common. However, this also means that the kind of chance processes expected in island bumblebees may help to cross adaptive valleys, and therefore give rise to new evolutionary innovations that would be unlikely to occur in large and stable populations (Barton 1984). With this in mind, we tested a variety of populations of *B. terrestris* (both from the mainland and several islands) in several behavioural paradigms (Fig. 1). Our first question was whether there were between population differences in behaviour at all, indicating evolutionary plasticity. We then explored whether such differences would reflect adaptation to different environmental conditions, or if they might be the results of evolutionary chance, pleiotropy, or history. We also searched for new evolutionary innovations that might first arise in island populations exposed to repeated bottlenecks.

Distribution and colouration of *B. terrestris*

Bombus terrestris is a widespread pollinator species in Europe and adjacent territories. It occurs in North Africa as well as all southern, central and eastern European countries; its eastern boundary seems to stretch from the Ural Mountains through the Caucasus to Israel. It also occurs in southern Scandinavia and throughout the British Isles. It is the only bumblebee species that has

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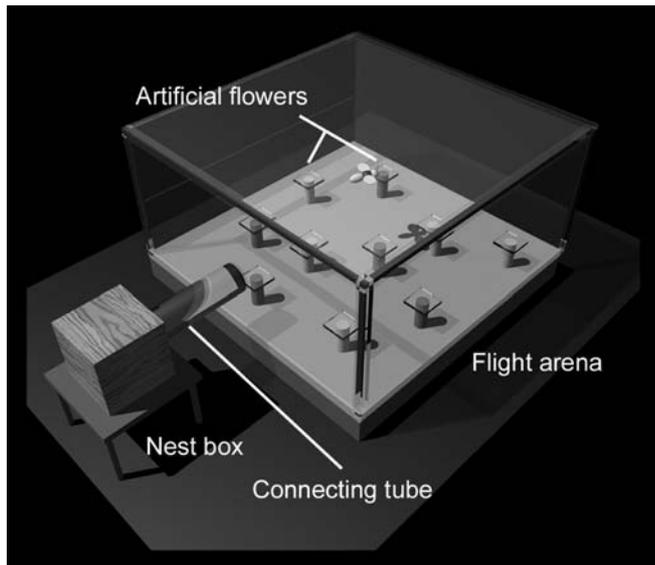


Fig. 1 Schematic drawing of basic setup for laboratory behavioural experiments reported here. A nestbox, which contains the bee colony, is connected to a flight arena via a clear Plexiglas tube. The arena contains one or more types of artificial flowers, which can differ in colour and reward amounts. Flowers were positioned at random coordinates on the arena floor. For most experiments, flowers were plastic chips of 25 mm×25 mm with a central well, placed on a glass peduncle. For experiments measuring detection times, circular flowers were placed flat on the arena floor (without a peduncle). Figure design courtesy of R.B. Lotto

colonised all major Mediterranean Islands, and some Atlantic Islands (Madeira, and all of the Canary Islands except Fuerteventura and Lanzarote) (Estoup et al. 1996; Widmer et al. 1998). The island populations of *B. terrestris* are genetically differentiated from each other and from the mainland population, whereas the entire mainland population appears to be genetically more homogenous (Widmer et al. 1998). This is also apparent in their colour coats: there is little differentiation in the mainland European population of *B. terrestris terrestris*, but some of the island populations look so different that they might be taken for different species. *B. terrestris canariensis* from the Canary Islands and *B. terrestris xanthopus* entirely lack the yellow bands of the mainland *B. t. terrestris*. *B. t. canariensis* has a white tip of the abdomen (Fig. 2b), whereas *B. t. xanthopus* has a red-brownish tip, and also brown (rather than black) legs (Fig. 2e). *B. terrestris sassaricus* combines brown legs with a lack of the yellow band of on the thorax in workers, whereas the yellow band is present in males (Fig. 2c, d). Yet, members of all these populations can be interbred, and can therefore be considered one biological species (Fig. 2d; Chittka and Wells 2004; DeJonghe 1986).

Unfortunately, the diversity of bumblebee populations is currently under threat from indiscriminate import of bee colonies for commercial greenhouse pollination. *Bombus terrestris dalmatinus* (from the Balkans, Greece and Turkey) is currently being shipped to crop growers throughout Europe including Sardinia and the UK (where a different subspecies, *B. t. audax*, is

native). Sardinian *B. t. sassaricus* has long been shipped to southern Europe, and there is anecdotal evidence that these bees are now established in southern France (P. Rasmont, personal communication). Thus, there is a severe danger that the behavioural and sensory differences between bumblebee populations may soon vanish because of grand-scale commercial movement of bumblebees, with very little concern for preserving fragile island pollination systems.

Innate colour preferences

We started our investigations by looking at a behavioural trait that can be easily quantified for large numbers of individuals, colonies and populations: the innate colour preferences of *B. terrestris*. Many newly emerged insects, that have never seen flowers, prefer certain colours over others (Chittka and Wells 2004). Such innate colour preferences help naive insects to find food and, possibly, to select profitable flowers among those available. Floral preferences can be overwritten by learning to some degree, but there is evidence that in some situations (for example when rewards are similar across flower species), bees will revert to their initial preferences (Banschbach 1994; Heinrich et al. 1977). A commonly accepted hypothesis is that these innate preferences reflect the traits of local flowers which are most profitable for bees.

We tested innate colour preferences of colonies obtained from eight populations. Three colonies of *B. t. terrestris* from Holland were obtained from Koppert Biological Systems (Holland), *B. t. terrestris* from Germany (20 colonies raised from queens caught in the wild), *B. t. dalmatinus* from Israel (from Kibbutz Yad Mordechai, Israel; five colonies), Turkey (obtained from Bunting Brinkman Bees, Belgium; five colonies) and Rhodes (five colonies raised from queens caught in the wild, provided by Koppert Biological Systems), *B. t. sassaricus* from Sardinia (five colonies purchased from Koppert Biological Systems, one raised from a queen caught in the wild), *B. t. xanthopus* from Corsica (three colonies raised from queens caught in the wild), and *B. t. canariensis* from the Canary Islands (five colonies purchased from Koppert Biological Systems, one raised from a queen caught in the wild). All colonies were laboratory raised, i.e. their workers had never been exposed to flowers or colours prior to experiments. Nest boxes were connected to a flight arena (120 cm × 100 cm × 35 cm), where foragers were allowed to forage for sucrose solution from clear, UV-transmitting Plexiglas squares (25 mm × 25 mm) placed on clear glass cylinders (Ø = 10 mm; 40 mm height). Foragers were individually marked with Opalith number plates. Workers were then removed from the arena, and 18 unrewarded flowers with six colours (i.e. three flowers of each colour) were set up at random positions in the arena. The “flowers” were painted Plexiglas squares on glass cylinders (dimensions as above). Only one forager at a time was admitted into the arena for

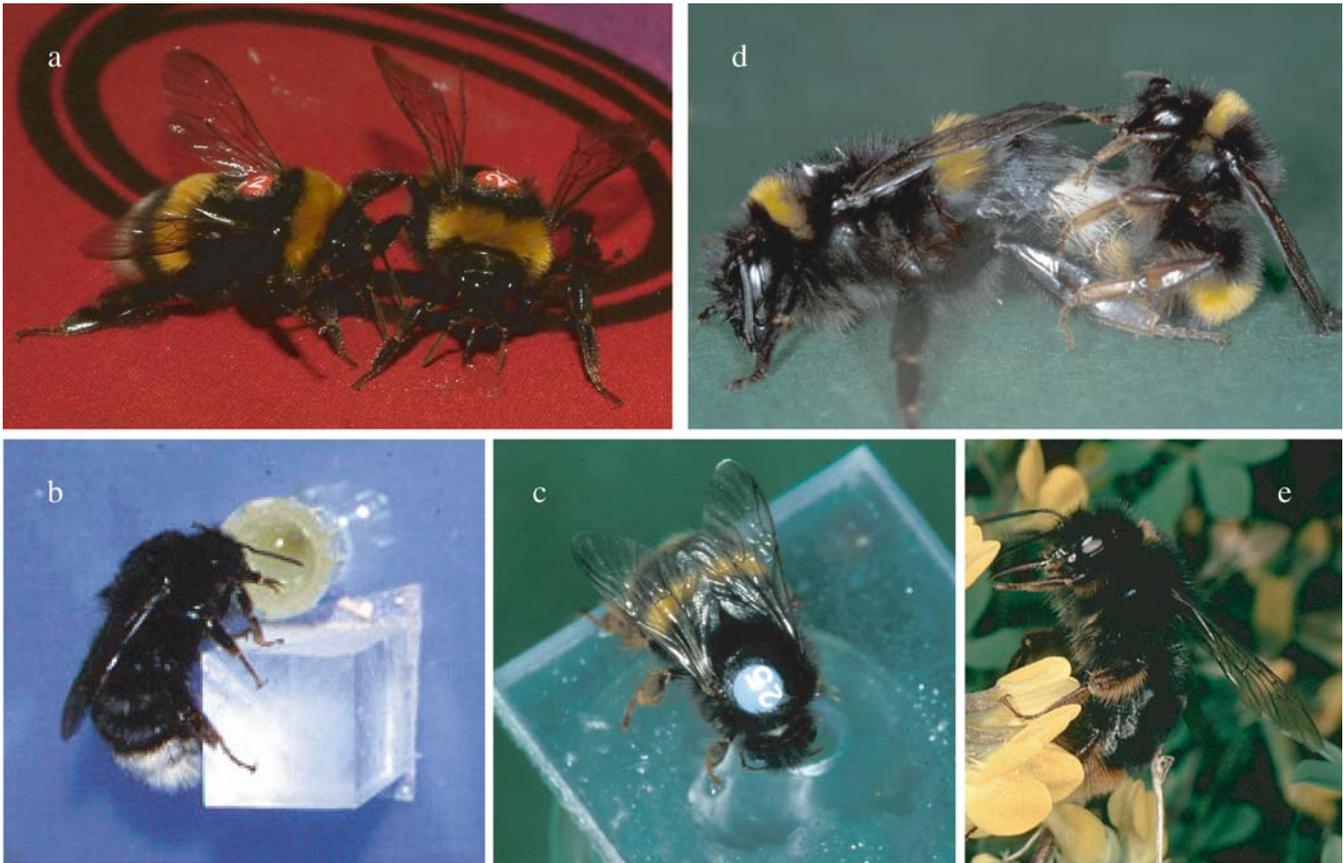


Fig. 2a–e Colour coat variation in *B. terrestris* populations. **a** Two *B. t. terrestris* workers, displaying the typical colour coat found on the mainland. Number labels are attached to the bees for individual recognition. **b** Worker from the Canary islands, *B. t. canariensis*, entirely lacking the yellow bands (photo by A. Dornhaus, with permission). **c** Worker from Sardinia, *B. t. sassaricus*, with brown legs and an absence of a yellow band on the thorax. **d** A German *B. t. terrestris* queen mating with a Sardinian *B. t. sassaricus* male. Males from the Sardinian population retain the yellow band on the thorax, but have brown legs like the workers. **e** Worker from Corsica, *B. t. xanthopus*, with a brown abdomen and brown legs, and no yellow bands (photo by P. Rasmont, with permission)

testing, and each forager was tested only for a single foraging bout.

We gave individuals a choice between the colours violet (bee UV-blue), blue (bee blue), white (bee blue-green), yellow, orange and red (all bee green). All populations preferred colours in the violet to blue range of the spectrum, but there were some differences in the relative preference for violet and blue (Fig. 3). Some island populations, however, exhibit an additional red preference (Chittka et al. 2001). In *B. t. sassaricus*, this preference is stronger than that for blue colours in some colonies, and is highly significant in all colonies. In *B. t. canariensis*, five of six colonies tested showed a significant preference for red over yellow and orange. Thus, there clearly is evolutionary plasticity in flower colour preference within *B. terrestris*, and tests with laboratory-bred offspring colonies show that the between population differences are heritable (Chittka and Wells 2004).

Adaptive explanations for flower colour preferences?

Could the consistent preference for violet and blue colours be a reflection of the profitability of flowers with these colours? Indeed, in an investigation of 154 flower species from a nature reserve near Berlin, violet and blue flowers offered high nectar rewards with the highest probability (Giurfa et al. 1995). However, in that study, floral nectar production rates were not actually measured, but were categorised into high and low nectar plants according to beekeeping literature. In order to obtain a more direct assessment of the nutritional quality of flowers with different colours, we measured the colours and nectar production rates of flowers in the vicinity of Würzburg (59 species) and in Sardinia (region of Monte Padru; 56 species). In both of these regions, UV-blue flowers and blue flowers were those with the highest nectar rewards (Fig. 4; Schikora 2001). The most highly rewarding (and also most heavily visited) species in Sardinia was UV-blue *Borago officinalis* in the spring (Schikora 2001). In autumn, *Arbutus unedo*, with white-pink (bee blue-green) flowers, was the *only* species visited.

To be sure, we need data from more habitats, but the overall picture that appears to emerge is that violet (bee UV-blue) and blue (bee blue) flowers appear to produce, on average, more nectar than species with flowers of other colours. Thus, the consistent preference for such

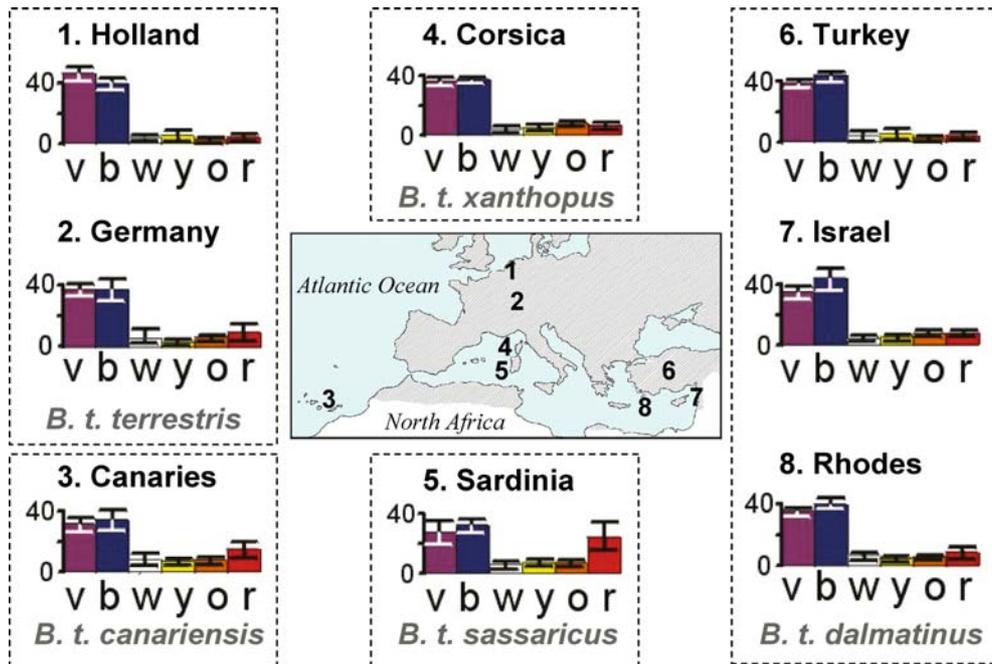


Fig. 3 Biogeography of floral colour preferences in *B. terrestris*. Bees were individually offered the colours: *V* violet (bee UV-blue), *B* blue (bee blue), *W* white (bee blue-green), *Y* yellow, *O* orange, *R* red (the latter three are bee green). Column height denotes the mean (± 1 SE) of colony choices. At least five colonies were tested per population. The shaded area shows the distribution of *B. terrestris* (this range was provided with kind permission of P. Rasmont). Numbers of workers tested were (with number of choices in brackets): *B. t.* from Holland: 125 (1,870), *B. t. terrestris* from Germany: 399 (9,670), *B. t. dalmatinus* from Israel: 156 (5,731), *B. t. dalmatinus* from Rhodes: 150 (5,335); *B. t. dalmatinus* from Turkey: 120 (3,401); *B. t. sassaricus* from Sardinia 185 (6,500), *B. terrestris xanthopus* from Corsica: 88 (3,428), and *B. t. canariensis* from the Canary Islands 179 (4,540)

colours in a variety of bumblebee populations appears to be adaptive.

But can we also find an adaptive reason for between population differences in colour preferences? An obvious adaptive explanation for why Sardinian and Canary island bumblebees prefer red, UV-absorbing flowers, might be that such flowers occur in these islands more commonly (and provide more nectar) than in the other habitats. Therefore we measured flower spectral reflectance of large numbers of plant species in a variety of locations (Germany: Nature Reserve Lange Dammwiesen, Brandenburg (Gumbert et al. 1999), and from the vicinity of Würzburg, Bavaria; Sardinia: Monte Padru, Nurra and Sassarese, Monte Arci and Costa Rei; Norway: Dovrefjell) (Schikora 2001). We compared these with a published dataset from Mediterranean habitats in Israel (Menzel and Shmida 1993) (Fig. 5).

Red, UV absorbing flowers were rare in all of these locations (Schikora 2001; Schikora et al. 2002) (Fig. 5). The highest prevalence was in Israel, where five species were found (out of over 100). In Israel, however, bumblebees do not show red preference, and the red flowers there appear to be predominantly visited by beetles

(Dafni et al. 1990). In Sardinia (where bumblebees showed the strongest preference for red flowers), we found only a single red, UV-absorbing flower species (*Adonis annua*). Four other red species (*Anagallis arvensis*, *Papaver rhoeas*, *Lathyrus cicera*, *Tetragolobus purpureus*) reflect UV light strongly, and another red species had a reflectance peak in the blue (*Fumaria capreolata*). Conspicuously, most of the red species (including those that reflect UV) in all habitats tested are pollen-only flowers which do not contain any nectar (Dafni et al. 1990). This includes several red *Papaver* species, and some Ranunculaceae, including *Adonis annua* in Sardinia and *Ranunculus asiaticus* in Israel.

Thus, the red preference of the Sardinian bees (*B. t. sassaricus*) is certainly not explicable in terms of nectar foraging, the behavioural context in which we tested our foragers: we tested only workers which had been previously observed as nectar foragers, and had been fed pollen ad libitum into the nest (thus removing their need to forage for pollen). Red flowers possibly still represent a useful pollen source, despite their low species numbers. However, there is no reason to expect that the importance of such flowers is higher in Sardinia than at the other sites tested.

The Canary Islands harbour several orange–red flower species. These are possibly relics of a Tertiary flora, and some seem strongly adapted to bird pollination (Vogel et al. 1984). Bird visitation has been observed in at least some of these species, but it is unknown whether bees use them (Olesen 1985). Thus, we are left with an interesting observation: flower colour preferences are clearly variable within *B. terrestris*, but we cannot easily correlate the colour preferences in different habitats with differences in local flower colours. The possibility that genetic drift has produced the colour preferences in some island populations therefore deserves serious consideration.

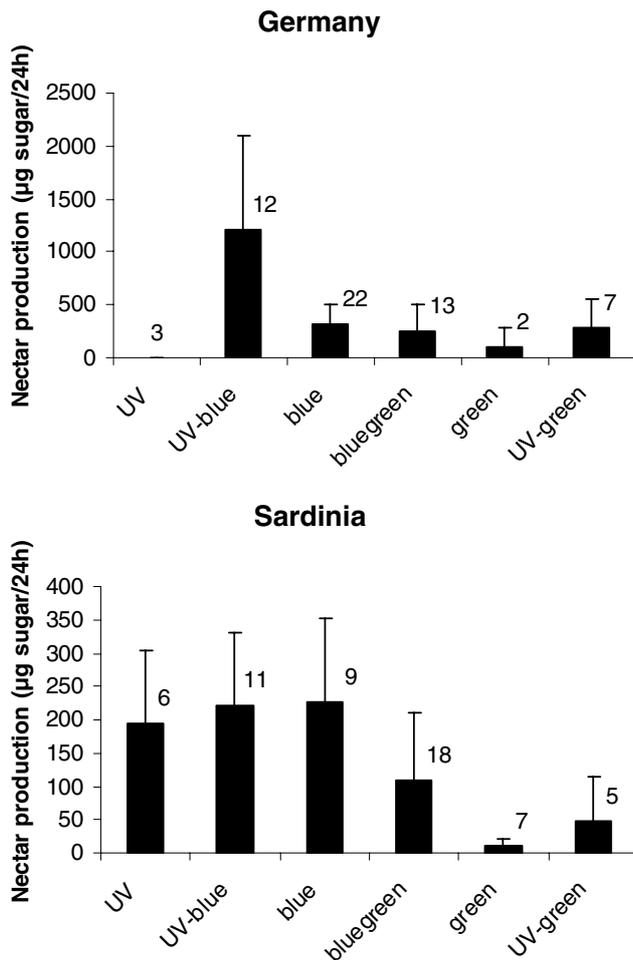
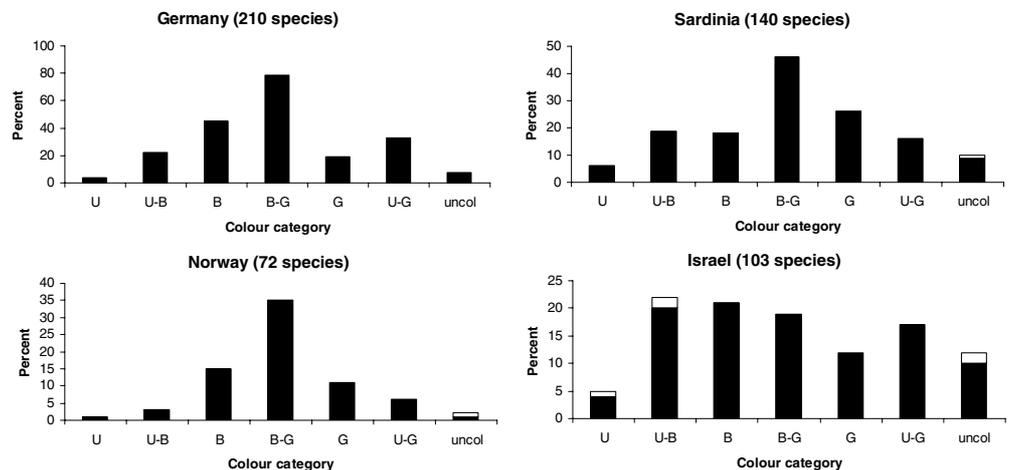


Fig. 4 Nectar production rates for flower species in six bee-subjective colour categories. Flowers were protected from visitation with gauze for 3 h after emptying. Then nectar volume was quantified for at least 30 flowers per species; nectar concentration was measured with a pocket refractometer (Atago, HSR-500). Note that production is given over 24 h, not the measured 3 h period. Numbers next to columns are numbers of species tested in each colour category

An alternative explanation is that colour preference in the context of feeding is a pleiotropic by-product of colour preference in species recognition or mate choice

Fig. 5 Frequencies of plant species from Germany, Sardinia, Norway and Israel in seven bee-subjective colour categories: *U* UV, *U-B* UV-blue, *B* blue, *B-G* blue-green, *G* green, *U-G* UV-green, *uncol* uncoloured. The overall pattern appears similar across habitats. Red flowers (with UV reflectance below 7%) are indicated in *white*



(Smith et al. 2004). Could red preference in some bumblebee species be explained by the fact that red is an important component in these bees' coat colour? Unfortunately, this explanation is unlikely, since the strongest component of red in the body colouration of *B. terrestris* occurs in Corsica (Fig. 2e), where bees show no red preference. On the other hand, bees from the Canary islands show a relatively strong preference for red, but their coat colour lacks red entirely (Fig. 2b). Generally, it appears that coat colouration in bumblebees is largely aposematic, rather than being used for within species signalling (Plowright and Owen 1980).

Red vision in island bumblebees?

Most solitary and all social bee species tested to date possess only UV, blue and green receptors (Briscoe and Chittka 2001). Red flowers, therefore, are harder to detect for mainland *B. terrestris* workers than flowers of other colours (Spaethe et al. 2001). Why would bees preferentially visit flowers which are hard to make out? Could it be that the red preference in some island bee populations is explained by the presence of specialised red receptors? In a first approach, we compared workers from two populations, *B. t. terrestris* and *B. t. sassaricus* in a behavioural paradigm. We measured the time taken by a worker to detect for red flowers of two sizes in a flight arena (see Spaethe et al. 2001). *B. t. sassaricus* workers were not significantly faster at detecting large red flowers (28 mm; Mann Whitney $U=9$; $P=0.180$) but they were substantially faster for small flowers (15 mm; $U=2$; $P=0.032$; Fig. 6). This means that the red-preferring Sardinian bumblebees (*B. t. sassaricus*) are in fact better at detecting small red flowers, which is consistent with the interpretation that they have higher sensitivity at longer wavelengths (i.e. to red light). However, there are alternative explanations. One possibility could be that they simply fly faster, but this is not the case (see below). It is also conceivable that the optics of Sardinian bees' eyes are superior to those of mainland bees, especially so since they have a larger average body

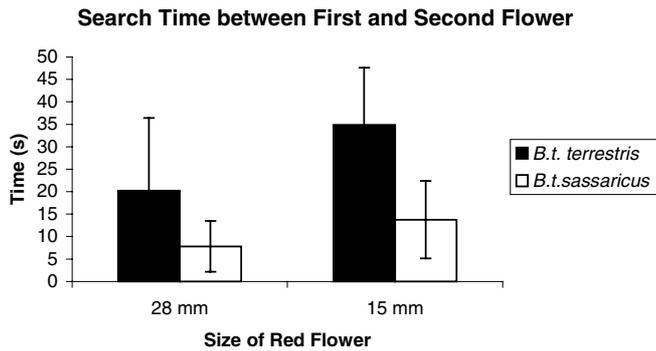


Fig. 6 Search time for red artificial flowers in a flight arena, by European mainland *B. t. terrestris* and Sardinian *B. t. sassaricus*. Search times were measured for two different floral sizes. Individual workers had to search for three red disks placed at random positions on the arena floor. Each flower contained 30 μ l 1.5 M sucrose solution

size, which is correlated with eye optical quality both within populations (Spaethe and Chittka 2003), and across species (Jander and Jander 2002). Clearly, we need intracellular measurements of photoreceptor spectral sensitivity to confirm the suspicion that Sardinian *B. terrestris* have specialised red receptors.

Learning ability

We also explored whether there might be between population differences in learning ability. Since floral rewards differ strongly among plant species and vary over time, bees need to assess such differences, and respond accordingly. For this reason, learning floral traits such as colour, pattern and scent, are vital to efficient foraging (Chittka et al. 1999). We tested bumblebees in a simple foraging situation in which they had to distinguish yellow, rewarding artificial flowers from blue, unrewarding ones (Chittka and Reinhold 1999). Bees were raised entirely in the laboratory and were therefore unbiased by previous experience at the start of the experiments. A nest box was connected to a flight arena, in which workers were pre-trained to bi-coloured blue and yellow plastic chips with a central well to hold “nectar” rewards. During training, individual workers encountered ten blue and ten yellow artificial flowers. The yellow flowers contained 15 μ l of sucrose solution (50% volume), while blue flowers were empty. The bees’ choices of flower were recorded and errors (visits to the unrewarding colour) were evaluated as a function of the total number of flowers visited (Fig. 7). First order exponential decay functions are fitted to the data from each individual, using the following formula in Microcal Origin (Chittka and Thomson 1997):

$$y = y_0 + Ae^{-(x-x_0)/t}$$

where y_0 is the Y offset, the asymptotic value of the Y value (handling times in our case) for large X values; x_0 is the X value at which the curve starts (in our case the

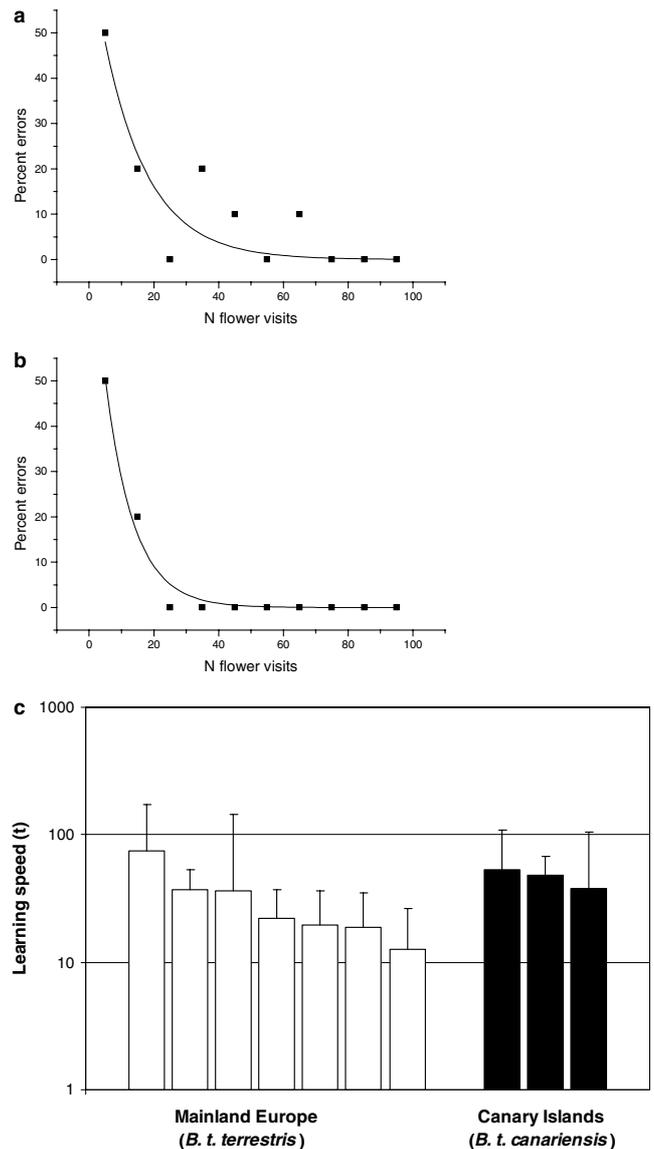


Fig. 7a–c Learning behaviour of bees at artificial flowers. Learning curves of a relatively slow learning individual bee (**a**) and a relatively fast one (**b**) These were generated from bees foraging in a flight arena with rewarding, yellow and unrewarding, blue artificial flowers. Each individual bee’s choices of flower were recorded and errors (visits to the unrewarded flower colour) were evaluated as a function of the total number of flowers visited. **c** Learning speed in two *B. terrestris* populations: *B. t. terrestris* from the European mainland, and *B. t. canariensis* from the Canary islands. t the decay constant is small for rapid learners, and high for slow learners. Each column represents the mean value for one colony, and error bars show the interindividual variance (± 1 SD)

trial number at which a treatment starts); t is the decay constant (it is small when the curve approaches y_0 rapidly, and large when the slope is shallow); t is thus a measure of the learning speed. A is the amplitude; it specifies the height of the curve above y_0 . Here we focus on t , which is a direct indicator of learning speed: high values of t correspond to slow learning, whereas low t values are generated by fast learners.

We tested workers from seven colonies from the European mainland (*B. t. terrestris*; Germany) and compared their performance with three colonies from Tenerife (*B. t. canariensis*). At least 15 workers were tested per colony. There were intriguing differences both within and between populations (Fig. 7). Bumblebees from the Canary Islands tend to learn more slowly than those from Germany, although they were not outside the variation exhibited by mainland colonies. Since all colonies were raised under identical conditions, it is likely that the observed differences are genetically determined. At present, it is unclear whether the between population difference might be adaptive or it might have arisen through evolutionary chance. We need to study the “pollination market” in the Canary Islands in more detail, to see if, for example a high nectar supply by very few plant species makes rapid learning less crucial.

Foraging performance and reciprocal transplant experiments

In the preceding paragraphs we attempted to search for adaptive explanations for observed between-population behavioural differences by searching for elements in each population’s habitat which might have favoured these differences. A more direct way of testing the adaptiveness of each population’s behaviour is by testing their foraging performance under natural conditions. A necessary corollary of the notion that each population is best adapted to foraging in its own habitat is that native bees should outcompete colonies from other populations in terms of foraging performance in their native environment. Therefore, we set up a reciprocal transplant experiment in which we compared the foraging performance of *B. t. terrestris* from central Europe with *B. t. sassaricus* from Sardinia and *B. t. canariensis* from Tenerife. All colonies were obtained from commercial breeders (Koppert Biological Systems and Bunting Brinkman Bees). They had been raised under identical conditions, with ad libitum provision of nectar and pollen. We therefore conjecture that between-population differences in foraging performance, if any, are genetically determined. Colonies were in comparable stages for all experiments, i.e. colonies were young and vigorous, and had 30–50 workers at the start of the experiments.

We measured nectar collection rate (weight of nectar collected per unit foraging time) in three sites: Costa Rei (southern Sardinia, autumn 2000), Monte Padru (Gallura; northern Sardinia, spring 2001), and near Würzburg (Germany, summer 2002). In three sites, the foraging performance of nine colonies (three from each population) was tested. All foragers were individually marked, their flight departure and arrival times and weights were noted. There was no selection of foragers to be tested, i.e. we simply monitored all bees that volunteered to forage.

We expected that Sardinian *B. terrestris* would perform better in their native Sardinian habitats than

German bees and those from the Canary Islands. Likewise, we expected that mainland *B. terrestris* would be superior foragers in their native Germany. We also predicted that *B. t. canariensis*, not native to either of these sites, would perform most poorly. Surprisingly, however, *B. t. canariensis* performed best at all three sites. *B. t. sassaricus* consistently came second, but performed better than German *B. t. terrestris* not only in its native Sardinia, but also at the German experimental site (Fig. 8; T.C. Ings, J. Schikora and L. Chittka, unpublished). Thus, our hypothesis that each population is best adapted to its native habitat in terms of foraging behaviour cannot be upheld.

Differences in body size

One possible explanation for between-population differences in foraging performance could be that members of different populations differ in body size, since body size is a good predictor of foraging rate within populations (Goulson et al. 2002; Spaethe and Weidenmüller 2002). We measured body mass for all foragers tested, since mass is highly correlated with size (Goulson et al. 2002). Indeed, it turns out that body sizes of the three

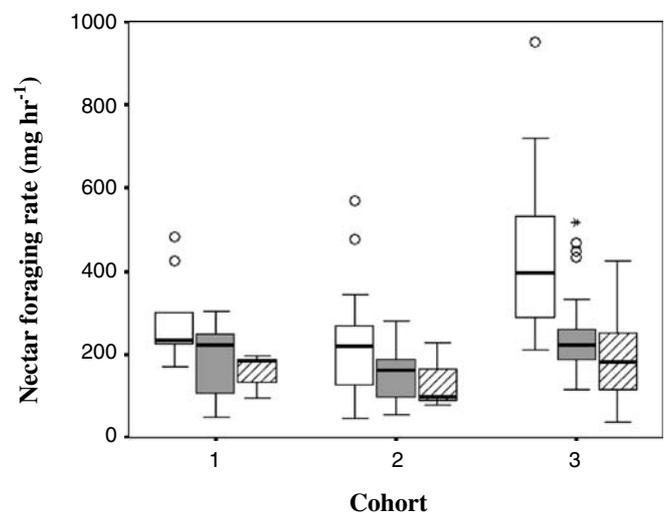


Fig. 8 Box and whisker plots comparing the nectar foraging rates of individual workers from three populations of *B. terrestris* in Sardinia during the autumn of 2000 (T.C. Ings, J. Schikora and L. Chittka, unpublished). White boxes represent *B. t. canariensis*, light grey boxes represent *B. t. sassaricus* and hatched boxes represent *B. t. terrestris*. The thick bar in each box represents the median, the lower and upper edge of the boxes represent the lower (25%) and upper (75%) quartiles respectively. Whiskers represent the maximum and minimum values that are not outliers. Empty circles indicate outliers and stars extreme values. Foraging rates are given as amount of nectar (mg) collected per unit time (hour) by marked bees. As foraging performance of individual bees can vary, only mean nectar foraging rates of marked bees observed foraging on three or more occasions were used in the analysis. Cohorts represent three sets of experiments carried out sequentially at each location and are treated separately. This is because NFR differed significantly between cohorts, possibly reflecting changes in floral resources and climatic factors

populations tested fall into the following order: *B. t. canariensis* > *B. t. sassaricus* > *B. t. terrestris* (Fig. 9), i.e. exactly the same rank order as that established for foraging rates. These body size differences are not a consequence of variation in foraging performance: all colonies were fed pollen and nectar ad libitum prior to the onset of tests with freely foraging bees. The duration of tests with individual hives was shorter than the minimum development time for workers (about 3 weeks from newly laid eggs to eclosion—Heinrich 1979); thus worker sizes could not be a result of foraging performance during the period of testing.

These results show that worker size is an important factor in determining the foraging intake of a bumblebee colony, in fact, perhaps so important that between-population differences in forager size may obscure the effects of other traits, such as those of colour preference or foraging performance. Why are larger foragers better nectar harvesters? One well established factor is visual acuity: a one third increase in body size is paid off by a doubling in precision of floral detection (Spaethe and Chittka 2003), so that large foragers can save valuable foraging time by being better at both detecting flowers from longer distances, and detecting smaller flowers.

It has also been suggested that superior nectar foraging rates in larger workers could be due, at least in part, to larger bees being able to fly faster (Goulson et al. 2002; Spaethe and Weidenmüller 2002). It is therefore possible that flight speeds could explain the differences in nectar foraging rates we observed between populations. However, in an experimental study of flight speeds of *B. t. terrestris* and *B. t. sassaricus* over three spatial scales (0.3, 1 and 50 m) we did not find support for this hypothesis (Stüber 2002). At the smaller spatial scales (0.3 and 1 m) there was significant variation in flight speeds between colonies and populations, but at the 0.3 m scale *B. t. sassaricus* flew slightly faster than *B. t. terrestris* with the

opposite occurring at 1 m. At the largest scale (50 m) no significant differences in flight speeds were observed between colonies or populations. Similar inconsistencies across spatial scales were apparent when examining the effects of body size on flight speed. For example a significant positive correlation was observed between flight speed and forager mass of *B. t. sassaricus* at the 0.3 m scale, but at the larger scales (1 and 50 m) negative relationships (only significant at 1 m scale) were observed. In contrast, no relationship between flight speed and forager mass was observed at the 0.3 m scale for *B. t. terrestris*, but at larger scales (1 and 50 m) heavier workers tended to fly faster (only significant at 1 m scale). Therefore, although some significant trends between body size and flight speed were observed, it appears that larger workers are not consistently faster fliers (Stüber 2002).

But why are island foragers larger in the first place? In general, small bodied animals tend to be larger on islands than on the mainland (“Island Rule”; Foster 1964). Palmer (2002) showed that beetle body size increases with island size to an optimum, and then subsequently decreases with further increases in island size. Favoured explanations for the island rule are that ecological release from predators and competition leads to an initial increase in body size, whilst resource limitation leads to size reductions at larger island size (Brown and Lomolino 1998). Clearly we need data on resource availability and predation levels on islands and the mainland to resolve this issue.

Conclusion

Our analysis reveals several behavioural differences between populations of the bumblebee *B. terrestris*, for example in colour preference, learning speed, and floral detection. Such differences show that these behavioural traits are evolutionarily plastic: hence there is the possibility for adaptation to local conditions. This should make our study system, bumblebee island populations, an ideal model to study behavioural adaptation. Islands are natural laboratories, which have provided major key insights for many evolutionary biologists. Some of the observed behavioural differences, however, defy simple adaptive explanations. For example, population differences in red floral preferences do not show a clear correlation with the local frequency or profitability of red flowers. The possibility that these population differences are the result of evolutionary chance processes needs to be taken seriously. Other observed differences, for example those in learning ability, still await adaptive explanations. One direct test of adaptation to local conditions, the reciprocal transplant experiment, did not reveal a pattern by which native bees outcompete those introduced from different habitats. Instead, worker body mass was a strong determinant of foraging performance across habitats. Worker size, however, might be under selective pressures wholly unrelated to foraging, for example predator pressure (Dukas and Morse 2003), so

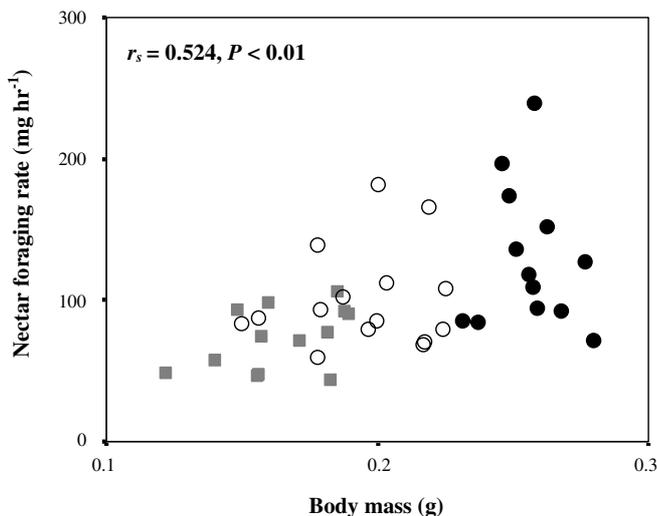


Fig. 9 Scatter plot of nectar foraging rate against body mass of individual workers (T.C. Ings, J. Schikora and L. Chittka, unpublished). Grey squares, *B. t. terrestris*; open circles, *B. t. sassaricus*; filled circles, *B. t. canariensis*

that apparent foraging adaptations may in fact be exaptations (i.e. the result of traits evolved for other purposes). In conclusion, our population biological approach to the evolution of behaviour has yielded intriguing, but not necessarily easily interpretable patterns of between population variation. It appears that we can only understand the evolution of behaviour if we consider that behavioural traits might sometimes be under multiple constraints that might be related to environmental conditions not obviously related to the trait in question. In addition, it is quite conceivable that behavioural traits might occasionally evolve by mere stochastic processes, especially in animals with low or highly variable population sizes. Ultimately, we will be better able to understand evolutionary adaptation if we also consider alternatives to adaptation.

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References

- Adkison MD (1995) Population differentiation in Pacific salmon: local adaptation, genetic drift, or the environment. *Can J Fish Aquat Sci* 52:2762–2777
- Banschbach VS (1994) Colour association influences honey bee choice between sucrose concentrations. *J Comp Physiol A* 175:107–114
- Barton NH (1984) Genetic revolutions, founder effects and speciation. *Annu Rev Ecol Syst* 15:133–164
- Barton NH (1998) Natural selection and random genetic drift as causes of evolution on islands. In: Grant PR (ed) *Evolution on islands*. Oxford University Press, Oxford, pp 102–123
- Briscoe AD, Chittka L (2001) The evolution of color vision in insects. *Annu Rev Entomol* 46:471–510
- Brown JH, Lomolino MV (1998) *Biogeography*. Sinauer, Sunderland
- Chittka L, Reinhold H (1999) Towards an individual-based approach to insect learning. In: Elsner N, Eysel U (eds) *Proceedings of the 27th Göttingen neurobiology conference*. Thieme, Berlin, p 257
- Chittka L, Thomson JD (1997) Sensori-motor learning and its relevance for task specialization in bumble bees. *Behav Ecol Sociobiol* 41:385–398
- Chittka L, Wells H (2004) Color vision in bees: mechanisms, ecology and evolution. In: Prete F (ed) *How simple nervous systems create complex perceptual worlds*. MIT, Boston, pp 165–191
- Chittka L, Thomson JD, Waser NM (1999) Flower constancy, insect psychology, and plant evolution. *Naturwissenschaften* 86:361–377
- Chittka L, Spaethe J, Schmidt A, Hickelsberger A (2001) Adaptation, constraint, and chance in the evolution of flower color and pollinator color vision. In: Chittka L, Thomson JD (eds) *Cognitive ecology of pollination*. Cambridge University Press, Cambridge, pp 106–126
- Dafni A, Bernhardt P, Shmida A, Ivri Y, Greenbaum S, O'Toole C, Losito L (1990) Red bowl-shaped flowers: convergence for beetle pollination in the Mediterranean region. *Isr J Bot* 39:81–92
- DeJonghe R (1986) Crossing experiments with *Bombus terrestris* (Linnaeus 1758) and *Bombus terrestris xanthopus* (Kriechbaumer 1870) and some notes on diapause and nose-mose (*Nosema*) (Hymenoptera, Apoidea). *Phegea* 14:19–23
- Dornhaus A, Chittka L (2004) Why do honeybees dance. *Behav Ecol Sociobiol* 55:395–401
- Dukas R, Morse DH (2003) Crab spiders affect flower visitation by bees. *Oikos* 101:157–163
- 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
- Ford EB (1955) Rapid evolution and the conditions which make it possible. *Cold Spring Harb Symp Quant Biol* 20:230–238
- Foster JB (1964) The evolution of mammals on islands. *Nature* 202:234–235
- Giurfa M, Núñez J, Chittka L, Menzel R (1995) Colour preferences of flower-naïve honeybees. *J Comp Physiol A* 177:247–259
- Goulson D, Peat J, Stout JC, Tucker J, Darwill B, Derwent LC, Hughes WOH (2002) Can alloethism in workers of the bumblebee, *Bombus terrestris*, be explained in terms of foraging efficiency? *Anim Behav* 64:123–130
- Gumbert A, Kunze J, Chittka L (1999) Floral colour diversity in plant communities, bee colour space and a null model. *Proc R Soc London B* 266:1711–1716
- Heinrich B (1979) *Bumblebee economics*. Harvard University Press, Cambridge
- Heinrich B, Mudge PR, Deringis PG (1977) Laboratory analysis of flower constancy in foraging bumblebees: *Bombus ternarius* and *B. terricola*. *Behav Ecol Sociobiol* 2:247–265
- Jander U, Jander R (2002) Allometry and resolution of bee eyes (Apoidea). *Arthropod Struct Dev* 30:179–193
- 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
- Olesen JM (1985) The Macaronesian bird-flower elements and its relation to bird and bee opportunists. *Bot J Linn Soc* 91:395–414
- Palmer M (2002) Testing the 'Island Rule' for a tenebrionid beetle (Coleoptera Tenebrionidae). *J Ecol* 223:103–107
- Plowright RC, Owen RE (1980) The evolutionary significance of bumble bee color patterns: a mimetic interpretation. *Evolution* 34:622–637
- Schikora J (2001) Blütenfarben auf Mittelmeerinseln und die Rolle von genetischer Drift bei den Farbpräferenzen von Hummeln: "Zoologie II." Julius-Maximilians-Universität, Würzburg
- Schikora J, Spaethe J, Brockman A, Chittka L (2002) Colour vision and colour preference in *Bombus terrestris*: a population biological approach. *Zoology* 105:28
- Smith C, Barber I, Wootton RJ, Chittka L (2004) A receiver bias in the origin of threespine stickleback mate choice. *Proc R Soc London B* 271:949–955
- Spaethe J, Chittka L (2003) Interindividual variation of eye optics and single object resolution in bumblebees. *J Exp Biol* 206:3447–3453
- Spaethe J, Weidenmüller A (2002) Size variation and foraging rate in bumblebees (*Bombus terrestris*). *Insect Soc* 49:142–146
- Spaethe J, Tautz J, Chittka L (2001) Visual constraints in foraging bumblebees: flower size and color affect search time and flight behavior. *Proc Nat Acad Sci USA* 98:3898–3903
- 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
- Stüber K (2002) *Sammel- und Flugverhalten bei Hummeln: ein Vergleich zwischen Populationen*. University of Würzburg, Würzburg
- Vogel S, Westerkamp C, Thiel B, Gessner K (1984) Ornithophilie auf den Canarischen Inseln. *Plant Syst Evol* 146:225–248
- 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