Part I

Foraging Decisions, Patterns, and Strategies

1 Measuring the Adaptiveness of Social Insect Foraging Strategies
An Empirical Approach[*]

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CONTENTS

INTRODUCTION

Foraging has been one of the key research areas to define the development of behavioral ecology as a discipline (Krebs and Davies 1993; Owens 2006). However, despite the considerable research effort devoted to studying foraging behavior, a number of fundamental questions with respect to the adaptiveness of foraging strategies remain relatively unexplored. Generally, we still understand very little about how foraging strategies contribute to the fitness of animals in the wild. How well does a given foraging strategy perform relative to strategies used by other individuals, colonies, or species? Does variation in foraging-related traits actually translate into real differences in fitness?

The rich history of studying foraging has revealed a great deal about the economics of foraging decisions, such as which types of food an animal should choose to consume (Pyke et al. 1977; Waddington and Holden 1979; Stephens and Krebs 1986), when to abandon a foraging patch (Kacelnik and Krebs 1985; Cuthill et al. 1990), how variance in food supply affects forager choices (Real 1981; Shafir et al. 1999; Fülöp and Menzel 2000; Chittka 2002), and what currencies animals use when making decisions about food quality (Schmid-Hempel et al. 1985; McNamara et al. 1993). But can we conclude that the improvements in foraging success or efficiency brought about by these behavioral strategies actually lead to increases in fitness? In a field study of bumble bee foraging, Schmid-Hempel and Heeb repeatedly removed a large percentage of foragers (10–15% of all workers) at regular intervals during the colony cycle. Interestingly, they found no significant effects of this forager workforce decimation on colony growth, life history, or ultimate colony reproductive success in a natural environment (Schmid-Hempel and Heeb 1991). So how can the precise

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subtleties of minute-to-minute foraging strategies of specific individuals matter if even the existence of those individuals does not appear to affect colony reproductive success? Schmid-Hempel and Heeb's findings are consistent with comparable worker removal studies in ants (Gentry 1974; Herbers 1980), and experiments in which food availability was restricted for bumble bee colonies (Sutcliffe and Plowright 1988) suggest that stress levels must be quite severe before colony development or reproductive output are adversely affected. Perhaps the real value of foraging strategies only becomes crucial under adverse conditions (Schmid-Hempel and Heeb 1991; Schmid-Hempel and Schmid-Hempel 1998), but this underlines the general point that we do not yet really understand how foraging strategies contribute to the fitness of animals under natural conditions.

The goal of this review is to determine whether particular behavioral traits represent actual adaptations in the context of foraging. To do this we revisit the central tenets of behavioral ecology, namely, the need to accurately quantify variation in behavior and then to use the subtle variation that exists in behavioral traits to test adaptive hypotheses (Krebs and Davies 1993; Owens 2006). We need to quantify variation in foraging-related traits, and then measure the fitness consequences associated with different competing behavioral strategies under the field conditions in which animals really operate. As assessing lifetime reproductive success is at best rather time-consuming and labor-intensive, and at worst impossible, it is perhaps unsurprising that there are very few studies of phenotypic selection on behavioral traits in the wild (Endler 1986; Kingsolver et al. 2001). The social bees provide a convenient and tractable biological system with which to examine the potential adaptiveness of a wide range of foraging traits under natural conditions. Bumble bees are particularly amenable to such studies, as their foraging behavior is easily studied in both the laboratory and field, and can be linked to colony reproductive success. Since bumble bee colonies produce males and new queens in proportion to the amount of food available to them (Schmid-Hempel and Schmid-Hempel 1998; Pelletier and McNeil 2003; Ings et al. 2006), we can use colony foraging performance as a robust proxy measure of colony fitness. Here, we focus on how empirical studies on social bees allow us to investigate the adaptiveness of foraging strategies.

First, we assess how the innate color preferences of bumble bees have been influenced by the particular floral markets in which they forage. Using a phylogenetic approach we compare the innate color biases of different bumble bee species, and distinct populations within a single bumble bee species, which are presumably adapted to forage in different conditions but diverged from a common ancestor. Second, we examine the hypothesis that local variation in flower traits drives selection for innate color biases. The performance of bees from nine colonies was compared in a laboratory color bias paradigm before assessing the foraging performance of the same colonies under the field conditions to which they should be locally adapted. Third, we examine the quantitative effects of variation in learning performance on fitness using a similar correlative approach. The learning performance of bumble bees from twelve colonies was evaluated in an ecologically relevant associative learning task under laboratory conditions, before testing the foraging performance of the same colonies under field conditions. Finally, we examine the ecological conditions in which the honey bee dance language is adaptive by comparing an experimentally manipulated foraging phenotype, in which the directional information component of the dance language is removed, to the normal behavioral phenotype.

THE ADAPTIVE SIGNIFICANCE OF SENSORY BIAS IN A FORAGING CONTEXT

Animals are constantly exposed to stimuli differing widely in their potential importance. Sensory systems and cognitive processes allow the animal to assess the relative salience of stimuli and select appropriate behavioral responses to the most important. One mechanism through which such adaptive behavioral outcomes are promoted is through sensory biases, within either the sensory system or subsequent cognitive processes, causing animals to respond more strongly to certain, more pertinent, stimuli (Basolo and Endler 1995; Endler and Basolo 1998). Although sensory biases have received attention in the context of animal signaling, predominantly relating to mate choice

(Dawkins and Guilford 1996; Collins 1999) and predator avoidance (Bruce et al. 2001), the potential adaptive role of such biases has only recently been studied in a foraging context where they could also be very influential (Smith et al. 2004). The flower choices of pollinators represent a good model system in which to study the adaptive role of sensory bias in the context of foraging. Flowers send out signals to attract the attention of potential pollinators in a competitive marketplace, and pollinators are attuned to particular traits, such as the color, morphology, scent, and temperature of the flowers they visit to find food (Heinrich 1979; Menzel 1985; Dyer et al. 2006; Raine et al. 2006a).

Naïve animals often initially use innate rules to find food. Pollinators, such as bees, use color as a cue to find flowers when first exploring the world (Lunau and Maier 1995; Chittka and Raine 2006). Therefore, sensory biases toward particular colors might help naïve bees find flowers, and perhaps even help them to locate the most profitable ones in the local area. Indeed, newly emerged bees, that have never seen flowers, show distinct sensory biases for certain colors (Giurfa et al. 1995; Lunau et al. 1996; Chittka et al. 2001). While these innate color preferences can be easily modified, or even reversed, as a result of individual experience (Menzel 1985; Raine et al. 2006b), there is evidence that in some situations (for example, when rewards are similar across flower species) bees will revert to their initial preferences (Heinrich et al. 1977; Banschbach 1994; Gumbert 2000). It therefore seems a reasonable hypothesis that these innate preferences reflect the traits of local flowers that are most profitable for bees.

Phylogenetic Approaches to Understanding Floral Color Preferences

Studying behavioral repertoires, such as those involved in foraging, can be complicated as animals typically proceed along multiple alternative evolutionary pathways to optimize foraging behavior, and constraints imposed by one foraging-related trait might easily be compensated for by modifications to another trait (Raine et al. 2006a). Therefore, attempting to identify evolutionary adaptations in foraging by focusing on a single species (Pyke 1978; Greggers and Menzel 1993), or sets of unrelated species (Dukas and Real 1991), can be problematic since optimality and correlation cannot be equated with adaptation (Maynard Smith 1978; Chittka 1996). However, interspecific comparisons can be more rewarding when applied to closely related species of known phylogeny. For example, we can infer that a trait is adapted for a particular task if it can be demonstrated 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; Losos and Miles 1994; Chittka and Briscoe 2001). 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; Ryan and Rand 1999; Phelps and Ryan 2000). Following earlier studies of adaptation in the foraging strategies in beetles (Betz 1998), birds (Barbosa and Moreno 1999), and primates (Clutton-Brock and Harvey 1977), this technique has more recently been applied to considering the adaptation in the innate floral color preferences of bees.

Giurfa et al. (1995) found a good correlation between the color preferences of naïve honey bees (*Apis mellifera* L.) and the nectar provided by different flowers in a nature reserve near Berlin. These honey bees preferred violet (bee UV-blue, i.e., flowers that stimulate the bees' UV and blue receptors most strongly) and blue (bee blue, i.e., stimulating predominantly the bees' blue receptors), which were also the colors most frequently associated with high nectar rewards. However, as correlation does not imply causality, a better test to examine whether color preferences actually evolved to match floral offerings would be to compare a set of closely related bee species that live in habitats in which the association of floral colors with reward is different.
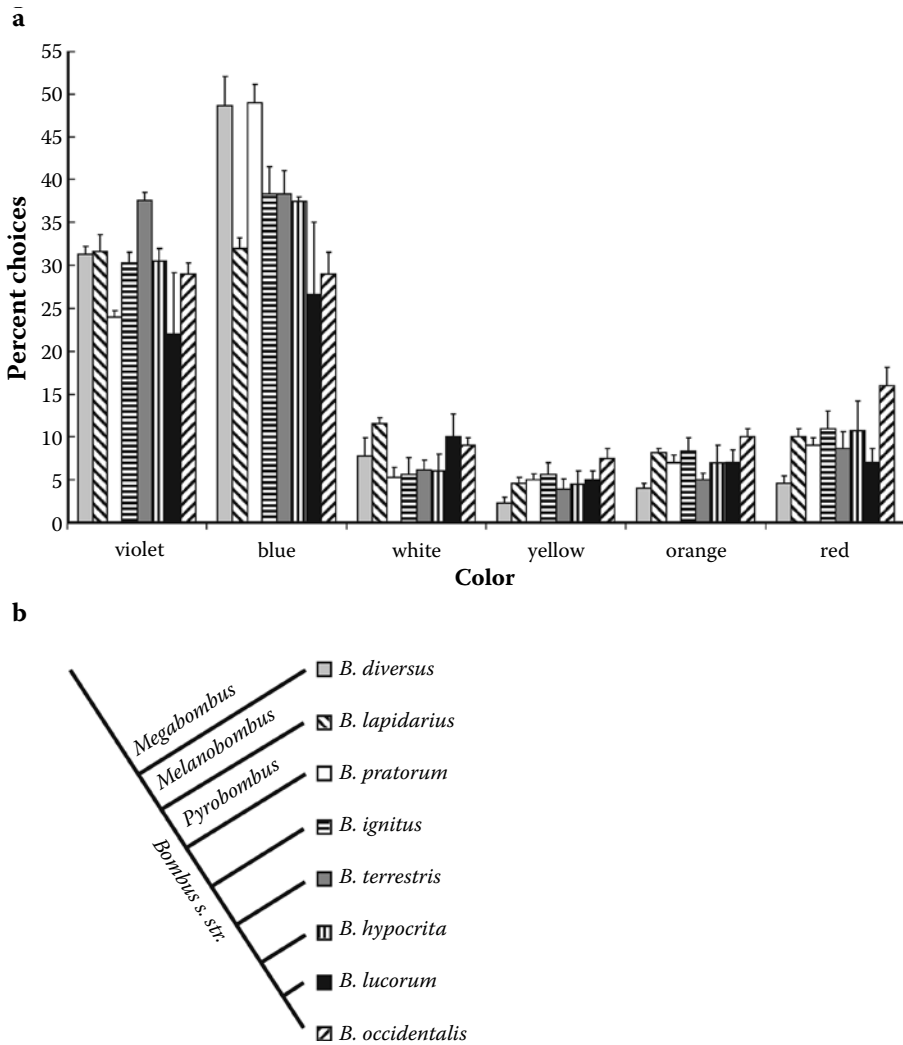
The innate color preferences of eight bumble bee species were tested by presenting them with artificial flowers in a laboratory flight arena: four species from Europe (*Bombus terrestris* L., *Bombus lucorum* L., *Bombus pratorum* L., and *Bombus lapidarius* L.), three from temperate East Asia (*Bombus diversus* Smith, *Bombus ignitus* Smith, and *Bombus hypocrita* Pérez), and one from North America (*Bombus occidentalis* Greene) (Raine et al. 2006a). Colonies from all species were

raised under identical temperature and humidity conditions in a dark laboratory, to minimize the chances that observed interspecific differences could be caused by nongenetic factors, and were never exposed to flower colors before experiments. The color preferences of each bee were tested individually by recording their choices in a flight arena containing eighteen unrewarding flowers of six different colors (i.e., three 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 the bees' green receptors most strongly).

As all eight species showed a strong sensory bias for colors in the violet-blue range, this indicates a phylogenetically ancient preference (Figure 1.1). This preference is likely to be advantageous, since violet and blue flowers have been found to contain high nectar rewards in a variety of habitats (Menzel and Shmida 1993; Giurfa et al. 1995; Chittka et al. 2004; Raine and Chittka 2007c). However, there were also differences among species. *B. occidentalis* had a much stronger preference for red than any other species tested. This is intriguing because this species 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). 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 et al. 2006a).

Comparing more recently diverged populations within the same species is also a useful approach to investigate patterns of adaptation among very closely related individuals operating under different ecological conditions. This can be especially true when comparisons include island populations that, by virtue of their small effective population size and risk of genetic bottlenecks, have increased potential for divergence from mainland populations either by chance processes or through more pronounced adaptation to local conditions due to limited gene flow with animals in different habitats (Ford 1955; Stanton and Galen 1997; Barton 1998; Chittka et al. 2004). Applying this phylogenetic approach to compare populations within a single species, Chittka and colleagues tested the innate color preferences of laboratory-raised colonies from eight *Bombus 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 Tenerife—using the same paradigm as above (Chittka et al. 2001; Raine et al. 2006a). All populations preferred colors in the violet-blue range, but there were some differences in the relative preference for violet and blue (Figure 1.2). This pattern is similar to that seen across different bumble bee species (see above), and makes biological sense since these floral colors are frequently the most rewarding across a variety of habitats (Menzel and Shmida 1993; Giurfa et al. 1995; Chittka and Wells 2004; Raine and Chittka 2007c). Interestingly however, some island populations displayed a different pattern of color preference. *B. t. sassaricus* and *B. t. canariensis* exhibited a secondary red preference (Chittka et al. 2001; Raine et al. 2006a). Coupling this observation with the fact that both island populations are genetically differentiated, both from one another and the mainland population (Estoup et al. 1996; Widmer et al. 1998), and that such population differences are heritable (Chittka and Wells 2004), indicates evolutionary plasticity in flower color preference within *B. terrestris*.

The adaptive significance of the red preference shown by the Sardinian and Canary Island populations is not easy to explain. Red, UV-absorbing, pollen-rich flower species exist at the eastern end of the Mediterranean (e.g., Israel). However, the Israeli *B. terrestris* population shows no secondary red preference, and red flowers there are predominantly visited by beetles (Dafni et al. 1990; Menzel and Shmida 1993). In Sardinia, Chittka et al. (2004) found only a single red, UV-absorbing flower species (out of 140 measured). Conspicuously, almost all the red flower species (including those that reflect in the UV) in each habitat tested were pollen-only flowers, containing no nectar (Dafni et al. 1990; Chittka et al. 2004). Thus, a red preference would not be advantageous to the Sardinian population in terms of nectar foraging (the behavioral context tested by Chittka et al. 2004). Whether red flowers represent a particularly attractive pollen source remains to be tested,

a

b

FIGURE 1.1 Color preferences of eight bumble bee species superimposed on their phylogeny (following Cameron et al. 2007). Each bee was color naïve 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 fifteen workers per colony. Bees were individually tested in a flight arena in which they were offered the colors violet (bee UV-blue), blue (bee blue), white (bee blue-green), yellow, orange, and 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 (a), left to right, maps onto those from the phylogeny (b), top to bottom; hence, the leftmost column is *Bombus diversus*. (Data from Chittka et al. 2001, 2004, and Chittka and Wells 2004. Figure revised from Raine et al. 2006a. Copyright © 2006 Elsevier. Reproduced with permission.)

but there is no reason to expect the importance of such flowers species is higher in Sardinia than elsewhere. Several orange-red flower species are found on the Canary Islands (Vogel et al. 1984), which seem strongly adapted to bird pollination (Olesen 1985). Although birds visit several of these species (Valido et al. 2002), *B. t. canariensis* has not been observed to do so in the wild (Stelzer et al. 2007; Ollerton et al. 2009).

Thus, we are left with an interesting observation: flower color preferences are clearly variable among *B. terrestris* populations, and these differences are heritable (Chittka and Wells 2004).
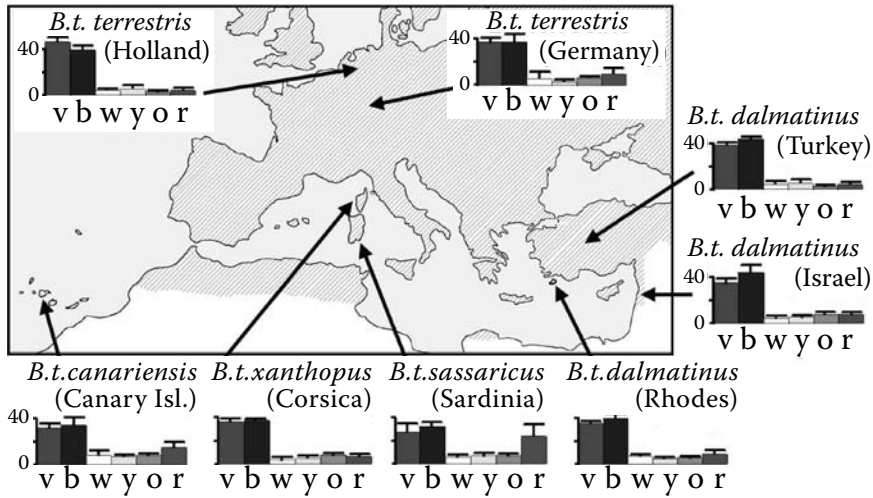
FIGURE 1.2 Biogeography of floral color preference in *Bombus terrestris* populations. Bees were individually offered the following colors: v, violet (bee UV-blue); b, blue (bee blue); w, white (bee blue-green); y, yellow; o, orange; and r, red (the latter three are bee green). Column height denotes the mean percentage (+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 the kind permission of Pierre Rasmont). (Data from Chittka et al. 2001, 2004. Figure after Raine et al. 2006a. Copyright © 2006 Elsevier. Reproduced with permission.)

However, 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—especially since a secondary preference for red flowers does not appear to be selected against. However, it is also possible that the red preference of these bumble bee populations is a "behavioral fossil" that dates back to an age when red, bird-pollinated flowers were common in Europe (Raine et al. 2006a). If this is true, and if bumble bees exploited some of these flowers (as some species do in North America; Chittka and Waser 1997), then the red preference of some *B. terrestris* populations might be a result of historical adaptation rather than either recent adaptation or chance. Physiological data also suggest that Sardinian bees might be more sensitive to detecting red flowers than mainland conspecifics (Skorupski et al. 2007). However, differences between Sardinian and mainland populations in the peak wavelength sensitivity of their green photoreceptors (λ_{max}: *B. t. sassaricus* = 538 nm, *B. t. dalmatinus* = 533 nm) are insufficient in themselves to significantly improve wavelength discrimination in the red region of the spectrum. The clear behavioral differences between *Bombus terrestris* populations in color preference are probably not explained by any simple change at the photoreceptor level, but must instead be based on differences in postreceptor neuronal wiring.

SENSORY BIAS AND FORAGING PERFORMANCE

Innate preferences for violet and blue flowers appear to represent a useful sensory bias at the species and population level, but what about variation in sensory bias among colonies within a population? Can floral traits drive selection for local adaptation in bumble bee color preferences? In the flora near Würzburg, Germany, the average violet flower provides more than twice as much sugar reward as each blue flower (Raine and Chittka 2007a, 2007c), the next most productive flower color. If local floral traits do drive selection for local color biases, bees with a stronger sensory bias for violet (over blue) flowers should forage more effectively in this environment. As social insects, bumble bee reproduction is restricted to a subset of individuals within each colony. Hence, for bumble bees,

intercolony (rather than interindividual) trait variation allows us to test the adaptive benefits of sensory bias variation when foraging in the local environment. Since bumble bee colonies produce males and new queens in proportion to the amount of food available to them (Schmid-Hempel and Schmid-Hempel 1998; Pelletier and McNeil 2003; Ings et al. 2006), we can use colony foraging performance as a robust measure of colony fitness. This approach explores intercolony variation of floral color bias within a natural population to measure the extent to which such sensory biases can be regarded as adaptive, i.e., improving colony foraging performance in their natural environment. This was achieved by comparing the performance of nine bumble bee (*B. t. terrestris*) colonies in color bias tests under laboratory conditions with the foraging performance of the same colonies under natural conditions. Using this approach allowed us to directly correlate trait variation in sensory bias with a proxy measure of colony fitness (foraging performance).

Colonies were raised in the laboratory from nest searching queens caught around Würzburg. Color preferences of color naïve workers (10–15 bees per colony, 101 in total) were tested in laboratory flight arenas using methods similar to those used in comparisons among species and populations—see above (Chittka et al. 2001; Raine et al. 2006a). The preference of each individual forager for violet (bee UV-blue) over blue (bee blue) was assessed in an arena containing sixteen unrewarded artificial flowers (eight of each color). After completion of laboratory tests, the nectar collection rate (mass of nectar collected per unit foraging time) of the same nine colonies was measured in the field (near Würzburg) in June–July 2002. The area is typical central European bumble bee habitat, giving colonies access to multiple flower species in bloom in dry grassland, deciduous forest, and farmland (Raine and Chittka 2007a).

Colonies with a stronger innate preference for violet (over blue) in the laboratory also harvested more nectar per unit time under natural conditions (Figure 1.3). Colonies with the strongest violet preference brought in almost 41% more nectar than the colony with the least strong bias when foraging from real flowers in the field. As violet flowers were on average twice as rewarding as blue flowers (the next most rewarding flower color) in the local area (Raine and Chittka 2007a, 2007c), these results support our hypothesis that colonies biased toward the more highly rewarding violet flowers collect more nectar per unit time. Comparing these findings with results from an earlier study (Raine and Chittka 2005) confirms that the pattern was very similar for consecutive years at the same location.
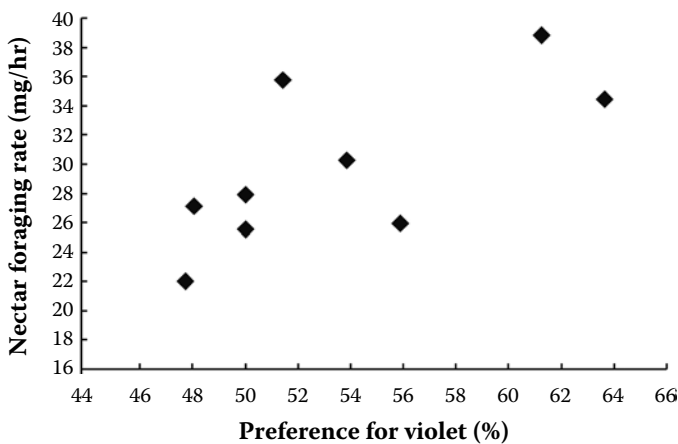
FIGURE 1.3 Correlation between strength of innate floral color preference for violet (over blue) in the laboratory and nectar foraging performance in the wild, measured for nine bumble bee colonies (*Bombus terrestris*) near Würzburg ($r_s = 0.678$, $n = 9$, $p = 0.045$). Each data point represents the colony median value for each of these traits. (After Raine and Chittka 2007a. With permission.)

It is easy to imagine how these innate color preferences help naïve bees to find flowers on their first foraging trip, as very few objects in natural landscapes are blue or violet except flowers. Presumably, color preferences lead bees to investigate violet or blue objects (flowers) in preference to leaves, rocks, etc. Following the same logic, if violet flowers are consistently more rewarding, it would make adaptive sense to prefer them (over blue). As bees gain foraging experience, by visiting hundreds or thousands of flowers each day (Heinrich 1979; Raine and Chittka 2007b), they establish an increasingly detailed picture of which flower species (or colors) are most profitable and when. Bees are easily able to learn to associate multiple floral traits, including color (Giurfa et al. 1995; Gumbert 2000), morphology (Laverty 1994; Raine and Chittka 2007d), and scent (Menzel 1985), with reward levels, and such learned associations allow individual foragers to modify, or even overwrite, their inbuilt sensory biases within a short time (Menzel 1985; Gegear and Laverty 2004; Raine et al. 2006b; Raine and Chittka 2008). Since overall flower visitation rates are largely dominated by the informed choices of experienced bees, rather than the result of the sensory biases of naïve foragers, this presumably prevents selection for flowers to exploit innate color preferences by reducing the amount of reward they provide while still maintaining similar pollination success (Raine and Chittka 2007a).

Earlier studies correlating color bias variation among bumble bee species (Chittka and Wells 2004; Raine et al. 2006a), or among populations within a single bumble bee species (Briscoe and Chittka 2001; Chittka et al. 2004), with differences in their respective foraging environments have provided valuable insights into patterns of bee color bias evolution within a phylogenetic framework. Changing the emphasis and focusing on the potential adaptive significance of color preference at the colony level adds the missing link, i.e., how variation in color biases actually affects foraging performance. Quantifying the level of local intercolony variation in a foraging-related trait (violet-blue bias) and assessing its potential effect on foraging performance (a robust proxy measure of reproductive success) using the same set of colonies provides a more direct test of the potential adaptive value of this sensory bias. This approach, linking demonstrations of trait variation in the laboratory with its effect on animals operating in their natural environment, represents a valuable tool that has the potential to be usefully applied to studying the adaptive value of many other foraging-related traits.

LEARNING AND FORAGING PERFORMANCE: BUMBLE BEES GAIN FITNESS THROUGH LEARNING

Learning, or the adaptive modification of behavior based on experience, affects virtually every aspect of animal behavior. However, despite the abundance of research on the mechanisms of learning in a wide variety of animal taxa, we still know very little about how learning performance is actually adapted to real ecological conditions (Shettleworth 1998; Dukas 2004). As different individuals or species vary widely in their learning capacities, it is commonly assumed that these differences reflect adaptations to the natural conditions under which such animals operate (Gallistel 1990; Dukas 1998; Shettleworth 1998). While it is intuitively appealing to assume that such variation in learning performance is adaptive (Johnston 1982; Dukas 1998), few studies have yet been conducted to specifically examine this link under natural conditions.

Laboratory studies, using grasshoppers (Dukas and Bernays 2000) and parasitoid wasps (Dukas and Duan 2000), suggest that animals able to form associations between cues (such as color, odor, or location) and rewards perform better than animals prevented from learning. Other laboratory studies, applying artificial selection to the learning ability of fruit flies, provide evidence for potential fitness costs associated with enhanced performance in associative learning (Mery and Kawecki 2003, 2004) or long-term memory (Mery and Kawecki 2005) tasks. While these results suggest that the ability to learn is useful (compared to being unable to learn) in highly controlled laboratory situations, and that enhanced learning appears to incur higher costs, they do not yet inform us directly about the potential fitness payoffs for animals with different learning abilities under natural conditions. Circumstantial evidence for the adaptive value of learning comes from comparisons between

species (Dukas and Real 1991; Sherry and Healy 1998; Healy et al. 2005); for example, vole species with larger home ranges typically have better spatial memory, and their hippocampi (brain areas that store spatial memories) are typically larger (Sherry and Healy 1998). While such studies suggest that learning performance and ecologically important measures (such as home range size) are correlated, the species compared also vary in numerous other ecological requirements. Therefore, to make further progress in understanding the evolutionary and ecological relevance of learning abilities, the next step is to quantify how and to what extent learning differences within species affect animal fitness in nature (Papaj and Prokopy 1989; Dukas and Duan 2000).

We set out to address this question using the same successful approach applied to investigate the adaptive value of local color preferences (see "Sensory Bias and Foraging Performance" section): we directly correlated variation in learning performance with field foraging performance (a robust measure of fitness) for twelve bumble bee (*B. terrestris dalmatinus*) colonies (Raine and Chittka 2008). In laboratory learning trials, the bees' task was to overcome their innate preference for blue (Lunau et al. 1996; Chittka et al. 2004; Raine et al. 2006a) and learn to associate yellow as a predictor of floral reward. This is a simple associative task that bumble bees are able to learn, but individuals and colonies vary in their speed and accuracy (Chittka et al. 2004; Raine et al. 2006b). The task is ecologically relevant because foraging bees use a variety of cues, including floral color, pattern, and scent, to recognize, discriminate, and learn the flowers from which they collect nectar and pollen (Menzel 1985; Chittka and Raine 2006). We measured the nectar collection rate of the same twelve colonies in the field (Queen Mary College, London) in July–August 2005. Once outside the nest, bees could forage freely in an area containing abundant floral resources growing in numerous private gardens, several large parks, and other areas of open land (e.g., canal or railway embankments).

We found that colonies with higher learning speeds (in the laboratory tests) also harvested more nectar per unit time under field conditions (Figure 1.4). This positive correlation between learning and foraging performance indicates the slowest-learning colonies brought in 40% less nectar than the fastest-learning colonies. As foraging performance represents a robust proxy measure of fitness, these results indicate higher learning speed is closely associated with increased bumble bee colony fitness under natural conditions (Raine and Chittka 2008).

As bees forage in a complex and dynamic flower market in which rewards differ strongly among plant species and vary over time (Heinrich 1979; Willmer and Stone 2004), individual foragers must assess such differences and respond accordingly (Chittka 1998; Menzel 2001; Raine and Chittka 2007d, 2008). Rapid learning of salient floral cues, such as color, presumably assists bees to track
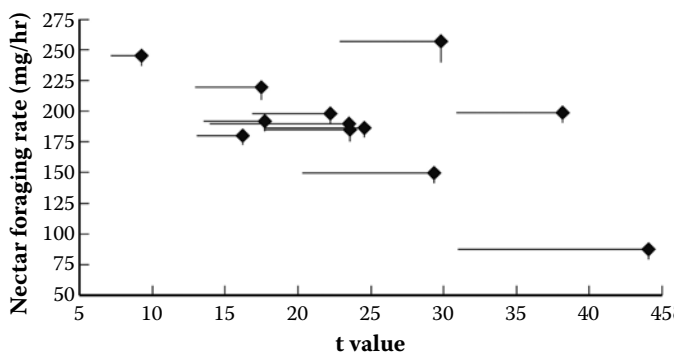
FIGURE 1.4 Correlation between learning speed and nectar foraging performance for twelve bumble bee (*Bombus terrestris dalmatinus*) colonies. High *t* values correspond to slow learning, while low values are generated by fast learners. Data presented are colony mean values (–1 SE) for both *t* value and foraging performance. On average, colonies with higher learning speeds (lower *t* values) brought in more nectar per unit time (Pearson's correlation: $r = -0.588$, $n = 12$, $p = 0.044$). (After Raine and Chittka 2008. With permission.)

changes in the floral rewards on offer, thereby improving bee foraging efficiency by allowing them to preferentially visit the current most profitable flower type (Raine et al. 2006a, 2006b). It would be interesting to examine whether colonies that learn more quickly in visual tasks (e.g., learning color associations) also show better learning performance in other modalities (e.g., odor or tactile cue learning). Laboratory studies (using the proboscis extension response paradigm) suggest that individual honey bees that are more sensitive to sucrose stimuli show improved learning in both odor and tactile conditioning experiments (Scheiner et al. 2001a, 2001b). These results suggest that performance levels in an associative learning task using one modality might indicate the relative performance for other modalities.

To date, discussion of the potential adaptive value of learning has concentrated on the environmental conditions under which learning is favored. Learning is predicted to be favored in most environments, except those that are either so changeable that prior experience has no predictive value, or so consistent (across generations) that genetically preprogrammed innate behaviors alone are sufficient (Johnston 1982; Shettleworth 1998; Dukas 2004). However, these studies do not allow assessment of how the subtle variation that exists between individuals in natural populations translates into fitness benefits. The correlative approach used here represents a first step toward examining potential fitness effects attributable to variation in learning performance under the real conditions to which animals are adapted (Raine and Chittka 2008). However, although variation in learning performance among bumble bee colonies appears the most likely explanation for observed differences in their foraging performance, further evidence is needed to establish a causal link. Ultimately, developing a more general understanding of the adaptive value of learning would require a direct examination of the fitness effects of variation in learning performance across a range of animal species and the environments to which they and their cognitive abilities are adapted.

MANIPULATION OF FORAGING PHENOTYPE: THE HONEY BEE DANCE

The honey bee dance language is regarded by many as one of the most intriguing communication systems in nonhuman animals (von Frisch 1955, 1967; Chittka 2004). A successful scout bee returns and advertises the location of a newly discovered food source to nestmates using a repetitive figure-eight-shaped sequence of movements. Shortly after these "waggle dances" commence, scores of newly recruited foragers will arrive at the food source being advertised (von Frisch 1955, 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?

Dornhaus and Chittka (2004b) investigated the potential adaptive significance of the dance language by measuring the foraging performance of honey bee (*A. mellifera*) colonies under natural conditions and comparing this to conditions under which the information flow between dancers and recruits was disrupted. Information transfer from dancer to recruit is disrupted with a simple trick. Under normal conditions in the darkness of the hive, 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 (von Frisch 1955, 1967). However, rotating the combs into a horizontal position eliminates the bees' ability to use gravity as a reference. Therefore, bees perform dances in random directions, effectively removing the directional information component. Having "interpreted" these nondirectional dances, recruits leave the hive in random directions (von Frisch 1967; Dornhaus and Chittka 2004a, 2004b). However, if bees can see the sun (or polarized light), then returning foragers can perform correctly oriented waggle dances on a horizontal surface using the sun rather than gravity for reference (von Frisch 1955, 1967). Using hives with horizontally arranged combs, Dornhaus and Chittka (2004b) controlled the ability of returning foragers to perform oriented dances by either covering or uncovering a window on the top of the hive (see Figure 7.1, p. 137).

Initially, the foraging success of colonies that were able, or unable, to communicate the direction of profitable food sources was compared in two temperate habitats: a typical Mediterranean habitat in the Sierra Espadán Nature Reserve, Spain, and a site near Würzburg, where agricultural land is

mixed with natural meadows. A pair of hives, each containing about five thousand workers, was placed at each site. Each colony was switched from oriented to disoriented dancing every 2 days, by uncovering or covering the window on top of the hive. Foraging success was assessed using the daily weight gain of hives, which predominantly reflects nectar intake (Seeley 1995). Surprisingly, no differences in weight gain were recorded between days in which colonies could follow oriented or disoriented waggle dances from returning foragers at either site (Dornhaus and Chittka 2004b). These findings were confirmed by repeating the same experiment with two additional hives monitored in Würzburg from May to September (Dornhaus and Chittka 2004b).

Why do honey bees bother communicating the direction of profitable food sources if it makes no difference to foraging efficiency? It seems highly counterintuitive, especially when considering the enormous efficiency of the dance language to recruit bees to single points in space (Gould 1975; Towne and Gould 1988; Dyer 2002). Perhaps honey bee ecological history could help us understand their current behavioral patterns? It seems most likely that the evolutionary origins of the dance occurred in an open-nesting tropical ancestor of extant honey bees (Dyer and Seeley 1989), which foraged under conditions wholly different from those in which modern *A. mellifera* colonies operate. In tropical forests, an individual tree, or a local aggregation of trees, frequently offers many thousands of flowers at a very precise spatial location (Roubik 1992; Condit et al. 2000; Pitman et al. 2001), which might only persist or provide rewards for a short period of time (Stone et al. 1998, 2003; Raine et al. 2007). Under such conditions, it seems likely that an ability to accurately communicate the distance and direction of such foraging bonanzas to other foragers in the hive would be highly advantageous. 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; Seeley 1995) and are easily located by individual foragers.

To test if the dance language is more important to efficient foraging in tropical than in temperate habitats, Dornhaus and Chittka repeated their experiment in an Indian tropical dry deciduous forest (Bandipur Biosphere Reserve). In this environment removing the direction component of the honey bee dance information reduced the number of successful foraging days by 85% (Figure 1.5).
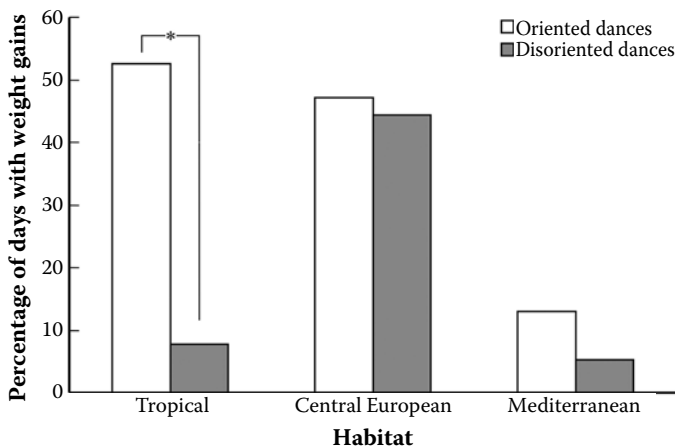
FIGURE 1.5 Foraging performance of honey bee *(Apis mellifera)* colonies with (oriented dances) and without (disoriented dances) the ability to communicate directional information about the location of food sources to nestmates through their dance language. Columns indicate the percentage of days on 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. (Reprinted from Dornhaus and Chittka 2004a. Copyright © 2004 EDP Science. With permission.)

The median hive weight gain on days with oriented dances was 5 g, compared with a loss of 65 g on days when direction information was disrupted (Dornhaus and Chittka 2004b).

Maps of the flower patches visited by a hive can be made by decoding the dances of returning foragers (Visscher and Seeley 1982). Using this technique confirmed foraging sites were very patchily distributed within the Indian tropical forest (Dornhaus and Chittka 2004b), compared to temperate habitats for which comparable forage maps are available: temperate forest (Visscher and Seeley 1982), disturbed suburban habitat (Waddington et al. 1994), and disturbed habitat mixed with more natural open moors (Beekman and Ratnieks 2000).

These findings suggest that the honey bee 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 temperate habitats. Here, it might be 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) showed the precision of direction communication is higher in tropical than in temperate species. When food is less patchily distributed than in tropical forest, foraging by individual initiative, or communication through floral scent, may be as efficient as dance communication (Chittka 2004). Alternatively, stabilizing selection might have occurred through nonforaging dance applications, such as indicating the location of nesting sites (Weidenmüller and Seeley 1999; Beekman et al. 2008).

GENETIC BASIS OF FORAGING BEHAVIOR

Current questions being addressed in behavioral ecology require increasingly detailed understanding of the genetic and physiological mechanisms that underlie behavioral traits (Owens 2006). If we uncovered the genetic basis of foraging behavior it would clearly improve our 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). Honey bee foraging is one of the best-understood behaviors at the genetic level (Fitzpatrick et al. 2005; Hunt et al. 2007; Oldroyd and Thompson 2007).

Although in some instances a single candidate gene can have profound behavioral effects—for example, a single genetic element (Gp-9) is responsible for determining variation in fire ant colony social organization (Ross and Keller 1998)—it seems likely that most behavioral traits are polygenic and linked through pleiotropies, i.e., correlated characters (Amdam et al. 2004; Owens 2006), which suggests that selection on any individual gene might have complex effects (Rueppell et al. 2004a, 2004b; Hunt et al. 2007). Studies investigating the genetic architecture and the physiological and molecular basis of a variety of foraging-related traits in honey bee behavior appear to confirm this idea (Robinson et al. 1989; Page and Robinson 1991; Page and Fondrk 1995; Pankiw et al. 2002; Rueppell et al. 2004a; Hunt et al. 2007). Page and colleagues started by selecting two strains of honey bee 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 that differed strongly in the relative effort they devoted to nectar and pollen foraging. The resulting bee strains differed in multiple aspects of foraging behavior that could be linked, either directly or indirectly (via pleiotropic effects), to pollen foraging. The "high strain" colonies (those that hoarded more pollen) not only had more pollen foragers, and collected larger pollen loads, but 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 sucrose concentrations (Page et al. 1998), perhaps explaining their higher relative acceptance level for poor-quality nectar (Pankiw and Page 2000). Indeed, high-strain bees have higher sensitivity to other chemosensory stimuli, e.g., brood pheromones (Pankiw and Page 2001). This suggests a potential for overall improvement of sensory function in these bees, which could

explain their superior performance in both olfactory and tactile learning paradigms (Scheiner et al. 2001b). 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 high-strain bee brains. Both enzymes play a role in memory consolidation and avoidance conditioning (Shobe 2002). It has also been proposed that these differences are pleiotropically linked to reproductive behavior (Amdam et al. 2004, 2006a), perhaps suggesting that division of labor in honey bee foraging evolved from an ancestral reproductive regulatory network (Hunt et al. 2007).

What are the implications of these findings for future studies 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 therefore that the raw material for selection exists (under both natural and experimental conditions). How quickly the genetic basis of behavioral trait variation will be uncovered will depend on the number of genetic elements involved and the strength of potential pleiotropic effects in each case (Oldroyd and Thompson 2007). Once we have this quantitative genetic information, it opens up the possibility of studying the adaptive benefits of these traits in the wild. However, the interpretation of the potential differences in fitness will be difficult 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.

CONCLUDING REMARKS

In this review, we have illustrated the value of several empirical approaches to study the adaptive nature of foraging behavior under natural conditions. Comparing variation in a foraging trait among species, or geographically isolated subspecies, with a known phylogeny can allow us to distinguish adaptation from the effects of chance and history on the behavior in question (Clutton-Brock and Harvey 1977). Despite the potential power of the phylogenetic method, studies on the innate color preferences of bumble bees presented here (Chittka et al. 2001; Chittka and Wells 2004; Raine et al. 2006a) are among the few that use this approach to study behavioral traits related to foraging (e.g., Betz 1998). This could be because the method relies on well-supported phylogenies, which are not universally available, or that levels of trait variation among species are unpredictable. If traits are conserved across all species tested, for example, a strong preference for blue and violet flowers across all bumble bee species tested, this does not inform us about the adaptive value of this trait without testing additional outgroups with different ecological requirements. However, where trait variation exists among tested species, and can be linked to strong differences in ecology, this approach provides relatively strong, indirect evidence for trait adaptation, for example, the secondary preference for red in *Bombus occidentalis*, which robs nectar from bird-pollinated flower species.

Using a correlative approach, combining laboratory and field studies on the same animals (or colonies) represents a novel approach to studying whether variation in foraging-related traits actually translates into real differences in fitness. Positive correlations between two foraging-related traits in the laboratory and field foraging performance suggest the potential for strong directional selection for both a more extreme sensory bias for violet (over blue; Raine and Chittka 2007a) and higher learning speed (Raine and Chittka 2008) in bumble bees. This approach is well suited to studies of social insects, as they are central place foragers, and a discrete subset of workers from the same colony can be used for laboratory and field experiments. Furthermore, the foraging behavior of social insects (particularly bees and ants) is comparatively well studied, and numerous proxy measures or correlates of colony fitness are known. Although bumble bee foraging performance is strongly correlated with colony fitness (Schmid-Hempel and Schmid-Hempel 1998; Pelletier and McNeil 2003; Ings et al. 2006), it would be even better to determine a more direct measure of fitness, such as the number or biomass of sexual offspring (males and queens) produced. While this has been done in some field studies of parasitism in bumble bees (Müller and Schmid-Hempel 1992; Baer and Schmid-Hempel 1999), colony manipulations in these studies were minimal and could be

conducted at (or before) the earliest stages of colony development, allowing colonies to grow and mature under field conditions. In contrast, the length of time needed to accurately quantify behavioral trait variation in the laboratory necessarily restricts the period of time during which colonies can develop in the natural environment. Under such conditions, it would be impossible to attribute any differences in colony reproductive output solely to differences in field foraging performance. While it is becoming potentially easier to monitor the foraging activity of social insect colonies, using radio frequency identification (RFID) technology to automatically monitor when workers enter and leave the nest (Streit et al. 2003; Sumner et al. 2007; Molet et al. 2008), there is no obvious solution to reducing the time required to quantify variation in foraging-related traits in the laboratory. Hence, given these constraints, foraging performance appears to be the best measure of colony fitness that can be achieved using this approach.

Manipulating the behavioral phenotype can allow a direct test of the potential adaptive value of a trait, particularly when the manipulation is completely reversible, allowing the opportunity to compare the manipulated and unmanipulated phenotype of the same individual (or colony). With their manipulation of the honey bee dance language, Dornhaus and Chittka (2004b) were able to elucidate that the dance language is highly advantageous when floral resources are highly clustered in time and space. The drawback of this approach is that there are very few, if any, other behavioral traits that would be amenable to such simple but effective, reversible manipulation. While this does not reduce the potential power of this approach, it means it is unlikely to be generally applicable.

Perhaps a more promising approach for future research would be manipulation of the foraging phenotype via the insight gained from studies of variation in behavioral traits at the genetic level. Researchers are closing in on isolating the genes that encode particular behavioral traits (Fitzpatrick et al. 2005; Hunt et al. 2007; Oldroyd and Thompson 2007), so it might soon be possible to selectively modify behavioral phenotypes by knocking out their expression using double-stranded RNA interference (dsRNAi; Fire et al. 1998), or perhaps by creating more traditional knockout mutants (Wolfer and Lipp 2000; Lipp 2002). While it is occasionally possible to create behavioral phenotypes for traits without genetic techniques, such as removing the ability to encode directional information in the honey bee waggle dance (see "Manipulation of Foraging Phenotype: The Honey Bee Dance" section), 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. This dsRNAi approach is already being used to study functional mechanisms by knocking out gene function. Blocking the octopaminergic pathway renders honey bees unable to learn an odor paired with sucrose reward, as octopamine mediates the unconditioned stimulus (the reward) in this associative learning task (Farooqui et al. 2003, 2004). Downregulation of vitellogenin activity using dsRNAi increases the gustatory responsiveness of workers, suggesting that vitellogenin is an important regulator of long-term changes in honey bee behavior (Amdam et al. 2006b). Continued advances in the search for other behaviorally important genes and refinements in dsRNAi techniques could herald the beginning of a very powerful future tool for the study of adaptation in behavioral ecology. The choice of study organism for such an approach is a trade-off between availability of techniques and its tractability for fitness studies under natural conditions. Social bees have long been a model system in the study of behavior. Now with recent advances in understanding social bee genetics, particularly since sequencing the honey bee genome (Honey Bee Genome Sequencing Consortium 2006), the combination of availability of techniques like dsRNAi and their tractability for fitness studies suggests social bees have a bright future for tests of the adaptiveness of foraging behavior under natural conditions.

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