
Adaptation, Genetic Drift, Pleiotropy, and History in the Evolution of Bee Foraging Behavior

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I. INTRODUCTION

The formal study of foraging behavior began in the mid 1960s, using an approach that later became known as optimal foraging theory (Emlen, 1966; MacArthur and Pianka, 1966). Practitioners would use modeling to identify an optimal strategy for an animal facing a given number of foraging options, and then compare this to the strategy actually chosen by the animal (Maynard Smith, 1978; Orzack and Sober, 2001; Stephens and Krebs, 1991). This approach was instrumental in predicting quantitatively which types of food an animal should choose to consume (Pyke *et al.*, 1977; Stephens and Krebs, 1991; Waddington and Holden, 1979), when to abandon a patch of food (Cuthill *et al.*, 1990; Kacelnik and Krebs, 1985), how variance in food supply might affect forager choice (Fülöp and Menzel, 2000; Real, 1981; Shafir *et al.*, 1999), and what currencies animals use in making decisions about food quality (McNamara *et al.*, 1993; Schmid-Hempel *et al.*, 1985). The field thrived and expanded rapidly throughout the 1970s and 1980s, receiving further impetus from studies on the neurobiological mechanisms that underlie and constrain foraging during the 1990s (Chittka *et al.*, 1999; Clayton, 1995; Clayton and Krebs, 1994; Greggers and Menzel, 1993), and from studies into the genetic basis of foraging behavior (Ben-Shahar *et al.*, 2002; Rueppell *et al.*, 2004a).

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Despite these successes, a number of fundamental questions with respect to the adaptiveness of foraging strategies remain relatively unexplored. In a study on bee foraging in a natural environment by Schmid-Hempel and Heeb (1991), a large percentage of foragers were removed at regular intervals during the colony cycle. The authors found no significant effects of this apparent decimation of the forager workforce on colony growth, life history, or ultimate colony reproductive success. So how can the precise subtleties of minute-to-minute foraging strategies of individuals matter, *if not even the individuals' existence matters* for colony reproductive success? Perhaps foraging strategies are crucial only under adverse conditions (Schmid-Hempel and Schmid-Hempel, 1998), but the point here is much more general: we do not yet understand at all well how foraging strategies contribute to the fitness of animals in the wild. How well does a given strategy perform relative to other strategies, used by another individual or species? The shape of the adaptive landscape with respect to foraging remains relatively unexplored. If foraging strategies are sometimes placed on fitness plateaus, rather than steep adaptive peaks, genetic drift may make traits meander in random directions, before an animal falls down the cliff of severe fitness loss. In small populations, the effects of evolutionary chance should be especially pronounced (Adkison, 1995; Crow and Kimura, 1970; Ford, 1955), which is why we have devoted special attention to island bumblebee populations.

In other cases perhaps, we might be better able to explain an extant animal's foraging behavior by its evolutionary history, rather than the conditions under which it presently forages. While the power of studying adaptive hypotheses in foraging behavior through comparisons between species, or individuals, with different behavioral strategies was recognized early on (Clutton-Brock and Harvey, 1977; Maynard Smith, 1978; Stephens and Krebs, 1991), these methods have received relatively little attention. Instead optimality modeling remained the favored tool of the trade.

Here, we advocate using the toolbox of modern evolutionary biology, which has already been successfully applied to study adaptive patterns in many branches of animal behavior (Alcock, 1996), to the study of foraging in bees. We employ a comparative approach (Harvey and Purvis, 1991) to correlate differences in foraging styles, at both the species and population level, with features in the bees' respective environments. We use reciprocal transplant experiments (Kawecki and Ebert, 2004; Riechert and Hall, 2000), comparing the foraging performance of native bees with those stemming from populations operating in different (foreign) environments, to test hypotheses about local foraging adaptation. We manipulate the foraging environment to remove the possibility that bees can use particular foraging strategies (Schmid-Hempel and Schmid-Hempel, 1998), such as forming traplines, to tease apart the effects of each of these strategies individually. We use experimental manipulations to create artificial

foraging phenotypes (Curio, 1973), selectively eliminating the foraging-related abilities of wild-type bees, to determine the adaptive significance of the manipulated traits. Where such manipulations are not possible, we use agent-based simulations to assess the success of phenotypes that are not naturally available (Dornhaus *et al.*, 1998).

We focus especially on the following traits: flower constancy, floral color preference, learning behavior, traplining, and communication about food sources. We also correlate some of these with foraging performance. In some cases, we show that forager behavior has been tuned to function adaptively in a given niche. In other cases, however, the observed differences in behavior patterns can be better explained by chance processes, or by the historical conditions under which bees operated in their evolutionary past.

II. COMPARISON BETWEEN SPECIES: FLOWER CONSTANCY

Aristotle observed that “during each flight the bee does not settle on flowers of different kinds, but flies, as it were, from violet to violet, and touches no other till it returns to the hive” (quoted in Christy, 1884). This phenomenon, now termed flower constancy, is defined as follows: an individual insect is flower constant if it visits only a restricted number of flower species, even if other species are available and equally rewarding, and if the insect has no innate or imprinted predisposition to visit only flowers of a restricted plant taxon, which must be confirmed by the observation that other individuals of the same insect species visit other plant species within the same array (Chittka *et al.*, 1999; Waser, 1986).

Is flower constancy an optimal foraging behavior? It is hard to see how such behavior could be adaptive per se, since there is rarely only a single best food source, and specializing on one flower type, while skipping other valuable resources encountered *en route*, is not necessarily the best strategy to maximize energy intake rate (Chittka, 2002; Chittka *et al.*, 1999; Waser, 1986). Thus, flower constancy can only be considered adaptive in the face of behavioral limitations that might make switching between species costly. Short-term memory limitations are one likely explanation (Chittka, 1998; Chittka *et al.*, 1997, 1999; Raine and Chittka, 2005a). While generalist bees are able to store the sensory cues and motor patterns for several flower species in long-term memory, there appear to be delays in retrieving the sensory cues of flowers that have not been visited in the bee’s immediate history (Bar-Shai *et al.*, 2004; Chittka and Thomson, 1997; Greggers and Menzel, 1993). In addition, several workers have found that switching between plant species with different morphologies increases flower handling time. While such costs are often negligible for easily accessible flowers

(Chittka *et al.*, 1997; Lavery, 1994), they can be substantial when bees have to retrieve multiple but drastically different motor patterns from memory (Chittka and Thomson, 1997; Woodward and Lavery, 1992). Under these conditions, when flowers of the same and novel species are available at equal distances, foraging insects should remain flower constant to minimize switching costs. Conversely, as travel time between flowers increases, or if all flowers are poorly rewarding, the costs of bypassing alternative species may exceed the costs of switching, which should favor inconstancy (Chittka *et al.*, 1999).

In reality, it is difficult to rigorously test these specific predictions in the economy of nature because controlling the range of floral species, morphologies, and patterns of reward provision available to free foraging bees is virtually impossible. An alternative, and perhaps more direct, test of the adaptive benefits of flower constancy could be to examine bumblebee species that differ consistently in the extent to which they are flower constant and to compare their relative foraging performance. Do we actually find that more flower constant species forage more effectively? In a study where foraging bumblebees were monitored in a meadow, containing five plant species near Berlin, Germany (Chittka *et al.*, 1997), *Bombus terrestris* (L.) switched in 15% of 107 observed flights (transitions) between plants, *Bombus lapidarius* (L.) switched in 18% of 867 transitions, and *Bombus pascuorum* (Scopoli) switched in 26% of 2368 transitions. In this study, *B. pascuorum* switched significantly more often than *B. lapidarius* ($\chi^2 = 19.52$, $p < 0.00005$), but *B. lapidarius* and *B. terrestris* did not differ ($\chi^2 = 0.78$, $p > 0.1$: Chittka *et al.*, 1997). We consistently found the same rank order of flower constancy, among the same three bumblebee species near Würzburg, Germany, in controlled field trials (“bee interviews,” *sensu*; Thomson, 1981), where bee choices between specific pairs of plant species were observed (Chittka *et al.*, 2001; Raine and Chittka, 2005a; Fig. 1). Likewise, in a study near Southampton, England, *B. terrestris* foragers were observed to be more constant than *B. pascuorum* (Stout *et al.*, 1998). The results of all of these studies suggest that *B. terrestris* is consistently more flower constant than *B. lapidarius* and *B. pascuorum*. To what extent, then, is this consistent difference in foraging strategy mirrored in the foraging performance of these bee species?

In a first approach, we placed colonies reared from wild-caught queens of *B. lapidarius* (two colonies in 1999, three colonies in 2001) and *B. terrestris* (two colonies in 1999, five colonies in 2001) at a field site near Würzburg, Germany (Raine and Chittka, 2005a). We were unsuccessful at rearing *B. pascuorum* from wild-caught queens, but in 1999, we found a small colony in the wild, placed it into a nest box, and raised the colony to a relatively large size in the laboratory before placing it in the field, alongside

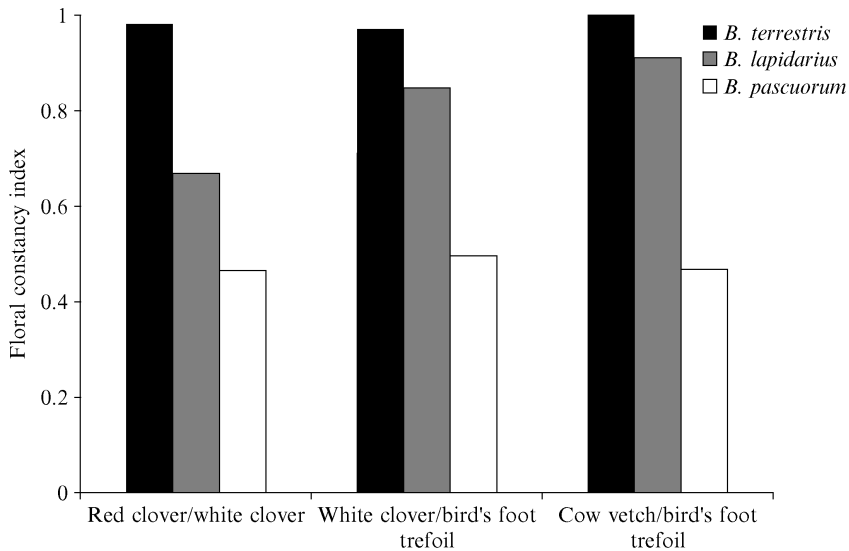


FIG. 1. Consistent differences in flower constancy across three bumblebee species. Bees were tested using the bee interview technique (Thomson, 1981) using three pairs of plant species. The plant species used were red clover (*Trifolium pratense* L.), white clover (*Trifolium repens* L.), bird's foot trefoil (*Lotus corniculatus* L.), and cow vetch (*Vicia cracca* L.). Common plant names are given on the *x*-axis labels. Higher values of the flower constancy index indicate that bees are more likely to move between individual plants of the same species when foraging. Constancy indices were calculated according to Chittka *et al.* (2001) and can vary from 1 (complete constancy), through 0 (random flights between species), to -1 (complete inconstancy). Data from Raine and Chittka (2005a) with permission.

two colonies each of *B. terrestris* and *B. lapidarius*. The field site was typical central European bumblebee habitat, including dry grassland, deciduous forest, and farmland within the bees' foraging range (Darvill *et al.*, 2004; Dramstad, 1996; Osborne *et al.*, 1999; Walther-Hellwig and Frankl, 2000). Individually marked foragers were weighed at the start and the end of each foraging trip, allowing us to determine the foraging rate of individual workers by dividing the difference in body mass (i.e., return minus outgoing weight) by the trip duration (Chittka *et al.*, 2004; Ings *et al.*, 2005b; Raine and Chittka, 2005a; Spaethe and Weidenmüller, 2002).

At first inspection, the more flower constant *B. terrestris* foragers performed consistently better in both 1999 and 2001 than the less constant *B. lapidarius* (Fig. 2; Frauenstein, 2002; Raine and Chittka, 2005a). From this, one might conclude that a higher degree of floral constancy is beneficial in this habitat. However, there are several complications with this

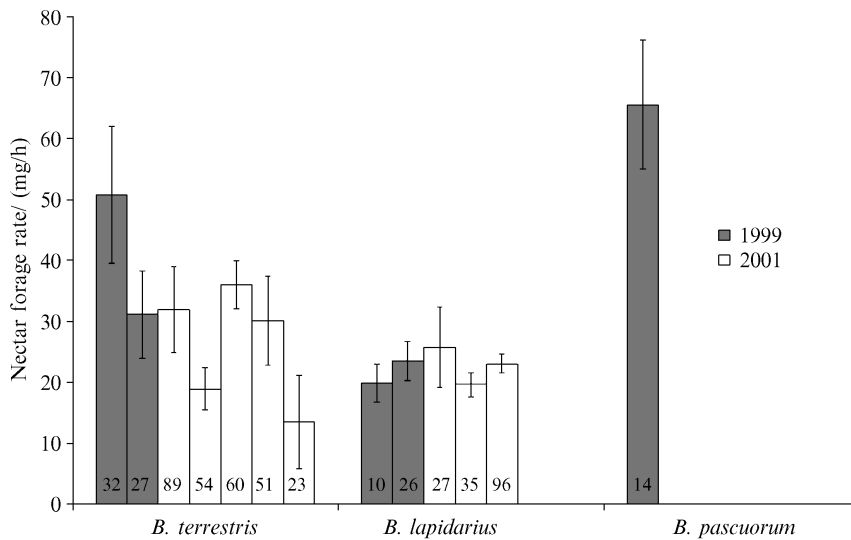


FIG. 2. Interspecific comparison of foraging performance in three bumblebee species. The foraging rate of individual workers from each colony was determined by dividing the difference in body mass (i.e., incoming minus outgoing weight) by the duration of their foraging trip. Colony foraging performance was evaluated by averaging each bee's performance across all foraging bouts, then averaging across all bees tested. Column heights are colony mean (± 1 SE) foraging rates/flight durations in each year tested. The number of foragers evaluated per colony is indicated at the foot of each column. For two species (*B. terrestris* and *B. lapidarius*), the experiment was performed in two different years (1999 and 2001), while for *B. pascuorum* it was only performed in 1999. Data from Raine and Chittka (2005a) with permission.

interpretation. *B. pascuorum*, the least flower constant species, performed even better than *B. terrestris*: hence flower constancy appears to be a poor predictor of foraging performance at the species level. This suggests that factors besides flower constancy may be decisive in determining foraging performance. Body mass might be one such factor as larger bees appear to bring home more nectar per unit time (Chittka *et al.*, 2004; Goulson *et al.*, 2002; Ings *et al.*, 2005b; Spaethe and Weidenmüller, 2002). While body size puts the larger *B. terrestris* (mean body mass ± 1 SD = 166 ± 43 mg) at an advantage over the smaller *B. lapidarius* (mean body mass = 114 ± 35 mg), once again it cannot explain the superior performance of *B. pascuorum* (mean body mass = 138 ± 18 mg), which is much smaller than *B. terrestris*. Tongue length and foraging range could be other important factors. *B. pascuorum* has a longer proboscis than *B. terrestris* or *B. lapidarius* (Goulson and Darvill, 2004; Hagen, 1990; Prys-Jones and Corbet, 1991), which allows *B. pascuorum* workers to collect nectar from flowers with

longer corolla tubes that would not be accessible to the other two species (Barrow and Pickard, 1984). *B. pascuorum* also flies shorter distances to foraging patches than other species (Darvill *et al.*, 2004; Free and Butler, 1959; Goulson, 2003; Hedkte, 1996), which might give it an additional edge. Hence, even if flower constancy is an important factor in determining foraging performance, each bee species might effectively choose microhabitats with a plant species composition best suited to its particular foraging strategies (Chittka *et al.*, 1999; Thomson and Chittka, 2001). We conclude that using species comparisons to determine the adaptive significance of foraging strategies in the field is difficult because species will typically differ with respect to multiple foraging-related traits. This is an important general lesson about the evolution of foraging behavior: typically animals proceed along multiple alternative evolutionary pathways to optimize foraging behavior, and constraints imposed by one foraging-related trait might be easily compensated for by alterations of another trait.

III. COMPARISON BETWEEN SPECIES: FLORAL COLOR PREFERENCE

Comparisons between species can be more rewarding when we compare many closely related species of known phylogeny. Attempts to identify evolutionary adaptations in foraging by focusing only on a single species, or sets of unrelated species, were common in earlier studies (Dukas and Real, 1991; Greggers and Menzel, 1993; Pyke, 1978). However, this is problematic since correlation and optimality cannot be equated with adaptation (Chittka, 1996a; Chittka and Dornhaus, 1999; Maynard Smith, 1978): in order to show that a trait is adapted for the task we think it is, we need to demonstrate that the ancestors of the animal in question which did not share the same environment also do not share the trait under scrutiny (Brooks and McLennan, 1991; Chittka and Briscoe, 2001; Losos and Miles, 1994). The comparative phylogenetic method, which seeks to reconstruct the traits of ancestral species through comparing closely related extant species, is a powerful tool to study patterns of adaptation (Armbruster, 1992; Chittka and Dornhaus, 1999; Phelps and Ryan, 2000; Ryan and Rand, 1999). This has been used to some extent to study adaptation in the foraging strategies of beetles (Betz, 1998), birds (Barbosa and Moreno, 1999), and primates (Clutton-Brock and Harvey, 1977) but not, to our knowledge, bees.

We start by applying this method to a foraging-related trait, the floral color preferences of bees. Many newly emerged insects that have never seen flowers prefer certain colors over others (Briscoe and Chittka, 2001; Chittka and Wells, 2004; Lunau *et al.*, 1996). Such innate color 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; Gumbert, 2000; Heinrich *et al.*, 1977). Our hypothesis is that these innate preferences reflect the traits of local flowers that are most profitable for bees.

In one study, Giurfa *et al.* (1995) found a good correlation between the color preferences of naive honeybees (*Apis mellifera* L.) and the nectar offerings of different flowers in a nature reserve near Berlin. These honeybees preferred violet (bee UV-blue, i.e., stimulating most strongly the bees' UV and blue receptors) and blue (bee blue, i.e., stimulating predominantly the bees' blue receptors), which were also the colors most associated with high nectar rewards. However, correlation does not imply causality. Hence, to show that color preferences actually evolved to match floral offerings, we could compare a set of closely related bee species that live in habitats in which the association of floral colors with reward is different.

We tested the color preferences of eight bumblebee species from three subgenera: four species from central Europe (*B. terrestris*, *B. lucorum* (L.), *B. pratorum* (L.), and *B. lapidarius*); three from temperate East Asia (*Bombus diversus* (Smith), *Bombus ignitus* (Smith), and *Bombus hypocrita* (Pérez)); and one from North America (*Bombus occidentalis* (Greene)). Note that all data were collected by naive observers, who were given no background information on the bees' foraging biology (Chittka *et al.*, 2001). We rotated observers between the experimental setups containing different species to minimize any effect of observer bias on observed interspecific patterns.

All colonies were raised under identical temperature and humidity conditions in a dark laboratory. Feeding and other necessary colony manipulations (e.g., marking workers) were conducted under dim red light, otherwise colonies were kept in unlit conditions. Bees had never been exposed to flower colors prior to experiments. This rearing procedure minimizes the risk that any observed between-species differences were caused by nongenetic factors. One cannot entirely exclude the possibility that different species respond differentially to identical rearing conditions, but we think that any effect of this on color preferences is most unlikely. Colony nest boxes were connected to a flight arena ($120 \times 100 \times 35 \text{ cm}^3$), where workers were allowed to forage for sucrose solution (50% w/w) from colorless, UV-transmittent Plexiglas square chips ($25 \times 25 \text{ mm}^2$) placed on transparent glass cylinders (diameter = 10 mm; height = 40 mm). Workers that foraged on these transparent chips were individually marked with Opalith numbered tags. To test bee color preference, these rewarding, colorless

Plexiglas chips were replaced by 18 unrewarding “flowers” of 6 different colors [i.e., 3 flowers of each color: violet (bee UV–blue), blue (bee blue), white (bee blue–green, i.e., producing a strong signal in the blue and green receptors of bees), yellow, orange, and red (all bee green, stimulating most strongly the bees’ green receptors)]. These “flowers” were painted Plexiglas squares on glass cylinders (dimensions as above) located at random in the arena. Only one forager was allowed into the arena for testing at a time, and each bee was tested for a single foraging bout during which the number of times it chose flowers of each color was recorded. Flowers were changed between each foraging bout to ensure that the next bee received no odor cues from the previously tested forager.

We superimposed the behavioral data from these species onto their phylogeny, as established by Williams (1994). All species tested preferred the violet–blue range, which therefore presumably represents a phylogenetically ancient preference (Fig. 3). This preference is likely to be advantageous, since flowers of these colors have been found to contain high nectar rewards in a variety of habitats (Chittka *et al.*, 2004; Giurfa *et al.*, 1995; Menzel and Shmida, 1993). Since all tested species share this trait, it is impossible to conclude that it has been adapted specifically by bumblebees in the context of flower visitation. However, we did also find interspecific differences in color preference. *B. occidentalis* had a much stronger preference for red than any other bumblebee species tested. This is particularly intriguing because *B. occidentalis* is frequently observed foraging, or robbing nectar, from red flowers whose morphology seems well adapted for pollination by hummingbirds (Chittka and Waser, 1997; Irwin and Brody, 1999). Our comparative phylogenetic analysis strongly suggests that this preference is derived and is therefore likely to represent an adaptation to this unique foraging strategy of *B. occidentalis* (Chittka and Wells, 2004; Raine and Chittka, 2005b). We conclude that the approach of superimposing foraging-related traits onto the known phylogeny (Harvey and Purvis, 1991) is a powerful tool to study evolutionary adaptation of foraging behavior, so we recommend that this approach be used more frequently in similar such studies to determine the adaptiveness of foraging traits.

IV. COMPARISON BETWEEN POPULATIONS: FLORAL COLOR PREFERENCES

Comparisons between populations of the same species are attractive because they reveal patterns of adaptation among very closely related individuals operating under divergent ecological conditions. We became especially interested in island populations, which are “natural laboratories” because of their relatively small population sizes, risk of genetic

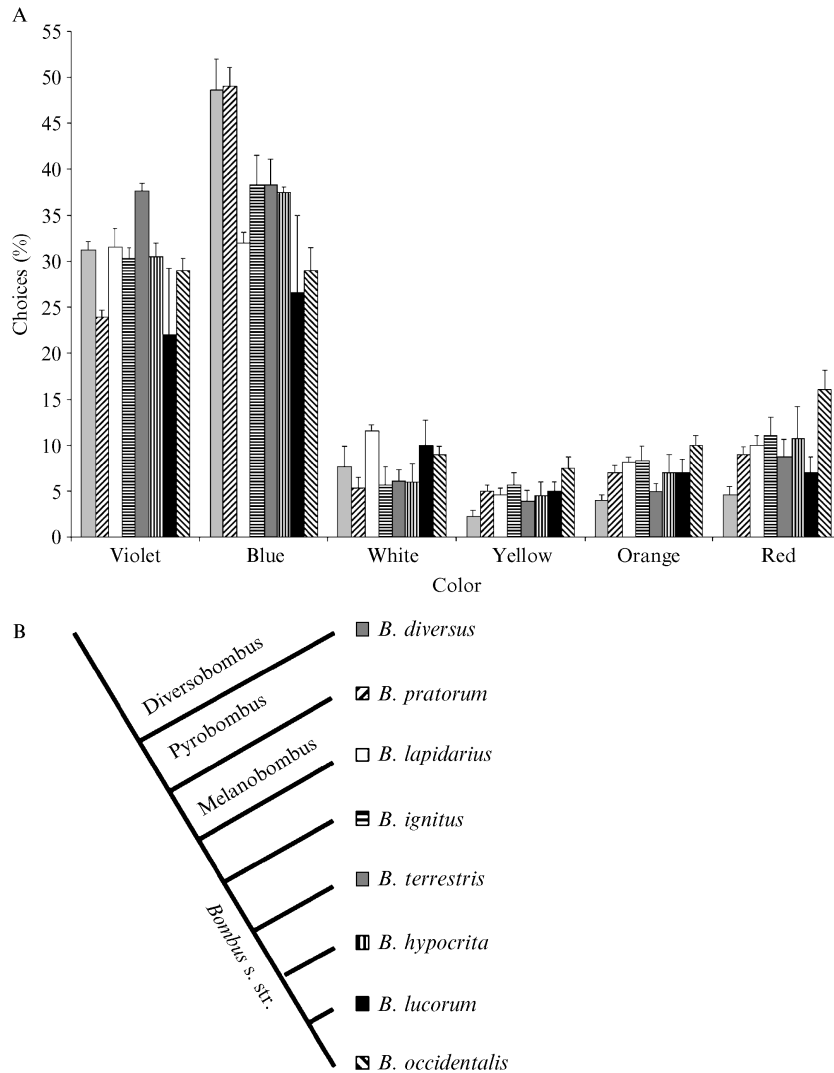


FIG. 3. Color preferences of eight bumblebee species superimposed on their phylogeny (following Williams, 1994). Each bee was experimentally naive at the start of the experiment, and only the first foraging bout was evaluated. At least three colonies were tested per species and at least 15 workers per colony. Bees were individually tested in a flight arena in which 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 mean (± 1 SE) of choice percentages. The sequence of species in the histogram (top panel) left to right maps onto those from the phylogeny, top to bottom; hence the leftmost column is *B. diversus*. Data from Chittka *et al.* (2001, 2004) and Chittka and Wells (2004).

bottlenecks, and occasionally more pronounced local adaptation because of disruption to gene flow with other populations adapted to different conditions (Adkison, 1995; Barton, 1998; Chittka *et al.*, 2004; Ford, 1955; Stanton and Galen, 1997). As well as being one of the commonest bumblebee species in Europe, *B. terrestris* has managed to colonize all Mediterranean islands. These island populations of *B. terrestris* are particularly interesting because they are genetically differentiated from one another and from the mainland population (Estoup *et al.*, 1996). In contrast, the entire mainland population, stretching across central, southern, and eastern Europe, appears to be much more genetically homogeneous (Widmer *et al.*, 1998).

We tested the unlearned color preferences of laboratory-raised colonies obtained from eight *B. terrestris* populations: *B. t. terrestris* (L.) from Holland and Germany; *B. t. dalmatinus* (Dalla Torre) from Israel, Turkey, and Rhodes; *B. t. sassaricus* (Tournier) from Sardinia; *B. t. xanthopus* (Kriechbaumer) from Corsica; and *B. t. canariensis* (Pérez) from the Canary Islands. Color preference tests and rearing conditions were identical to those in Section III.

All populations preferred colors in the violet to blue range of the spectrum, but there were some differences in the relative preference for violet and blue (Fig. 4). This largely matches the picture seen in most species tested in Section III, and this preference for violet and blue flowers makes biological sense since these flowers have been identified as most rewarding in a variety of habitats (Chittka *et al.*, 2004; Giurfa *et al.*, 1995). One might ask why flowers have not exploited these preferences, so that flowers with colors that are innately preferred might ultimately produce *less* nectar, while maintaining the same pollination success. It is necessary to bear in mind that innate preferences typically govern only the first few flower visits of a naive bee so that overall visitation rates of plants will largely be governed by informed choices of experienced bees.

However, some island populations displayed a different pattern of color preference. *B. t. sassaricus* and *B. t. canariensis* exhibited an additional red preference (Chittka *et al.*, 2001). Thus, there clearly is evolutionary plasticity in flower color preference within *B. terrestris*, and tests with laboratory-bred offspring colonies show that such between-population differences are heritable (Chittka and Wells, 2004).

The adaptive significance of such a red preference is not easy to understand. Some red, UV-absorbing, pollen-rich flowers exist in the Mediterranean basin, particularly toward the eastern end, with the highest concentration in Israel (Dafni *et al.*, 1990). However, in Israel, bumblebees do not show a red preference, and the red flowers which grow there appear to be predominantly visited by beetles (Dafni *et al.*, 1990). In Sardinia, red, UV-absorbing flowers are neither more common than on the European

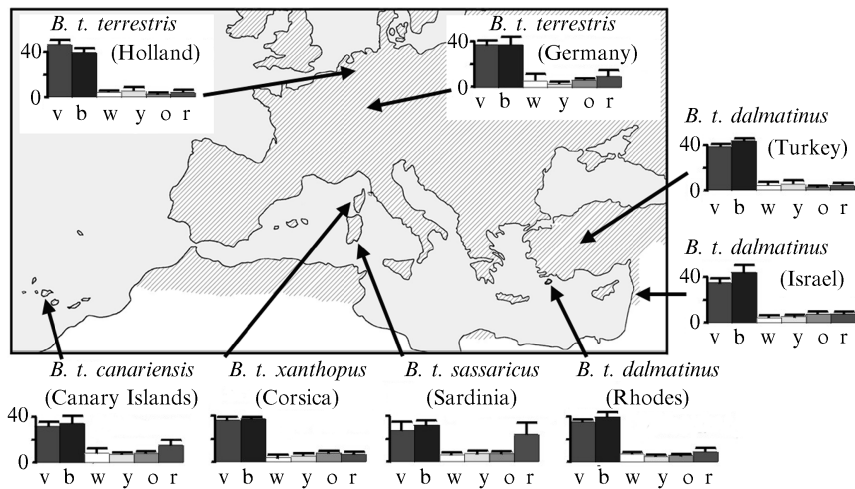


FIG. 4. Biogeography of floral color preference in *B. terrestris*. Bees were individually offered the colors: V, violet (bee UV-blue); B, blue (bee blue); W, white (bee blue-green); Y, yellow; O, orange; R, red (the latter three are bee green). Column height denotes the mean (± 1 SE) of colony choices. 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). Data from Chittka *et al.* (2001, 2004).

mainland nor more rewarding than flowers of other colors in Sardinia (Chittka *et al.*, 2004). The Canary Islands do harbor several orange-red flower species (Vogel *et al.*, 1984), which are most probably relics of a Tertiary flora, and some species seem strongly adapted to bird pollination. In fact, bird visitation has been observed in at least some of these species (Olesen, 1985; Valido *et al.*, 2002), but it is not known whether bumblebees use them at all. Thus, we are left with an interesting observation: flower color preferences are clearly variable within *B. terrestris*, and these differences are heritable (Chittka and Wells, 2004). But we cannot easily correlate the color preferences in different habitats with differences in local floral colors. The possibility that genetic drift has produced the color preferences in some island populations certainly deserves consideration. However, it is also possible that the red preference of these bumblebee populations is a “behavioral fossil,” which dates back to an age when red, bird-pollinated flowers were common in Europe. The discovery of fossil hummingbirds in the Old World (Germany) provides putative pollinators for such bird-pollinated flowers (Mayr, 2004). Mayr conjectured that some flower species, seemingly adapted to bird pollination, might be relics from

times when these birds were common in Europe. If this is true, and if bumblebees exploited some of these flowers (as some species do in North America: Chittka and Waser, 1997), then the red preference of some of our *B. terrestris* populations might be a result of history rather than either recent adaptation or chance.

V. VARIATION WITHIN POPULATIONS: COLOR PREFERENCE AND FORAGING PERFORMANCE

Many scientists studying insects have long ignored interindividual variation in behavior: some have even regarded it as noise that needed to be eliminated by averaging (reviewed in Chittka and Dornhaus, 1999). However, heritable differences between individuals represent the raw material for evolution. If no such variation exists (as in the number of legs in insects), selection has nothing to act on. In the social bumblebees, matters are somewhat more complicated because reproduction is restricted to a subset of individuals: here then, the unit of selection is not the individual, but the entire colony, which works together to maximize the contribution of sexually active individuals to the next generation. Hence, for bumblebees, intercolony, rather than interindividual, variation allows us to test the adaptive benefits of foraging behavior within a given ecological framework.

To test if floral color preference, or any foraging-related trait, is adaptive, one would ultimately want to show that the trait confers greater fitness to its bearers, compared to animals lacking the trait, or that have it in a modified form (Chittka and Briscoe, 2001). One indirect measure of biological fitness is foraging performance (Alcock, 1996, p. 159), as the amount of food available to a bumblebee colony is positively correlated with the production of males and new queens (Ings *et al.*, 2005a, 2006; Pelletier and McNeil, 2003; Schmid-Hempel and Schmid-Hempel, 1998). Here we explore within-population variation of floral color preference, a heritable foraging-related trait, to measure the extent to which such preferences can be regarded as adaptive, that is, improving the foraging performance of individual bees, and hence indirectly colony fitness.

In the vicinity of Würzburg, Germany, we made two interesting observations. First, that plant species with violet (bee UV-blue) flowers contain the highest nectar rewards (Chittka *et al.*, 2004). Second, that there is appreciable variation among colonies in the extent to which bees prefer either blue or violet flowers (Raine and Chittka, 2005b; Fig. 5). To establish any potential correlation between a preference for violet (highly rewarding) flowers and good foraging performance, we needed to test both for each colony. To enable us to achieve this within the lifespan of a single

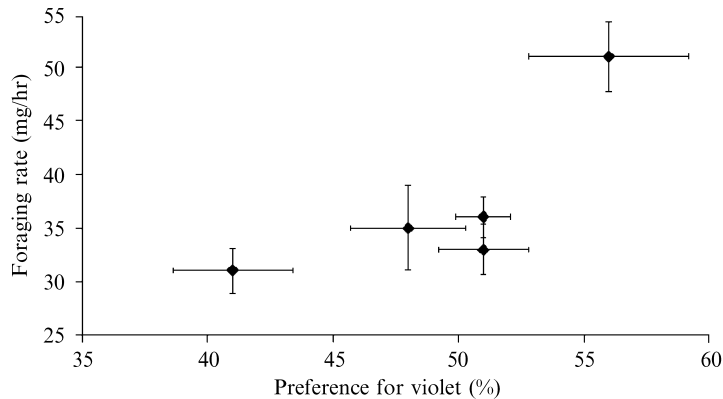


FIG. 5. Correlation of unlearned floral color preference and foraging performance in the wild measured in the bumblebee *B. terrestris* near Würzburg ($r_s = 0.82$; $N = 5$; $p = 0.089$). Each data point represents mean (± 1 SE) performance for each of these traits for one test colony. Data from Raine and Chittka (2005b).

colony, we simplified the laboratory color preference tests from those in Section III. We tested the color preference of each forager individually in a flight arena, which contained eight violet and eight blue artificial flowers (Frauenstein, 2002; Raine and Chittka, 2005b). Each bee was tested for a single foraging bout, after which the flowers in the arena were changed to ensure that the subsequent test bee received no odor cues. We tested 12 foragers from each of 5 colonies (i.e., 60 bees in total). All five tested colonies were subsequently taken into the field and their foraging performance tested over a 3-week period in July 2001 (see Section II; Chittka *et al.*, 2004; Raine and Chittka, 2005b for site description and methods).

In the five colonies tested, the average percentage preference for violet over blue ranged from 41 to 56% (Raine and Chittka, 2005b), although other colonies tested in a separate study exhibited a violet preference of up to 62% (Frauenstein, 2002). In our study, colonies with a higher average unlearned preference for violet in the laboratory harvested more nectar per unit time in the field (Raine and Chittka, 2005b; Fig. 5). This is as one might expect, given that the violet flowers around Würzburg appear to contain more nectar than blue flowers (Chittka *et al.*, 2004), but the correlation narrowly misses statistical significance ($r_s = 0.82$, $N = 5$, $p = 0.089$; Raine and Chittka, 2005b) possibly because of the small sample size. We left these test colonies in the field for a further 5 weeks after the foraging

tests to allow us to quantify the production of new queens (gynes) from each one—a more direct measure of biological fitness than foraging performance. We reduced the nest entrance diameter to 7 mm to prevent the escape of newly emerged queens from their natal nest, while allowing the smaller foraging workers to pass freely (worker thorax width 3–7 mm: Goulson, 2003; Goulson *et al.*, 2002). Queen productivity per colony ranged from 4 to 39, with the highest number of queens being produced by the colony with the strongest violet preference (Raine and Chittka, 2005b). However, while the overall correlation between violet preference and queen production was positive, it was far from significant ($r_s = 0.46$, $N = 5$, $p = 0.43$; Raine and Chittka, 2005b). In conclusion, while there is an overall trend for colonies with a stronger violet preference to perform better in an environment with highly rewarding violet flowers, we need more data to ascertain whether this trend is actually biologically meaningful.

This study clearly illustrates a number of the challenges faced when trying to quantify the fitness impacts of foraging-related traits in bees. First, the traits of interest (e.g., color preference) and foraging performance must both be measured for a large number of colonies, which requires a large and motivated workforce. Second, even if the traits under examination are somehow correlated with foraging performance, they may have no measurable impact on biological fitness within one generation. However, even if any fitness effect is difficult to measure within a single generation, the effects of that trait may still be important over evolutionary relevant time scales. Finally, other traits, notably parasite resistance (Baer and Schmid-Hempel, 1999), may be so important that they obscure the potential impact of the trait(s) under examination. This is further complicated by the fact that the parasite load may itself also affect foraging behavior (König and Schmid-Hempel, 1995; Otterstatter *et al.*, 2005; Schmid-Hempel and Stauffer, 1998) and learning performance (Mallon *et al.*, 2003). Therefore, this is not just a lesson in the difficulties involved in *measuring* adaptive significance—it is also a lesson related to the evolution of foraging behavior itself. If the effects of foraging-related traits on biological fitness are relatively hard to measure, or are often obscured by other unrelated traits, then selection on foraging strategies may itself be relatively weak. Thus, foraging-related traits may well be sitting on relatively broad adaptive peaks, where deviations from the optimum may not be strongly penalized in terms of fitness costs because of the shape of the adaptive landscape (Gilchrist and Kingsolver, 2001; Whitlock, 1997). If variation in foraging strategies is sometimes selectively neutral, evolutionary chance processes may play a greater role in between-species or between-population differences than is generally thought.

VI. VARIATION WITHIN POPULATIONS: LEARNING BEHAVIOR

The “pollination market” in which bees forage will typically contain dozens of flower species, which differ greatly in the nectar and pollen rewards on offer, their handling costs, and spatial distribution. The average rewards in a flower species may change rapidly over the course of the day, depending on patterns of reward production and the activities of other flower visitors (Harder, 1990; Heinrich, 1979; Inouye, 1978; Stone *et al.*, 2003; Willmer and Stone, 2004). Since floral rewards differ strongly among plant species and fluctuate rapidly over time, generalist foragers, such as bumblebees and honeybees, need to assess such differences in reward and respond accordingly (Chittka, 1998; Menzel, 2001). For this reason, learning floral traits, such as color, pattern, and scent, as predictors of floral reward is vital to efficient foraging (Chittka *et al.*, 1999). But is the speed at which bees form associations, such as those between floral color and reward, adaptive?

To examine this question, we set out to assess the variability in colony learning performance within the British population of *B. terrestris* (*B. t. audax* (Harris)). We tested bumblebee workers (240 workers from 16 colonies) in a simple foraging situation in which they had to distinguish yellow, rewarding artificial flowers from blue, unrewarding ones (Raine *et al.*, 2006). Test colonies, produced from wild caught queens, were raised entirely in the laboratory and were therefore unbiased by previous experience at the start of the experiments. During testing, each bee foraged alone in a flight arena containing 10 blue and 10 yellow artificial flowers. The yellow flowers contained a sucrose reward (15 μ l of 50% sucrose solution w/w), while blue flowers were empty (unrewarded). The behavior of each test bee was observed until it approached, or landed on, at least 100 flowers after it first fed from (probed) a yellow flower. The learning performance of each bee was quantified as the number of errors made, that is, choices of unrewarding (blue) flowers, as a function of the total number of flowers chosen.

We found striking variation in learning performance among the 16 bumblebee colonies tested. First, we found significant variation in the average number of flower choices made by a bee before probing a yellow flower, the point at which associative learning between yellow flowers and reward could begin (Raine *et al.*, 2006). While the vast majority (88%) of bees probed their first yellow flower after fewer than 100 flower choices, bees from some colonies did not feed from a yellow flower until after several hundred choices, and the highest recorded number of choices was 373. There was also significant intercolony variation in the speed at which bees subsequently learned to associate yellow flowers with reward (Raine

et al., 2006). A comparison of the learning curves for the fastest (A99), a medium (A62), and the slowest (A228) learning colonies shows that they differed most in the number of errors they make during the earlier stages of the learning process, predominantly during the first 60 choices (1–60) after probing their first yellow, rewarding flower (Fig. 6). In all colonies, the largest improvement in task performance happened during the first 10 flower choices after, but including, the first time the bee probed a yellow, rewarding flower. However, the magnitude of this improvement in task performance varies greatly among colonies. The task performance of the fastest learning colony (A99) improved by 70% during the first 10 flower choices after probing a yellow flower, while the slowest learning colony improved by 49%. After this very large improvement in task performance, learning continues, but the rate at which task performance improves declines until the bee's task performance eventually saturates.

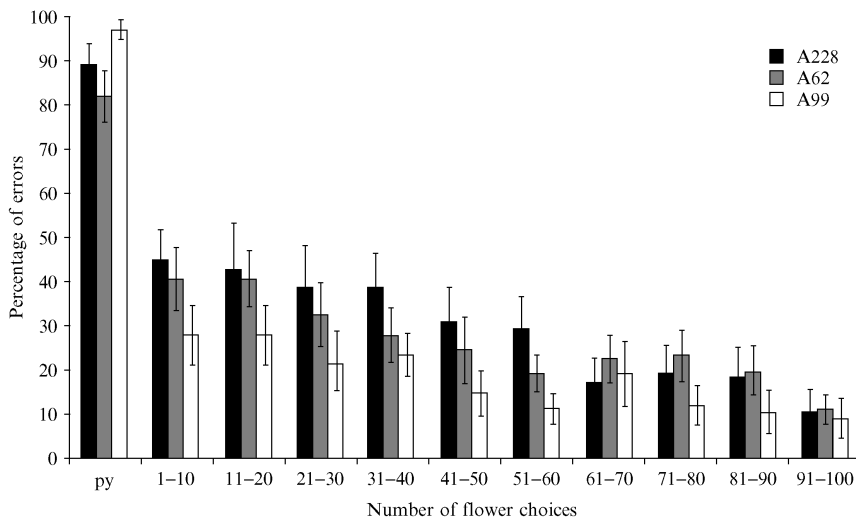


FIG. 6. Learning performance of bees from a fast (A99), medium (A62), and slow (A228) learning colony. The behavior of 15 bees in each colony was observed for 100 flower choices after they first fed from (probed) a yellow, rewarding flower. An “error” was categorized as a bee approaching or visiting (landing on) a blue, unrewarding flower. The first column (py) represents the mean (± 1 SE) percentage of errors made by bees from each colony during the first 10 flower choices they made in the test arena, that is, before they probed a rewarding, yellow flower. The remaining columns ($N = 10$) represent the colony mean percentage error for each consecutive sequence of 10 flower choices made after probing the first yellow flower (choices 1–10, 11–20, and so on). Data from Raine *et al.* (2006).

We can therefore conclude that there is significant variability in the ability of bumblebee colonies to learn color as a predictor of floral reward. This raises the question whether there might be an optimal learning speed for foraging under natural conditions. We often tacitly assume that behavioral traits (including learning ability) are sitting on narrow adaptive peaks (Price *et al.*, 2003) so that deviations from the most common wild type will be strongly penalized in terms of losses in fitness. Indeed, tests with honeybees (Benatar *et al.*, 1995; Brandes, 1988; Scheiner *et al.*, 2001) and fruit flies (Lofdahl *et al.*, 1992; Tully, 1996) have shown that measurably faster or slower learners can be bred in very few generations. If artificial selection can easily produce faster-than-wild-type learners, why has natural selection not done the same? The fact that bees do not learn as fast as they could do, indicates that natural selection stabilizes learning ability at an intermediate level, and that both faster and slower learners might have lower fitness and are therefore selected against. But why would faster learning be selected against?

In nature's dynamic pollination market in which the most profitable flower type is constantly changing, it would seem advantageous for foragers to be able to learn new associations quickly to keep pace with changing floral rewards. However, if the speed with which bees form associations compromise the fitness returns of a second trait (Mery and Kawecki, 2004), then this could produce a trade-off between learning speed and this other trait. One such potential trade-off could be between learning speed and efficient memory retrieval (Chittka, 1998). Foraging bees are continually amassing experience, learning many new associations, such as those between floral morphology, scent or color and reward, and new sensorimotor skills to obtain rewards from flowers effectively. While long-term memory has sufficient capacity to store much of this information (Chittka, 1998; Greggers and Menzel, 1993; Menzel, 1990), problems might arise regarding the organization and retrieval of this stored information. Since information is very hard to eliminate once stored in long-term memory (Chittka, 1998) and information retrieval becomes both slower (Chittka and Thomson, 1997) and less efficient (Chittka *et al.*, 1995, 1997) as more information is stored, it makes adaptive sense to limit both the amount and the rate of information input to long-term memory. One potential way to regulate this problem is by limiting the input to long-term memory to information which has shown its salience in large numbers of trials.

The high levels of intercolony variation we have demonstrated in learning performance also raise some important methodological considerations of sample size. Clearly, care must be taken when making comparisons between species or populations based on small number of colonies, or when examining correlations between learning performance and other

parameters. While there was no overall correlation between bee age and learning performance, we did find significant correlations between bee age and learning speed in 3 out of 16 colonies (2 positive and 1 negative correlation: Raine *et al.*, 2006). Thus, randomly selecting a single colony from this population would produce a significant correlation between age and learning speed in almost 1 in 5 (20%) cases. Thus, when designing experiments it is important to consider the potential significance of variation among, as well as within, colonies when deciding how to allocate finite sampling effort.

Animal species differ widely in their cognitive capacities, and it is commonly assumed that such differences reflect adaptations to the natural conditions under which these animals operate (Dukas, 1998; Gallistel, 1990; Shettleworth, 1998). The evidence for this view comes from interspecific comparisons and correlative studies (Dukas and Real, 1991; Sherry, 1998). For example, vole species with larger home range size have, on average, better spatial memory, and the hippocampi (brain areas which store spatial memories) in such animals are typically larger (Sherry and Healy, 1998). An alternative way to address the question of the adaptive value of variation in cognitive capacities could be to examine the link between intraspecific variation in learning ability and fitness under ecologically relevant conditions. As the colony represents the unit of selection in social insects, the intercolony variation we have demonstrated represents the raw material on which selection for learning ability might act. This forms a solid basis from which to explore the potential adaptive value and constraints imposed on such variation in the economy of nature.

VII. RECIPROCAL POPULATION TRANSPLANT EXPERIMENTS: A TEST OF LOCAL ADAPTATION

A rarely used but potentially powerful method of testing the adaptiveness of a (foraging) behavior is by testing an animal's (foraging) performance under natural conditions in its native habitat and then transplanting this animal into a second animal's native environment and retesting its performance. Crucially, the second animal's foraging performance must also be measured in both its native habitat and that of the first animal—hence a reciprocal transplant experiment (Chittka *et al.*, 2004; Ings *et al.*, 2005b; Riechert and Hall, 2000). A necessary implication of the notion that animals are best adapted to foraging in their own habitat is that native animals should outcompete animals from other populations in terms of foraging performance in their native environment. Therefore, we set up reciprocal transplant experiments 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 the Canary Islands. All 27 tested colonies had been raised under identical conditions, including *ad libitum* provision of nectar and pollen. We therefore conjecture that any between-population differences at the start of the foraging career of individuals would be genetically determined. Test colonies were at a comparable developmental stage at the start of each experiment, that is, colonies were young and vigorous, and had 30–50 workers.

We measured the nectar collection rate (weight of nectar collected per unit foraging time) of bee colonies from each of these populations at three sites: Costa Rei (southern Sardinia, autumn 2000), Monte Padru (northern Sardinia, spring 2001), and Würzburg (Germany, summer 2002). Ideally we would have liked to test our bee populations at a field site in the Canary Islands, but this was impossible as local authorities prohibit the import of nonnative bees. At the three sites chosen, we tested the foraging performance of nine bee colonies, that is, three from each population. All foragers were individually marked, and their flight departure and arrival times and weights were recorded for each foraging bout. There was no selection of foragers to be tested: we simply monitored all bees motivated to forage (Chittka *et al.*, 2004).

We expected that Sardinian *B. terrestris* would perform better in their native Sardinian habitat than either bees from Germany or the Canary Islands. Likewise, we expected that mainland *B. terrestris* would be the superior foragers in their native Germany. We also predicted that *B. t. canariensis*, as a nonnative of either site, would perform worse than either native population in their native habitats. Surprisingly, however, *B. t. canariensis* performed best at all three sites. *B. t. sassaricus* was consistently second: it performed better than German *B. t. terrestris* not only in its native Sardinia but also most surprisingly in Germany (Fig. 7; Ings *et al.*, 2005b). Thus, our hypothesis that each population is best adapted to its native habitat in terms of foraging behavior cannot be upheld.

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 of all foragers tested as body mass is highly correlated with size (Goulson *et al.*, 2002). It turns out that body sizes of the three populations tested fall into the following order: *B. t. canariensis* > *B. t. sassaricus* > *B. t. terrestris*, that is, exactly the same rank order as that established for foraging rates (Chittka *et al.*, 2004; Ings *et al.*, 2005b). These differences in body size are not a consequence of variation in foraging performance as all colonies were fed pollen and nectar *ad libitum* prior to the start of field

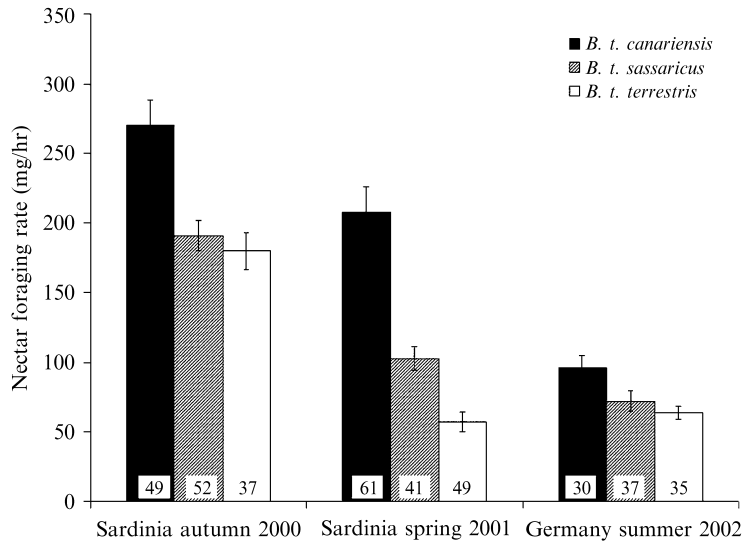


FIG. 7. Nectar foraging performance of three populations of *B. terrestris* in different test locations. One “native” bee population (*B. t. sassaricus* in Sardinia and *B. t. terrestris* in Germany) is compared against two nonnative bee populations at each test location. Columns represent pooled mean (± 1 SE) nectar foraging rates of bees from three colonies per population at each location. Numbers in bars are sample sizes, that is, the number of bees that performed three or more foraging trips. Data from Ings *et al.* (2005b).

trials using freely foraging bees. We monitored each nest for less time than it takes for a worker to develop (ca. 22 days from newly laid eggs to eclosion: Duchateau and Velthuis, 1988; Shykoff and Müller, 1995), so worker size could not be a result of colony foraging performance during the experiments.

These results strongly suggest 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 color preference (Ings *et al.*, 2005b). There are a variety of reasons why larger foragers might be better foragers, 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: Foster’s (1964) “Island Rule.” Palmer (2002) showed that beetle body size increases with island size until reaching its maximum and then subsequently decreases with further increases in island size. One explanation for the island rule is that ecological release from predators and competition leads to an initial increase in body size, while resource limitation leads to

size reductions at larger island size (Brown and Lomolino, 1998). Clearly we need comparative data on resource availability and predation levels on islands and the mainland to resolve this issue. But one important lesson here is this: since worker size might be under selective pressures wholly unrelated to foraging, for example, thermoregulation (Bishop and Armbruster, 1999; Corbet *et al.*, 1993; Willmer and Stone, 2004) or predator pressure (Dukas and Morse, 2003), apparent foraging adaptations may in fact be exaptations: that is, the result of traits historically evolved for other purposes (Gould and Lewontin, 1979).

VIII. MANIPULATION OF THE FORAGING ENVIRONMENT: SCENT MARKING AND TRAPLINING

One possible approach to studying the adaptive significance of a foraging strategy is to manipulate the environment in such a way that the foraging strategy cannot be used. For example, bees use the scent marks they deposit when visiting a flower as an olfactory cue to minimize the risk of revisiting recently emptied flowers (Giurfa and Núñez, 1992, 1993; Goulson *et al.*, 2000; Saleh *et al.*, 2006). In order to test the adaptive benefits of bees' ability to respond to these cues, Giurfa and Núñez (1992) eliminated these floral scent marks by means of an air extractor in a flight arena and found that this resulted in significant decrease in the number of recently visited flowers rejected when the fan was turned on (mean \pm 1 SE = 11.43 ± 0.79 rejections per flower visit with fan off vs 0.13 ± 0.05 with extractor on: $t = 14.24$, $p < 0.001$; Giurfa and Núñez, 1992), suggesting that the ability to correctly interpret scent marks is a highly important and adaptive component of bee foraging.

Here we test the adaptive significance of another foraging strategy, traplining. In analogy with a trapper checking his traps in a fixed stable sequence, bees often visit flowers, or patches of flowers, in repetitive orders (Collett, 1993; Heinrich, 1976; Manning, 1956; Thomson, 1996; Thomson *et al.*, 1982, 1987, 1997). In a field study, Williams and Thomson (1998) found that traplining bees harvested more nectar per unit time than casual foragers (bees foraging opportunistically within the same flower patch). But how can the advantages of traplining be explained? Williams and Thomson (1998) found that the greater efficiency of traplining bees in collecting rewards primarily resulted from greater selectivity. Traplining bees could select, on average, more rewarding flowers within a patch than those selected by casual foragers. This ability to select the most profitable flowers appeared to be the result of the fact that traplining bees were better able to reject recently visited, resource-depleted flowers, that is, those

bearing scent marks (Williams and Thomson, 1998). But why did trapliners respond more strongly to such scent cues? One possibility is that bees with extensive local experience might be better able to respond to repellent scent cues within a floral patch. Traplining bees would build up such local experience while making repeated circuits of visits to the same flowers, plants, and flower patches. In addition, bees might also be able to distinguish their own scent marks from those deposited by other bees (Giurfa and Núñez, 1993). If so, traplining foragers might use scent marks as a backup strategy to minimize the risk of visiting recently depleted flowers (Thomson and Chittka, 2001).

In order to tease apart the relative benefits of using scent marks and traplining, we used an experimental design that removed the possibility for bees to visit flowers in a stable sequence, that is, they could no longer trapline. Bumblebee workers (*Bombus impatiens* Cresson) were trained to empty six large artificial flowers (colored plastic chips, diameter = 3 cm), each containing a sucrose solution reward, placed in a flight arena (Thomson and Chittka, 2001). We ensured workers needed to visit all six flowers by adjusting the total volume of sucrose solution available in the flowers to the size of their honeycrop. Since bumblebee foragers vary in size (Goulson *et al.*, 2002), and therefore in honeycrop capacity (Spaethe and Weidenmüller, 2002), we needed to determine maximum honeycrop load size for each individual worker to be tested. This was done by presenting each bee with 15 large artificial flowers, each containing a 10 μ l sucrose solution reward, and counting the number of flowers it visited per foraging bout (Thomson and Chittka, 2001). For subsequent tests, each large flower was filled with a reward equal to one-sixth of the test bee's honeycrop volume. Two groups of bumblebees were tested for 40 foraging bouts per individual. We evaluated the performance of each forager in the final 20 bouts to ensure that bees had reached saturation level in terms of familiarizing themselves with the task (Thomson and Chittka, 2001). Bees in the first group found the flowers in fixed positions in subsequent bouts, while flower positions varied randomly between foraging bouts for bees in the second group. Thus, bees foraging from the random arrangements of flowers had no opportunity to form traplines: that is, they had to seek out the positions of the six flowers *de novo* in each successive foraging bout. Large flowers (diameter = 3 cm) were used in all of these tests, irrespective of whether the spatial arrangement of flowers was held constant, or randomized, between subsequent foraging bouts (Thomson and Chittka, 2001). We measured the search time taken by each bee to find all six rewarding flowers: that is, the flight time from entering the flight arena to when the bee first visited the sixth rewarding flower minus the time spent feeding from the other five flowers.

Surprisingly, bees foraging from large flowers appeared to be entirely unaffected by being unable to form traplines. The total flight time taken to find all six flowers was statistically indistinguishable between bees allocated to the random or the constant spatial arrangement of flowers (Mann–Whitney $U = 13$, $p = 0.86$; Thomson and Chittka, 2001; Fig. 8A). Also, while the number of revisits made to already emptied flowers was higher in the group of bees foraging from the random (mean = 3.4) as opposed to the constant flower arrangement (mean = 2.0), this difference was not significant ($U = 8.5$, $p = 0.29$; Thomson and Chittka, 2001). Bees foraging from the constant arrangement of flowers clearly visited flowers in a highly repeatable sequence (Thomson and Chittka, 2001), but this gave them no measurable advantage over bees that had to actively search for all six flowers in each new foraging bout. So does this mean traplining represents a behavioral pattern without adaptive benefits?

It is possible that using a stable sequence of flight vectors (traplining) is particularly advantageous when flowers are hard to find, that is, when they

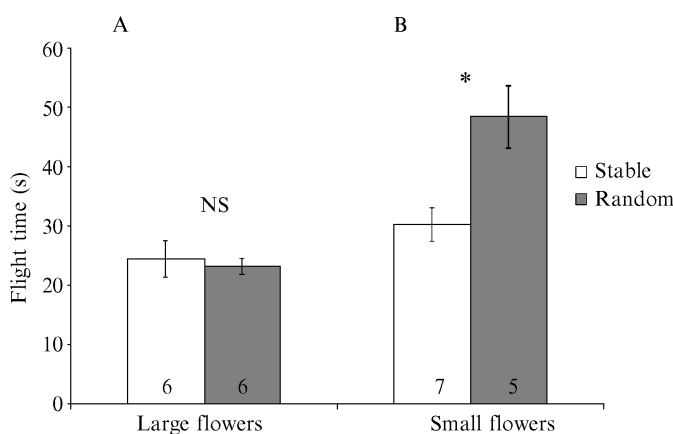


FIG. 8. The relative benefits of traplining (visiting flowers in a stable sequence) depend on whether flowers are (A) large or (B) small. Bumblebees (*B. impatiens*) were trained to empty six artificial flowers placed in a spatial arrangement which either remained stable (open columns) across, or was randomized between (shaded columns), subsequent foraging bouts. Bees foraging from flowers in a constant, stable arrangement could form traplines, those foraging from randomly arranged flowers could not. In the first experiment (A) all bees foraged from large flowers (diameter = 3 cm), while in the second (B) all flowers were small (diameter = 1 cm). Column heights indicate the mean flight time (± 1 SE) for bees to find all six flowers in each test group (minus the time spent on flowers and imbibing nectar). Numbers in each column are the number of bees tested in each treatment ($N = 40$ foraging bouts per bee tested). Significant differences between stable and random arrangements of flowers for each experiment are indicated with an asterisk. Data from Thomson and Chittka (2001) and Saleh and Chittka (unpublished).

are either far apart or sufficiently small that they are difficult to detect. Flowers with a diameter of 3 cm, like the large ones used in our first test above, would be detectable from a distance of 34 cm: given that a target (here a flower) needs to subtend an angle of approximately 5° to be detected by an average-sized worker bumblebee (Spaethe and Chittka, 2003; Spaethe *et al.*, 2001). Thus, a forager in our test flight arena (floor dimensions: $105 \times 75 \text{ cm}^2$), containing six randomly arranged large flowers, will almost always be able to detect the nearest flower(s) from wherever it is currently foraging. Thus, it might simply not be very challenging for bees to locate such large flowers at a relatively high density.

In a scenario in which flowers are smaller, and thus more difficult to detect, a bee would probably need to search considerably harder to find each flower (unless the bee already knows their location). For a bee foraging in such an environment, a strategy allowing it to memorize flower locations, and learn to link them with a set of flight vector instructions (e.g., “first, fly 50 cm in a northeast direction, then 20 cm west,” and so on), might have a clear advantage over a strategy in which flowers must to be located afresh in each foraging bout. To test this idea, we repeated our first experiment with flowers of smaller size: diameter = 1 cm (Thomson and Chittka, 2001; Saleh and Chittka, unpublished). In this situation, randomizing the spatial arrangement of flowers from one bout to the next had a strong effect ($U = 31, p = 0.023$; Thomson and Chittka, 2001; Saleh and Chittka, unpublished): the time taken to locate all six flowers increased by more than 60% (Fig. 8B). Likewise, the mean number of revisits to previously emptied flowers increased from 2.4 (stable) to 4.9 (random), and this difference was also highly significant ($U = 29, p = 0.009$; Thomson and Chittka, 2001; Saleh and Chittka, unpublished).

As bees in all treatments had equal access to the scent marks (those the forager itself left) on flowers, any differences in the frequency of revisits to empty flowers could only have been produced by differences in the spatial arrangement of flowers. Our findings strongly suggest that bees use a combination of traplining and scent-marking flowers to avoid revisiting resource-depleted flowers. However, it seems that the adaptive benefits of traplining are context dependent: in situations where flowers are hard to detect (because they are either small and/or widely spaced), traplining gives bees a clear advantage over others which do not implement a stable flight route connecting memorized flower locations. When floral detection imposes no constraints on foraging performance, that is, when flowers are large (highly apparent) and/or closely packed together, more “random” spatial movements do not appear to be detrimental to foraging performance. In accordance with these findings, wild bumblebees (*Bombus ternarius*) foraging from natural flowers displayed a clear tendency to trapline when foraging from widely spaced sarsaparilla (*Aralia hispida*

Vent.) plants (Thomson *et al.*, 1982), whereas they show no such tendency when foraging from dense stands of goldenrod (*Solidago* spp.) plants (Thomson and Chittka, 2001).

IX. MANIPULATING FORAGING PHENOTYPES: THE HONEYBEE DANCE

The honeybee dance language is regarded by many as one of the most intriguing communication systems in nonhuman animals (Chittka, 2004; Frisch, 1955). A successful scout bee returns from the field and advertises the location of a newly discovered food source to nestmates. To do this, the forager performs a repetitive figure-eight-shaped sequence of movements, the so-called “waggle dance.” In the darkness of the hive, the successful forager waggles her abdomen from side to side, while moving forward in a straight line: the “waggle (wagtail or wagging) run.” Then she runs in a half circle to the left, back to her starting point, before performing another straight waggle run, after which she circles to the right to reach her starting point once again, thereby completing a waggle dance circuit. This pattern is repeated multiple times and is eagerly attended by bees in the hive. Shortly after such dances commence, scores of newly recruited foragers will arrive at the food source being advertised (Frisch, 1967; Seeley, 1995). But what were the ecological conditions under which such a dance language evolved, and what are its benefits to colony foraging performance? An ideal approach to studying this question would be to study a knockout animal, or mutant, in which dance communication is disrupted, but which otherwise functions completely normally. Unfortunately, such study systems are not currently available in honeybees. Therefore, we examined this question by creating experimental phenotypes in which the location information of the dances was eliminated.

In order to try to understand the adaptive significance of the dance language, we decided to measure the performance of bee colonies under natural conditions and compare it to conditions under which the information flow between dancers and recruits was disrupted (Dornhaus, 2002; Frisch, 1967; Kirchner and Grassler, 1998; Sherman and Visscher, 2002). To these ends, we used a simple trick to disrupt the normal process of information transfer from dancer to recruit. Under normal conditions, the angle of the forager’s waggle run relative to the direction of gravity on the vertical comb indicates the direction of the food source relative to the azimuth of the sun (Frisch, 1955, 1967). However, by tilting the combs into a horizontal position we eliminated the possibility for bees to use gravity as a reference (Dornhaus and Chittka, 2004). Therefore bees performed dances in chance directions, so that dances lose their directional

information component. Having “interpreted” these nondirectional dances, recruits leave the hive in random directions (Dornhaus, 2002; Frisch, 1967; Kirchner and Grasser, 1998). However, if bees are offered a direct view of the sun or polarized light, then a returning forager can perform a correctly oriented waggle dance (with respect to the sun rather than to gravity) on a horizontal surface (Frisch, 1967). We used specially constructed hives in which combs were arranged horizontally. The top was fitted with a window, so the first comb would be exposed to the sun if the window was uncovered. Hence covering this window allowed us to eliminate the directional component of a returning forager’s waggle dance (Dornhaus, 2002; Dornhaus and Chittka, 2004).

Initially, we compared the success of colonies that were able, or unable, to communicate the direction of profitable food sources in two temperate locations representative of the present distribution of European honeybees, *A. mellifera*, in spring. The experimental sites were a typical Mediterranean habitat in the Sierra Espadán Nature Reserve, Spain, and a site near Würzburg, Germany, where agricultural land is mixed with natural meadows. We placed a pair of hives with 10 horizontal combs and ca. 5000 workers in each location. This is the sort of colony size one might expect to find in the wild, and it ensured that colony foraging would not be limited by the space available for honey storage. Each colony was switched from oriented to disoriented dancing every 2 days by uncovering or covering the window on top of the hive, respectively. Colony success was assessed using the daily weight gain of hives, which predominantly reflects nectar intake (Seeley, 1995).

Surprisingly, we found no difference in weight gain, at either European site, between days in which colonies were able to follow oriented or disoriented waggle dances from returning foragers (Dornhaus and Chittka, 2004). To confirm that this was not simply a consequence of the time of year, we repeated the same experiment with two three-comb hives monitored from May to September in Würzburg, Germany. However, even over this extended timescale, we again found no effect of obscuring the directional dance information (Dornhaus and Chittka, 2004). In both experiments, hive net weight changes were quite often negative, that is, the hive lost weight over a 24-hr period, except on those days when bees apparently discovered a rich nectar flow. This is similar to the patterns Seeley (1995) has found in his foraging experiments in North America.

So why bother communicating the direction to profitable food sources? Are the elaborate dances of European honeybees a useless behavioral feat? It seems highly counterintuitive, especially when one considers the enormous efficiency of the dance language to recruit bees to single points in space (Dyer, 2002; Frisch, 1967; Gould, 1975; Towne and Gould, 1988).

However, to understand why animals behave the way they do, we must consider their ecological history as well as the conditions under which they currently operate. *A. mellifera*, the European honeybee in which the dance language was first described, occurred historically in temperate habitats west of the Iranian desert (Ruttner, 1987). The honeybee spread unassisted into sub-Saharan Africa from Europe via Arabia, whereas its colonization of the new world tropics and Australia is the result of human intervention (Ruttner, 1987). However, *A. mellifera* shares the dance with all other species of honeybees (genus *Apis*), most of which are limited in their distribution to tropical Asia (Ruttner, 1988). The evolutionary origins of these dances are therefore thought to have occurred in an open-nesting tropical ancestor of extant honeybees (Dyer and Seeley, 1989). These ancestral honeybees foraged under conditions wholly different from those in which modern European *A. mellifera* colonies find themselves. In tropical forests, floral food sources are predominantly arboreal and patchily distributed in space. Individual trees frequently offer many thousands of flowers at a very precise spatial location within the forest, and there are often large distances between trees flowering at the same time (Bawa, 1983, 1990; Roubik, 1992). This is in marked contrast to most temperate habitats in which widely distributed herbs and shrubs form a significant component of a bee's diet (Heinrich, 1979).

To test if the dance language is more essential to efficient foraging in tropical than in temperate habitats, we repeated our experiment with *A. mellifera* in the tropical dry deciduous forest of Bandipur Biosphere Reserve, India. We found no difference in the foraging capability of hives with vertical combs (the natural comb orientation) compared to hives with horizontal combs in which bees could perform oriented dances (i.e., the window atop the hive was uncovered: Dornhaus and Chittka, 2004). But scrambling the information content of the dance, by covering this window, reduced the number of successful foraging days by 85% (Fig. 9). The median weight gain on days with oriented dances was 5 g compared to 65 g on days when location communication was disrupted (Kolmogorov-Smirnov Test, $p = 0.02$, $N = 45$: Dornhaus and Chittka, 2004). In a similar study, Sherman and Visscher (2002) showed that season may also be a factor influencing whether the waggle dance actually increases foraging success.

One explanation for differential effects of preventing bees from communicating in different habitats or seasons is different spatial distribution of resources. Since mapping the actual flower distribution in the bees' foraging range ($\sim 100 \text{ km}^2$; Seeley, 1995) is effectively impossible, we used the information that the bees themselves provide in their waggle dances to map the locations where they forage (Visscher and Seeley, 1982). Using this

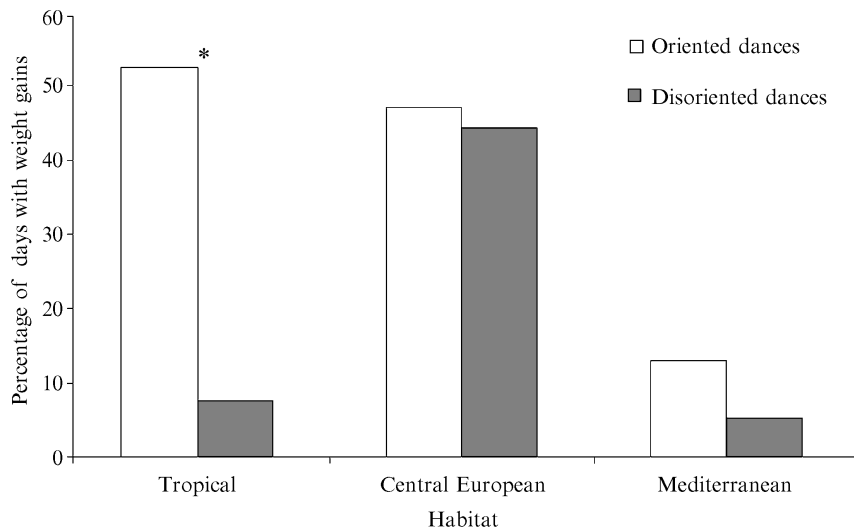


FIG. 9. Foraging performance of *A. mellifera* colonies with (oriented dances) and without (disoriented dances) the ability to communicate directional information about the location of food sources to nestmates through their dance language. Columns indicate the percentage of days on which each colony increased in weight. A significant effect of disrupting information between dancers and recruits was found in the tropical (indicated by the asterisk), but not in the two temperate habitats, where bees foraged equally well with and without directional communication about location of food sources. Data from Dornhaus and Chittka (2004).

approach, we created foraging maps for the Indian site by extracting information on the distance and direction of foraging sites from the hive from videotaped dances of returning foragers (Dornhaus and Chittka, 2004). This method has previously been used to create forage maps of honeybees in several habitats: temperate forest (Visscher and Seeley, 1982), African tropical forest (Schneider, 1989), a disturbed suburban habitat (Waddington *et al.*, 1994), and a disturbed habitat mixed with more natural open moors (Beekman and Ratnieks, 2000). To see if the degree of clustering varied between different habitats, we calculated the patchiness of foraging sites (following Clark and Evans, 1954) for our maps and those previously published. We found that bees at our Indian site foraged up to 10 km from the hive, but that most dances indicated foraging sites much closer (ca. 500 m) to the colony. Honeybee foraging sites were very patchily distributed within the Indian dry deciduous forest (Dornhaus and Chittka, 2004). Indeed it appears that floral resources are significantly more patchily distributed in tropical forests (Dornhaus and Chittka, 2004; Schneider, 1989) than temperate habitats (Beekman and Ratnieks, 2000; Visscher

and Seeley, 1982; Waddington *et al.*, 1994). There was also appreciable variation in the patchiness of honeybee foraging sites among these temperate habitats, with temperate forests showing the most aggregation of floral resources. Therefore, the degree of forest cover could be an important factor determining the patchiness of honeybee food sources.

Our findings suggest that the honeybee dance language is an adaptation to the tropical conditions under which the genus *Apis* diversified and may no longer be essential for efficient foraging in the temperate habitats studied. Here, it may have been maintained simply because it confers no selective disadvantage. In support of the argument that the dance language is more crucial under tropical conditions, Towne and Gould (1988) found that the precision of direction communication is higher in tropical than in temperate species. When food is less aggregated in space than in tropical forest, foraging by individual initiative, or communication through floral scent, may be as efficient as dance communication (Dornhaus and Chittka, 1999). Alternatively, stabilizing selection might have occurred through nonforaging applications of the dance such as indicating the location of nesting sites (Weidenmüller and Seeley, 1999).

X. GENETIC BASIS OF FORAGING BEHAVIOR

If we understood the genetic basis of foraging behavior, that is, the identity and number of genes involved, this would clearly give us a better understanding of the evolvability of traits that influence foraging and the extent to which foraging behavior is adapted to a given niche (Ben-Shahar *et al.*, 2002; Whitfield *et al.*, 2003). It is likely that most behavioral traits are polygenic, and linked through pleiotropies, that is, correlated characters (Amdam *et al.*, 2004; Chittka *et al.*, 2001), and therefore selection on any of them might have complex effects (Rueppell *et al.*, 2004a,b). This notion is confirmed by a series of studies by R. E. Page and colleagues, who have explored the genetic architecture, as well as the physiological and molecular basis of a variety of foraging-related traits in the behavior of the honeybee (*A. mellifera*: Page and Robinson, 1991; Page *et al.*, 1995; Pankiw *et al.*, 2002; Robinson *et al.*, 1989; Rueppell *et al.*, 2004a,b). They started by selecting two strains of honeybee colonies for a single characteristic: the amount of pollen collected and stored (Page and Fondrk, 1995; Page *et al.*, 1995). Within a few generations, they had selectively bred two lines of bees that strongly differed in the relative effort they devoted to nectar and pollen foraging. The resulting bee strains differed in multiple aspects of foraging behavior that could either be linked directly or through pleiotropies to pollen foraging. The “high strain” colonies (those which hoarded

more pollen) not only had more pollen foragers, and collected larger pollen loads (Pankiw and Page, 2001), but they also initiated foraging at a younger age and collected smaller and less concentrated nectar loads (Pankiw and Page, 2001). However, because foraging loads were not measured as a function of foraging flight duration, these data are not indicators of differential foraging performance. On the sensory level, proboscis extension reflex experiments showed that “high strain” bees were more sensitive to low concentrations of sucrose (Page *et al.*, 1998), and the authors conjecture that this might explain their higher relative acceptance level for poor nectar quality (Pankiw and Page, 2000). Indeed sensitivity to other chemosensory stimuli, such as pheromones produced by the brood, might also be elevated (Pankiw and Page, 2001). This suggests that there might be an overall improvement of sensory function in these bees, which could in turn explain their superior performance in both olfactory and tactile learning paradigms (Scheiner *et al.*, 2001). However, there may also be changes at the level of the central nervous system: Humphries *et al.* (2003) found higher levels of protein kinases A and C in the brain of bees selected for high pollen hoarding—both of these kinases play roles in memory consolidation and avoidance conditioning (Shobe, 2002). Also, Amdam *et al.* (2004) proposed that all of these differences might be pleiotropically linked to reproductive behavior.

There are multiple implications of these findings for the study of the adaptiveness of foraging behavior. The good news is that researchers are homing in on the genetic architecture underlying foraging behavior, that several foraging-related traits are heritable, and that therefore the raw material for selection, both natural and experimental, exists. This opens up the possibility to study the adaptive benefits of these traits in the wild, especially since nonlethal DNA sampling techniques have been refined for bees (Châline *et al.*, 2004; Holehouse *et al.*, 2003). However, the interpretation of the potential differences in fitness will be difficult. This is because selection on any one trait is likely to drag along a host of other traits, which may all operate under a variety of environmental constraints, and might therefore affect fitness in different ways.

XI. MODELING

In behavioral ecology, two types of models have traditionally been used to study adaptation (Judson, 1994; Ydenberg and Schmid-Hempel, 1994). Mathematical descriptions of a behavior and its fitness consequences are often very abstract, and therefore simplified, but generally applicable (Maurer and Séguinot, 1995). They can usually be solved analytically, making predictions about the optimal trait value that maximizes fitness

and how fitness will change away from that optimum. Computational models, on the other hand, cannot be solved without using numerical values for the parameters involved (Grimm, 1999). Such models can, for example, be rule-based descriptions of behavior and its fitness consequences, as is often the case in individual-based simulation models, or they can be equation-based models that are too complex to be solved analytically.

Both of these model types are powerful tools to test whether animals are adapted to particular environments; however, each also has its own potential pitfalls, which may tempt the observer to infer optimality of behaviors for the wrong reasons. For example, mathematical models of optimal foraging and load size predict that bees should return from a food source without collecting a full load if the bee is trying to maximize energetic efficiency rather than reward collection rate (Schmid-Hempel, 1987; Schmid-Hempel *et al.*, 1985). However, several other models also predict such submaximal loads (Cuthill and Kacelnik, 1990); for example, those assuming diminishing returns at the food source (Ydenberg and Hurd, 1998), or those cases where there is some chance of sharing (Varju and Núñez, 1991, 1993) or receiving (Dornhaus *et al.*, in press) information on high-quality food sources when the bee returns. Each of the models by itself can be used to argue that not collecting a full load at a food source is the optimal strategy. Unless some of these models use assumptions that do not reflect the situation of foraging bees, the bee's load size is the result of the combined effects of all these factors. In this case, none of the models alone would be sufficient to explain the full deviation from the maximal load size in foraging bees. It is therefore important not to exclude alternative hypotheses because an observed effect is consistent with one model. Like all scientific hypotheses, models that are falsified can ultimately be more interesting than those that are consistent with data, because we can deduce how the biological system does not work; whereas models that are consistent with data may, or may not, reflect the true mechanisms underlying real biological processes.

There is an additional difficulty associated with the "exact" solutions achieved in analytically solved models. In such models, analysis often focuses on the mathematically "interesting" areas. However, it might well be that what is mathematically interesting is not biologically relevant. While a model might show a trait to have several optima, only one of these may be at biologically feasible values of that trait. It is therefore crucial to apply the model to experimental data and to check that the concluded effects apply in a biologically relevant region of parameter space (Grimm, 1994; Kacelnik *et al.*, 1986; May, 2004). Similarly, it is important to derive quantitative predictions from a model (Orzack and Sober, 1994), for example, about foraging behavior. Not only should the model make quantitative predictions about the optimal value of the studied foraging trait, it should

also predict the magnitude of the benefits of optimizing this trait. In other words, it should estimate how big an advantage is gained by optimizing this particular trait, something that is seldom addressed in studies of optimal foraging. Very small effects can be hard to detect in biological data, and may indeed be too small to cause significant selection pressure in the predicted direction. Also, if effects predicted by a model were much smaller than those observed, this would indicate that additional factors influence the measured trait, and that the model does not provide a full explanation. By quantifying the trait values predicted by a mathematical model, one loses some of its generality and exactness; but at the same time, one makes a more accurate assessment of the biological relevance of the model's predicted effects.

Computational models avoid such difficulties because they require the experimenter to think about relevant parameter values from the start. However, estimation of biological parameters is inherently inexact. This means that we cannot base conclusions on the assumption that any particular estimate is correct; we have to conduct a sensitivity analysis to test for the effects of all parameters involved, within their biologically plausible limits (Chittka *et al.*, 1992). If this is not done systematically, it is all too easy to tune parameter values so that a particular result is achieved (Ginzburg and Jensen, 2004). However, with proper sensitivity analysis, computational models can be powerful tools in understanding which environmental and other factors are likely to have contributed to the evolution of observed traits (Chittka, 1996b; Judson, 1994).

Full (or even limited) sensitivity analyses are very rarely published with computational modeling studies (exceptions are Bautista *et al.*, 2001; Chittka *et al.*, 1992; Schmid-Hempel *et al.*, 1985). However, a full sensitivity analysis was performed in a study of benefits of recruitment to food sources in bees (Dornhaus *et al.*, 2006). Recruitment systems vary considerably between species of social bees (Chittka and Dornhaus, 1999; Dyer and Seeley, 1989; Lindauer and Kerr, 1958), and to develop hypotheses about the evolution of such systems, it is necessary to identify which social or ecological factors favor the evolution of recruitment. In the study by Dornhaus *et al.* (2006), an individual-based model of honeybee foraging was developed to quantify the benefits of recruitment. These were measured under different spatial resource distributions and colony sizes. Benefits of recruitment in the simulations were found to be strongly dependent on resource patch quality, density, and variability. Communication was especially beneficial if patches were poorly rewarding, few in number, and variable (Fig. 10; Dornhaus *et al.*, 2006). This result would not have been achieved had the interaction effect of environmental parameters on bee foraging success in the model not been studied. A sensitivity analysis was carried out in which each parameter value put

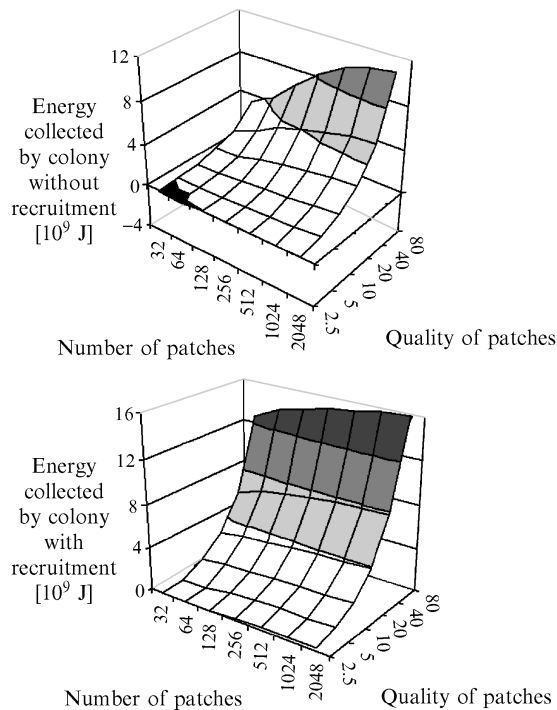


FIG. 10. Foraging success in the individual-based model was dependent on environmental parameters such as resource density and quality. Unsurprisingly, most energy was collected by the bee colony when there were many high-quality resources. The model also predicts that recruitment has different effects under different conditions. The highest relative increase in energy collected is achieved by recruitment under conditions of few and poor resources. Each data point represents the average of 10 simulation runs. The shading on each model landscape indicates the amount of energy collected (same as y-axis; black is a net energy loss) in the period simulated (50 hr). Data from Dornhaus *et al.* (2006).

into the model was varied to study its effect on foraging success of the modeled bees. Such a sensitivity analysis can be very time consuming, particularly if many parameters are involved, which is often the case particularly in individual-based models. In the cited study, 4600 simulation runs were carried out and analyzed (Dornhaus *et al.*, 2006). Some parameters that were varied within their biologically plausible limits had no effect at all; while others strongly influenced colony foraging success. The sensitivity analysis showed, for example, that under conditions of high resource density, recruitment could even become detrimental if foraging bout duration was short, the tendency to scout was high, or the recruits

needed a long time to find communicated locations. Colony size, the other main factor studied, has often been suspected to influence recruitment evolution but had no significant effect in the model (Dornhaus *et al.*, 2006). These results may explain the experimental findings that in honeybees, benefits of waggle dance recruitment seem to vary seasonally and with habitat (Dornhaus and Chittka, 2004; Sherman and Visscher, 2002).

Finally, when predictions of any models are compared with experimental results, it is important to distinguish between adaptive (“optimal”) behaviors and the mechanisms that enable animals to achieve them (Kacelnik, 1984). These mechanisms may not be identical with the way the optimal decision is computed in a model. Animal behavior arises from natural selection in a given environment, and certain rules of thumb may lead to the optimal behaviors in this environment but not necessarily in very artificial laboratory test situations (Herre, 1995). Such a situation would show animals behaving nonadaptively, but that does not prove that the trait under consideration is not under selection. Any modeling studies that produce quantitative predictions about traits and their fitness values, that provide full sensitivity analyses, and that test predictions by comparing them with the behavior of animals in their natural environment will advance our understanding of the evolution of these traits.

XII. DISCUSSIONS

We have illustrated the value of a number of approaches taken from the toolbox of the modern evolutionary biologist, which can be used to study the adaptive nature of foraging behavior. When trying to establish the role and importance of the extant behaviors, we must consider the evolutionary processes by which these traits have been forged: adaptation, chance, and history are all likely to have played their part. So to determine the adaptiveness of a particular behavioral trait we must conceive our experiments such that we can distinguish adaptation from the effects of chance and history on the behavior in question (Adkison, 1995; Clutton-Brock and Harvey, 1977). Putting this into practice in the economy of nature is never as straightforward as it may sound, due to the interrelated nature of many behavioral traits. Animals will typically be able to proceed along multiple evolutionary pathways to optimize foraging behavior, and constraints imposed by one foraging-related trait might be easily compensated for by alterations in another trait (cf. Endler *et al.*, 2001). For this reason, it is often necessary to use several different approaches to tease apart the effects of different traits and to establish whether, or under what conditions, any (or all) of them are adaptive.

The essential first step is to quantify the raw material for selection of any behavioral trait of interest, that is, variation among individuals and/or colonies in the case of social insects. Where such variation exists, we can then attempt to correlate the trait with foraging performance in the wild, and ideally, with biological fitness (Maynard Smith, 1978). Where such variation is lacking, selection might have eliminated it in the past (Chittka *et al.*, 2001), which makes a direct study of the adaptiveness of these traits more challenging. In such cases, modeling (McNamara *et al.*, 1993), manipulations of the environment (Schmid-Hempel and Schmid-Hempel, 1998), or alterations of the behavioral phenotype (Curio, 1973) help us to understand the adaptive benefits conferred on their bearer by a given trait. Reciprocal transplant experiments are a useful tool to examine hypotheses of local adaptation (Kawecki and Ebert, 2004), and the comparative phylogenetic method (Harvey and Purvis, 1991) allows us to identify patterns of adaptation by comparing closely related species. We have applied this package of methods to a variety of foraging-related behavior patterns, that is, flower constancy, flower color preference, flower color learning, traplining behavior, and bee communication about floral resources.

We also aim to highlight some of the promising areas of future research: further foraging-related traits which deserve attention using existing approaches to study their potential adaptive value (e.g., risk sensitivity, memory dynamics, and pollen foraging) and new techniques which could potentially be used to great effect in the study of adaptation (e.g., correlating foraging performance with actual biological fitness, and molecular genetic methods).

Foraging bees face a complex challenge to assess accurately the floral rewards being offered in the dynamically changing pollination market. When trying to assess which flower type is currently the most profitable, a foraging bee must not only contend with differences in quality and quantity of reward among flower species but also the variation among plants within a species and even across flowers on an individual plant. There are many experimental laboratory studies on bee "risk" sensitivity to variance in reward (Chittka, 2002; Chittka and Wells, 2004; Fülöp and Menzel, 2000; Shafir *et al.*, 1999; Waddington, 2001). There are also many models that examine the potential adaptive benefits of responsiveness to reward variance and the mechanisms underlying it (Bateson and Kacelnik, 1998). Given this complex foraging problem, it would seem intrinsically interesting to investigate the potential effect of a bee's risk sensitivity on its foraging performance, exploiting between-species variation in this trait, or by examining performance in natural environments that differ in reward variance.

Memory dynamics and recall seem to be important in many aspects of bee foraging behavior, such as associative learning of floral cues and reward, and spatial learning of flower positions in traplining. Menzel (2001) has suggested that honeybee working memory dynamics are tuned to the flight interval between flower visits (ca. 3–5 sec). However, while such adaptive speculations for these cognitive capacities might seem intuitively appealing, the ideas require rigorous testing. If memory dynamics are tuned to the foraging process, then related insects which do not forage from flowers (e.g., some cleptoparasitic bees; Roubik, 1989) would be expected to have memory phases with different temporal dynamics. Likewise, studying the foraging performance of learning mutants, should these become available in bees, may be a rewarding avenue of future research; in *Drosophila melanogaster*, scientists can make use of a wide variety of memory mutants in which only specific phases of memory are rendered nonfunctional (Reif *et al.*, 2002; Tully, 1991).

The vast majority of foraging studies on bees concentrate on the collection of nectar. This is not altogether surprising as nectar foraging provides a convenient and much more easily manipulated model system. However, pollen collection is also crucial to the success of any bee colony, and the intrinsic differences between pollen and nectar mean that bees collect them in different ways. Given the need for bees to develop such divergent strategies to harvest these distinct floral resources, we cannot reasonably extend conclusions drawn from studies investigating nectar foraging bees to questions concerning pollen collection. When collecting nectar bees automatically receive instant feedback on its quality via taste receptors (Kuwabara, 1957) and quantity via stretch receptors as the honeycrop is filled (Neese, 1988). In contrast, bees gain only indirect information on the pollen quantity from the mass they collect in their corbiculae (Ford *et al.*, 1981; Harder, 1990; Robertson *et al.*, 1999; Schikora and Chittka, 1999), and any information about pollen quality (such as the relative composition and richness of essential amino acids) is harder to collect (Erhardt and Baker, 1990), except perhaps by odor (Dobson *et al.*, 1996; Robertson *et al.*, 1999), taste, or indirect feedback through colony development. Pollen quality may be particularly important because many bees which will opportunistically collect nectar from a variety of different flower species are much more particular about finding specific flower species from which to collect pollen (Waser *et al.*, 1996; Westrich, 1989). This all begs the obvious question: what are the strategies that bees use in harvesting pollen and are these strategies adaptive?

To show the biological relevance of a foraging-related trait, we should ideally be able to quantify its impact on fitness. However, in foraging

studies fitness is seldom directly measured but is frequently inferred through changes in proxy measures or correlates of fitness. In social bees, foraging performance is well correlated with colony production of sexuals (males and new queens), which will leave the nest, mate and set up the next generation (Ings *et al.*, 2005b; Pelletier and McNeil, 2003; Schmid-Hempel and Schmid-Hempel, 1998). As such, foraging performance represents a good, but indirect, measure of fitness, while the number (or biomass) of sexuals produced by a colony gives us a more direct measure of fitness. To really understand the adaptiveness of (foraging) behavior, we need to link variation in a behavioral trait to changes in fitness. Measuring the fitness consequences of traits is challenging but obviously a desirable thing to do. While this has been done in some studies of parasitism in bees (Baer and Schmid-Hempel, 1999; Müller and Schmid-Hempel, 1992), it still needs to be achieved in the field of foraging behavior.

Another desirable avenue of future research would be to gain an insight into the adaptiveness of behavioral traits at the genetic level. Researchers are closing in on isolating the genes that encode particular behavioral traits (Ben-Shahar *et al.*, 2002, 2003; Rueppell *et al.*, 2004a,b; Whitfield *et al.*, 2003). In the future, it might be possible to modify behavioral phenotypes by knocking out their expression using double-stranded RNA interference (dsRNAi: Fire *et al.*, 1998) or perhaps by creating more traditional knock-out mutants (Lipp, 2002; Wolfer and Lipp, 2000). While it is occasionally possible to create behavioral phenotypes for traits without genetic techniques, such as removing the ability to encode distance information in the honeybee waggle dance (Section IX), the use of dsRNAi could extend the potential of this powerful approach (i.e., modification of natural behavioral phenotypes) for many other traits of interest. dsRNAi is being used to study functional mechanisms by knocking out gene function (Booth, 2004; Marie *et al.*, 2000). Farooqui *et al.* (2003) have modified the behavioral phenotype using dsRNAi techniques to block the octopaminergic pathway in the antennal lobe of honeybees. As a result, these bees were unable to learn an odor paired with a sucrose reward because octopamine mediates the unconditioned stimulus (the reward) in this associative learning task. Continued advances in the search for other behaviorally important genes and refinements in the dsRNAi techniques could herald the beginning of a very powerful future tool for the study of adaptation in behavioral ecology.

XIII. SUMMARY

Our goal in this chapter is to determine whether particular behavioral traits represent actual adaptations in the context of foraging. Social bees are our chosen study system because they provide a convenient and tractable

biological system with which to study the potential adaptiveness of a wide range of foraging traits such as flower constancy, floral color preference, learning to associate floral color as a predictor of reward, traplining, and communication about food sources.

This variety of behavioral traits allows us to demonstrate the strengths and weaknesses of applying five approaches (four experimental and one theoretical) to the study of foraging at the species, population, and colony level. (1) The comparative approach allows us to contrast behavioral traits of extant species with those of their common ancestor. We correlated differences in floral color preference between closely related species (and populations), with a known phylogeny, with features in each bee's respective environment. (2) Reciprocal transplant experiments allowed us to test for local adaptation. We compared the relative foraging performance of distinct bee populations in both of their respective native environments. (3) Manipulating the foraging environment to eliminate specific behavioral traits permitted a direct comparison of animals' foraging performance in their normal and experimentally manipulated environment, allowing us to quantify the effect of the trait in question (traplining) on foraging performance. (4) Manipulating the foraging phenotype to eliminate specific behavioral traits is another valuable approach. Unless suitable behavioral mutants, knockouts, or molecular techniques to selectively block gene expression are available, creating such artificial foraging phenotypes is only possible for a very small number of specific traits, for example, the honey-bee dance language. (5) Integrating biologically realistic modeling with experimental studies allows us to test predictions about the adaptive significance of foraging-related traits not amenable to experimental manipulation and to identify the ranges over which these traits might affect fitness.

Do these approaches provide evidence that foraging behaviors are adaptive? In some cases, we show that forager behavior has indeed been tuned to function adaptively in a given niche, although the adaptive benefits of such behavioral traits are often strongly context dependent. However, in other cases, the observed patterns of behavior were more parsimoniously explained by chance evolutionary processes, or by the historical conditions under which bees operated in their evolutionary past.

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