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The effect of plant density on departure decisions: A test of the marginal value theorem

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THE EFFECT OF PLANT DENSITY ON DEPARTURE DECISIONS:

A TEST OF THE MARGINAL VALUE THEOREM

A Thesis

Presented to

The Faculty of the Department of Biology

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In Partial Fulfillment

Of the Requirements for the Degree of

Master of Arts

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by

Donald A. Cibula

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APPROVAL SHEET

This thesis is submitted in partial fulfillment of

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Donald A. Whittle
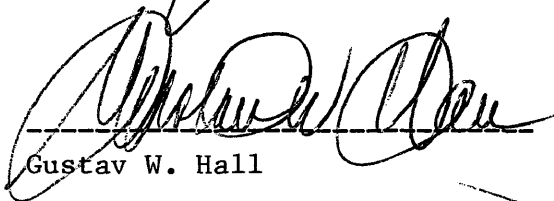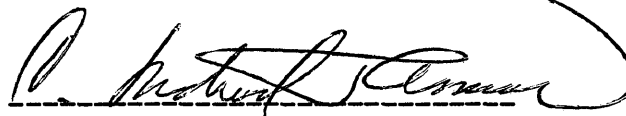
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ABSTRACT

The discrete, stochastic analog of the marginal value theorem predicts that bees should respond to increases in interplant flight costs by increasing the percentage of open flowers that they visit per inflorescence. This prediction was tested using Bombus flavifrons workers foraging for nectar in naturally occurring populations of Delphinium nelsonii. The results of these tests were consistent with the prediction. It was shown that bees also compensate for increased foraging costs by flying with greater relative frequency to nearby inflorescences. However, there was no clear-cut indication of whether bees assess flight costs directly (via interplant flight distances) or indirectly (via visual perception of plant density).

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THE EFFECT OF PLANT DENSITY ON DEPARTURE DECISIONS:

A TEST OF THE MARGINAL VALUE THEOREM

INTRODUCTION

A number of models have been developed in recent years which attempt to explain and predict various aspects of foraging behavior. Collectively, these models constitute a body of knowledge which has been termed optimal foraging theory (for reviews, see Schoener, 1971; Covich, 1976; Pyke et al., 1977). Underlying this theory is the hypothesis that animals forage in ways which maximize some measure of fitness (Pyke et al., 1977). The rate of net energy intake while foraging is usually assumed to be the relevant measure of fitness; Schoener (1971) showed that animals with either fixed energy requirements (time minimizers) or fixed amounts of time for foraging (energy maximizers) should maximize fitness when they maximize their rates of energy intake. Thus, within the range of possible foraging behaviors for a given population, the optimal foraging behavior is usually considered to be that which maximizes the rate of net energy intake.

Many animals utilize resources which occur in discrete clumps or patches. An animal which visits many patches during a foraging bout must continually decide whether to remain in its present patch or move to another. One of the questions optimal foraging theory attempts to answer is "How long should a forager remain in each patch in order to maximize its rate of net energy intake?"

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Charnov (1976) addressed this question from a theoretical standpoint and developed the marginal value theorem in order to predict when an optimally foraging animal should leave a given patch and move to another. An important assumption in this model is that a forager's rate of net energy intake decreases deterministically and continuously with time spent foraging in a given patch. This assumption is made because search time is assumed to increase as an animal removes more and more food from a patch; by feeding, the forager depresses the availability of food in that patch (Charnov et al., 1976). If an animal continues to forage in a patch after it has significantly reduced the availability of food, its rate of net energy intake will be less than the rate which it could have achieved by moving sooner to another patch. But, if a forager leaves patches too soon, it will spend too much time and energy on interpatch movements and its rate of net energy intake will again be sub-optimal. The marginal value theorem predicts that a forager will maximize its overall rate of net energy intake if it leaves a patch and moves to another when its rate of net energy intake in the present patch falls below the average rate of net energy intake for the entire habitat. A number of tests of the marginal value theorem have been carried out (Krebs et al., 1974; Cowie, 1977; Pyke, 1978a, 1982; Heinrich, 1979; Hodges, 1981; Zimmerman, 1981a; Best and Bierzychudek, 1982) and in general, the results are consistent with its predictions.

The marginal value theorem, as formulated by Charnov (1976), is only applicable to a system in which an animal's rate of net energy intake decreases deterministically and continuously with time spent

foraging in a given patch (Pyke, 1978a). Pyke (1978a, 1981) has modified the model, making it applicable to a discrete, stochastic system. An animal foraging for nectar in patches of flowers (e.g. inflorescences) constitutes one such system. In this case, food occurs at fixed, discrete points (i.e., flowers) on an inflorescence, and the amount of energy that is obtained at each flower is a random variable which may be correlated with the amount of energy obtained at a previously visited flower (Pyke, 1978a). For these conditions, the pertinent question is <u>how</u> <u>many</u> flowers per inflorescence an optimally foraging animal should visit, not <u>how</u> <u>long</u> it should stay on each inflorescence. The optimal departure rule, modified for a discrete, stochastic system, states that an optimally foraging animal should leave its present inflorescence and move to another whenever the rate of net energy intake it would expect to achieve by visiting another flower on the present inflorescence is less than the average rate of net energy intake for the entire habitat. This expected rate is obtained by dividing the time it would take to move to another flower on the present inflorescence and remove the nectar there, into the amount of energy that this flower is expected to contain. If the expected rate exceeds the average rate, a forager will maximize its rate of net energy intake by moving to another flower within the present inflorescence.

According to the discrete, stochastic analog of the marginal value theorem, foragers make departure decisions based on the outcome of a comparison between two rates: (1) the expected rate of energy intake at another flower on the present inflorescence and (2) the average rate

of net energy gain for the entire habitat. The latter rate is a function of time and energy costs for interpatch movement and changes in these costs affect departure decisions (Cowie, 1977). Specifically, if costs for interpatch movement increase, the discrete, stochastic analog of the marginal value theorem predicts that an optimally foraging animal should visit more flowers per inflorescence. If the distances between flower patches in a given habitat are increased by reducing plant density, then a forager may travel greater distances when moving between patches and thereby incur increased foraging costs (Waddington, 1980). If other factors remain constant, an increase in these costs should result in a decrease in the average rate of net energy intake for the habitat. If the average rate is lowered, a greater percentage of the flowers on inflorescences will provide energy at a rate which exceeds the standard for comparison (i.e., the average rate of net energy intake for the habitat). Thus, the discrete, stochastic analog of the marginal value theorem predicts that if the average distance between patches in a given habitat is large and flight distances are consequently longer, foragers should visit a greater percentage of open flowers per inflorescence than when the average interpatch distance is relatively small and flight distances are shorter (Zimmerman, 1981a). Zimmerman (1981a) tested this prediction using Bombus flavifrons workers foraging for nectar on Polemonium foliosissimum. He compared the mean percentage of open flowers visited per plant for two plant populations which differed significantly in density. These populations occurred at locations which are 8 kilometers apart and which differ in elevation. Zimmerman (1981a)

reported that B. flavifrons and B. bifarius workers visited nearby plants and heterospecific plants with significantly greater relative frequency at the low density site than at the high density site. However, the mean percentage of open flowers visited per plant did not differ significantly between the two sites (Zimmerman, 1981a). This result could have been obtained because uncontrolled differences (other than in plant density) between the two sites might have affected foraging behavior in such a way that differences in the mean percentage of open flowers visited per plant were masked.

The present study tested the same prediction using B. flavifrons workers foraging in naturally occurring populations of Delphinium nelsonii. In contrast to Zimmerman's (1981a) study, this prediction was tested by altering plant spacing distances at a single site. The density of a population of D. nelsonii was experimentally reduced by bagging plants with nylon netting. The percentage of open flowers that B. flavifrons workers (the primary pollinators of D. nelsonii) visited per plant was monitored as a function of plant density and mean flight distance. This design permitted comparisons in the mean percentage of open flowers visited per plant at different densities (and mean interplant distances) while eliminating any variability in foraging behavior which is attributable to difference in location.

Bumblebees are excellent experimental animals for testing optimal foraging theories. While foraging, the sole activity of the worker is to collect nectar and pollen. Therefore, it is reasonable to assume that the foraging behavior of bumblebee workers represents adaptations for collecting food only. Since workers forage for a colony,

individual variability in hunger and motivation should have minimal effect on foraging behavior. Because colony growth and reproduction are dependent on their foraging success, there should be selection for foraging behavior that maximizes the rate of net energy intake.

Delphinium nelsonii was chosen for this study because resource presentation in this species meets all of the criteria of the discrete, stochastic model for optimal departure decisions. It is an herbaceous species which bears flowers on a single vertical inflorescence. Thus, each plant or inflorescence may be considered to be a single, discrete patch. Plants are self-compatible and protandrous (Pyke, 1978b). There is a negative correlation between height of a flower on the raceme and standing crop of nectar (Pyke, 1978b). Bees exhibit stereotypic behavior when foraging on this plant, commencing at bottom flowers and moving up the vertical inflorescence (Pyke, 1978b). Given the correlation and systematic movement just described, it is possible that a bee foraging on a given D. nelsonii inflorescence can accurately estimate the rate of net energy intake it may expect at any flower on that inflorescence. In short, it is expected that bees foraging for nectar on D. nelsonii could use the departure rule predicted by the discrete, stochastic analog of the marginal value theorem. If indeed they do, this result would be consistent with previous studies which show that B. flavifrons workers optimize other parameters when foraging on D. nelsonii. It has been shown that the movement patterns of B. flavifrons workers flying between (Pyke, 1978c) as well as within (Pyke, 1979) D. nelsonii inflorescences are those patterns which are thought to be optimal. In addition, Hodges

(1981) and Zimmerman (1982) have shown that the departure decisions made by B. flavifrons workers in response to the standing crops of nectar encountered on D. nelsonii inflorescences are consistent with predictions from the marginal value theorem.

METHODS

Fieldwork was conducted during June and July, 1980, at two sites. The first study was conducted at Horse Ranch Park (elevation 2,743 meters), an open meadow in the Gunnison National Forest, 19 kilometers west of Crested Butte, Colorado. A second, similar study was conducted in a meadow at Kebler Pass (elevation 3,048 meters), 11 kilometers west of Crested Butte.

A study plot was established in dense, non-clumped populations of D. nelsonii at both sites. The plot at Horse Ranch Park was 11 square meters while that at Kebler Pass covered 20 square meters. All D. nelsonii plants within the plots were marked by tying two differently colored pieces of embroidery thread to their stems. Thus, each plant could be identified by its unique color code. X and Y coordinates were measured for each plant within the plots and its location was plotted on a map. The number of open flowers on each inflorescence was counted every other day.

Bombus flavifrons workers were observed as they foraged for nectar within the study plots. As a bee flew from plant to plant, the color codes of the plants which were visited and the number of flowers visited were recorded. Using the plant maps and flower census data, foraging bouts were recreated and the percentage of open flowers that the bee visited per plant, flight distances, distance ranks of visited

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plants and interplant spacing distances were determined. Interplant distance was measured as the distance between a plant and the nearest plant which had at least one open, available flower. The distance rank of a visited plant indicates whether that plant was the closest or second, third, etc., closest neighbor of the plant which had just previously been visited.

The experiments can be divided into three distinct phases. During phase I, foraging bouts were observed under the naturally occurring plant densities. During phase II, the density of D. nelsonii was reduced by bagging (with nylon netting) a fraction of the populations in the plots. The bagged plants were chosen randomly, using a random numbers table. This netting prevented bees from visiting flowers. Therefore, bagged plants were considered to have no available flowers and were not measured during this phase. Foraging bouts were then observed under these experimentally reduced densities. All plants were then unbagged and again, foraging bouts were observed (phase III).

RESULTS

The mean interplant distances at Kebler Pass (Table 1) differ significantly between phases (k-sample van der Waerden test; $W = 6.36$; 2 df; $p = 0.042$; $N = 395$). Since plants were bagged during phase II, one would expect that the mean interplant distance for the experimental period would be significantly greater than the means for the controls (phases I and III). This expectation was met in part; Table 2 shows that the mean interplant distance for phase II is significantly greater than that for phase I, but is not significantly greater than the mean for phase III. Contrary to the design of the experiment, unbagging plants at Kebler Pass did not restore plant spacing distances to their original values; the mean interplant distance for phase III is 9.1 percent greater than the mean for phase I. The reason for this is flower senescence; in the six days between phase I and phase III, 15.9 percent of the plants in the plot lost all flowers. Flower mortality increased plant spacing distances enough to make the difference in mean interplant distance between phases II and III non-significant.

At Horse Ranch Park, the means for interplant distance (Table 1) do not differ significantly between phases (k-sample van der Waerden test; $W = 1.35$; 2 df; $p = 0.509$; $N = 468$); thus, bagging did not produce the intended results. Bagging increased the mean interplant distance by 8.3 percent (relative to the phase I value). This increase

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is much smaller than the corresponding increase at Kebler Pass (42.7 percent) and was the result of bagging a relatively small fraction of a population which had relatively high density. 51.8 percent of the plants at Kebler Pass were bagged while 32.0 percent were bagged at Horse Ranch Park. Since plant density before bagging at Horse Ranch Park was nearly twice as high as that at Kebler Pass (Table 1), the fraction of plants bagged at Horse Ranch Park was too small to significantly increase plant spacing distances.

Since the mean interplant distance for phase II at Kebler Pass is significantly greater than that for phase I, one might expect that bees flew greater distances between plants during the experimental period than during phase I. This expectation was not met. Although the means for flight distance (Table 1) differ significantly between phases (k-sample van der Waerden test; W = 10.66; 2 df; p = 0.005; N = 125), the mean for phase II is significantly smaller than the means for phases I and III (Table 2). This is exactly opposite the expected result. A k-sample van der Waerden test shows that the means of the frequency distributions of the distance ranks of visited plants (Table 1) differ significantly between phases (W = 8.63; 2 df; 0.025 > p > 0.01; N = 122;). Post hoc contrasts indicate that the mean distance rank of visited plants for phase II is significantly smaller than that for phase I (Table 2). When plant spacing distances were significantly greater, bees flew with greater relative frequency to nearby plants. Bees also visited nearby neighbors with significantly greater relative frequency during phase II than during phase III (Table 2) even though mean interplant distance did not differ significantly between these two

phases. However, the mean interplant distance for the experimental phase was substantially (30.8 percent) greater than that for phase III. This increase is comparable to that observed between phases I and II (42.7 percent) and it may have been large enough to trigger the same response (i.e., increased visitation of nearby plants) as a statistically significant increase in mean interplant distance.

The mean interplant distances at Horse Ranch Park do not differ significantly between phases. Bagging increased plant spacing distances by only 8.3 percent (relative to the phase I value). Since this increase is relatively small, one might not expect the mean flight distances to differ significantly between phases and indeed, they do not (k-sample van der Waerden test; $W = 1.96$; 2 df; $p = 0.375$; $N = 116$). The means for distance ranks of visited plants also do not differ significantly between phases (k-sample van der Waerden test; $W = 5.93$; $0.10 > p > 0.05$; $N = 124$). Except for phase II versus III at Kebler Pass, when interplant distances did not differ significantly, bees did not change their pattern of flight distances relative to the plant spacing distances they encountered.

At Kebler Pass, the percentage of open flowers that bees visited per plant is not independent of the number of open flowers on a plant ($x^2 = 24.87$; 4 df; $p < 0.005$; $N = 145$). A test for trend shows that bees visited lower percentages of the flowers on plants having fewer open flowers than on plants with larger numbers of open flowers; the percentage of open flowers visited per plant decreases monotonically with the number of open flowers per plant ($\hat{\beta} = -0.430$; $x^2 = 22.61$; $p < 0.005$; $N=145$). Departure from monotonicity is not significant ($x^2 =$

2.26; 3 df; p > 0.10; N = 145). A similar relationship has been shown to exist for two hummingbird species (Selasphorus platycercus and S. rufus) foraging for nectar on Ipomopsis aggregata (Pyke, 1978a). Since the percent of open flowers visited per plant is not independent of the number of open flowers available, if the mean number of open flowers on visited plants changed during the course of the experiment, one might expect changes in mean percentage of open flowers visited per plant which cannot be attributed to increased interplant flight costs. At Kebler Pass, the mean number of open flowers on of visited plants (Table 1) does differ significantly between phases (k-sample van der Waerden test; W = 6.62; 2 df; 0.05 > p > 0.025; N = 148). To eliminate the confounding effects of changes in the mean number of open flowers per plant, this variable was treated as a covariate and analysis of covariance was used to determine whether or not the mean percent of the open flowers visited per plant differs between phases. Variance due to changes in the numbers of available flowers on visited plants was removed prior to determining variance due to interplant flight distance (the main effect).

A covariate analysis of the Kebler Pass data indicates that the means for percentage of open flowers visited per plant differ significantly between phases (Table 3). A Student-Newman-Keuls test (α = 0.05) shows that, contrary to prediction, bees visited, on average, significantly greater percentages of the open flowers per plant (Table 1) during the experimental phase than during phases I and III. The adjusted means for the control phases do not differ significantly.

It has been shown that mean flight distances do not differ significantly between phases at Horse Ranch Park. Therefore, one would not expect the adjusted means for percentage of open flowers visited per plant to differ significantly between phases. Covariate analysis indicates that indeed, they do not differ significantly (Table 4).

Data from Kebler Pass and Horse Ranch Park were combined in order to test for a correlation between the means of flight distance and the percentage of open flowers that bees visited per plant. For reasons discussed below, the data from phase II at Kebler Pass were excluded from this analysis. Preliminary correlations indicated a significant, negative relationship between the percentage of open flowers visited per plant and the number of available flowers per plant ($r = -0.435$; $p < 0.001$; $N = 171$) as well as a significant correlation between mean flight distance and mean interplant distance ($r = 0.3936$; $p < 0.001$; $N = 171$). If the means of interplant distances or number of open flowers on visited plants differ significantly between phases in the combined data, a correlation between the percentage of open flowers visited per plant and mean flight distances could be spurious. Thus, a partial correlation, controlling for the effects of changes in the mean number of open flowers per plant and for interplant distance, was indicated. The results of this test show that there is a significant, positive relationship between the means of flight distance and the percentage of open flowers that bees visited per plant ($r = 0.142$; $p = 0.032$; $N = 169$). As one would predict, during phases in which mean flight distances were greater, bees visited larger percentages of the open flowers per plant than during phases in which the mean flight

distances were smaller.

To test further for the existence of an overall trend in the percent of open flowers visited per plant with increases in mean flight distance, the sign of the difference in the adjusted mean percentage of open flowers visited per plant was calculated for a pair of phases in the combined data (excluding phase II at Kebler Pass). Then, the sign of the difference in mean flight distance was determined for the same pair of phases. The signs of the differences were compared. One would predict that if the mean flight distance increased between a given pair of phases (i.e., the difference was negative), then the mean percentage of open flowers visited per plant should have likewise increased for that pair of phases. Conversely, if the mean flight distance decreased between a given pair of phases (i.e, the difference was positive), one would predict a corresponding decrease in the mean percentage of open flowers visited per plant. This procedure was carried out for all non-redundant pairs of phases in the combined data. For 9 of the 10 pairs, the sign of the difference in the adjusted means for percent of open flowers visited per plant matches the sign of the difference in the means for flight distance. A binomial probability test shows that this trend is highly significant (p = 0.011, one-tailed).

The combined data (excluding phase II at Kebler Pass) were also used to test for a correlation between the percentage of open flowers visited per plant and mean interplant distance (per phase). Since the number of open flowers per plant has been shown to be negatively correlated with the percentage of open flowers visited per plant, a partial correlation controlling for the effects of changes in the mean

number of open flowers per plant was run. The results show that the percentage of open flowers visited per plant is positively correlated with mean interplant distance ($r = 0.1312$; $N = 170$; $p = 0.043$); bees visited greater percentages of open flowers per plant when plant spacing distances were large than when they were smaller.

DISCUSSION

The prediction that bees should respond to increased plant spacing distances by visiting greater percentages of the available flowers on inflorescences is based on the assumption that interplant distance and (therefore) interplant flight costs are greater when plant spacing distances are large than when they are small. In this study, mean interplant distances were positively related to mean flight distances, with the exception of the experimental phase at Kebler Pass. Recall that during this phase, mean interplant distance was the greatest, but the mean flight distance was the smallest. Thus phase II at Kebler Pass does not meet the planned experimental conditions for testing the prediction, and for this reason, it will be regarded as a special case and discussed separately below.

Mean interplant distances did not differ significantly between phases at Horse Ranch Park. Since bees did not alter their pattern of flight distances relative to the plant spacing distances they encountered, one would not expect mean flight distances to differ significantly between phases at this site and indeed, they did not. If all else was constant during the study, one can assume that the bees' average rates of net energy intake did not differ significantly between phases. Thus, the discrete, stochastic analog of the marginal value theorem predicts that the percentage of open flowers that bees visit

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per plant should not differ significantly between phases at Horse Ranch Park. The results of the covariate analysis are in accord with this prediction. One can also assume that the mean rates of net energy intake for phases I and III at Kebler Pass did not differ significantly. As the model predicts, the means for percentage of open flowers visited per plant did not differ significantly between these phases. It should be noted, however, that statistical significance does not necessarily imply biological significance. The reverse may also be true; statistically non-significant changes in mean flight distances may be meaningful to bees and may trigger measurable changes in foraging behavior which, although not statisticlly significant, are nevertheless real. The significant, positive correlation between mean flight distances and the percentage of open flowers that bees visited per plant (during phases in the combined data which did not differ significantly in mean percentage of open flowers visited per plant) supports this contention. In addition, this overall trend is in the direction predicted by the discrete, stochastic analog of the marginal value theorem; when flight distances were great (and flight costs were high), bees visited, on average, greater percentages of open flowers per plant than they did when flight distances were small (and flight costs were low). Only once in 10 cases did an increase in mean flight distance (between pairs of phases in the combined data) occur without an accompanying increase in the mean percentage of open flowers visited per plant. Thus, bees appear to be responding to statistically non-significant changes in mean flight distance. Although their response did not produce significant changes in the mean percentage of

open flowers that they visited per plant, the results of the partial correlation and binomial probability test indicate that non-significant changes in the percentage of open flowers visited per plant are part of an overall trend which is in the predicted direction and is statistically significant. This significant trend suggests that bees are indeed using the departure rule proposed by Pyke (1978a).

Despite the fact that plant spacing distances were the greatest during the experimental phase at Kebler Pass, bees flew, on average, significantly shorter distances during this phase than during the control periods. If reduced flight distances necessarily imply lowered foraging costs, interplant flight costs may have been lowest during phase II (instead of being highest, as called for in the experimental design). Therefore, one could assume that bees actually had the highest rates of net energy intake during the experimental phase. If this assumption is valid, the discrete, stochastic analog of the marginal value theorem predicts that bees should have visited smaller percentages of the available flowers on plants during phase II than during phases I and III. The results at Kebler Pass were not consistent with this prediction; the mean percentage of open flowers visited per plant during the experimental phase was significantly greater for phase II than for the control phases. Two possible explanations for this result are proposed below.

First, the assumption that bees had the highest overall rates of net energy intake during the experimental phase may not be valid. Recall that flight distances were shorter during phase II, not because interplant distances were shorter, but because bees visited nearby

plants with greater relative frequency during the experimental phase than during the control phases. For bees foraging for nectar on D. nelsonii, this response may actually lower the average rate of net energy intake, even though it serves to reduce foraging costs.

It has been shown (Pleasants and Zimmerman, 1979; Zimmerman, 1981b) that the dispersion pattern of standing crops of nectar in D. nelsonii is patchy; thus, a population consists of localized areas containing plants with similiarly high nectar rewards ("hot spots") and other areas within which all plants have similarly lower rewards ("cold spots"). Furthermore, Pyke (1978c) has shown that under such conditions bees should maximize their rates of net energy intake by increasing their turning angles and flying short interplant distances after encountering high reward plants. These responses increase the probability that bees will remain in areas of high reward. Conversely, bees should avoid low reward areas by reducing their turning angles and flying long distances after encountering plants with low rewards. However, when plant spacing distances are relatively large (as for phase II at Kebler Pass), bees may not base interplant flight distances on the quality of reward, but instead, attempt to cut potentially high flight costs by visiting nearby plants with higher frequency. Zimmerman (1981a) has demonstrated that B. flavifrons workers foraging for nectar on P. foliosissimum respond to increased plant spacing distances in a similar way. Pleasants and Zimmerman (1979) have shown that the proportion of plants with large standing crops of nectar to those with small standing crops in D. nelsonii populations is low. If one assumes that this proportion remained constant during the course of

the study at Kebler Pass, then by increasing the relative frequency of visits to near neighbors, bees may have remained longer in cold spots and visited a greater percent of low reward plants during phase II than during the control phases. Thus it is possible that bees had the lowest average rates of net energy intake during the experimental period. If so, then the fact that the mean percentage of open flowers visited per plant is significantly greater for phase II than for the controls is consistent with the optimal departure rule proposed by Pyke (1978a).

If the increase in the relative frequency of flights to close neighbors (which was observed during the experimental phase at Kebler Pass) does lower the average rate of net energy intake for the habitat, why would selection maintain this response to low density? One possible reason is that if bees foraging on D. nelsonii always based the lengths of their interplant flights on nectar reward, then when plant spacing distances were great, bees might have to fly much farther in order to avoid low reward areas than they would under higher density conditions. The high flight costs associated with this "strategy" might lower the average rate of net energy intake even more than failing to avoid low reward areas. Thus, the response which has been demonstrated to be optimal when interplant distances are within normal ranges (Pyke, 1978c) may be sub-optimal when plant density is very low. One would expect that selection would maintain behavioral flexibility which allows bees to maximize their rates of net energy intake under changing environmental conditions.

So far, the results of this study have been interpreted under the

assumption that bees directly assess their costs of interplant flights (based on their actual flight distances) and that their overall rates of net energy intake are partly based on this assessment. Thus, in testing the hypothesis that bees should respond to increased foraging costs by visiting greater percentages of open flowers per plant, greater mean flight distances were assumed (except for phase II at Kebler Pass) to be indicative of lower overall rates of net energy intake. Under this assumption, the results were consistent with the hypothesis. Recall however, that the the results at Kebler Pass were consistent only if it was assumed that short flight distances actually lowered the overall rate of net energy intake under the low density conditions in phase II.

It is possible, however, that bees do not assess flight costs based on their actual flight distances but rather, use plant spacing distances as an index of potential foraging costs. Thus, bees may indirectly estimate their average rates of net energy intake for the habitat based partly on a visual assessment of interplant distances. Under this assumption, the discrete, stochastic analog of the maginal value theorem predicts that bees should respond to increases in mean interplant distance by increasing the percentage of open flowers that they visit per plant. When plant spacing distances and flight distances are positively correlated (as they are for all phases except phase II at Kebler Pass) the predicted responses to changes in mean interplant distance are identical to those predicted for changes in mean flight distance. Thus, although the significant, positive partial correlation between mean interplant distance and the percentage of open

flowers visited per plant is consistent with the optimal departure rule, it provides no information on whether changes in mean interplant distance or mean flight distance are the causal factor. However, if one assumes that bees are responding to plant density rather than flight distances, one may propose a second explanation for the results at Kebler Pass. Bees may have significantly increased the percentage of open flowers that they visited per plant during phase II because plant spacing distances were larger during this phase and thus the estimated average rate of net energy intake was lower. Simultaneously, bees may have increased the relative frequency of visits to nearby plants as a second, independent means of compensating for the estimated increase in foraging costs.

For those phases in which flight distances are positively correlated with interplant distances, the experimental results suggest that bees do respond to changes in foraging costs in the manner predicted by the discrete, stochastic analog of the marginal value theorem. If smaller flight distances necessarily imply reduced foraging costs, then the results for phase II at Kebler Pass are not consistent with the prediction. There are at least two possible explanations for this apparent inconsistency; (1) for bees foraging on D. nelsonii, shorter flights may not necessarily increase the average rate of net energy intake because of the presence of "cold" spots in these plant populations; (2) bees may not assess flight costs via flight distances but rather, via their visual perception of plant spacing distances. The results at Kebler Pass point out the need for further experimental work on how bees actually assess foraging costs.

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TABLE 1

Means for variables measured at Kebler Pass and Horse Ranch Park.

	KEBLER PASS			HORSE RANCH PARK		
	Phase			Phase		
	I	II	III	I	II	III
Interplant distance (m.)	0.110	0.157	0.120	0.125	0.131	0.134
Plant density (no. plants/m.)	8.50	4.10	7.15	16.18	11.00	13.55
Flight distance (m.)	0.468	0.322	0.768	0.541	0.622	0.418
Distance ranks of plants	7.67	3.03	7.55	19.54	18.54	11.19
Size (no. open flowers/plant)	3.78	3.51	3.33	3.85	3.04	3.42
Percent flowers visited	42.80	54.67	45.65	50.19	52.40	45.05

TABLE 2

Results of simultaneous post hoc confidence interval procedures (subsequent to van der Waerden tests) for pair-wise comparisons of the mean ranks for normal scores. Values shown represent 95 percent confidence intervals for the comparisons. Confidence intervals which do not include zero are significant. Comparisons are for Kebler Pass only.

Phases compared	Interplant distance	Flight distance	Distance ranks of visited plants
I vs II	-0.334+0.324*	0.05+0.48*	-0.45+0.45*
I vs III	-0.104+0.274	-0.28+0.60	0.17+0.57
II vs III	0.230+0.033	-0.78+0.64*	0.62+0.61*

* significant at   = 0.05

TABLE 3

Results of analysis of covariance used to test null hypothesis that the means for percentage of open flowers visited per plant do not differ between phases. Plant size (number of open flowers on visited plants) was used as a covariate. Data are from Kebler Pass.

Source of Variation	df	SS	MS	F	p
Covariate: Plant size	1	0.724	0.724	18.98	0.000
Main effect: Phase	2	0.369	0.185	4.84	0.009
Explained	3	1.093	0.364	9.55	0.000
Residual	125	4.770	0.038		
TOTAL	128	5.863	0.046		

TABLE 4

Results of analysis of covariance used to test null hypothesis that the means for percentage of open flowers visited do not differ between phases. Plant size (number of open flowers on visited plants) was used as a covariate. Data from Horse Ranch Park.

Source of Variation	df	SS	MS	F	p
Covariate: Plant size	1	1.397	1.397	29.12	0.000
Main effect: Phase	2	0.089	0.044	0.93	0.399
Explained	3	1.486	0.495	10.32	0.000
Residual	122	5.835	0.048		
TOTAL	125	7.339	0.059		