Behavioral Ecology Vol. 7 No. 2: 158–164

Trapline foraging by bumblebees: I. Persistence of flight-path geometry

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By setting out arrays of potted plants of *Penstemon strictus*, I tested whether freely foraging bumblebee (*Bombus* spp.) workers would establish regular foraging routes that reflected the geometry of the array. They did, passing through an asymmetrical array in a pattern that minimized interplant flight distances. After the array was changed to a symmetrical pattern, however, the experienced bees continued to show their previous asymmetrical flight patterns. New bees without experience on the asymmetrical array showed no asymmetry on the symmetrical array. I term this persistence of flight-path geometry "trapline holdover," and discuss its implications for the study of animals' learning and foraging behavior. *Key words:* bee, *Bombus*, foraging, foraging area, movement rules, orientation, *Penstemon strictus*, spatial learning, trapline. *[Behav Ecol 7:158–164 (1996)]*

Scientists interested in animal behavior have often chosen bees as exemplars for study, and when optimal foraging theory stimulated a wave of new questions in the mid-1970s, numerous researchers chose worker bumblebees as nearly ideal for testing theory (reviewed by Morse, 1982; Plowright and Laverty, 1984). Articles frequently listed their virtues, including abundance, ease of marking and observation, lack of mating as a distraction from foraging, little apparent predator-avoidance behavior, easily characterized and manipulated natural food sources, willingness to feed on artificial flowers in lab conditions, and (in contrast to honeybees) independence of individuals.

As studies accumulated, we learned much about various aspects of choice behavior and their relationship to resources. However, most study has been concentrated on small-scale phenomena. Following Pyke (1978a,b, 1979), several workers aimed to characterize "decision rules" that assessed bees' movements within and between inflorescences in terms of efficient strategies for finding resources (e.g., Hodges and Wolf, 1981; Kipp et al., 1989; Schmid-Hempel, 1984; Waddington, 1980; Waddington and Heinrich, 1979; Zimmerman, 1979). Others were more concerned with variance and risk aversion (e.g., Harder and Real, 1987; Real, 1981), pollen versus nectar rewards (e.g., Galen and Plowright, 1985), and still other questions. Despite the diversity of questions, most of these formulations asked about the utility of the behavior, usually in terms of net energy gain per unit time. They also assumed, implicitly or explicitly, that the bees were *searching* without prior knowledge of the locations and values of rewards. Bees were shown to use information from recently visited flowers to make decisions about their next flights (Pyke, 1979), but they were seldom considered to be intimately familiar with the plants in a small foraging area. Indeed, the two essential ingredients of most movement rules are that travel costs ought to be reduced by efficient flight paths and that "a bumble bee should never choose a flower known to have been already visited" (Pyke, 1979).

An absolute prohibition against revisitation is surely an oversimplification; the time scale must be specified. It has long been known that bumblebees and honeybees frequently confine their foraging to small areas within dense stands of flowers (Bonnier, 1906; Free, 1993; Heinrich, 1979; Manning, 1956; Müller, 1882; Ribbands, 1949; Schneider and Glass, 1990; Singh, 1950). Although immediate returns to the same plant may be undesirable, if one looks at larger temporal and spatial scales, such returns are one of the most conspicuous features of the foraging. Indeed, the scale of observation need not be expanded very much to see returns: in both *Aralia hispida* and *Penstemon strictus*, at least some marked bees do all of their foraging on 20 to 50 plants, in an area of 100 m^2; they revisit individual plants *within* foraging bouts, at intervals on the order of 10 to 20 min, and they return to the area for as long as 15 days. Furthermore, they frequently revisit particular plants in a somewhat predictable sequence, that is, they show a tendency toward "trapline" foraging (Anderson 1983, Heinrich 1976, 1979; Thomson et al., 1982, 1987, and unpublished data). *Searching* comprises a minor component of the behavioral repertoire of such foragers; if they are optimizing anything, it ought to be the *harvesting* of rapidly renewing sources of nectar and pollen [see Possingham (1988, 1989) for theory and Gill (1988) for application to hummingbirds]. Predictions made for searching bees—for example, that they should alternate left and right turns to maintain a long-term directionality—may apply in many cases, but may simply be irrelevant to a traplining bee repeating a circuit.

Although studies of bumblebees have tended to be restricted to small scales, there is a strong and separate tradition in honeybee research, where long-distance orientation to feeding sites has long been of interest (e.g., Cartwright and Collett, 1983; Chittka and Geiger, 1995; Chittka et al., 1995; Collett, 1992; Dyer, 1991; Gould, 1986; von Frisch,1967). These mechanistic studies tend to ask *how* bees find their way to foraging sites rather than assessing the utility of the behavior. Although some studies in this tradition have used small-scale experimental arenas (Collett et al., 1993), most of the findings concern landmarks and other orientation cues that bees use to move across landscapes—usually over hundreds of meters. It is not clear how many of these findings can be extrapolated down to the intermediate scale of traplining within an individual's foraging area. On the other hand, by demonstrating that at least honeybees use truly impressive spatial skills in their foraging, these studies collectively warn us that any picture of quasi-amoeboid bees following simple "movement rules" may leave out important aspects of their foraging, particularly at intermediate and large scales. I contend that trapline foraging represents an area that has not been well inves-

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Received 3 February 1995; revised 15 May 1995; accepted 16 May 1995.

1045-2249/96/$5.00

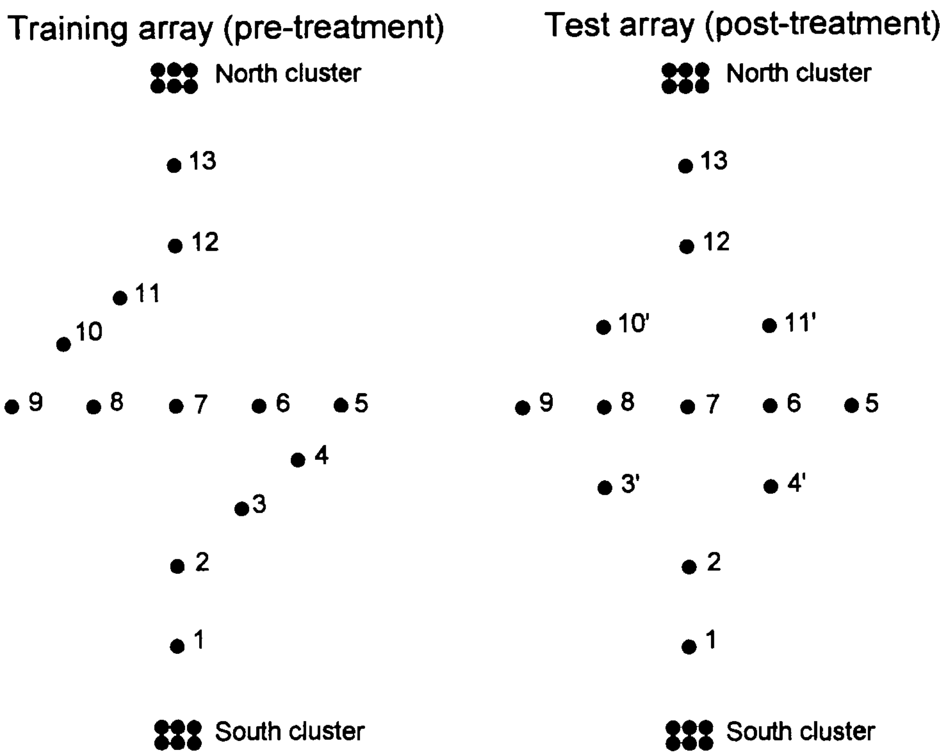

Figure 1
Maps of the asymmetrical training array and the symmetrical test array. Dots indicate locations of potted *Penstemon strictus* plants. Spacing is approximately 1.5 m.

tigated by either of these research traditions. Rather, it falls into an intermediate territory. Concepts and techniques from both traditions may be useful, but first it is necessary to build up a clear descriptive picture of what remains a poorly known phenomenon.

Here I consider only one aspect of traplining, that of "trapline holdover:" the question of whether bumblebees, once they have established a particular flight path through a stand of flowers, will persistently follow that path despite changes in the arrangement of the flowers. In other words, does the contemporary architecture of a trapline reflect only contemporary conditions, or is it burdened by history? If it is so burdened, it supports the idea that trapline structure is learned, in the sense of comprising "an enduring internal representation of the external environment" (Dudai, 1989; Mangel, 1993). If traplines are learned, and if they function to promote efficient foraging, we can begin to establish connections between the observed phenomenon of traplining and the developing theory on how animals gain fitness by tracking shifting resources through sampling and memory (e.g., Mangel 1990, 1993; McNamara and Houston 1985, 1987; Stephens 1987, 1993). Traplining does entail spatial constraints beyond the scope of these models; for example, a bee's response to a plant might well depend on the characteristics of surrounding plants as well as those of the focal plant. Still, some of the general conclusions regarding memory, "optimal forgetting" (Mangel, 1990), and the effects of unrewarding encounters (Papaj et al., 1994) seem particularly relevant to trapline holdover.

METHODS

This field study used experimental arrays of potted plants of *Penstemon strictus* (Scrophulariaceae). This penstemon grows abundantly at lower altitudes, especially as a roadside weed, but it is absent from the vicinity of Irwin, Colorado (107°06'00"W, 38°52'35"N, elevation 3140 m), where observations were made (in a subalpine meadow rich with other flowers). Therefore, all experience of the test subject bees with *P. strictus* must have come from the plants in the array. Although there were only 25 pots, the largest plants each presented nearly 50 flowers, and the flows of nectar and pollen were sufficient to draw numerous bees to the array. Some marked individuals spent virtually all of their time foraging in the array, while others were seen less often. Some of the latter bees were foraging elsewhere on other plant species, as evidenced by non-*Penstemon* pollen loads and direct observation, but others may simply have been in the nest when not on the array.

Preliminaries

The array was set out in a gravel driveway about 6 m wide. There were no potential landmarks within the array except for the plants themselves, but there were numerous landmarks available at the sides of the array, including two observers seated near plants 2 and 12 (Figure 1).

As the plants came into bloom in early August 1992, the pots were kept in a tight circular cluster. A substantial number of bumblebees (mostly *Bombus flavifrons* and *B. bifarius* workers) discovered the patch and began visiting regularly. Early on 16 August, before bees became active for the day, the pots were moved into the "pretreatment" arrangement shown in Figure 1, with a spacing of 1.5 m between plants. As bees appeared at the array, two observers netted them and gave them individual color marks by daubing Floquil® hobby paint on their thoraxes while the bees were immobilized in a fold of the net. We marked approximately 30 bees, about 20 of which were seen again on the array. Several resumed foraging immediately after marking, suggesting that the marking procedure is not very traumatic.

On 17 August, three observers followed marked bees, audiotape-recording the sequence of plants visited. The array was designed to provoke a particular behavior in bees that had become familiar with the array. Based on previous observations, we expected that bees would spend considerable time foraging at the two concentrations of plants at the north and south ends of the arrays, but that, as resources became depleted at one end, they would leave and "commute" to the other end, visiting the intervening plants in numerical order (or reverse numerical order). Visiting plants in strict sequence would amount to always visiting the nearest neighbor not just visited, a behavior attributed to bumblebees in general (Pyke, 1978b) and observed in other studies of *P. strictus* at Irwin. [Of 1497 interplant transitions in a hexagonal array of 37 plants (also at 1.5 m spacing), 86% were to nearest neighbors; J. D. Thomson, unpublished data.] Because the array was asymmetrical, nearest neighbor moves required northbound bees to turn right at plant 2 and left at plant 12, and southbound bees to turn right at plant 12 and left at plant 2. We continued to mark new bees on 17 August.

The frequencies of different classes of interplant movements (e.g., right versus left turns) were analyzed using the BIOM-PC package (Rohlf, 1987) for replicated goodness-of-fit tests (Sokal and Rohlf, 1995), and StatXact (Cytel, 1989) for Fisher's exact tests of $r \times c$ contingency tables and Zelen's exact test of log-odds ratio homogeneity for replicated 2×2 contingency tables.

Experiment

On 18 August we began long vigils at plants 2 and 12. An observer at each plant recorded the timing of each arrival, the number of flowers visited, the identity of the bee if marked, and the identities of the plants that the bee came from and departed to. Observations continued from 0828 to 1301 on 18 August (when bad weather caused foraging to decline) and from 0900 until 1130 on 19 August. Unfortunately the voice tapes from plant 12 on 18 August were either lost or accidentally erased, so these data are missing.

Unmarked bees continued to arrive during this period. We did not want to disturb these bees by catching and painting them, but we gave some of them temporary marks by brushing fluorescent powder on their dorsa as they left flowers. These marks faded as the bees groomed, but by refreshing the marks at intervals, we could keep individuals recognizable indefinitely. Because we had only five colors of powder, we reused a color if a bee had not been seen for 2 h. However, some of the older bees did return, so then we had duplicates. Therefore, powder marks served to denote bees that had fed in the array on 18 August, but unlike the paint marks, did not reliably distinguish individuals.

At 1130 on 19 August, we rapidly moved plants 3, 4, 10, and 11 to the new "posttreatment" positions indicated by the "prime" notations in Figure 1. Observations at plants 2 and 12 resumed at 1132 and continued until 1435.

RESULTS

Preliminaries

Although many of the marked bees continued to visit the array regularly for the entire experimental period, there was a continual turnover, and new unmarked bees kept appearing throughout the experiment. By the afternoon of 17 August, almost all the bees on the array were marked, but by 19 August only 56% of the visits were by marked bees. A small number of regular visitors contributed a large fraction of the visits; for example, of the 151 visits to plant 2 on 18 August, 26 were by Blue, 15 by Green, 11 by Red, and 10 each by White and Yellow. (Blue, then, averaged one visit to this plant every 9.8 minutes.)

Bees observed on 17 August frequently did follow the expected pattern of visiting the numbered plants in sequence. For example, the three longest sequences for Green were: 6 7 8 9 10 11 12 11 10 9 8 2 3 4 6 3 2 1; S 1 2 3 4 6 7 8 9 10 11 12 13 N; and 5 6 7 8 10 11 12 13 N. Blue's four longest were N 1 2 3 4 6 7 8 9; 2 1 S 1 2 3 6 12 13 N; 9 10 11 12 13 N 13; and N 13 12 11 10 9 8 7 (briefly lost) 3 2 1.

These bees were particularly systematic individuals, however. It was not unusual for a bee to break sequence, often making a looping flight above the array and then settling down on a different plant. Sometimes these breaks seemed to be induced by encountering another bee in a flower, but more often they seemed to follow a series of very short visits, perhaps indicating that the bee had been encountering unrewarding plants (Taneyhill, 1994). When otherwise systematic bees skipped only a single plant without flying above the array, the plants skipped were most often numbers 5 and 12, those at acute corners.

Experiment-classification of data

With bees arriving at less than 2 min intervals, frequently in clusters, it was not always possible to note the plants from which bees came (henceforth, "points of origin" or simply "origin"). This was particularly true for southbound bees at plant 2 and northbound bees at plant 12, so we ignored them and concentrated on bees moving in the opposite directions. ("Northbound at 2" describes any bee that, having left plant 2, moved to any plant other than 1 or S.) The bees' destinations on leaving the focal plants were much easier to score, so these records are virtually complete; the few instances to the contrary have been eliminated from the analysis. It is necessary, however, to classify the remaining data by whether the point of origin was observed or not. Where the origin was observed, it was overwhelmingly either 1 or S for bees at focal plant 2, and 13 or N for bees at plant 12. The very few exceptions have been removed from the "origin observed" category and placed in the "origin not observed" category for analysis; therefore, the "observed" label really indicates "known to be from S or 1," and the "not observed" label means "truly unknown or known to be from other than S or 1." I assume that many of the "origin unknown" bees actually came from S or 1 also, but have no direct evidence.

Testing the hypotheses requires scoring left and right turns. These must also be subdivided. For bees at plant 2 in the pretreatment array, I define "tight right turns" as those whose destination is plant 3. Moves to plants 4, 5, or 6 are "other right turns." Straight-ahead moves to plants 7, 12, 13, or N are ignored because these lack information on handedness. Moves to plants 8, 9, 10, or 11 are left turns; in the asymmetrical pretreatment array, there are no "tight left turns." In the symmetrical posttreatment array, moves to plant 4' are "tight right turns;" "other right turns" are to plants 5, 6, or 11'; "tight lefts" are to plant 3', and "other lefts" are to plants 8, 9, or 10'. Moves from plant 12 are, of course, scored analogously.

Experiment—tests

To make this section less tedious, I invert the usual procedure by first presenting tests of the pooled data (Table 1), then dissect the data to determine whether any artifacts have been introduced by the pooling.

1. *In the asymmetrical pretreatment array, do bees make mostly right turns, as would be expected from a tendency to visit nearer neighbors?* Yes, right turns outnumber lefts by 110 to 13; goodness-of-fit $G = 87.51$, 1 df, $p < .0001$.

2. *In the symmetrical posttreatment array, do bees make equal numbers of left and right turns, as would be expected from a tendency to make decisions based on flight distance?* No, there

Table 1

Summary of turns made by *Bombus* workers at the focal plants 2 and 12

Direction of movement	Origin observed				Origin unobserved				All bees, pooled across direction, date, and origin class
	Northbound bees at plant 2		Southbound bees at plant 12		Northbound bees at plant 2		Southbound bees at plant 12		
Pretreatment baseline, asymmetrical array									
	8/18	8/19	8/19 only		8/18	8/19	8/19 only		
Right turn	26 + 3	17 + 1	14 + 0		30 + 0	9 + 0	10 + 0		110
Left turn	1	0	2		6	1	3		13
Posttreatment baseline, symmetrical array									
	Mark	No mark	Mark	No mark	Mark	No mark	Mark	No mark	
Right turn	15 + 2	8 + 0	17 + 0	11 + 0	13 + 1	5 + 0	7 + 0	5 + 0	84*
Left turn	5 + 0	2 + 0	1 + 0	9 + 0	2 + 0	5 + 0	1 + 0	5 + 0	30*

"Origin observed" indicates that the bees on plant 2 came there directly from either S or 1 and that the bees on plant 12 came there directly from N or 13. "Origin unobserved" indicates that bees appeared on the focal plant without their prior location being observed, but then departed northbound from plant 2 or southbound from plant 12. Pretreatment observations were made on 18 and 19 August, but data from plant 12 for 18 August were lost. All posttreatment data were gathered on 19 August. These data, but not the pretreatment data, are broken down by whether the bee was marked or not.

* Pooled across direction and mark and origin classes.

is still a significant preponderance of rights (84) over lefts (30), $G = 26.6$, 1 df, $p < .0001$.

3. *In the posttreatment array, do marked bees (which had experience with the pretreatment array) make a higher proportion of right turns than do unmarked bees (which may lack such experience)?* Yes, a 2 × 2 contingency table is highly significant (marked right, 55; marked left, 9; unmarked right, 29; unmarked left, 21: Fisher's exact test, $p = .0012$). Indeed, the unmarked bees show no preference (goodness-of-fit $G = 1.3$, 1 df, ns).

The above conclusions seem clear-cut, but might they be artifacts caused by inappropriate pooling of data over subclasses? First, I consider whether the missing data from plant 12 on 18 August might have distorted the results. This could occur if (1) there were different processes controlling lefts versus rights at plants 2 and 12 (e.g., an east-west bias), or if (2) data from 18 August and 19 August were different (e.g., due to bees' increasing experience with the array). I tested the first of these with a 2 × 6 contingency table for the 19 August data [(plant 2 versus plant 12) × (the six subcategories of turns)], and the second with a similar 2 × 6 table comparing the 18 August data for plant 2 to the 19 August data for plant 2. Neither table even suggested significant interaction; $p = .44$ (Fisher's exact test) in both cases. There is no obstacle to pooling the pretreatment data from both days and plants.

The second question is whether turns of known and unknown origin can be pooled. For question 1 above, if the data are separated into these categories and tested by replicated goodness-of-fit tests, the subsets differ significantly: $G_{\text{heterogeneity}} = 5.08$, $p < .05$. Therefore, these data sets reflect somewhat different processes, and pooling is questionable. However, the difference is a matter of strength of effect, not direction. Bees known to come from plants S or 1 (N or 13) are more likely to turn right at plant 2 (12) than those whose direction was not noted. The preponderance of right turns is still highly significant in either subset considered above (known or unknown) however, so question 1 can still be answered affirmatively (turns of known origin, 61 right to 3 left, $G = 64.5$, 1 df, $p < .0001$; turns of unknown origin, 49 right to 10 left, $G = 28.1$, 1 df, $p < .0001$).

For question 2 above (posttreatment data), a similar replicated goodness-of-fit analysis reveals that each subset is again significant by itself (known origin, 51 right to 10 left, $G = 30.1$, 1 df, $p < .0001$; unknown origin, 31 right to 13 left, $G = 7.6$, 1 df, $p < .01$), but in this case the subsets are homogeneous ($G_{\text{heterogeneity}} = 2.6$, 1 df, $p > .05$).

For question 3 above, I divided the data into two 2 × 2 contingency tables—origin known and origin unknown—and tested the tables for homogeneity of log-odds ratios using Zelen's exact test. The tables are homogeneous ($p = .64$), and each remains significant ($p < .05$) if tested separately. In conclusion, examination of the internal structure of the data sets reveals no need to change the answers to the three questions posed above.

Of course, the statistics pertain to the entire set of choices, pooled over individual bees. We might also ask whether bees are heterogeneous; if so, pooling data would be inappropriate. Such analyses can only be done for the paint-marked bees, which means that only a few bees have sample sizes large enough to test with any power at all. I tested the four bees scored most frequently (Blue, Green, Yellow, and White). They were homogeneous in their preference for right turns over lefts in the pretreatment data (2 × 4 contingency table, $p = .78$). Blue disappeared about the time of the treatment, but the other three were also homogeneous in the posttreatment data (2 × 3 table, $p = .24$). Additionally, Zelen's test shows that the latter three bees had homogeneous ($p = .69$) responses to the treatment [(right versus left turns) × (pre- versus posttreatment periods)].

DISCUSSION

Trapline holdover

These patterns challenge an assumption that was implicit in several of the earliest and most influential treatments of bumblebee foraging—the assumption that an animal's choice at any point in space and time is purely a function of its immediate assessment of the choices available, perhaps conditioned by its very recent experience or by internal motivational factors such as hunger level. The decision can then be predicted by "rules" that integrate those sources of information. In this approach, each movement decision is treated as a fresh problem that the animal must solve de novo. This is a reasonable way to frame a model, and it may provide an accurate picture of an animal that is truly searching unknown or forgotten territory. It is not the most appropriate way to view these site-faithful *Penstemon* bees, however. Usually they will have confronted the same decision at the same plant numerous times before, sometimes hundreds of times over several days.

In the experiments described here, there is no reason to expect bees to turn right preferentially in the posttreatment array; if the bees are solving a problem de novo, it is hard to envision a "foraging rule" that would promote such a bias in a symmetrical arrangement of plants. Indeed, less experienced bees show no such bias, but bees accustomed to asymmetrical choices retain asymmetrical biases for some time after their decision problem has become symmetrical. (In laboratory experiments with three artificial flowers arranged in an equilateral triangle, Cheverton (1982) found that individual *Bombus lapidarius* workers displayed an arbitrary "handedness" or bias toward left or right turns. If naive bees showed such behavior in the symmetrical posttreatment array here, individual biases canceled out in the pooled data. Cheverton also found a fairly even distribution of handedness across bees.)

This experiment shows that flight-direction decisions of bumblebees, while they may well be shaped by hardwired rules of thumb, also reflect previous foraging history. This is hardly surprising or novel. Importantly, however, this result does not depend on the behavior of captive bees in a lab situation, but on that of freely foraging wild bees. Had this "trapline holdover" effect been demonstrated in the lab, it could illuminate the learning processes of bees (cf. Collett et al., 1993). It would not, however, answer the important ecological question of whether unconstrained bees showed enough site fidelity for such effects to matter in nature. If bees did not return frequently to a small stand of plants, they could not develop familiar paths through it, nor could those paths show persistence in the face of changing resource arrangement. In fact, in this study, enough bees were site-faithful for the statistical ensemble of bee movements to show both of these properties.

How typical is the extreme site fidelity displayed by at least some of the bees in this experiment? There are too few studies to generalize. However, in most studies where bumblebee workers have been marked at a particular locality, at least some of them have been seen again at that spot [e.g., Heinrich, 1976, 1979; Manning, 1956; Morse, 1982 (review); Taneyhill, 1994; J. D. Thomson, unpublished data from *Penstemon whippleanus, Solidago, Digitalis,* and *Frasera*; Thomson et al., 1982, 1987]. Similar observations exist for honeybees [e.g., Free 1993 (review); Müller, 1882; Singh, 1950], and Ribbands (1949) described a honeybee worker that usually began a foraging bout on the same individual flower. Free (1993, p. 35ff) suggests that the size of a restricted foraging area is likely to vary with the type of plants being visited, but that bumblebees may typically use smaller areas than honeybees. In short, bees may not always show site fidelity, but it appears to be a very common behavior. It may occur at various spatial scales, from the tens of square meters used by *Apis* and *Bombus* workers on rich resources, to the extremely large (many square kilometers) areas of forest patrolled by euglossine females (Janzen, 1971).

If bees are site-faithful, they may in addition be "traplining" their plants. Traplining requires that a set of plants be repeatedly visited in a particular sequence (Anderson, 1983). This ideal definition is hard to make operational. We expect any animal's behavior to vary somewhat, but it is not clear how many imperfections might be allowed in the replication of sequences before one decides that the bee is not traplining. A companion paper (J. Thomson, M. Slatkin, and B. Thomson, in preparation) that argues that observed sequences must simply be more predictable than expected from an appropriate null model of foraging. Constructing such a model is controversial, and detecting traplining is statistically onerous, and I have not attempted to do it from the data gathered for this experiment. Indeed, the high repeatability of the sequences flown by the bees in the asymmetrical array can be easily explained by the simple null (i.e., nontraplining) hypothesis that bees prefer to make short flights without revisiting plants. Therefore, I apply the term "trapline holdover" to these experimental results only because other data sets (from hexagonal arrays of *Penstemon strictus*) have shown that repeated sequences by individual bees are significantly individualistic and self-similar.

How does the present demonstration of trapline holdover differ from previous studies? Darwin (1876, p. 246) concluded that bumblebee workers knew the locations of particular plants in a garden because they flew in straight lines toward those plants even when sight lines were obscured. Manning (1956; see also Tinbergen, 1958) removed plants that marked bumblebees had been visiting, and reported that the bees continued to return to the locations for some time. Janzen (1971) did much the same for euglossine females. To test bumblebees visiting *Aralia hispida,* Thomson (1988) set out matched, cut inflorescences in vases at fixed stations within a large stand. Some were artificially enriched with nectar and pollen; gradually, the visitation rate to the enriched stations increased. Then the enrichment was removed, making all stations equal in everything except history. Bees continued to make more visits to the stations that had once been enriched. Other studies (Thomson et al., 1982, 1987) indicated that *Bombus* traplined *A. hispida*, and I described the persistently elevated visitation to formerly enriched plants as "trapline holdover." I hypothesized that it occurred because bees were continuing to fly particular paths that they had developed during the enrichment phase. However plausible, this hypothesis lacked direct support, because the visitation rate data said nothing about flight paths. The same is true of the other studies cited above. The *Penstemon* experiment described here was designed to examine flight-path conservation directly.

The design further sought to isolate *directionality* itself as the cause of the observed holdover. Two alternative explanations for a persistent right turning could be imagined. First, bees might appear to conserve turning direction while actually just continuing to visit a particular plant that they had become accustomed to visiting. The design prevented this, because plants 3 and 11, which were the ones most visited by right-turning bees in the asymmetrical array, were the ones moved to the left side. Second, if the right-hand plants in the symmetrical array happened to have more flowers, the apparent holdover effect could be due to a simple preference for larger inflorescences. This potential confounding was avoided by making sure that plants 3 and 11 had slightly more open flowers (26 and 21) on 19 August than did plants 4 and 10 (18 and 15). These precautions help bolster the conclusion that the persistent bias toward right turns is truly a holdover of flight-path geometry.

In this respect, the *Penstemon* work may be compared to that of Collett et al. (1993), who showed that honeybees learned sequences of motor instructions when they were trained to fly through a maze to a food source. Changes in maze geometry were met with behaviors that suggested persistent spatial memories. The principal difference is that in one case bees were learning the spatial arrangement of obstacles to food-getting; in the other they were learning the arrangement of multiple food (reward) sources. Different learning processes could thus be involved, although the orientational capacities demonstrated are probably similar. Collett (1993) also trained honeybees to visit feeders in a fixed stable order by withholding reward when a feeder was visited out of sequence. The *Penstemon* experiment differed in that bees were free to organize their own flight sequence; but this may be an unimportant distinction: there seemed to be only one "correct" path through the pretreatment array, and all bees converged on it. Again, however, the *Penstemon* experiments are considerably closer to a natural foraging situation, bolstering the relevance of such learning to behavior in the field.

Traplining, tracking of fluctuating resources, and forgetting

What are the consequences of trapline holdover to the bees? This question is not amenable to direct experimentation; although one can measure the foraging efficiency of bees in the field, one cannot easily create bees with different intensities or styles of traplining. Therefore, we turn to models. Current models of traplining and memory (e.g., Stephens, 1987) do not include the explicit spatial constraints that would be necessary for them to fit exactly the case of bees that develop repeated foraging routes. Nevertheless, they may provide insights. Indeed, Mangel (1990, p. 317) prefaces a general theoretical treatment of information processing with a hypothetical example of a bee faced with changing and unpredictable nectar rewards. The appropriate general tactics for tracking such resources are (1) sample and remember information about resource quality, but (2) forget older information.

Both of these components seem to characterize traplining bees. For example, bumble bees working *Aralia hispida* do adjust their foraging areas to track spatial changes in reward (Thomson, 1988; Thomson et al., 1982, 1987). Day-to-day changes in traplines are consistent with the hypothesis that bees (1) regularly trapline a set of "core" plants on every pass through the stand, but also (2) sample peripheral plants, (3) eventually adding rewarding peripheral plants to the trapline, while (4) deleting consistently unrewarding plants. By this mechanism, or something like it, bees shift their traplines into experimentally created patches with higher rewards.

If we grant that a bee's trapline is a learned pattern, based on sampling, that represents an energetically efficient set of behaviors, the phenomenon of holdover might seem to reduce this efficiency. We detect trapline holdover, after all, by observing anachronistic behaviors that persist even after their former value has been lost because the resources changed. Could trapline holdover constitute, in Mangel's construct, a failure to forget fast enough?

If so, the costs are probably minimal. In general, fitness functions for memory length are likely to be broad, without sharply defined optima (Mangel, 1990). For the specific case of bees and flowers, Papaj et al. (1994) suggest that the speed with which bees can assess and reject should render them less affected by unrewarding experiences than other insects (e.g., parasitoids of drosophilids) that require a long time to assess a substrate for the presence of hosts. In addition, Thomson et al. (1982) describe how bumblebee visitors to *Aralia hispida* will reject an entire plant, which may bear hundreds of flowers, after sampling only one or two empty flowers. Although seemingly reckless, this behavior certainly provides for low cost assessment.

Consider the probable distribution of rewards encountered by bees on *Penstemon strictus*. Bumblebees' foraging areas are not exclusively held territories. Although nectar secretion is continuous, at visitation rates of 0.5 bee/min, most of the plants visited by any particular bee will have recently been emptied by another. Much less frequently, one of the same plants will have escaped recent visits and will be highly rewarding. No plant will be rewarding all of the time. The difference between good plants and bad ones, from a bee's point of view, is that good ones will be unrewarding somewhat less frequently. Bad plants may be receiving such intense visitation by a set of faithful bees that there are virtually never any "openings" until one of the faithful dies. Such plants may still be worth sampling, because mortality rates of *Bombus* workers are high [about 5% per day in a study by Rodd et al. (1980)]. Alternatively, plants may be bad because they have too few flowers or lower nectar secretion rates. These plants are less likely to repay sampling.

With this sort of distribution, the most appropriate sort of memory might have different dynamics for rewarding and unrewarding encounters. That is, bees should sample; if a plant is unrewarding, they should "forget" this information within a few minutes and be willing to sample it again. If a plant is highly rewarding, however, bees should remember it for hours. A single good encounter should cause a bee to add a novel plant to its trapline, but it should take a run of bad encounters for a bee to delete a plant that was once rewarding. This view is oversimplified, of course: it suggests that traplines would tend to expand without limit, and it does not reconcile how bees can "forget" single disappointments in the short term but remember runs of them in the longer term. Still, if this view captures the essentials of the resource tracking problem, the bees' persistent interest in formerly rewarding plants or flight paths may not be a failure to forget fast enough, but simply an expression of the inherent conservatism that makes traplining effective for tracking resources. Trapline structure must be somewhat flexible to track important shifts in resources, but a bee with too much flexibility will be tracking noise, not signal.

I thank B. A. Thomson for help with every phase of the work. L. Chittka, M. Mangel, D. Taneyhill, and N. Williams provided helpful critiques. The U.S. National Science Foundation provided support for write-up (IBN 9316792). This is contribution number 938 in Ecology and Evolution, State University of New York at Stony Brook.

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