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POLLINATOR FORAGING ON FOXGLOVE (*DIGITALIS PURPUREA*): A TEST OF A NEW MODEL

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Plant-pollinator relationships have been recognized as excellent systems in which to test optimal foraging theory (Pyke et al., 1977). In particular, Pyke (1978a, 1978b, 1978c, 1979) has considered the movements of hummingbirds and bumblebees within and among inflorescences to determine the extent to which the behavior of these organisms can be considered "optimal," i.e., that the net rate of energy gain is maximized. Pyke's (1978c, 1979) predictions of how an optimally foraging bee should behave have been based on general theoretical arguments rather than on precise quantitative considerations of the energetic "costs" and "rewards" of foraging. In addition, recent work by Waddington and Heinrich (1979) has revealed new information about the flexibility of response of foraging bees to changes in the presentation of rewards. In this paper we examine the relationship between *Digitalis purpurea* (Scrophulariaceae) and its most frequent visitor, *Bombus flavifrons dimidiatus*.

We construct a quantitative model for the foraging behavior of energy-maximizing bees on *Digitalis*, predicting where on the inflorescence bees will begin foraging, the direction of their movement, and at what flower position they will leave. We then seek to answer the following questions, raised by the model: 1) Is the spatial arrangement of nectar rewards within the inflorescence exploited by foraging bees in the manner predicted by our model? 2) Does the plant's pattern of nectar rewards

elicit bee behavior which promotes pollen transfer?

It is important to note at the beginning that we do not attempt to answer the additional question of whether the foraging behavior of *Bombus* on *Digitalis* is learned and that our tests do not allow us to measure differences in bee behavior on inflorescences with alternative reward structures. Evidence from laboratory studies of other researchers on this issue are presented in the Discussion. Because *Digitalis* is one of many genera (especially in the Scrophulariaceae) which display their flowers in a distinct vertical spike, the general findings of this paper should be applicable to many other species.

Floral Biology

Digitalis purpurea is a European biennial that is well-established in western Washington state and British Columbia. It was probably introduced into the area in the early 1800's by settlers (M. Denton, pers. comm.) and is now common along shaded roadsides and other disturbed sites. Its large, purple or white bell-shaped flowers are pollinated by bumblebees, which are by far the most common visitors. The basal rosette of leaves produces a vertical inflorescence about one meter tall that blooms for a period of about one month, from mid-June to mid-July (Fig. 1a). Individual flowers remain open for about ten days. Each day the lowest (oldest) flower on the inflorescence withers and drops and a new bud at the top of the inflorescence unfolds. The flowers are protandrous (Percival and Morgan, 1965); that is, the anthers mature first and only after they have begun to dehisce does the stigma become receptive. Thus individual

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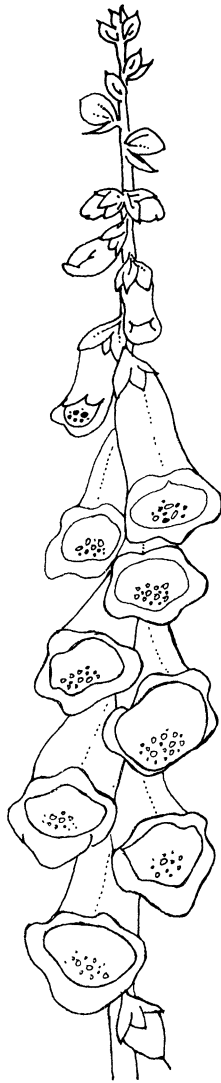


FIG. 1a. The vertical inflorescence of *Digitalis purpurea*.

flowers pass sequentially through male and female stages with little overlap. The spatial arrangement of the anthers and stigma also effectively prevents self-fertilization (Fig. 1b), though the flowers are self-compatible (Stead and Moore, 1979). Any inflorescence, then, usually consists of (from top to bottom) a cluster of closed buds, several newly-opened buds, male flowers, female flowers, and maturing seed capsules. The mean number of flow-

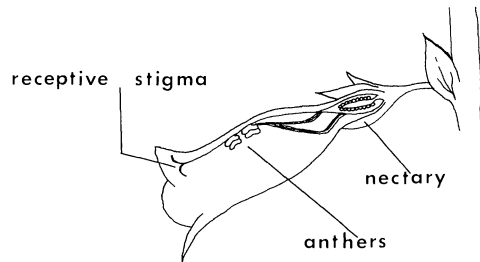


FIG. 1b. Longitudinal section through a *Digitalis* flower.

ers open at any one time is 10.0 (SD = 3.0) per inflorescence.

Since individual inflorescences had different numbers of flowers, measurements were standardized for comparative purposes by assigning each measured flower a position value from 1 to 10, with 1.0 being the position of the lowermost, oldest flower and 10.0 being the position of the most newly opened flower. Thus, on an inflorescence of nine open flowers, the fifth flower from the bottom was given a position value of 5.6.

In any individual bagged plant we found a consistent relationship between the position of the flower on the inflorescence and the caloric value of the nectar it contained; because the calorie gradient is steeper in plants with fewer flowers, relative flower position is a much better measure of expected sugar content than absolute position. Controlling for position, the calories per flower is independent of inflorescence size. For this reason all number values assigned to flowers will be their relative flower positions unless otherwise stated. The older, lower flowers contain a greater reward than the younger, upper ones (Fig. 2). Moreover, when the data from all mature plants measured were lumped together, a significant linear relationship was found (Student's *t*-test, $P < .001$) between these two variables. The considerable scatter is primarily due to interplant variance in energy resources and vigor (Fig. 3) (Fahn, 1949). Our data were collected in the middle of the blooming season, when few immature or very old inflorescences were present.

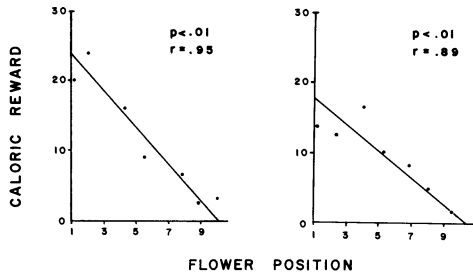


FIG. 2. The relationship between calories and flower position for two individual *Digitalis* plants. The correlations are significant ($r = .89$, $r = .95$, respectively; $P < .01$).

MATERIALS AND METHODS

We collected data in June and July of 1975, 1977, and 1978, from two populations of feral plants in Redmond, Washington, about 10 mi NE of Seattle. Nine hundred fifty-eight flowers on 116 inflorescences were examined to assess the sexual stage of flowers in various positions. A flower was judged to be male if it was in the process of shedding pollen, female if the two lobes of the stigma had begun to curl backwards, exposing the receptive surface.

Each inflorescence was enclosed by a plastic bag for 24 h prior to measurement to prevent nectar removal by animals or rain. This was judged to be sufficient time for the renewal of any nectar which might have been removed the previous day. Nectar was collected from the flowers and measured by means of capillary pipettes (Drummond "microcaps"). Once the height of the nectar in the pipette had been recorded to the nearest millimeter, some of the nectar was transferred to a Bausch and Lomb pocket refractometer to measure its sugar concentration in sucrose equivalents. *Digitalis* nectar is primarily sucrose but contains some fructose and glucose, which have about one-half the refractive index (Percival, 1961). Therefore, it is possible to measure a mixed solution in sucrose equivalents and convert the value to calories per microliter by multiplying concentration by nectar volume (Hainsworth and Wolf, 1972; Gill and

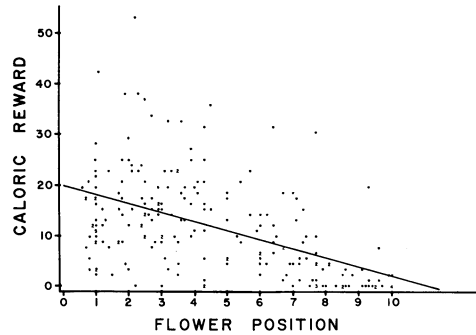


FIG. 3. The relationship between calories and relative flower position for all measured flowers. The equation for the regression line is $y = -1.70x + 20.19$, and is highly significant ($P < .001$, Student's t -test). (Numbers indicate two or more identical points.)

Wolf, 1975) and then by the caloric equivalent of sugar, 3.7 cal/mg (Heinrich, 1972). Two hundred sixteen flowers from 46 different plants were chosen randomly for measurement. The bagging and measurement were always done in midafternoon.

The movements of worker bees were observed during the same periods when nectar production was being measured, as well as on several additional dates. Movements were observed on both unprotected plants, which contained a high proportion of empty flowers, and on plants which had been protected for 24 h. Although *Bombus melanopygus*, *B. mixtus*, and *B. occidentalis* workers and both workers and males of *B. flavifrons* visited the previously bagged flowers, only measurements from *B. flavifrons* workers were used for the calculations and to test our predictions because of their much greater abundance. (It should be noted that all species follow the same general pattern of foraging.) For each visit the following data were recorded: 1) the amount of time that bees spent in each flower, 2) the traveling time between adjacent flowers on the same plant, 3) the traveling time between plants, 4) the sequence and positions of all flowers visited on a plant, 5) time of day, and 6) weather conditions. Only data from bees

foraging for nectar were included in the analysis. Finally, bees were collected and weighed while alive.

Predictions of Bee Foraging Behavior

To the foraging bee, each individual inflorescence represents a foraging patch; that is, food is found only in the inflorescence and the bee must spend time traveling between inflorescences. A foraging bee, therefore, makes three separate decisions: 1) whether or not to forage in a particular patch, 2) how to forage within an acceptable patch, and 3) when to leave the patch. The problem is similar to that posed by Charnov (1976) but is different because of the highly structured nature of each patch. We did not directly test any predictions about the first decision. Instead, we focused our efforts on how bees should forage within the inflorescence and when they should leave it.

Many complicating variables can be disregarded in the case of bees because they perform very few activities other than foraging, and the reproductive output of the colony should be directly related to the amount of food that the workers can harvest. Although pollen is the primary larval food, nectar provides the fuel that pollen-foragers need, and also fuels the workers within the hive (Pyke, 1978a). Thus, they fit the criteria for energy-maximizers (Schoener, 1971). In this system we can deal with questions of energy and time with precision. By combining the information obtained on nectar caloric value and distribution of nectar in *Digitalis* inflorescences with the data for time spent by bees harvesting nectar and flying, it is possible to calculate accurately the return that the bees may expect at each flower position on the inflorescence.

The bees averaged 3.3 sec (SE = 0.597, $N = 84$) flying between two flowers on the same plant. There was no significant difference in the times spent within the flowers at different positions on bagged plants on sunny days (interestingly, there was a negative linear correlation between flower position and time spent in the flower on

cool, overcast days); thus, the values from all positions were averaged for a mean handling time of 14.7 sec (SE = 1.12, $N = 87$, N of bees = 30). Thus, time and energy costs are approximately the same for visits to any flower and a foraging bee has a lower net energy intake the higher its position on the inflorescence. For example, at position 1 in a rewarding inflorescence (one that has not recently been visited by another bee) a foraging bee nets approximately 1 cal/sec, while at position 3 the return is down to about 0.84 cal/sec. At some position on the inflorescence a threshold will be reached at which the net energy return from continuing to forage on the inflorescence will be lower than that gained by seeking out and foraging on another rewarding plant. (In a field in which bees are actively foraging, the probability, P , that the next inflorescence encountered will have a full complement of nectar is always less than one.) The position at which the threshold is reached will vary from plant to plant; if a bee encounters a plant unusually rich in nectar, it should visit more flowers, a poor plant fewer. If it were to start in the middle of an inflorescence and move down, the risks of either visiting below average flowers or missing good ones are substantially increased and the net energy return reduced.

In addition, skipping (failure to visit each flower on an inflorescence in sequence) on a rewarding inflorescence will lower the energy intake rate because flowers on the next inflorescence visited are less likely to provide the same high return.

In summary, we can predict that in order to maximize the energy obtained per unit time, a bee should: 1) begin with the lowest flower on the inflorescence; 2) forage upward on the inflorescence; 3) avoid skipping flowers; 4) avoid revisiting flowers (because such flowers contain no available nectar); and 5) leave the inflorescence when the energy return expected in the next highest flower is lower than the average return expected from a new plant.

Because the standard flower position was found to be the best correlate of the

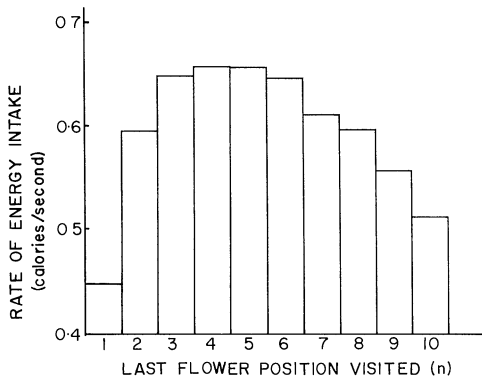


FIG. 4. The relationship between the last flower position visited on a plant and the rate of net energy intake calculated from the model. The rate is at a maximum when $n = 4$.

energy reward offered for mature inflorescences of all sizes (see Floral Biology above), we used position value to calculate the average energy intake rate as follows:

$$\text{Net energy intake rate} = \frac{P \sum_{i=1}^n E_i - E_b - PE_w(n-1) - PnE_f - E_e(1-P)}{T_b + PT_w(n-1) + PnT_f + T_e(1-P)}$$

where n is the last flower position visited by the bee (its departure point). The other parameters are defined and measured as follows:

E_i is the expected caloric reward for the i th flower position, calculated from the regression line of nectar vs. flower position.

E_b and T_b are, respectively, the energy and time expended flying between two plants. The observed bees weighed 0.20

g (SE = 0.01). Excluding times when they disappeared from sight, they spent an average of 4.4 sec (SE = 0.46, $N = 34$) flying between plants. Using an energy expenditure rate of 375 cal/g bee/h (Heinrich, 1975), $E_b = 0.09$ cal.

E_w and T_w represent the energy and time needed to fly between two flowers on the same inflorescence. Given a T_w of 3.3 sec, $E_w = 0.07$ cal.

E_f and T_f are the energy and time costs of emptying bagged flowers. The bees spent 14.7 sec in "full" flowers. Using an energy expenditure rate while walking, etc., of 29 cal/g bee/h (Kammer and Heinrich, 1974), $E_f = 0.02$ cal.

E_e and T_e are the costs of sampling "empty" flowers. Flowers from unbagged plants on which the bees visited only one flower and then left were assumed to be nearly empty. The mean time spent in such flowers was 8.9 sec (SE = 0.78, $N = 84$), which involves an energy expenditure of 0.01 cal. (Observations of bee behavior at recently drained flowers support this estimate. In 21 such visits bees spent an average 9.3 sec.)

P is the probability that a bee will encounter a plant not recently visited and drained of nectar; it was determined by the percentage of visits to unbagged plants in which bees stayed to visit at least two flowers. This approximation was checked by sampling nectar in unbagged plants to determine the number that fell in the range of rewards offered by bagged plants. $P = .375$ ($N = 192$).

We substituted all possible values of n (1–10) into the equation to determine which n yielded the maximum net energy/

TABLE 1. The effects of changes in T_f , T_b , T_e , and P on optimal n . In each case the maximum net energy intake rate is underlined.

n	Calories/second							
	$T_f = 6.8$ sec	$T_f = 25.2$ sec	$T_e = 3.5$ sec	$T_e = 16.1$ sec	$T_b = 1.7$ sec	$T_b = 7.1$ sec	$P = .25$	$P = .50$
3	0.930	0.458	0.731	0.559	0.714	0.589	0.524	0.730
4	0.991	<u>0.460</u>	<u>0.733</u>	0.589	<u>0.719</u>	0.616	0.558	<u>0.732</u>
5	<u>1.012</u>	0.451	0.717	<u>0.597</u>	0.707	<u>0.620</u>	<u>0.570</u>	0.717
6	1.008	0.436	0.693	0.591	0.684	0.611	0.568	0.693

time for the environment described by the parameters. The optimal n was found to be 4 (Fig. 4).

Some of the above field data have considerable variances. However, one advantage of this type of modeling is that it quickly points out which variations have a significant effect on the final result. A sensitivity analysis was performed by making small variations in one parameter at a time and observing any subsequent variation in the result. Given the distribution of nectar found in *Digitalis* plants, the optimal departure point is most sensitive to changes in T_b , T_e , T_f , and P . (Of course, the optimal departure point is sensitive to changes in the slope and intercept of the regression line determining nectar reward [see Fig. 3]. However, the slope may vary from -2.30 to -1.15 and the intercept from 30.0 to 15.0 without changing the optimal departure point predicted here. Over three years and among three different fields the actual range encountered was well within these limits.) Variations in T_b and P over two standard deviations and in T_e and T_f over 1.75 standard deviations can only change the optimal n from 4 to 5 (Table 1). Thus, we can predict that bees, in order to maximize the net energy return per unit time, should leave after visiting the fourth or fifth flower on a plant with ten flowers, and at the equivalent fourth or fifth flower position value in other plants.

RESULTS

The test of the predictions.—Four of our five predictions were supported by observations of bee behavior on the previously bagged plants. We predicted that the first visit should be to the lowest flower on the plant. Figure 5 shows the frequency distribution of 114 arrivals; 43.9% were to the lowest flower position, 75.4% to the lower third of the inflorescence. We predicted that bees should always move from lower positions to higher positions. 76.1% of moves on the inflorescences were to higher flowers, while 23.9% were to lower flowers ($N = 176$). We predicted that the bees should not revisit flowers.

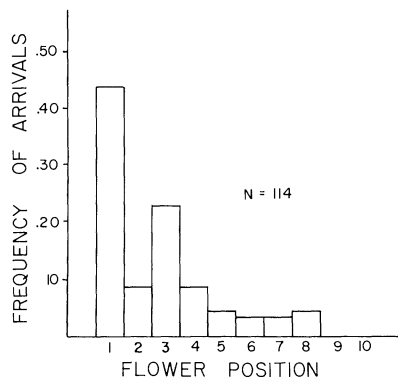


FIG. 5. Frequency distribution of arrivals of *Bombus flavifrons* on *Digitalis* inflorescences.

Only 1.3% of the observed moves ($N = 35$) were to flowers that had been visited previously by the same bee.

We also predicted that the bees should leave after visiting the fourth or fifth flower. They actually left after visiting a mean flower position of 4.55 (SE = 0.32, $N = 44$). That this was a response to reward structure and not a "fixed" behavior is illustrated by the fact that bees behaved quite differently on unbagged plants, which were exposed to bee visits throughout the day. By afternoon, 63% of the bees left these inflorescences after visiting only a single flower.

Finally, we predicted that the bees should not skip flowers. In fact, only 39.6% of moves were to adjacent flowers ($N = 134$). 43.3% of moves skipped one or two flowers, and 17.2% skipped more. Skipping results at least partly from the fact that bees tended to move straight up the stalk rather than visiting each flower in sequence in a spiral pattern. In large inflorescences (number of flowers ≥ 15), which tend to be more tightly packed, the incidence of skipping increased (see Table 2).

The plant's strategy.—The pattern of rewards offered by a plant should influence the behavior of its pollinators, and those patterns should evolve to maximize benefits to the plant. A plant benefits from pollination through the fertilization of pistillate flowers with pollen from another

TABLE 2. Incidence of skipping on large vs. small inflorescences. The difference is significant at $\alpha = 0.05$ ($\chi^2 = 5.00$, d.f. = 2).

Inflorescence size	Flowers skipped/move		
	0	1-2	3 or more
Large (flowers ≥ 15); $N = 68$	22 (32.4%)	31 (45.6%)	15 (22.1%)
Small (flowers < 10); $N = 32$	16 (50.0%)	14 (43.8%)	2 (6.3%)

plant, and the transfer of pollen from staminate flowers to stigmas of another plant. No data exist to suggest how much pollen is necessary to fertilize a female flower; Schall (1980) observed that *Bombus* carry pollen from *Lupinus texensis* farther than to the next flower they visit. In laboratory experiments, Thomson and Plowright (1980) found that most pollen picked up by *Bombus* from one *Erythronium americanum* flower was deposited within the next 10–15 flowers, although grains may be deposited sporadically on subsequent flowers, the longest carryover being 54 flowers. Our observations suggest that it is reasonable to assume that: 1) visiting one male flower leaves enough pollen on the bee to fertilize more than one female flower, and 2) pollen from the plant a bee is currently visiting generally supersedes that from the previous plant. If so, then a plant is best served if a pollinator visits at least one of its male flowers, and then first visits female flowers on the next plant, so it can deposit pollen before it is superseded by the current plant's pollen.

Flowers in positions 1 and 2 on a *Digitalis* inflorescence are almost always female, flowers in positions 3 through 7 are predominantly male, and the uppermost flowers are sexually immature (Fig. 6). The values in Figure 6 allow us to calculate the probability of pollen removal for any value of n . The probability that a bee will remove some pollen from a plant (i.e., that it will visit at least one male flower) can be expressed as:

$$\text{prob. of pollen removal} = 1 - (\text{prob. that no male flowers are encountered}).$$

Pollen removal probability increases with n ; at $n = 5$, it is already almost 1 (Table 3).

These probabilities are based on a standard inflorescence size of 10 flowers. If a plant has more flowers than that, one might expect that its probability of pollen removal would be close to unity at lower values of n . But because the switch from female stage to male stage occurs rather abruptly on the inflorescence (see Fig. 6), the actual number of flowers on an inflorescence does not affect this figure significantly. Even a plant with 20 flowers does not have a pollen removal probability of .99 until a bee reaches flower 4.5.

In summary, a *Digitalis* plant benefits when pollinators 1) visit the lowest (female) flowers on the inflorescence first, thus promoting outcrossing, and 2) visit the male flowers next, up to and including flower position 5. The reward structure of a *Digitalis* inflorescence prompts the bees to behave in just this way; if less nectar were offered in intermediate flowers or more in lower flowers, bees would not forage high enough on the inflorescence to reach male flowers. If more nectar were offered in higher flowers, bees would be "wasting" their visits (from the plant's point of view) on sexually immature flowers. And if the male flowers contained more nectar than the female ones, bees would be encouraged to visit the male flowers first. We believe that the existing pattern of nectar presentation is evidence that natural selection has favored careful regulation of the amount of reward in individual *Digitalis* flowers. Waddington and Heinrich (1979) and Pyke (1978c) suggested that this is the case in many plants. The degree to which coevolution between

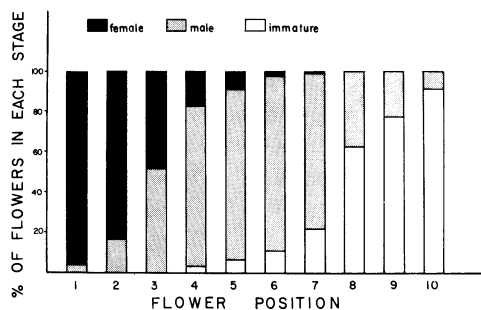


FIG. 6. The proportion of flowers in each sexual stage (male, female, immature) at each position. These proportions were used to calculate the values in Table 3.

TABLE 3. The probability of pollen removal for different values of n.

n	Probability
1	.039
2	.199
3	.613
4	.921
5	.988
6	.998
7	.999
8	.999
9	.999
10	.999

Digitalis and its pollinators has occurred is apparent in the close agreement we observed among: 1) the optimal departure point for the bees, 2) the optimal departure point from the point of view of the plant, and 3) the bees' actual departure point.

DISCUSSION

In this paper we have explored the relationship between *Digitalis* and bumblebees and presented a model for the foraging behavior of the bees based on theories of optimal foraging in "patchy" habitats. Four of the predictions are drawn from the model—that a bee will begin with the lowest flower, move up an inflorescence, avoid revisiting flowers, and leave the inflorescence at the flower position which will give the highest net energy intake rate for the habitat—are supported by the available data.

The only serious deviation from optimal foraging behavior is the skipping of flowers. One possible explanation for this behavior is that to avoid missing flowers a bee must spiral around the inflorescence, or zig-zag across it. In so doing it would be more likely to revisit flowers on the plant. This hypothesis is supported by the observation that skipping is related to the degree of complexity of the inflorescences. (Waddington and Heinrich [1979] found no skipping on extremely simple vertical arrays of nectar reward. The incidence of

skipping increases on large inflorescences of *Digitalis*.)

It is possible to calculate the cost of skipping versus that of repeating. For example, skipping in a pattern of 1-2-3-5, a bee would receive a return of 0.65 cal/sec compared to the 0.67 of a non-skipping, non-repeating bee. But repeating in a 1-2-3-2 pattern, the bee would only harvest at the rate of 0.52 cal/sec. In general, skipping is far less costly than repeating. Indeed, Pyke (1979) found that the difference in net rates of energy gain from several proposed "movement rules" for *Bombus* on *Aconitum columbianum* were almost entirely due to the difference in revisitation frequency. Pyke (1978c, 1979) suggests that bees might be using the simple "rule" of moving to the nearest flower that is vertically above them; the behavior we saw is consistent with this rule. If bees do follow this rule, then a spiral arrangement of flowers in effect provides the plant with several vertical routes for incoming pollinators, and thus makes it unlikely that one bee would drain all the flowers on a single visit. This would increase the number and genetic diversity of pollen donors and recipients.

It is noteworthy that these arguments depend upon the high cost of revisitation. This cost would be much reduced if bees could tell before entering a flower that it was depleted, as they can in several pollination systems (pers. observ.; van der Pijl, 1954; Frankie and Vinson, 1977; Kennedy, 1978; Copenhaver and D'An-

tonio, unpubl.). Modeling the conditions under which it is advantageous for plants to provide this information to pollinators would offer an excellent opportunity to test the extent to which plants can manipulate pollinator foraging to affect pollen flow.

Recent work by Waddington and Heinrich (1979), using artificial inflorescences, indicates that upward movement by bees on vertical inflorescences is stereotyped behavior, i.e., regardless of the pattern of rewards, bees usually moved up an inflorescence (although they could readily respond to varying reward structure by changing their arrival and departure points). They speculate that this tendency to move upward may be due to either their orientation when backing out of flowers and flying or negative geotaxis. However, the failure of bees to behave "intelligently" on artificial inflorescences with reverse reward structure does not mean that selection has not operated on this behavior to increase foraging efficiency. It is important to remember that flexibility in behavior can be costly in terms of mistakes made and is advantageous only as a response to changing or unpredictable circumstances. Since most, if not all, naturally-occurring vertical inflorescences have a nectar production pattern either similar to that of *Digitalis* or independent of height (Pyke, 1978a, 1978c; Robert W. Cruden, pers. comm.), there is little advantage to plasticity with respect to direction of movement, and selection would favor bees that had a tendency to move upward.

SUMMARY

We examine the relationship between *Digitalis purpurea* and its pollinators, bumblebees, and construct a model for the foraging behavior of the bees based on the theory for energy maximization in a "patchy" environment. The nectar reward in the vertical inflorescences of *Digitalis* shows a consistent pattern; the caloric value of the reward is greatest in the lowest, oldest flowers and decreases as one moves up the inflorescence. The model predicts whether or not bees should forage in a given

inflorescence, how they should forage on an acceptable inflorescence, and when they should leave a plant.

The behavior of bumblebees foraging on these inflorescences is consistent with the model. Bees begin foraging at the lowest flowers (those with the greatest reward), continue up the inflorescence, avoid revisiting flowers, and depart when the energy return expected from the next higher flower is lower than the average return expected from a new plant. Bumblebees skip flowers as they move up inflorescences with a spiral flower arrangement, thereby lowering their rate of energy intake. We suggest this behavior serves to prevent the more costly mistake of revisiting flowers.

Digitalis is protandrous; the lowermost flowers are predominantly female, and flowers 3 to 7 are male. The pattern of nectar rewards exhibited by this species encourages bees 1) to visit the female flowers first, fertilizing them with pollen from another plant, and 2) to remain on the plant long enough to remove pollen from at least one male flower, thus benefiting the plants by promoting outcrossing and increasing probabilities of pollen transfer. These findings suggest that natural selection has favored careful regulation of the amount of reward in individual *Digitalis* flowers.

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