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Pollinator individuality: when does it matter?

I have always regretted that I did not mark the bees by attaching bits of cotton wool or eiderdown to them with rubber, because this would have made it much easier to follow their paths.

Charles Darwin, cited by Freeman (1968)

The symposium that stimulated this book arose from the editors' conviction that botanists interested in biotic pollination would benefit from a consideration of recent research on the behavior and the sensory capabilities of flower-visiting animals. We hoped to offer perspectives that would correct misapprehensions, enrich future work, and open new questions. In this chapter, we continue in this evangelistic vein by indulging in long-standing personal interests in the individuality of pollinating animals. Ignoring the uniqueness of individuals will invite regrets like those expressed by Darwin in reviewing his work on the flight patterns of male bumble bees. Although he investigated this question for several years, Darwin never published his observations. Might he have considered his failure to mark the bees a fatal flaw?

Our goals are to outline some of the insights that are made possible by treating pollinators as individuals, and to show possible pitfalls of *not* doing so. Some well-known conclusions regarding pollinator physiology and behavior can be given alternative interpretations by invoking individuality. We hope that this chapter will stimulate more systematic approaches to pollinator individuality.

There are many relevant axes along which individual pollinators may vary, including gross behavioral aspects such as foraging-site preferences, food-plant preferences, and numerous aspects of foraging style (including sampling effort, level of flower constancy, giving-up thresholds, etc.).

These in turn may be underlain by variation in basic neurophysiological processes such as learning ability (speed, capacity, and duration), sensitivity to interference, efficiency at detecting flowers, etc. There are also multiple causes for observed variations in foraging behavior. These can be genetic, learning-related, age-dependent, or induced by parasites. In what follows, we are mostly concerned with cases where neglecting pollinator individuality may lead to erroneous conclusions.

Basic observations

Small foraging areas

Several studies showing that social insects use spatial memory in foraging date back to the penultimate century (e.g. Fabre 1879; Müller 1882). After many decades of detailed research on spatial memory of bees (e.g. Chittka *et al.* 1995; Menzel, this volume), most pollination biologists accept that such memory exists, but most associate it with finding the nest rather than finding food sources. Optimal foraging theory is partially responsible for this (Healy & Hurlly, this volume): some adherents of this theory proposed that pollinators forage using essentially the same rules as protozoans. The numbers of places visited during a foraging bout seemed to many biologists too high (often, several thousand flowers must be visited to fill the stomach of a bee) for bees to memorize much detail of the complex flight path.

Yet, if one catches bee workers at a patch of flowers, marks them, and releases them, one will frequently see some of them return to the site (Ribbands 1949; Heinrich 1976; Free 1993). This indicates that at least some individuals have established small foraging areas to which they return for all or most of their feeding. In one study, 37 plants of *Penstemon strictus* were planted in a meadow in a hexagonal pattern with 1.5 m between plants (Thomson *et al.* 1997). We marked bees and followed some of them intensively from 23–28 July 1990. Several bees did all of their foraging in this area; one worker in particular, *Bombus flavifrons* "Blue," worked the array for our entire period of close observations (23 July through 5 August 1990). She would visit the 37 plants (and some of other meadow species that grew interspersed with the *Penstemon*) essentially all day, disappearing for only a few minutes at *c.* half-hour intervals to drop off collected rewards at the nest. Bumble bees of other species have performed comparably on other plants (Thomson *et al.* 1987), but we do not know whether this site fidelity is typical.

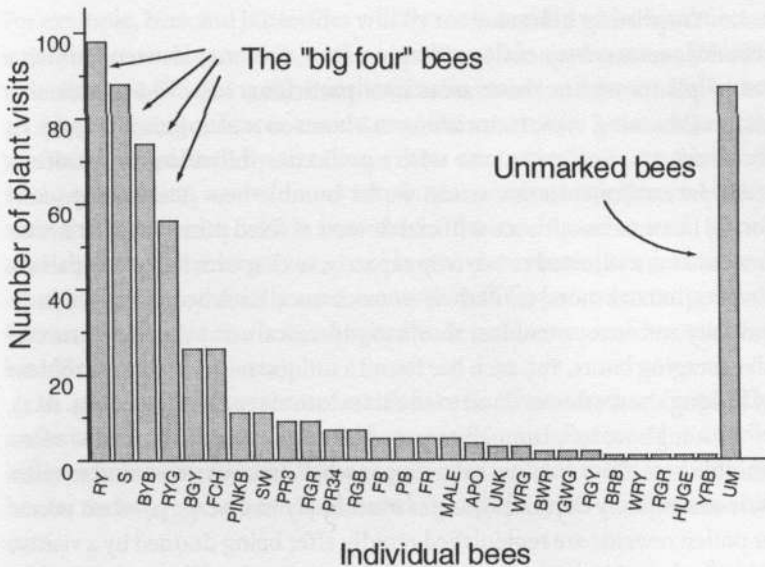


Fig. 10.1. Frequencies of visits in one day to a focal plant of *Penstemon strictus* by a number of marked bumble bees (Williams & Thomson 1998). Bee names mostly indicate painted color marks (e.g., RY = red-yellow), although a few distinctive bees were identified by natural attributes (e.g., HUGE).

In another study of *Penstemon strictus*, Williams & Thomson (1998) videotaped all visits to a single potted plant in a circular array of 27 plants. We had marked visitors on previous days. Four individuals made over half of the plant visits (Fig. 10.1); these bees returned to the focal plant at statistically regular intervals, with mean interarrival times of 5.36, 5.90, 7.07, and 7.91 min. Unmarked bees might have been vagabonds with no site fidelity, site-faithful bees that evaded marking, or site-faithful bees that were new arrivals.

Individual bumble bees may maintain more than one foraging area. Brian (1952) noted that *Bombus agrorum* (now *pascuorum*) workers tended to leave the nest in characteristic compass direction, but that some individuals had more than one departing direction. These bees also came back with different pollens when they left in different directions. Karen Goodell (personal communication) found that certain workers of *B. ephippiatus* collected one of two different sets of several pollen species on different trips in a montane Neotropical habitat. The most likely explanation for the covariation of several species is that the bees were going to two different localities, then foraging inconstantly in each place.

Traplining behavior

If bees do return frequently to foraging areas, they may also tend to visit a set of plants within those areas in a particular, somewhat repeatable circuit (Manning 1956; Heinrich 1976; Thomson *et al.* 1982, 1987, 1997). In fact, such traplining is a case where pollinator individuality manifests itself *par excellence*. In one study, we let bumble bees (*Bombus impatiens*) forage in an arena with six artificial flowers at fixed positions. The nectar rewards were adjusted to bee crop capacity, so that bees had to visit all six flowers (but not more) to fill their stomach once. Each bee was tested individually and encountered an absolutely identical array during 40 successive foraging bouts. Yet, each bee found a unique solution to the problem of linking the six flowers, and used this solution repeatedly (see Fig. 10.2).

Although we lack comparative studies that would indicate how often bumble bees show trapline behavior, or what circumstances tend to elicit it, it seems likely that traplining is most likely to emerge (1) when nectar or pollen rewards are replenished rapidly after being drained by a visitor, and (2) when there are spaces between plants, with sufficient landmarks to allow bees to orient. Bumble bees, especially *Bombus ternarius*, showed clear traplining behavior on scattered plants of *Aralia hispida* in central New Brunswick (Thomson *et al.* 1982); in dense stands of *Solidago* spp. (goldenrods) nearby, however, bees of the same species showed no discernable tendency to repeat their flight paths, although they were using small foraging areas (J.D. Thomson & W. Maddison, unpublished data).

Two aspects of bumble bee traplining are most relevant to this paper. First, although traplines are quite flexible – bees do not slavishly follow a fixed route, but rather add new plants and drop old ones as conditions change – there is a conservative tendency for bees to keep using accustomed flight paths (Thomson 1996) and to keep returning to plants that have been particularly rewarding in the past (Thomson 1988). For example, Manning (1956) described how bees that had been trained to visit potted plants still returned to those locations after the pots had been completely removed. Second, bees return to plants on their traplines at surprisingly brief intervals, *c.* 10 min in both *Penstemon strictus* and *Aralia hispida*.

Variation in working speed

When following marked pollinators, one is frequently struck by variations in the speed of individuals. Some of this variation is caused by differences in the nectar offerings of plants on which these individuals forage.

For example, bees and butterflies will fly more rapidly when more nectar is available, an observation with several possible explanations (Núñez 1970; Kunze & Chittka 1996). But there is also variation between individuals who are using the same resources at the same time. Some such variation can be explained by size: larger bees are faster fliers (Spaethe *et al.* 2000). In addition, some sensory attributes correlate with size and influence the speed with which bees detect flowers. Spaethe *et al.* (2000) recently found that larger bees have better visuo-spatial resolution, and are therefore substantially more accurate and faster at detecting small flowers. Furthermore, foraging speed is dependent on colony needs in bumble bees (Cartar 1992a).

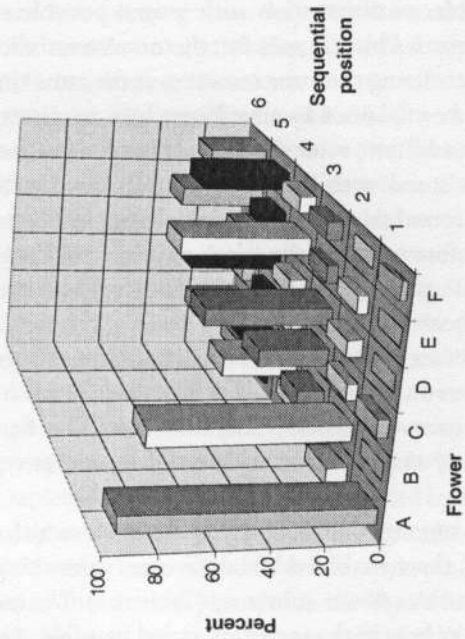
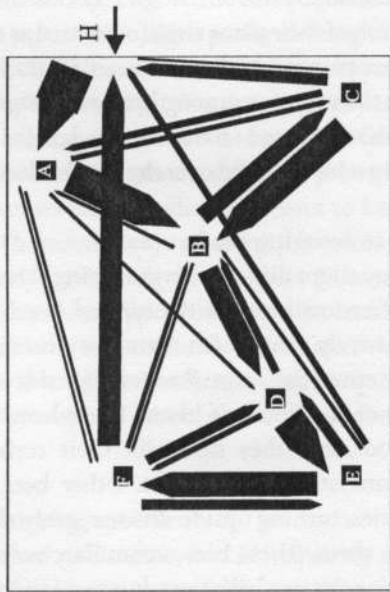
In studies with numerous marked bees, Thomson has frequently encountered a few individuals that seem to fly much faster and to handle inflorescences very quickly. Because such bees are hard to observe for long bouts, they may be underrepresented in certain types of observational data.

Even among the more stolid bees for which data are available, however, there are individual differences in working speed and in other aspects such as flower constancy (Table 10.1). The mean flower-handling times of 17 bees in the 1994 data varied two-fold. Recall that all of these data come from the same plant on a single day. Bees also varied about two-fold in the duration of their plant visits (measured as the mean number of flowers visited per plant visit), but plant-visit durations varied so much within bees that the variation among bees was insignificant. In addition to showing variation among individuals, the data for "Blue" suggest that this bee's foraging tempo slowed over the two weeks she was observed.

Variation in foraging mode

Different bees may adopt different ways of using flowers. One of the more conspicuous differences involves the type of floral reward – pollen or nectar – being actively sought. On *Penstemon strictus*, for example, most *Bombus* workers enter the large flowers rightside-up and tongue the paired nectaries at the filament bases. These bees usually accumulate small pollen loads, but they never fill their corbiculae, presumably because their honeystomachs fill first. Other bees, mostly *B. bifarius*, ignore the nectaries, turning upside-down to grasp the anthers and sonicate pollen from them. These bees accumulate very large pollen loads. Some bees combine the two behaviors, but most individuals tend to stick with one type of behavior over at least a few days. Still, changes occur; bees

Bee 1



Bee 2

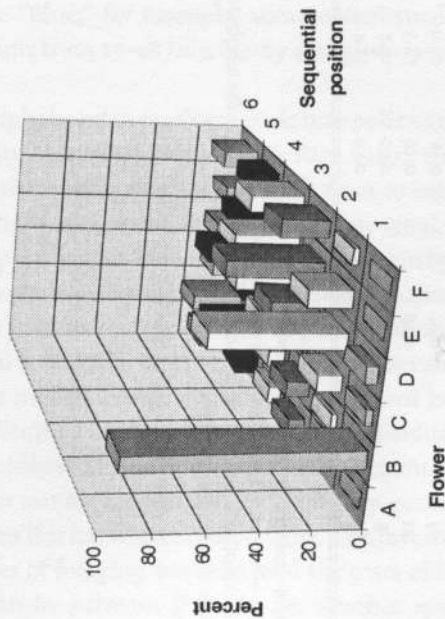
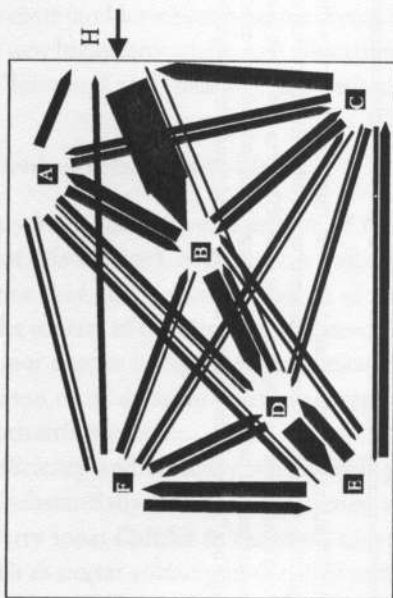


Fig. 10.2. Trapping of two bumble bees in a flight arena (105 cm \times 75 cm) with six artificial flowers. The left panels show the arrangement of flowers (black squares), and the frequency of flight paths within it. The arrow on the right marks the location of the nest entrance to the arena. The width of the arrows corresponds to the frequency each trajectory was taken. For example, in the upper left panel, the arrow from the hive to the closest flower corresponds to 38 of a total of 40 foraging bouts. The right panels show how often each flower occupied a given sequential position within a foraging bout. Note that the right panels contain only the first six visits of each foraging bout, whereas the left panels contain the information from all flights. Because bees often revisited flowers they had already emptied, a foraging bout can have more than six visits.

Table 10.1. Summary of movement patterns of three individual bees foraging in a hexagonal grid of *Penstemon strictus* plants set in a meadow with other plants

Bee	Moves to neighbors ^a				Constancy ^b				Summaries ^c		
	1 st	2 nd	3 rd	Far	P to P	P to Other	Other to P	Other to Other	Bateman's Index	Other/P	Mean bout
"Blue" early ^d	741	56	35	19	712	148	137	19	-0.10	0.21	22.0
"Blue" late ^d	304	28	11	6	282	74	72	41	0.19	0.26	55.3
"Red-Blue"	255	33	16	12	293	27	22	5	0.22	0.09	15.2
"Pink"	285	26	7	12	225	110	115	15	-0.31	0.49	13.4

Notes:

^a Counts of visits to first-nearest, second-nearest, third-nearest, farther-than-third-nearest neighboring *Penstemons*.

^b Frequencies of transitions between *Penstemons* and other flower species, where P = *Penstemon* and Other = any other species.

^c Bateman's Index (see Waser 1986) and the ratio of Other to P are given as summaries of constancy. The mean bout length (last column) is the number of plant visits observed before losing the bee; longer bouts indicate slow-moving bees that are easy to follow.

^d Data for bee "Blue" are divided into early (23-28 July) and late (5 August) periods.

that collected pollen while young may turn to nectar collecting with age, or vice versa. "Blue," for example, accumulated small corbicular loads during all bouts from 23–28 July, but by 5 August was no longer carrying visible loads.

Even though the relative efforts made into pollen and nectar foraging are genetically controlled (Robinson & Page 1989), there is also strong plasticity in the way in which individuals react to colony needs (Cartar 1992a; Plowright *et al.* 1993; Fewell & Bertram 1999). There have been recent attempts to understand such task allocation in bee colonies by self-organization models in which each bee is an automaton that differs from other colony members only in the response threshold to particular stimuli in and outside the nest (Bonabeau *et al.* 1997; Pankiw & Page 2000). Even if these models explain some of the observed behavior, there are potential difficulties, because they neglect the individuality of pollinators beyond their inborn thresholds. All animals encounter a basic difficulty when they set out to perform a novel skill: they generally need to *learn* that skill, even if it has innate components. The investments in learning different types of foraging activities (and the costs of interference when switching) can be substantial (Dukas & Visscher 1994); therefore, we cannot understand task allocation and task switching without quantifying these costs (and how bees perceive them). Surprisingly, however, one review of new breakthroughs in task allocation (Gordon 1996) avoids such terms as "learning" and "memory" altogether.

Learning-related individuality

Pollinators learn about diverse aspects of their environment (see other chapters of this volume). Because each pollinator's experience is unique, its behavior may also be unique. Much of this experience, however, is beyond the control of the observer. Moreover, each bee's experience (e.g., which flower species it experiences as rewarding) may in part be an epiphenomenon of its decision where to forage (see above) or may simply reflect stochastic processes.

The efficiency and accuracy with which pollinators handle flowers depends substantially on their experience with the respective flower type (Lavery 1994; Chittka & Thomson 1997). Some complex handling skills, such as nectar robbing in *Corydalis cava* (Fumariaceae) by bumble bee queens can take several days to develop (Olesen 1996). But handling efficiency on a given flower type can also be influenced by pollinators'

experience on other flower types. Depending on the similarity of motor patterns involved (and depending on the timing of visits to the two flower types), transfer or interference may occur (Chittka & Thomson 1997; Gegear & Laverty, this volume).

In the following paragraphs, we are concerned with the possibility of more formative types of learning, i.e., the possibility that early experience may substantially influence how a pollinator later reacts to flowers. Memory-through-metamorphosis has been invoked as a possible mechanism to determine foraging preferences in specialist bees (Dobson 1994), i.e., the possibility that bees become imprinted on particular scents (such as pollen odor) as larvae, and as adults show a preference for flowers with the same scent. The nervous system is entirely reorganized during metamorphosis; therefore a memory that persists through fundamental rewiring of neuronal circuitry is not trivial. However, Lindauer (1985) earlier found evidence for memory-through-metamorphosis in honeybees. The phenomenon, however, was also shown in grain beetles (Alloway 1972) and fruitflies (Tully *et al.* 1994), so it is not restricted to pollinators.

Does early experience shape the brain, as some studies on humans suggest (Elbert *et al.* 1995)? The mushroom bodies, a prominent structure in the insect brain, are essential in memory formation (Menzel, this volume). Interestingly, the size of the mushroom bodies in honeybees is correlated not only with age, but also with type of activity. Durst *et al.* (1994) showed that foragers have larger mushroom-body volumes than nurse bees of the same age, concluding that mushroom-body size is experience-dependent. The rationale was that more information storage requires more neural substrate (e.g. more neurons or dendritic proliferations). However, it was not clear whether the mushroom bodies increase in size as a result of experience, or whether the increased mushroom-body volume is a prerequisite in honeybees to switch from nursing to foraging activities.

To resolve this problem, Fahrbach *et al.* (1998) reared honeybees in an extremely deprived environment (social isolation and complete darkness). Mushroom-body volume increased even when bees collected no foraging experience, suggesting that the observed changes in brain structure served to *prepare* the animal for handling complex information in the context of foraging. But the correlation between brain-region size and storage capacity (or behavioral/cognitive ability) remains to be shown empirically.

Early learning may influence later learning without fundamental

changes in brain structure, however. We found that when bees were trained extensively on only a single artificial flower type, they had more difficulty in learning to switch between flower types than did bees that learned to switch without the prior phase of visiting only one flower type (Chittka & Thomson 1997). The effect extended to only a few hundred visits (or a few hours), so it may be marginal during a bee's several-weeks-long foraging career. On the other hand, the training phase also involved only a few hundred flower visits, and therefore was much shorter than what bees may really experience in nature. Some bees may spend the first several days of their life foraging in low-diversity situations – such as flowering trees – visiting tens of thousands of flowers of exactly the same type in rapid succession. Might such bees later have more difficulties in learning new flower types, or in learning to minimize interference when switching between flower types? Or do bees maintain complete flexibility, even if their foraging history includes phases where no flexibility is required?

The skill with which bees solve a particular foraging task depends substantially on their earlier experience with related tasks (Zhang & Srinivasan 1994). If bees are exposed to several flower types, some of which are rewarding and others not, bees are able to extract categories and concepts to predict the profitability of novel flowers (Dukas & Waser 1994, Giurfa *et al.* 1996). Whether or not bees acquire such complex skills depends substantially on the sequence with which different flower types are encountered (Zhang & Srinivasan 1994, Chittka & Thomson 1997). An entirely unresolved question is whether, in nature, this sequence is predominantly determined by the spatial arrangement of different flower types, or whether young bees actually choose to forage in diverse floral patches in order to gain the experience necessary for complex cognitive abilities.

Effects of genotype

Menzel (1985) claimed that the information available to a foraging bee comes from two sources: its own individual experience, and the “species experience” which is derived from evolutionary history and which is written into the species' genome. The implication here is that the “species memory” is identical in all members of the species. This is strictly true only when there is no genetic variability for the trait in question, either because of constraint, or because selection or drift have eliminated variance in the

past. However, recent studies have shown that there is heritable variation in learning speed (Brandes 1988), and several other foraging related traits (see references in Waddington, this volume) which means that the *limitations* of the plasticity discussed elsewhere in this chapter are variable and subject to selection. Thus, just as much as foraging is shaped by individual experience, it is also determined by individual genetic histories.

We hope for more studies of heritable variation of sensory and behavioral traits related to foraging. To confirm a hypothesis that a trait is adaptive, we should ideally show that animals *with* that trait have greater fitness than animals *without* that trait, or with a different quantitative expression of the trait. Is traplining adaptive, for example? Is flower constancy a strategy (Menzel, this volume) or a suboptimal solution (Gegear & Lavery, this volume)? Do bumble bees with red preference perform better on some islands than on the mainland, whereas bumble bees without such preference outcompete those with red preference in European mainland habitats (Chittka *et al.*, this volume)? We need to exploit heritable variation to understand whether the cognitive, behavioral, and sensory attributes of pollinators are truly sitting on narrow adaptive peaks, as many workers assume.

Parasite-induced changes in forager behavior

Certain parasites may force changes in foraging behavior. Late-instar larvae of conopid flies, which occupy much of the host's abdomen, prevent filling of the honey crop (Schmid-Hempel & Schmid-Hempel 1991); these bees concentrate on pollen foraging. On the other hand, parasitism by the protozoan *Crithidia bombi* is associated with reduced pollen foraging (Shykoff & Schmid-Hempel 1991). These parasites can be common. Shykoff & Schmid-Hempel (1991) found 20.2% and 35.7% infection rates by conopids and *C. bombi*, respectively, in bumble bees in the Swiss Alps. Schmid-Hempel & Stauffer (1998) also found that parasites affected floral preferences and switching behavior, but since both parasite load and experience may correlate with age, these changes might also have been driven directly by experience.

Effects of age

Cartar (1992a) and Dukas & Visscher (1994) found that efficiency increases over roughly the first week of a bee's foraging career (an effect which can

likely be attributed to learning what, where, and how to forage, and more complex foraging rules). Dukas & Visscher also observed that foraging efficiency declines later in life, but this effect need not necessarily be related to an age-related decline in cognitive ability. In fact, controlled studies show no effects of age on learning ability in honeybees (Bhagavan *et al.* 1994) or bumble bees (Chittka & Reinhold 1999). Several factors affecting foraging efficiency are potentially correlated with age of foragers, for example parasite load (Schmid-Hempel & Stauffer 1998) or wing wear (Cartar 1992b). Having seen several marked bumble bees die during foraging bouts, one of us (JT) can state with certainty that they slow down greatly as their time runs out. In honeybees, a decline in foraging efficiency with age might also be explained by assuming that seasoned foragers invest more time into scouting for new food sources than into harvesting.

Problems in neglecting interindividual variance: foraging strategies

One can fall into various misinterpretations by aggregating heterogeneous sets of individuals and therefore obtaining spurious correlations. Here we are dealing with specific, pollination-related manifestations of a general statistical problem. If bees do vary substantially in performance, but are treated statistically as equivalent replicates, the interbee variation can pop out in a variety of spurious relationships. For example, Pyke (1978) hypothesized that optimally foraging bees ought to show area-restricted search, i.e., they should fly shorter distances between plants after they have just received larger than average rewards. Because it is hard to know how much nectar a bee has received, Pyke and many others have substituted the time spent at a flower as a surrogate variable for the amount of reward received. This is reasonable, as it takes more time to extract more nectar (Harder 1986; Kato 1988). Making this substitution, one then tests for area-restricted search by testing for positive correlation between the time spent at one flower and the distance flown to the next. Pyke found this pattern. Although this procedure would be trustworthy for observations of a single bee, suppose that some bees in a population – say, those with tattered wings – work all flowers more slowly, and always tend to fly shorter distances. If one then combines data from fast and slow bees, one could obtain the expected positive correlation, even if no individual bee shows area-restricted behavior (Thomson *et al.* 1982).

Analogous difficulties attend field studies of flower constancy. Here, an attractive hypothesis is that a flower visitor should be more willing to switch to another species of flower after having received little reward. This flexibility would allow individuals to track the relative values of different resources and concentrate on the best ones. If flower-handling time is used as a surrogate for reward, if interbee variation in constancy is correlated with variation in working speed, and if data are pooled across bees, however, spurious correlation can cause the hypothesis to be accepted when it should be rejected, or vice versa.

Problems of this sort arose in a study of constancy in many unmarked bumble bees that were followed for as long as possible as they foraged freely in a meadow with several suitable flower species (Chittka *et al.* 1997; L. Chittka, unpublished data). The authors initially classified flower-handling times into two categories, either above or below the grand median for all bees. In this data set, bees were significantly more likely to switch plant species if their last (several) visits had been shorter than the median, and more likely to stay constant if their last visits had been longer than the median. This seems consistent with the hypothesis that bees switch when they are dissatisfied, but when each bee's visit times were re-scaled by the median for *that* bee's bout (rather than the grand median), the effect disappeared. Further exploration of the data suggested that the heterogeneity causing the spurious correlation arose not so much from interbee variation as from temporal variation. In the morning, all bees handled flowers slowly, presumably because nectar levels were high, and all bees tended to be constant. In the afternoon, visits were shorter and constancy dropped overall, so the relationship between visit length and subsequent constancy could not be clearly attributed to short-term behavioral flexibility. In fact, Chittka *et al.* (1997) resurrected the flexibility hypothesis; they reanalyzed the data within bouts, considering not just the upper and lower halves of the visit times but the upper and lower quartiles. Then, bees *were* more likely to switch following very short visits, and more likely to be constant following very long visits.

This example illustrates not just the danger of spurious correlation but also a reasonable way of handling existing data to avoid problems. Although marking animals is not always feasible, more trustworthy results will be obtained by restricting analyses to comparisons within bees, as well as considering other cryptic sources of heterogeneity (such as time of day). One investigation of flower constancy that apparently did

not include such precautions is a study of skippers by Goulson *et al.* (1997). They used exactly the procedure initially tried by Chittka *et al.* (1997), except that they used means rather than medians for dividing the data, and they reached the same initial conclusion. It might be worthwhile to analyze their data further, along the lines of Chittka *et al.* (1997), assuming that the bout lengths are long enough.

Modes of foraging

As Galen & Plowright (1985) showed, bumble bees that forage for nectar on *Epilobium angustifolium* visit the vertical inflorescences differently from those that seek pollen from the same plant. These authors interpreted their results in terms of reward maximization criteria, as if members of a group of equivalent bees first made a decision to specialize on pollen or nectar, then adjusted their movements accordingly. One would also like to know, however, whether parasitic infections also played a role in the food-type decisions; if so, then the population might be more profitably viewed as comprising heterogeneous groups of infected and uninfected individuals with different behaviors.

From the plant's point of view, it is clear that the adoption of pollen- or nectar-collecting behavior by a visitor can greatly change the fitness value of that visitor to the host-plant (Galen & Plowright 1985; Shykoff & Schmid-Hempel 1991; Wilson & Thomson 1991).

Familiarity with individual plant characteristics

Ignoring pollinator individuality can lead not only to spurious correlations, it can hamper insight regarding the adaptive problems that animals or plants are "trying" to solve. Knowledge of individuals can lead one to pose questions that would otherwise go unasked. For example, researchers concerned with pollinators' responses to variation in plant phenotypes tend to assume that the plant's visitors are influenced only by the characteristics, such as inflorescence size, that the plant presents at the moment. However, the behavior of bees that return frequently to particular plants might also be sensitive to qualities that the plant displayed previously but no longer does. For example, *Aralia hispida* plants change sex from male to female phases several times during a flowering season. When floral rewards were manipulated in male-phase inflorescences (Thomson 1988), bumble bee visitation increased to the richer inflorescences. When all of the variable male-phase inflorescences were replaced with uniform female ones, simulating the natural sex change, the bees

preferentially visited female inflorescences that were located where the richer males had been. This result highlighted an ambiguity in interpreting selection on floral displays in terms of sex allocation theory: nectar secreted by a flower in male phase can increase the visitation rate to that flower in female phase. Should the cost of producing that nectar be considered a male or a female cost?

Even without special subtleties due to sex roles, early flowers can influence visitation rates to later flowers if pollinators show "trapline holdover," as bumble bees sometimes do (Thomson 1988, 1996). This effect could provide adaptive explanations for some aspects of floral biology, such as the tendency of many plants to burst into bloom with many flowers, then to taper off flower production. Here, the early flowers may benefit the plant not only through their own gametes but also by recruiting a faithful set of individual pollinators that will continue to serve the plant through its blooming period (cf. Thomson 1988). Without knowing the site fidelity of individual pollinators, one cannot fully interpret how pollinator-based selection might act on inflorescence architecture.

Scent-marking at flowers

We have long had indications that bumble bees scent-mark flowers and respond to those marks (e.g., Cameron 1981; Kato 1988; Schmitt & Bertsch 1990), but this evidence has not yet been well incorporated into the thinking of many who study foraging primarily from an energetic point of view. The energetic viewpoint has interpreted bees' decisions at flowers as being driven mostly by direct assessment of rewards gained at a blossom, rather than indirect olfactory assessment of recent visitation. This is partly because the evidence for scent marks has been mostly indirect and partly because the interpretation has been somewhat confusing. Schmitt & Bertsch (1990) review the evidence up to that date for bumble bees and honeybees; they indicate that some chemicals deposited on flowers may serve as attractants that denote rewarding flowers, while others, probably more volatile and short-lived, may serve as repellents that signal bees not to revisit flowers that have recently been drained. Schmitt & Bertsch interpret their results as strong evidence for an attractant role. Conversely, Giurfa & Núñez (1992) found evidence that marks recently left by honeybee foragers act as repellents. More recently, Goulson *et al.* (1998) have reported field evidence from bumble bees for a repellent role, a finding reinforced by experimental application of extracts from bee tarsal glands

to flowers (Stout *et al.* 1998). To date, however, it is not clear if bees use more than a single scent to mark flowers, nor whether scent-marking is an active process (Chittka *et al.* 1999). It is equally possible that tarsal secretions are used for adherence of bee feet to flowers, and are used as scent marks only as an epiphenomenon: bees might use the scent marks as repellents if the flowers are known to refill slowly, and as attractant if they remember the flowers as having high refill rates.

Our goal in considering scent marks in this chapter is not to resolve controversies but to show how an individualistic perspective can help clarify how these marks should be interpreted. If one adopts an adaptationist viewpoint of bees as optimal foragers that search widely for food, scent-marking is hard to understand. Of course, it is easy to see that a short-lived repellent mark might be useful in helping an individual avoid revisiting flowers that it has just probed, but it is harder to see how it could be adaptive to leave long-lived attractive marks on rewarding flowers. It would seem to require some special conditions. First, there must be an expectation that the bee who does the marking will return in time to benefit from the mark. This condition is easily met if bees use small foraging areas. Second, and more onerous, the mark must be expected to be of *more* benefit to the bee who left it than to other bees that may also detect it. It will do an individual little good to flag a rich resource if the primary result is to help competing bees exploit that resource. This paradox could be explained by kin selection if most of the visitors to a plant were sisters. In honeybees, which might combine scent-marking of flowers with site-specific dance information in the hive (von Frisch 1967), this may sometimes be the case. In bumble bees, however, these conditions probably do not apply: they lack a site-specific recruitment system (Dornhaus & Chittka 1999); workers range too far, workers per colony are too few, and colony densities are too high (Cumber 1953; Harder 1986), for sibling encounters to be frequent.

On the other hand, if a traplining individual is making a substantial fraction of the visits to a plant (Fig. 10.1), that bee may reap enough benefits from attractive scent marks to offset the possible advantage given to competitors. Some analogous mechanism might help explain a puzzling observation by Williams & Thomson (1998) in the 1994 data mentioned above. Modeling nectar production and removal with some simple assumptions, they estimated that the bees that visited the focal plant most often – i.e., the regular trapliners – gained more reward per plant visit than did the casual visitors that arrived less often. Interestingly, the

trapliners achieved their edge not by arriving at times when the plant had more reward overall, but rather by being better at selecting the flowers that had not been visited recently by others. Positing scent cues does not in itself dispel the puzzle, for the casual visitors presumably have as much access to scent cues as the trapliners do. Conceivably, the trapliners simply pay more attention to these cues for some reason; an interesting alternative is that bees can leave some private cues that are not accessible to others. Individual-specific trail marks are known in some species of ants (Maschwitz *et al.* 1986). In laboratory tests, scent marks left by bees on artificial flowers have also been shown to be more efficient in repelling the individual which left them than other bees (Giurfa 1993), but whether this effect holds up in the field remains to be shown. If it does, trapliners that return at regular intervals might be able to make the best use of marks left by themselves and those left by other bees.

Problems in neglecting interindividual variance: pollinator sensory physiology

Many physiologists have treated all variance between individuals as noise, and eliminated it by averaging the responses from several animals. A typical example is a study by Peitsch *et al.* (1992), who measured the color-receptor wavelength positions of several species of Hymenoptera. They found that differences between species, although slight, exceeded differences between individuals of the same species, and concluded that variance between data from animals of one species was entirely caused by measurement error. This may be correct; however it would also be worthwhile to take the possibility seriously that there might be *real* (i.e., heritable) variation between individuals. While such variation may be a nuisance for the physiologist trying to extract smooth functions from noisy data, it is a resource for the evolutionary biologist interested in predicting how animals will respond to directional selection.

A more serious (and common) error in physiological work is caused by equating intraindividual variance with interindividual variance. Many authors regarded it as legitimate to take repeated measurements from the same individual animal, and treat these as if they had taken independent measurements from different animals. In fact, numbers of individuals tested are not even available in some behavioral or physiological studies of honeybees; instead, only total numbers of choices or measurements are given. The result is that the numbers of observations, in such studies, is often drastically inflated. It is trivial to most biologists that one cannot

obtain a sample size of 150 leaf diameters by measuring 3 leaves 50 times over. Yet, this is precisely what some physiologists do in their data analyses. This is especially dangerous when comparisons between groups of animals are performed. For example, Vorobyev *et al.* (1999) tested honeybees' ability to detect artificial "flowers" of different colors on a green background. They used the total n of choices (270) as a basis for the conclusion that white was more easily detectable than gray, but the number of individuals tested (which should have been used for statistics) for white flowers was only three! Clearly, within-individual behavior is noisy, and therefore one needs several data points from each animal. However, behavioral variance across individuals can be large, particularly in honeybees whose experience before and between experiments is outside the control of the experimenter. Thus, once each animal's behavior is quantified (if necessary, with several tests), only a single data point per animal may be used for comparison between groups of individuals (see, e.g., Chittka & Thomson 1997; Chittka *et al.* 1997).

Because interindividual differences were regarded as noise, many authors pooled data from individuals without testing for heterogeneity. This can be hazardous. For example, Scherer & Kolb (1987) tested innate floral color preferences of *Pieris* butterflies. They found that colors both in the blue and the red part of the spectrum were preferred, and conjectured that a neuronal mechanism summing up the responses from blue and red receptors might drive this behavior. This mechanism is simple and therefore attractive, but there are alternative explanations. In essence, Scherer & Kolb (1987) used average *group* behavior to deduce the neuronal mechanisms implemented in *individuals*. When only pooled data are presented, it is equally possible that group behavior is caused by some individuals preferring red, others blue. If this were the case, no single butterfly would use summed inputs from two receptors to search for flowers. Furthermore, pooling the data masks possible sequence effects. Say, for example, that butterflies tend to visit blue first (bypassing red flowers), then red (bypassing the blue flowers it has already found unrewarding); such a pattern would also suggest a different model of neuronal control.

Recommendations

Pollination biologists ought to consider the ways in which pollinator individuality may affect their interpretations of both pollinator behavior and pollinator-driven selection on plants. In addition to documenting variation among pollinators in characteristics such as constancy and the

mode and tempo of working flowers, future studies should concentrate first on how these traits covary across individuals, and second on how the variation and covariation change as individuals gain experience.

For any interpretation of how pollinators respond to variation among plants, and thereby exert selection pressure, it is important to know whether individual pollinators show site fidelity or traplining behavior. This is particularly important with respect to scent-marking behavior. In particular, we need to go beyond existing studies, which show only that *some* individuals trapline in some situations. We need to know whether this behavior is typical, and we need to know what circumstances promote it.

In our opinion, an interesting unanswered question in pollinator foraging ecology is, "How do individual animals choose foraging areas?" For example, do they preferentially forage in areas with rich spatial detail, so as to facilitate memorization of particularly rewarding patches (Cohen & Keasar 2000)? Does spatial memory develop "passively" as animals move between flowers based on simple foraging rules, or do animals first establish a "cognitive map" of their home range within which they then place the coordinates of profitable foraging sites (Menzel, this volume)? Heinrich (1979, p. 114) states that "Young bees wander about a great deal before settling down," but we know little about how their experiences while wandering affect their ultimate decisions to settle. We also do not know if the wandering phase simply serves searching for the most rewarding flowers, or whether pollinators "deliberately" visit many different flower types to extract more complex foraging rules, including, for example, categorization of food types, or optimal decision rules for when to leave floral patches. Perhaps bees whose early experiences have favored flower-constant behavior will preferentially choose foraging areas with monospecific stands of flowers that make it easy to be constant. Relationships of this sort would necessarily color our mechanistic interpretations of behavioral patterns, yet we tend to ignore them. Focusing on flower visitors as individuals – with individual histories of learning about the world – can be a useful corrective.

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