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Trapline foraging by bumble bees: III. Temporal patterns of visitation and foraging success at single plants

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We analyzed the temporal structure of visitation by bumble bee workers to a single *Penstemon strictus* plant growing in an array of conspecifics. When tested against a null distribution using a randomization model, the observed pattern of arrivals for the whole group of bees was random, but departures were clustered in time. Certain individuals visited the plant repeatedly and frequently throughout the day. These showed significantly regular arrival and departure schedules, which were likely produced by traplining. We explored whether these more frequent and regular foragers gained a higher reward than random or incidental plant visitors. Using an analytical model, Possingham predicted that a dominating forager that visited a simple, renewing resource in a regular pattern would garner higher and less variable rewards than random visitors. Inspired by these results, but interested in plant-level visitation, we constructed a simulation model of resource dynamics for a multiflowered plant with high visitation. The model incorporates the observed visitation schedules of all bees and independent reward dynamics for each flower on the plant. We calculated the rewards that observed bees would have collected given a range of resource-renewal parameters. More frequent visitors did not return to the plant when whole-plant resource levels were higher, but these visitors did get greater rewards. Their increased reward resulted from greater foraging efficiency, primarily through selecting (on average) more rewarding flowers than those selected by less frequent, random visitors. *Key words:* bee, *Bombus,* foraging, *Penstemon strictus,* Possingham model, renewing resource, simulation model, trapline, visitation pattern. *[Behav Ecol 9:612–621 (1998)]*

The two previous papers in this series concerned the spatial aspects of flight paths of individual bumble bees repeatedly visiting plants of *Penstemon strictus* (Scrophulariaceae). The most frequent visitors show a statistically significant tendency to ‘‘trapline,’’ or to visit a set of plants in individualistic, repeatable sequences (Thomson et al., 1997). Here, we treat the temporal structure of those revisits at a single plant within the set. The hypothesis is that trapline foraging might serve to bring individual bees back to plants at a schedule that increases their foraging success. We consider why such revisits should occur, and then we describe the observed timing of visits to plants and model the consequences of different bee behaviors.

In an early and influential application of optimal foraging theory to the movement patterns of foraging bees, Pyke (1978) made the assumption that, at the temporal scale of a bee's foraging bout, food was a nonrenewable resource. He then formulated movement rules that would reduce revisitation; there would be no energetic gain in visiting a flower that had just been drained of its nectar or pollen. Various other authors contributed similar studies at the level of local groups of plants and within plants (Best and Bierzychudek, 1982; Ginsberg, 1985; Heinrich, 1979; Kipp, 1987; Schmid-Hempel, 1985; Thomson et al. 1989; Waddington, 1980; Waddington and Heinrich, 1979; Zimmerman, 1979), establishing a body of work and a tradition of thinking about bee foraging at small spatial and temporal scales. At larger scales (multiple bouts), different considerations emerge. Revisits to flowers are certainly costly at short enough time scales, but as more time elapses between visits, flowers may replenish their available stocks of both nectar and pollen. Depending on the time scale, revisiting flowers may be advantageous rather than disadvantageous (Gill, 1988; Kadmon, 1992; Possingham, 1989).

Here, we present observational data on marked bumble bees. We first analyze the temporal structure of the visits, motivated by the idea that spatially systematic traplining behavior might produce temporally systematic visitation schedules. Second, we consider whether the temporal structure of an individual's visits is adaptive—i.e., whether it contributes to foraging efficiency. The question is not whether foraging behavior should discourage revisitation, but rather whether it should (and does) promote timely revisitation.

Modeling resource and rewards

The second question requires us to model the consequences of various temporal patterns of visitation. This entails some new approaches because renewing resources have also received less attention from theorists. An important exception is a model by Possingham (1989) showing that, depending on the shape of the refilling function, revisitation at regular intervals may be positively advantageous in one or both of two ways. Revisitation can reduce the variance of the reward encountered, and it can increase the mean amount of reward encountered. Modeling the dynamics of a single resource, for example nectar, Possingham makes a distinction between the ‘‘standing crop,’’ or the amount of nectar that could be revealed by sampling at random intervals, and the ‘‘encountered crop,’’ or the amount that would be discovered by a forager that does not necessarily visit at random intervals.

We can best understand the consequences of this distinction by comparing the expected foraging successes of two hypothetical foragers: a ‘‘resident,’’ which may visit repeatedly according to a systematic regular schedule; and an ‘‘intruder,’’ which by definition arrives at random. Under the model, a regular resident would at worst reduce the variance in its own

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encountered reward relative to that of the intruder and simultaneously reduce the value of the plant perceived by the intruder (i.e., the standing crop). At best, the regular resident would also increase its mean reward in addition to reducing the reward harvestable by the intruder. The nature of the resident's gains depends on the shape of the resource's refill function. If nectar refills as a linear function of time, returning at regular intervals does not increase the mean encountered crop experienced by a resident forager. It does, however, decrease the mean standing crop that would be encountered by a randomly arriving intruder. Therefore, systematic foraging may allow a resident to fend off intrusions by minimizing the rewards available to interlopers. If nectar refills as a decelerating function of time, returning with regularity decreases the mean standing crop but also increases the mean encountered crop; this provides a double benefit to the regular, resident forager.

To make his model analytically tractable, Possingham included several simplifying assumptions: visits to the resource drain it completely, visits are instantaneous relative to intervisit times, and visitors do not overlap at the patch. These assumptions allow interesting predictions, and they may often embody an adequate description of resource dynamics and forager visitation patterns at individual flowers (Possingham, 1988; Possingham, 1989; Kadmon, 1992). These assumptions may, however, prevent the application of the model to more complex situations, such as numerous bees visiting multiflowered plants. Because we were interested in the temporal pattern of plant visits, we developed a Possingham-inspired simulation model that let us include additional realistic factors, such as incomplete drainage of resources by foragers, long handling times, and overlapping visits.

In our experimental system, ''resource'' includes both nectar and pollen, but we treat it mathematically as a single quantity with a refill rate that can be measured by a single parameter. We distinguish ''resource'' from ''reward'' in that resource is what is in the flowers, and reward is what is taken by the bees. We model whole-plant resource dynamics based on resource refill functions and removal schedules for each flower. These schedules follow slightly modified assumptions of the analytical model. We keep track of resources by considering individual flower depletion in real time. Thus, depletion at the plant level takes time, and we can accommodate overlapping plant visits by different bees. With this model, we can estimate the dynamics of resource standing crop in a study plant and investigate the consequences of different visitation schedules for the foraging success (reward) of individual bees sharing the plant.

Traplining bees: individual versus aggregate visitation patterns

The visitation pattern of an entire assemblage of bees is generated by the foraging behavior of individuals. At our sites, *Penstemon strictus* plants are usually visited by numerous individual bees, at least some of which show a statistically significant tendency to trapline, or to repeatedly visit particular subsets of plants in individualistic, partially predictable sequences (Thomson et al., 1997; see also Heinrich, 1976; Manning, 1956; Thomson et al., 1982). Because the essence of traplining is repetition, we can recognize it only in those bees that return to the plants very frequently. The precise adaptive significance of traplining is obscure. It seemed reasonable (though by no means necessary) that the demonstrable regularity of foraging circuits might result in regularly timed returns to individual plants (as suggested by Corbet et al., 1984). If so, a function of traplining might be to ensure that foragers return to plants along the trapline at regular intervals. This in turn might allow the most regular trapliners to dominate a plant's rewards (Gill, 1988) if Possingham's simple model conclusions still hold in our more complicated situation. That is, the reason for repetitive patterns of movement in space might, in part, be to produce regular patterns in time. Therefore, the analysis of individual patterns is a central focus of this paper.

Nevertheless, we are also interested in the temporal patterns of plant arrivals and departures by the whole collection of bees that share the plants of a *Penstemon* stand. In part, this is because it is the aggregate pattern of exploitation that determines the time course of reward dynamics, which in turn determines whether individuals can increase their foraging efficiency by using particular visitation schedules. In part, it is because observing bees at plants suggested that aggregate patterns might have ''emergent'' properties that are not predictable from individual patterns alone. Temporal clustering of visits, if demonstrated statistically, would be consistent with some intriguing possibilities: bees might be moving in a coordinated fashion, as in a foraging flock of birds. Alternatively, bees might be producing independent but concordant estimates of when it would be particularly advantageous to visit a plant that had been refilling. If supported, either of these hypotheses would be a novel finding for bumble bees.

With these general issues in mind, we address the following specific questions: (1) at a closely observed focal plant within a stand of *P. strictus,* what are the temporal patterns of bee arrivals and departures, and do they deviate from random? We ask this question for the aggregate distribution of all bees and for a selection of the most frequently seen individual bees. (2) Using the simulation model to estimate plant resource dynamics, do observed patterns of revisitation by actual bees garner more reward than would random patterns? (3) Do bees that make more frequent visits to the focal plant garner more reward per visit than bees that visit more rarely? (4) Is the variation in reward reduced for more ''regular'' bees? Collectively, the answers indicate whether an individual can improve its foraging success in a system of renewing resources by spatiotemporally structuring its movements so as to dominate the local flow of reward, despite continuous visitation by other bees.

METHODS

Study site and data collection

We observed bumble bee visitation to focal *Penstemon strictus* plants on single days, 28 July 1990 and 14 August 1994, at Irwin, Colorado, USA (107°06′00″ W, 38°52′35″ N, elevation 3140 m). (No *P. strictus* grow naturally in Irwin, although abundant populations occur at lower elevations within several kilometers; our plants were imported to the study area.) In a pilot project in 1990, we recorded plant visits in the form of arrival and departure times of individually marked bees, from 0918 h to 1130 h and 1514 h to 1722 h, using audio tape and a stop watch. In 1994, we used a tripod-mounted video camera with audio narration to capture all visits from 0744 h to 1905 h. Because of the fine time resolution possible with video data, we were able to record (to the nearest 0.5 s) the start and finish of each flower visit within each plant visit: we numbered flowers individually, directly on the video monitor screen, and moved the tape frame by frame to note when each bee first touched each flower and when it left. In both years, the majority of visits were by individuals of a single species, *Bombus flavifrons* (99.3% *B. flavifrons* in 1994). Although new unmarked individuals entered the pool continually, most of the visits were by marked workers.

For several days before the observations, we marked all bees

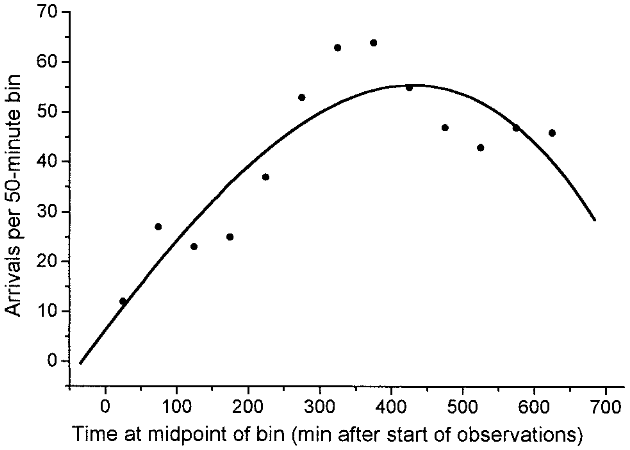

Figure 1
Diel trend in visitation rate at the focal plant, for all bee visits, 1994 data. Points represent the numbers of visits in time bins of 50 min. The fitted polynomial function $y = 6.332 + 0.1899x - 8.2817(10)^{-5}x^2 - 2.1445(10)^{-7}x^3$ was used extract the diel trend in the randomization procedure (see text).

in the foraging area, but we did not mark any bees on the observation day. All bees were marked on the scutum in front of the wing bases, using quick-drying paints in felt-tipped dispensers.

In 1990, 39 plants were planted directly into subalpine meadow habitat in a hexagonal array as described by Thomson et al. (1997). The focal plant was one of the corners of the hexagon. In 1994, 27 plants were grown in 2.5-gallon pots arranged in a ring with about 1 m between pots. Pots were watered daily. In 1994, the focal plant had 26 open flowers at the beginning of the observational day; four flowers opened at 1412, 1416, 1452, and 1638 h, and one flower dropped at 1410 h. Subsequent analyses keep track of the changing number of flowers.

Testing for nonrandomness of plant visit times: aggregate bee data and detrending procedure

The plant visit data include arrivals and departures, which we analyzed as separate time-series point processes. To assess patterns, we first broke each series into small "bins" of time and constructed a frequency histogram across the entire day. For both arrivals and departures in 1990 and 1994, aggregate visitation clearly peaked at midday, as Figure 1 shows for arrivals in 1994. Although this large-scale, nonrandom diel pattern is interesting and may reflect diel patterns in either resource production by the plants or in activity rhythms of bees, we were more concerned with finer-scale patterns: were visits clustered, random, or regularly spaced over time scales of minutes? To test for nonrandomness at this finer scale, we needed to remove the large-scale diel trend that would otherwise confound our test (see Plowright and Pallet, 1979, for discussion of how large-scale trends complicate the interpretation of small-scale processes).

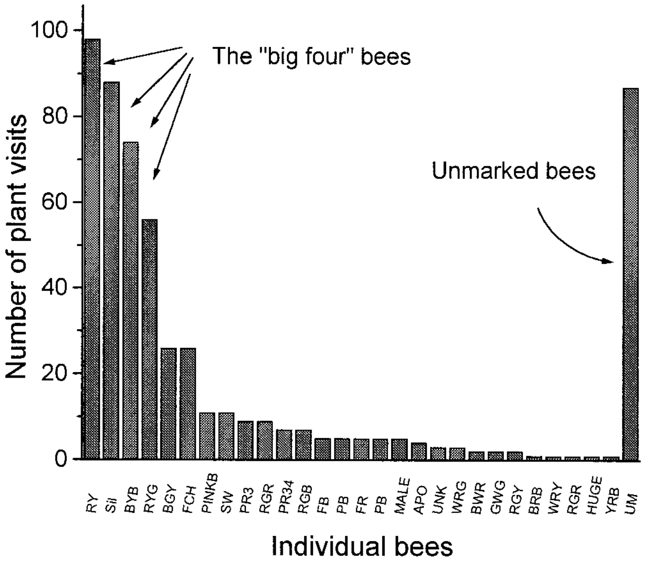

Figure 2
Frequency distribution of plant visits to the focal plant for the entire 1994 observation period. The "big four" individuals contributed over half of all the 553 visits. Two bees visited 26 times; only BGY was permanently marked. FCH was marked only with dye powder, as were several later visitors. For this reason, we are less confident that all 26 visits were made by a single individual and so decided a priori not to include this bee in further analyses.

We used a randomization procedure to produce a null distribution of "random" times from which the large diel trend had been extracted, as follows (FORTRAN code available on request). We first fitted the diel trend in the binned frequency distribution with the simplest polynomial function that seemed adequate to describe the trend; for example, Figure 1 shows a cubic function fitted to the 1994 arrival data. We then sampled n-2 points "randomly" across the time period, but we matched the density of random points to that defined by the cubic function. The two remaining points were constrained to equal the observed first and last visits. The procedure produced a set of null times that were random within the larger scale trend of the observed data. We calculated the variance in lengths of the interpoint time segments for the observed series and for 999 null series. Ranking all the variances allowed us to judge the statistical probability that our observed data could have been obtained from the process modeled by our null algorithm.

Visitation patterns of individual bees and variation among bees in visitation intensity

For 1994 only, we dissected the aggregate visitation data into sequences made by individual foragers. Bees varied dramatically in the intensity (i.e., number of plant visits) of their use of the focal plant (Figure 2), with four individuals contributing 316 (57%) of the 553 recorded plant visits. These bees, referred to as "the big four," were also faithful to the plant throughout the day (Figure 3), and confined virtually all of their foraging to the *Penstemon* array, as did the traplining bees analyzed by Thomson et al. (1997). We focused on these high-intensity bees as potential "residents" sensu Possingham. They were almost certainly traplining, and systematic behavior on their part would have the greatest potential to influence the standing crop encountered by less frequent visitors. A fifth bee visited 26 times, but no other marked bee visited more than 12 times.

First, we tested the visitation patterns for the bees that visited over an extended period of the day to see whether their individual foraging schedules suggested particular strategies that might not be evident from the combined pattern of all bees. Visitation was tested against random visitation in the same way as for the entire forager assemblage, but without detrending; null times were simply drawn from a uniform distribution over the period from the first to the last visit by an individual. Bees with low visitation intensities made too few visits to be statistically distinguished from random.

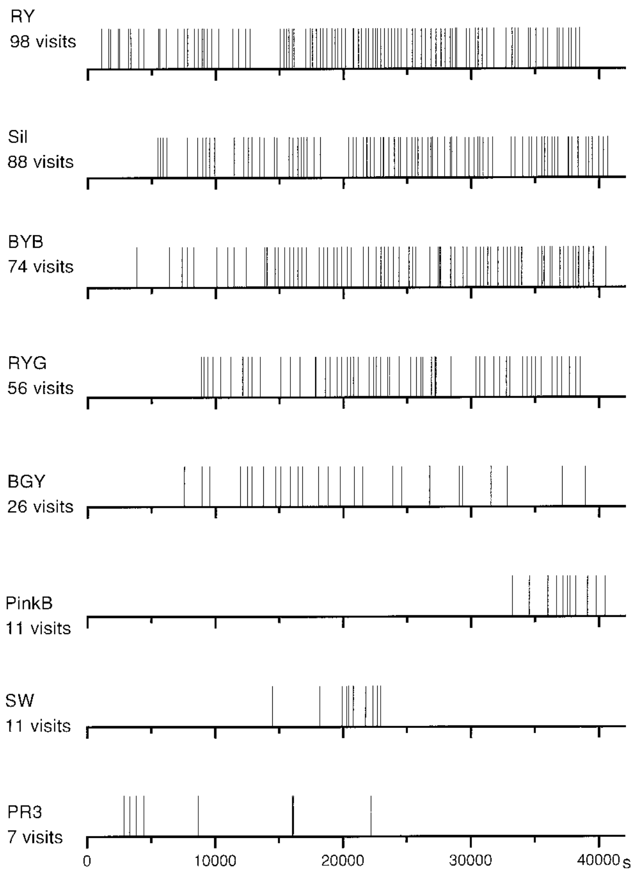

Figure 3
Temporal patterns of plant arrivals at the focal plant (1994) by the eight most frequent visitors.

Foraging success: modeling resources and rewards

Do bees that visit the plant more frequently outperform less intense visitors? Answering this question would require knowing which flowers a bee visits, when the visits occur, how much resource is available in each flower at the time of each visit, and how much resource the bee extracts each visit. Our data address only the first two processes, but with some simple assumptions about resource refilling rates and extraction efficiency, we could model the second two. In addition to estimating how much reward a particular individual obtained through an observed series of visits, we calculated how much would have been obtained by an unsystematic, randomly arriving individual with the same visitation intensity as the observed bee. As Possingham (1989) aptly showed, this random sample may not match the encountered reward for many individuals.

To model resource buildup by plants and withdrawal by bees, we assume that all flowers behave identically, and we scale each flower's resource state, or value, from 0 to 1. We assume that a flower visit always drains a flower's value to 0 at the moment the bee enters, and that immediately after the bee leaves, resource value is replenished at a constant rate until reaching 1 again, at which time replenishment stops. Resecretion following visitation and the plateauing function agree with nectar production patterns described for a range of flower species, including two *Penstemons* (Cruden et al., 1983). We modeled a range of refilling times, from 200 to 12,800 s. For our system, the function describes resource levels well because for all but the fastest refill time (200 s), visitation holds flowers in the initial linear part of the function. The exact refill schedule of *P. strictus* flowers is unknown, but unpublished data (J. Thomson) indicate that nectar refilling begins within minutes. Although we do not know how soon it levels off, if at all, flowers that have been unvisited for about 15 min elicit a strong feeding response in which bees probe both lateral nectaries. Analyses of reward data gave consistent results across the range of refill rates,; therefore, we usually present results from only one fast and one slow refill rate (400 and 3200 s).

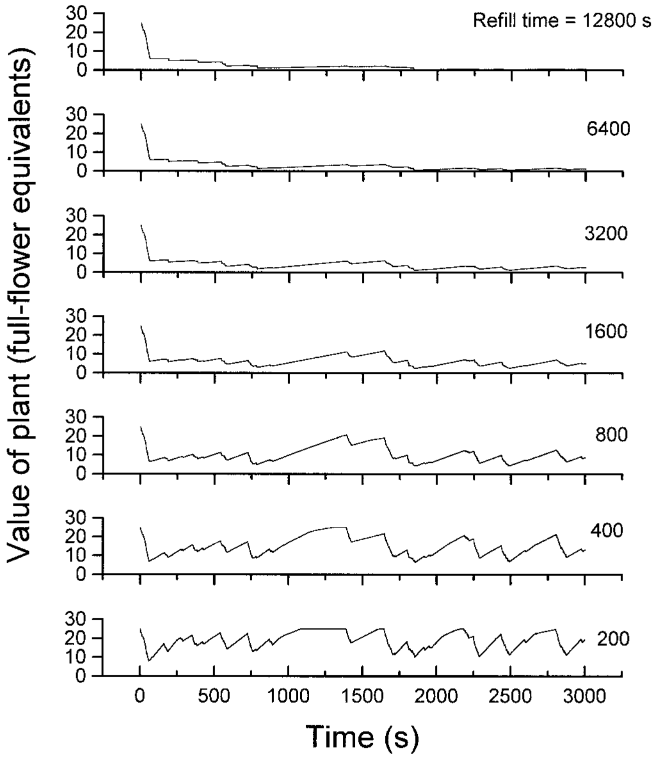

Figure 4
Simulation model: estimated plant standing crop of resource, or plant value, $V(t)$ versus time, plotted for the first 3000 s of the observation period. In this figure, all flowers had a value of 1.0 at time 0, whereas in the models discussed in the paper, flowers began with values of 0.5 so that $V(t)$ would reach equilibrium faster.

Our model estimated resource values of each flower on the focal plant and rewards extracted by all visitors for each second of the observation period. At each second, *t,* we calculated the value of the whole plant [$V(t)$] as the sum of the values of all flowers. When considering particular visits instead of continuous time, we define $V(i)$ as the value of the plant $V(t)$ at the time *t* when plant visit *i* begins (PASCAL code available on request).

We were unable to apply this model to the earliest portion of our video records because some flowers were initially hidden by others. Therefore, the modeled portion began at 1023 h, when the camera was repositioned, and continued through the rest of the record (31,161 s total). All flowers were arbitrarily initialized to be half full at 1023 h; depending on refill rates, flower values quickly reached a quasi-stable mean around which they fluctuated in a sawtooth fashion (Figure 4). For those simulations with the longest refill times, it took about nine plant visits before $V(t)$ apparently reached this equilibrium. We therefore excluded the first nine plant visits from analyses.

Plant's resource value at time of arrival

The analysis of a plant's resource value at the time of arrival follows the spirit of Possingham's model by asking, "Did systematic bees manage to arrive at the focal plant when its resource levels were particularly high (i.e., when it had not been visited lately)?'' The most frequent visitors came to the focal plant at regularly spaced times (see Results). We defined $V(i)$ for all visits by a focal bee, then compared the mean $V(i)$ per visit to that achieved either by (1) simulated null bees that made the same number of visits, but whose visits were made at random times or (2) other bees with different visitation intensities. For the first group, we used only the big four and ran 999 nulls for each observed data set to allow specification of a p value. This question echoes Possingham's distinction between ''encountered crop'' (the observed performance) and ''standing crop'' (the null prediction). For the second group, rather than separate particular bees or categorize visitation strategy for observed bees (faithful, regular, etc.), we regressed mean $V(i)$ against visitation intensity for marked bees.

For the second group, although we calculated resource available at each flower and plant [$V(i)$] for every bee-visit, we could not treat these estimates as independent observations for comparing among bees. Each plant visit by a bee represents a repeated measurement on the same individual, but repeated visits across individuals do not have serial correspondence, so standard repeated-measures analyses are not appropriate (von Ende, 1993). Still, to treat the data as independent would introduce a type of pseudoreplication. Additionally, because bees make different numbers of visits to the plant, they would contribute unevenly to correlation analyses if visits were used as individual observations. Therefore, we performed correlation analyses on mean data for each marked bee. In this way each bee produces a single datum. The procedure greatly reduces the power of the tests, but it is less likely to produce spurious effects. The resulting distribution of means deviates greatly from a bivariate normal; we therefore performed all correlations using Kendall's rank method (Sokal and Rohlf, 1995).

Reward obtained at each visit

We also asked whether visitation intensity was related, not to the resource in the plant at the bee's arrival, but to the estimated amount of that resource actually harvested by the bee. For example, a bee could arrive at a plant with many filled flowers but leave before discovering those flowers. Here, the reward harvested would be far lower than the resource available. We calculated total reward harvested per plant visit as the sum of the resource across all flowers visited. As above, we compared the mean total reward to visitation intensity to see if the more frequent visitors received more reward. To further investigate the discrepancies between plant resource values encountered by bees and the actual reward harvested, we also examined among-bee variation in a series of composite variables designed to illuminate different aspects of foraging efficiency. These are explained and defined below (Table 1).

Last, we consider variance in encountered reward. Variance in reward at an individual resource may have less effect on fitness than mean reward does to an organism, such as a bumble bee, which visits many plants per foraging trip and makes many trips per day. Nevertheless, the magnitude of variance reduction predicted by other models (Possingham 1989) warranted its consideration. We calculated the coefficient of variation in reward received (CV_{rd}) for all bees that made at least 10 plant visits. We then compared CV_{rd} against visitation intensity for these bees. We also compared CV_{rd} to CV of interarrival time (CV_{in}) for those bees that visited at least 10 times. A CV_{in} of 1.0 indicates independent visitation, because the probability distribution of interarrival times generated by random arrivals follows a negative exponential distribution with mean and standard deviation equal. CV_{in} is >1.0 for regular visits and <1.0 for clustered visits.

Table 1

Testing for advantages accruing to bees that visited the focal plant frequently and regularly

Variable	Definition
Response variables pertaining to floral resource levels, bee behavior, and floral rewards extracted by bees	
$V(i)$	Resource *value* of the focal plant at the beginning of plant visit i; the sum of the resource values of its open flowers
$R(i)$	*Reward* extracted from the focal plant by a bee during plant visit i; the sum of the resource values of the open flowers that the bee visited
$E(i)$	*Efficiency* of extraction of the available resource by a bee during a plant visit i; $R(i)/V(i)$
$N(i)$	*Number* of flowers visited on a plant visit i
$T(i)$	*Thoroughness* of flower visitation during plant visit i; $N(i)$/number of open flowers at the time of the visit
$S(i)$	*Selectivity* of flower choice during visit i; $R(i)$/the $R(i)$ that would have been obtained if the bee had chosen the richest $N(i)$ flowers on the plant at the time of the visit

Significance of nonparametric correlations of the means of the above response variables with the visitation intensities of the 15 most frequently recorded marked bees, for two selected refilling times. Values are Kendall's τ and associated (p values).

Response variable	Refill = 400 s	Refill = 3200 s
$V(i)$	0.089 (.322)	0.050 (.399)
$R(i)$	0.624 (.0006)	0.624 (.0006)
$T(i)$ (refill independent)	0.3883 (.022)	
$E(i)$	0.525 (.0032)	0.450 (.0097)
$S(i)$	0.545 (.0007)	0.617 (.0007)

RESULTS

Visitation patterns: whole assemblage

In 1990, at least nine bees visited the plant during the morning observation period (918 h and 1130 h), making 73 plant visits total. Between 1514 h and 1722 h, at least 11 bees made 87 plant visits. In 1994, at least 29 bees visited the plant, making 553 plant visits and 3111 total flowers visits during the continuous observation period of 683 min. Because there were unmarked bees, we could not know the exact number of individuals. Although these visitation rates are strikingly high—0.81 plant visits and 4.55 flower visits/min in 1994—similar rates were observed through most of the flowering of *Penstemon strictus* at Irwin. These rates may be somewhat higher than *P. strictus* typically receives in normal conditions, however, as the delayed blooming of the plants at Irwin's higher altitude meant that the plants flowered at the peak of *Bombus* worker abundance.

Despite the somewhat different observational techniques and different array geometries in the 2 years, the pattern of visits across time was consistent for both years. For 1994, both arrivals and departures were concentrated during the middle of the day, as illustrated for arrivals in Figure 1, and as evidenced by a significant quadratic term in a polynomial regression of the binned visitation data on time of day. For the separate observational periods of 1990, the morning period showed a significant linear increase in visits with time, and the afternoon period showed a significant linear decline. Despite the observers' impressions that bee activity was clustered in

Table 2

Temporal patterns of bumble bee visits to focal plants of *Penstemon strictus*

Aspect of visit	Data set	Detrended?	p	Pattern
Arrival times	1990 AM	Yes	.877	Random
	1990 PM	Yes	.416	Random
	1994 all bees	Yes	.436	Random
	1994 big four	Yes	.830	Random
	1994 BYB	No	.001	Regular
	1994 RY	No	.030	Regular
	1994 RYG	No	.002	Regular
	1994 Sil	No	.066 (.001)	Regular
	1994 BGY	No	.001	Regular
Departures	1990 AM	Yes	.024	Clustered
	1990 PM	Yes	.001	Clustered
	1994 all bees	Yes	.017	Clustered
	1994 big four	Yes	.830	Random
	1994 BYB	No	.001	Regular
	1994 RY	Yes	.005	Regular
	1994 RYG	No	.030	Regular
	1994 Sil	No	.089 (.001)	Regular
	1994 BGY	No	.001	Regular

Different data sets were compared to null expectations by the randomization procedures described in the text. ‘‘Detrended’’ indicates that the randomization procedure discounted the effects of the midday pulse in visitation. ‘‘Random’’ indicates that the observed data were indistinguishable from the expectations of the null model. For bee Sil, the first p value refers to the whole data set; the second refers to a trimmed data set from which three long gaps were removed (see text).

time, the times of all bees' arrivals did not differ from null expectation in any of the data sets after the large-scale diel trends were extracted (Table 2). Surprisingly, all of the matching sets of departure times differed significantly from null expectations: plant departures, but not arrivals, were clustered in time (Table 2). This pattern supports the observers' impression of clustered activity but does not support the possible explanation that bees were moving from plant to plant in coordinated groups.

Individual bees

We present more detailed results of individual bees for 1994 only. The uneven distribution of visits across bees, and the predominance of the big four, have been mentioned (Figure 2). Figure 3 shows the temporal patterns of the eight most frequently observed marked bees. For the big four (RY, Sil, BYB, RYG), there appears to be a tendency to return to the focal plant at fairly regular intervals, but periods of this regularity are occasionally broken by periods of absence. In contrast to other bees, the big four visited the plant over long periods of the day. The next most frequent visitor, BGY, showed the same type of visitation, but over a shorter portion of the day and with a longer intervisit time (mean = 20.10 min versus mean = 6.89 min, big four)

As was true for all bees, the combined arrival pattern for the big four as a group did not differ from random (Table 2). However, each individual within the set returned to the plant at regular intervals with respect to both arrivals and departures (Table 2). This kind of regularity contrasts strongly with the assemblage as a whole. RY, BYB, RYG, and BGY are highly significantly nonrandom, and Sil approaches significance. Sil had three periods during which it was away from the plant for more than 16 min. These long periods may have been times when the bee remained in the colony, or was foraging elsewhere, perhaps for a different resource (Cartar, 1992). When Sil's three long pauses were removed and the pattern reanalyzed, the pattern was significantly regular (Table 2), indicating that this bee returned to the focal plant systematically during its periods of heavy use. In summary, the most faithful visitors to the focal plant tended to visit at regular intervals, or ‘‘systematically’’ in Possingham's terminology. However, many bees were visiting, and the overall pattern of their arrivals was random.

Model results: floral resource dynamics

Unsurprisingly, temporal variation in plant value depends greatly on the rate at which individual flowers refill. Figure 4 shows $V(t)$ estimated for the first 3000 s of the observational period, for seven different refilling rates under the model described above. When refill rates are slow, the heavy visitation quickly drives standing crop to low levels; faster refill rates create a jagged $V(t)$ curve. Reward values were higher under faster times, but tests among bees were consistent across the range of refill rates.

Rewards received by individual bees

The hypothesis that systematically foraging bees could arrive at the plant at times of high resource abundance received little support. First, none of the big four arrived at times of significantly higher mean than expected from a null process of randomly timed arrivals, although the ‘‘big four’’ observed data sets all ranked in the upper half of the set of null realizations: RY, 737/1000; Sil, 565/1000; BYB, 788/1000; RYG, 522/1000. The less frequent visitor, BGY, ranked 406/1000. (This analysis is presented for a 800-s refill, although 400- and 3200-s refill times show a similar pattern).

Second, there is no correlation between visitation intensity and mean $V(i)$ across bees: casual visitors were just as likely as the most faithful bees to arrive when the plant reward was rich (Figure 5, Table 1). It is possible that using mean $V(t)$ may mask higher plant values encountered by faithful foragers at particular times. These faithful foragers visited at both ends of the day, and so may have gained higher rewards if $V(t)$ was higher during these lower bee-traffic times. We rule out this possibility for several reasons: our analyses began at 1023 h, by which time many different bees were visiting the plant; $V(t)$ under our refill model quickly stabilized (9 plant visits) to a consistent mean and $V(t)$ was higher only in the 20 min at each end of the foraging day; even if $V(t)$ is somewhat higher, plots of reward as a function of time (Figure 6) do not show higher reward gained at the ends of the foraging day. Reward is a function of $V(t)$ and of the number and identity of flowers actually visited.

Plots of the reward obtained per visit against the time of the visit (Figure 6) indicate the hit-or-miss nature of a bee finding a reward. Most visits were unproductive, either because the bee arrived at a time when the plant had a low $V(t)$ or because the bee left before probing the best flowers. On the other hand, at the modeled refill time of 400 s, a fraction of visits were highly rewarding, with bees sometimes obtaining the equivalent of 10 or more full flowers. The distributions of rewards received are uniform across bees.

There is a significant positive relationship between the number of visits made to the plant and the mean reward received per visit [$R(i)$, Figure 7, Table 1]. Bees that were more faithful and regular collected greater average rewards at the focal plant. If they did not arrive when resource levels were higher, then they must have been more efficient, i.e., extracted a greater fraction [$E(i)$, Table 1] of the resource that the plant contained when they arrived.

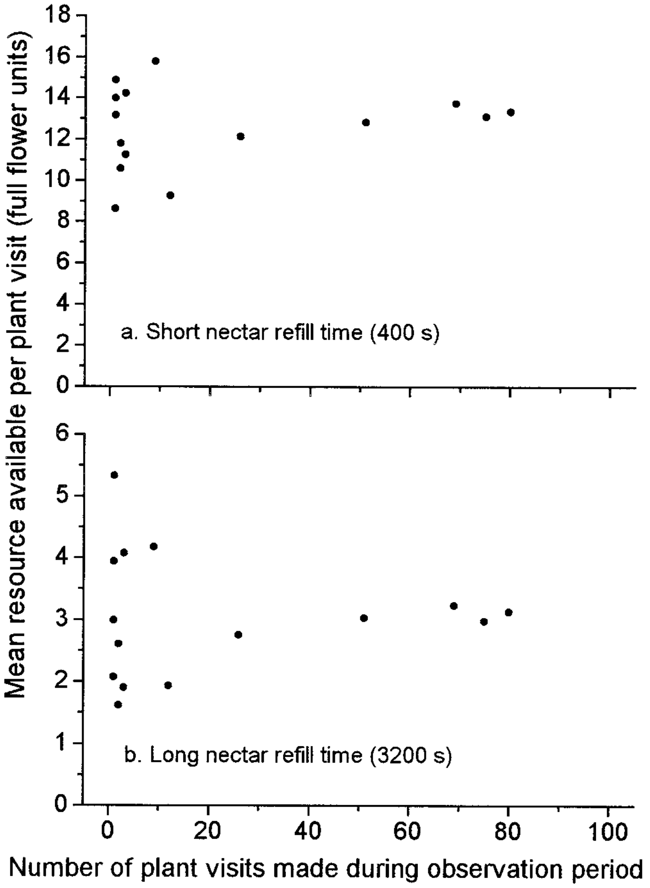

Figure 5
Plots of mean estimated plant value, *V*(*i*) versus visitation intensity, shown for two refill rates, 1994 data. Each point represents one bee. The bees that visited seldom were highly variable in the plant values they encountered due to low sample sizes, but the means show no relationship to visitation intensity.

Greater efficiency at the plant level can result from two mechanisms: thoroughness and selectivity. Table 1 examines each and presents results from regressions similar to those in Figures 5 and 7. First, the more faithful bees might have simply tended to visit more flowers per plant visit [i.e., to be more thorough; *T*(*i*), Table 1] in exploiting what the plant offered. There is a positive correlation, which is marginally significant, so this flower-number effect contributes in part to the greater reward received by the more faithful bees. Note that additional rewards gained by visiting more flowers would not necessarily increase foraging efficiency because handling time would increase as well.

More striking, it seems that the flowers chosen by the more faithful bees contained significantly more resource than those selected by more casual visitors, i.e., more frequent visitors were more selective in their flower choices [*S*(*i*), Table 1]. While faithful bees worked the plant harder, they achieved their gains by choosing the fullest flowers on average, rather than by simply visiting more flowers. Therefore, they gained a true efficiency advantage in terms of energy harvested per flower visit.

More frequent visitors did not encounter less variable rewards. Correlations of CV_{rd} and visitation intensity are not significant at either refill rate ($n = 7$, $t = -0.333$, $p > .1$; 400 and 3200 s refill). The direction of the relationship is consistent with the prediction of the analytical model (Possingham, 1989). The weak relationship is in part due to a single bee with a very low CV_{rd} that made few plant visits. When we compared CV_{rd} with CV_{in}, the correlation was again not significant ($n = 7$, $t = 0.2381$, $p > .1$). Here, too, the direction of the correlation is consistent with the analytical prediction. The single bee that had the low CV_{rd} also had a reduced CV_{in}, which again fits the prediction of the analytical model.

DISCUSSION

Possingham's (1989) model, although originally proposed as being particularly applicable to flower-feeding animals visiting nectar plants, appears to have stimulated only one prior empirical study of bees. Kadmon (1992) examined the temporal patterning of the arrivals of *Anthophora* spp. bees at focal flowers of *Anchusa strigosus* plants by recording sequences of 20 visits. He did not consider individual bees, but reported that the aggregate distribution of arrivals was significantly uniform, on the basis of the interarrival times having standard deviation/mean ratios < 1. A similar regular pattern of arrivals has been reported for one *Bombus pratorum* (Corbet et al., 1984). Kadmon estimated nectar refilling to be linear with time, and, following Possingham, he calculated that the regular arrivals of the whole suite of bees meant that they encountered nectar amounts 15–40% higher than would have been encountered by bees arriving at random intervals. As he lacked data on individual bees, he did not consider variation in foraging success among bees. He briefly considered mechanisms that might produce the uniform spacing of visits. Because of the large number of bees involved, he discounted the suggestion that traplining by individuals may have been responsible. Rather, he concluded that area-restricted searching accounted for the regularity of bee's arrivals at his focal flowers. Although he does not explain how this mechanism might work, we envision the following possibility: bees arriving at a full plant might work methodically through most of the flowers, draining the whole plant and rendering it for a time unattractive to subsequent visitors, who might leave the plant after visiting only one or two flowers (Thomson et al., 1982). Because Kadmon scored arrivals only at one focal flower on a many-flowered focal plant, bees that arrived while the plant's resources were depressed may have left the plant before getting to his focal flower. Therefore, plant arrivals might have been random or even clustered in time, even while focal flower arrivals were uniform, so our studies are not necessarily inconsistent.

Although our study also draws inspiration from Possingham's model, our data are different from Kadmon's, and they lead us to different questions. First, our long sequences of visits (3111 in 1994) allow us to consider patterns over an entire day. Second, our identification of individual, site-faithful foragers, which other studies on *Penstemon strictus* have shown to be traplining, naturally directs us to consider variation in foraging success among bees.

The components of temporal pattern

We obtained the consistent and striking result that the plant arrival times of all bees were essentially random, but that the departures of those same bees were clustered in time. Because visit duration depends on both arrival and departure times, the clustered departures alone would be sufficient to produce the alternating pulses of activity and lulls that struck the plant observers. However, if the arrivals of bees are truly random, and therefore independent events, it seems unlikely that coordinated movement of coherent flocks of bees could explain those pulses. Given the large number of bees involved, and assuming that their movements are largely independent, it is not hard to explain the random pattern of plant arrivals. The

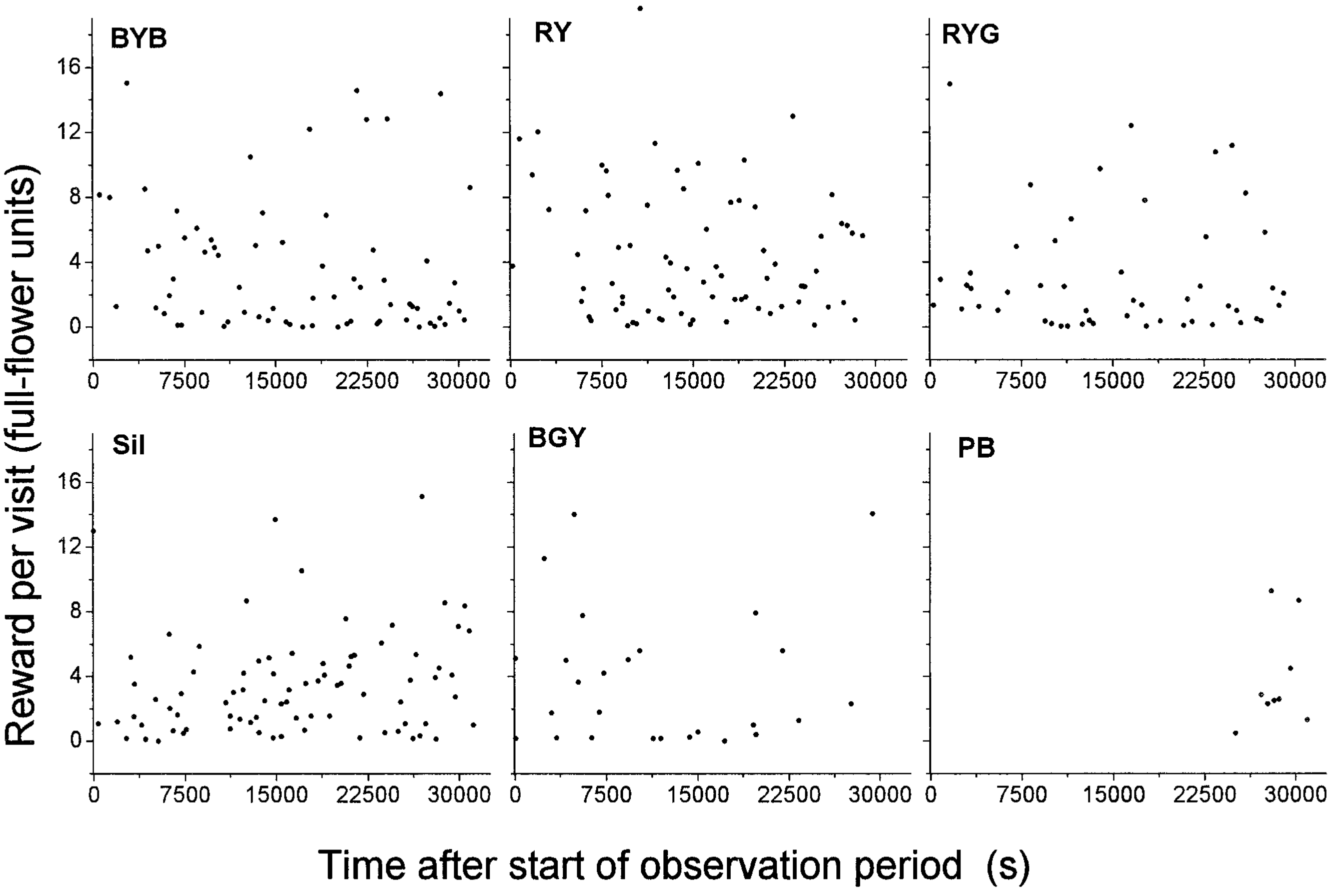

Figure 6
Estimated rewards obtained at each plant visit during the day by the six most frequent visitors, 1994 data.

temporal clustering of all departures does suggest some functional linkage among bees, however, and demands explanation. One possibility is that groups of bees leave at once because they are startled by an external stimulus, but we took care to avoid scaring the bees, and we seldom saw truly simultaneous departures. We prefer a hypothesis based on resource depression and rules for bee residence times on multiflowered plants (Cresswell, 1990; Hodges, 1985; Kadmon and Shmida, 1992; Taneyhill, 1994), as discussed above with respect to Kadmon's observations of regular arrivals at focal flowers. A multiflowered plant that has been neglected by visitors for some time will be rich; a visitor that arrives will find filled flowers and will start feeding systematically. Other visitors may then arrive independently while the first one is still working, and they too will initially encounter filled flowers. Soon, however, most flowers have been drained, and all the bees will start discovering empty flowers. Bees that arrive relatively later will likely encounter empty flowers sooner and so will move more rapidly through the plant and depart after a shorter residence. The process will produce relatively clustered departures. Even if bees do not overlap on the plant, this effect may hold. For example, bee A may find a full plant at $t = 0$, work until all the flowers are drained at $t = 100$ s, and leave. Bee B may arrive at $t = 110$ s, sample a few flowers (all still empty), and leave the plant at $t = 115$ s. The bees' departures are closer in time than are their arrivals.

Individual bees

The regularity of faithful bees remains hard to explain. Under the predictions of the analytical model (Possingham, 1989), regular foraging by a single individual that can dominate the resource dynamics will decrease reward variance and potentially increase net reward. However, no advantage accrues to a single regular individual if the overall pattern of visitation is random: there is no predictable pulse with which its regularity can coincide. Our simulation model, which was designed to supplant the analytical model with a set of assumptions better tailored to our situation, reached the same conclusion: the regular visitors did not return to the plant at better times than did casual visitors or simulated null visitors. Therefore, for this system we reject our hypothesis that traplining is advantageous because it generates regular returns to host plants.

Nevertheless, the faithful visitors, which are almost certainly traplining, do appear to extract more reward per plant visit than casual visitors (subject to our assumptions about refilling rates and complete extraction). They do this partly through greater thoroughness in visiting more flowers per plant visit, but principally through greater selectivity, choosing flowers with average higher standing crops. Bumble bees are known to be able to distinguish nectar-rich flowers from drained ones by scent (Heinrich, 1979; Marden, 1984) and can detect olfactory markings left by recent visitors (Cameron, 1981). There is no obvious reason, however, that faithful trapliners would have developed these abilities to a greater extent than other bees. It is tempting to speculate that the faithful bees are using extra information that they have gleaned during their more frequent visits. In life, if certain flowers had higher resource production rates, then it is easy to believe that very frequent visitors might learn their locations, while casual visitors would have to choose flowers without such knowledge.

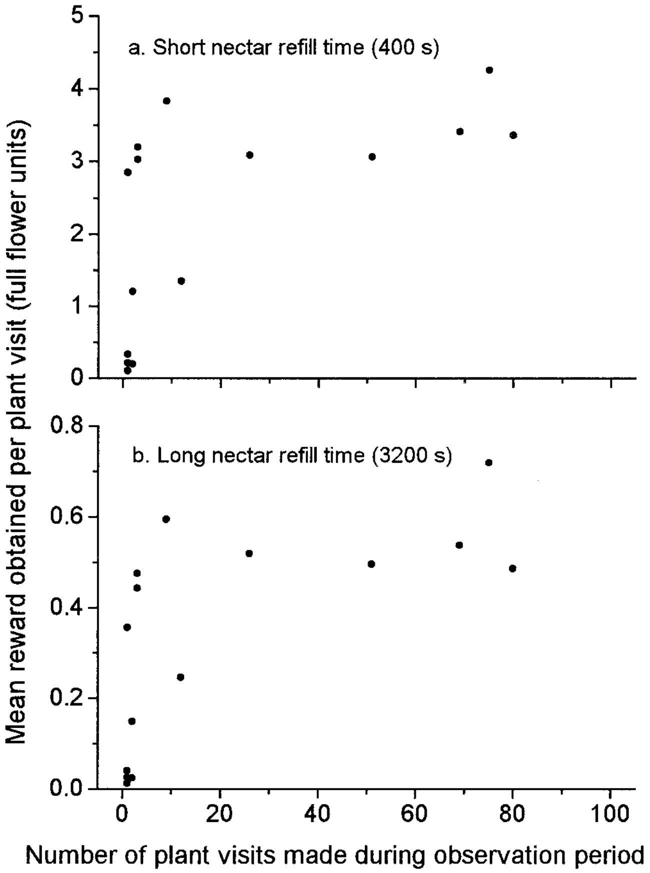

Figure 7
Plots of the mean estimated reward obtained, $R(i)$ versus visitation intensity, shown for two refill rates, 1994 data. The variance structure is similar to that in Figure 6, but here there is a significant relationship between mean $R(i)$ and intensity.

On a larger scale, Thomson (1988) showed that bumble bees do learn the locations of particularly rewarding inflorescences. This might, indeed, be an adaptive explanation for traplining within multiflowered plants. Recall, however, that our model assumed that all flowers have identical resource production characteristics. For the faithful bees to forage better than others in the model, they must be better at finding flowers that have not been recently drained. It is conceivable that they could manage this by remembering or marking which parts of the plant that they visited last.

If faithful individuals avoid flowers that they have recently visited, there will be less similarity between sets of flowers visited on consecutive pairs of plant visits than for more temporally distant pairs. This pattern would show that Pyke's rule of "avoiding revisitation" would still have some applicability even in this system characterized by traplining bees and flowers that are visited 100 times a day. For each bee, we calculated Sorenson and Baroni-Urbani and Buser similarity coefficients (S_S and S_{BU}, see Krebs, 1989) between sets of flowers visited on pairs of plant visits at lags of 1–4 visits. For example, if a bee visited the plant six times, we would calculate S for lag = 0, visits 1–2, 2–3, 3–4, etc.,

$$S_S = \frac{2a}{2a + b + c}$$

$$S_{BU} = \frac{\sqrt{ad} + a}{\sqrt{ad} + a + b + c}$$

where a = number of flowers common to both visits, b = number of flowers in visit i only, c = number of flowers in visit (i + lag) only, and d = number of flowers absent in both. The coefficients differ in assumptions about flower choice. S_{BU} considers flowers that were not visited at either lag to provide information about bee's flower choices, whereas S_S ignores unvisited flowers. We tested for changes in similarity between visit-pairs at increasing lags for each bee (Mann-Whitney U tests). Results were consistent between the two indices. There were no significant differences in S_S or S_{BU} over the first four lags, although Sil showed a nearly significant trend in the expected direction between lag 0 to 1 [$p = .064$ (S_S), $p = .058$ (S_{BU}) $n = 159$; all other bees $p > .2$ $n = 93$–151]. In *Penstemon strictus,* with such high visitation, bees do not seem to avoid their own revisitation on successive plant visits. In general, S values were low, regardless of the lag (mean S_S and S_{BU} across all lags for RY = 0.263, 0.380; Sil = 0.325, 0.398; BYB = 0.235, 0.320; RYG = 0.201, 0.301; BGY = 0.198, 0.232).

Conclusions

Although this work has revealed several interesting aspects of bee foraging on a plant with renewing resources, it has not shed much light on the functional significance of traplining. The principal hypothesis, that traplines ultimately produce benefits by returning foragers to plants at times of higher and less variable resource level, was rejected for this system. The mechanism fails simply because too many bees use each plant. Note, however, that such effects might be important in systems where a single trapliner dominates the resource dynamics. If regular foragers do no worse than other bees during intense visitation situations, as appears to be the case, and if during situations of lower visit intensity regularity produces a benefit, selection for a mechanism to produce regularity can still favor this mechanism as a general strategy. Less faithful, "random" visitors to the focal plant may also have been using a trapline but simply not including the focal plant in their core set of resources. Evidence of fixed strategies, or "rules of thumb," has been discusssed for simpler foraging decisions (Stephens and Krebs, 1986) and reported for bumble bees in other situations where it appears nonadaptive (Dukas and Real, 1993). The other advantage of traplining may lie in the way it allows a forager to become acquainted with the individual characteristics of a set of plants. Such knowledge could foster foraging efficiency by allowing the experienced forager to concentrate on more rewarding flowers within plants, as suggested above, or to drop chronically unrewarding plants and concentrate on good ones, as suggested by Thomson et al. (1982). It is possible, of course, that there is little direct advantage to traplining (repetitive, sequential visiting) per se beyond the general advantage of becoming familiar with a home space and the motor sequences required to move around in it (reviewed by Stamps, 1995).

The consequences of traplining behavior for foraging success will always be hard to quantify, even for bees, which are particularly amenable to field observations. With bees, the chief difficulties lie not in observing the animals but in measuring resource renewal dynamics of the flowers. The question of currency (pollen, nectar, or both?) is an additional complication. Because bees can be readily trained to visit artificial flowers, however, some real progress can be made with captive colonies of bumble bees, fed pollen ad libitum and visiting artificial flowers whose nectar secretion rates are controllable.

For continued work on the behavioral ecology of bees on real flowers, it will be necessary to pay particular attention to scale. As we have shown for the analysis of visit sequences (and as is commonplace in ecological sampling), the chosen time scale can determine whether a process appears regular, random, or clustered. Analogously, failing to appreciate the relationships between flower visits and plant visits can lead to muddled conclusions, particularly when trying to test theory that does not incorporate such spatial complexity. Models may treat plants as point sources that rise and fall in value, but bees are more likely to treat them as collections of flowers, each of which bears information about the whole.

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