Nordic Society Oikos

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Source: *Oikos*, Vol. 43, Fasc. 2 (Jul., 1984), pp. 154-158
Published by: Wiley on behalf of Nordic Society Oikos
Stable URL: http://www.jstor.org/stable/3544763
Accessed: 16/09/2014 11:12

OIKOS 43: 154–158. Copenhagen 1984

The effect of plant density on departure decisions: testing the marginal value theorem using bumblebees and Delphinium nelsonii

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Cibula, D. A. and Zimmerman, M. 1984. The effect of plant density on departure decisions: testing the marginal value theorem using bumblebees and *Delphinium nelsonii.* – Oikos 43: 154–158.

The discrete, stochastic analog of the marginal value theorem predicts that bumblebees should respond to increases in interplant distance by increasing the percentage of open flowers visited per inflorescence. This prediction was tested using *Bombus flavifrons* workers foraging for nectar in naturally occurring populations of *Delphinium nelsonii.* Results suggest that bumblebees respond as predicted to reductions in plant density. However, under experimental conditions, bees compensated for potentially high flight costs by visiting neighboring plants with increased relative frequency, thus reducing actual flight expenses. This result suggests that bumblebees may not assess flight costs directly, but rather, use plant density to estimate potential foraging costs. At times, this method of assessment could yield an overestimate of foraging costs, resulting in sub-optimal departure decisions.

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Дискретный стохастический аналог теоремы краевой величины предсказал чувствительность шмелей к увеличениям расстояний между растениями, проявляющуюся в повышении процента открытых цветков, посещаемых на одном соцветии. Это предсказание проверяли с помощью рабочих особей *Bombus flavifrons* собиравших нектар на природных популяциях *Delphinium nelsonii*. Результаты показали, что шмели реагируют, как было предсказано, на снижение плотности растений. Однако, в экспериментальных условиях шмели компенсировали потенциально высокие затраты на полет посещением соседних растений с повышающейся осноcительной частотой, уменьшая таким образом фактические затраты на полет. Эти исследования показали, что шмели не могут непосредственно регулировать траты на полет но, скорее, используют плотность растений для расчета потенциальных трат на фуражировку. Иногда этот способ может привести к переоценке трат на фуражировку, что приводит к субоптимальным отклонениям.

Accepted 14 September 1983

Introduction

Many animals utilize resources that occur in discrete clumps or patches. An animal that visits many patches during a foraging bout must continually decide whether to remain in the 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 (RNEI)?

Charnov (1976) addressed this question from a theoretical standpoint and developed the marginal value theorem to predict when an optimally foraging animal should leave a given patch and move to another. The model assumes that by feeding, a forager depresses the availability of food in a patch (Charnov et al. 1976), thus lowering its RNEI below what it could have achieved by an earlier move to another patch. But, if moves are made too soon too much time and energy are spent on interpatch travel yielding a sub-optimal RNEI. 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, 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 RNEI decreases deterministically and continuously with time spent foraging in a given patch (Pyke 1978a). Pyke (1978a, 1981) modified the model, making it applicable to a discrete, stochastic system such as animals foraging for nectar in patches of flowers (e.g. inflorescences). In this case, food occurs at fixed, discrete points (i.e. flowers) on an inflorescence, and the amount of energy obtained at any flower may be correlated with the amount of energy obtained at a previously visited flower (Pyke 1978a). The pertinent question is thus how many flowers per inflorescence an optimally foraging animal should visit, not how long it should stay on each inflorescence.

The average RNEI for the habitat is a function of time and energy costs of interpatch movement and thus changes in these costs affect departure decisions (Cowie 1977). As costs of interpatch movement increase, the discrete, stochastic analog of the marginal value theorem predicts that an optimally foraging animal should visit more flowers per patch because of three related variables. 1) As the distances between flower patches in a given habitat increase, a forager may travel greater distances when moving between patches and, thus, incur increased foraging costs (Waddington 1980). 2) If other factors remain constant, an increase in these costs should result in a decrease in the average RNEI for the habitat. 3) As this rate is lowered, there will be an increase in the number of flowers within any patch at which the expected RNEI exceeds the overall habitat rate. The purpose of our research was to test this departure prediction with *Bombus flavifrons* workers foraging in a naturally occurring population of *Delphinium nelsonii* whose density has been experimentally manipulated.

D. nelsonii is an ideal species for this test because resource presentation meets all of the criteria of the discrete, stochastic version of the marginal value theorem. It is an herbaceous species bearing flowers on a single vertical inflorescence. Thus, each plant or inflorescence may be considered to be a single, discrete patch. 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 species, commencing at bottom flowers and moving up the vertical inflorescence (Pyke 1978b). Given these nectar patterns and systematic bee movements, it is possible for bees to estimate the RNEI expected from any flower on an inflorescence. It is thus 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. Such behavior would be consistent with previous studies showing that *B. flavifrons* workers flying between (Pyke 1978c), as well as within (Pyke 1979), *D. nelsonii* inflorescences are, in fact, foraging optimally. In addition, Hodges (1981) and Zimmerman (1983) 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 optimal foraging theory.

Methods

Fieldwork was conducted during June and July, 1980, at Kebler Pass (elevation 3048 m a.s.l.), a montane meadow in Gunnison National Forest, 11 km W of Crested Butte, Colorado. A 20 m^2 study plot was established in a dense population of *D. nelsonii.* All *D. nelsonii* plants within the plot were distinctively marked by tying colored pieces of embroidery thread to their stems and their locations were mapped. The number of open flowers on each inflorescence was counted every other day.

B. flavifrons workers were observed as they foraged for nectar within the study plot. As a bee flew from plant to plant, the color codes of visited plants and the number of flowers visited were recorded. Using plant maps and flower census data, foraging bouts were recreated and the percentage of open flowers visited per plant, flight distances, nearest neighbor status of visited plants and interplant spacing distances were determined. Interplant distance was measured as the distance between a plant and the nearest conspecific individual having at least one open, available flower. The nearest neighbor status of a visited plant indicates whether that plant was the closest or second, third, etc., closest neighbor of the plant just visited.

The experiment was divided into three phases. During phase I, foraging bouts were observed under naturally occurring plant densities. During phase II, density of *D. nelsonii* was reduced by randomly bagging (with nylon netting) a fraction of the population. Because the netting prevented bees from visiting flowers, bagged plants were considered to have no available flowers and were not censused during this phase. Foraging bouts were observed under this experimentally reduced density. All plants were then unbagged and again, foraging bouts were observed (phase III).

Results

Bagging plants reduced density by 51.8% relative to phase I and 42.7% relative to phase III. The mean interplant distances (Tab. 1) differ significantly among phases (k-sample van der Waerden test (Marascuilo and McSweeney 1977); $W = 6.36$; 2 df; $P = 0.042$; $N = 395$). 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 (Tab. 1). Contrary to the design of the experiment, unbagging plants did not quite restore plant spacing to their original values. Flower mortality over the course of the study reduced plant density and resulted in non-significant differences in interplant distances between phases II and III.

The percentage of open flowers that bees visited per plant is not independent of plant size (i.e. the number of open flowers on a plant) ($\chi^2 = 24.87$; 4 df; $P < 0.005$; $N = 145$). A test for trend shows that bees visited higher percentages of flowers on small plants than on larger plants. The percentage of open flowers visited per plant decreases monotonically with plant size ($\hat{\beta} = -0.430$; $\chi^2 = 22.61$; $P < 0.005$; $N = 145$). Departure from monotonicity is not significant ($\chi^2 = 2.26$; 3 df; $P > 0.10$; $N = 145$). The mean size of visited plants (Tab. 1) differs significantly among phases (k-sample van der Waerden test; $W = 6.62$; 2 df; $0.05 > P > 0.025$; $N = 148$) so plant size was treated as a covariate and analysis of covariance was used to determine whether the mean percentage of open flowers visited per plant differed among phases. Variance due to size class was removed prior to determining variance due to interplant distance (the main effect).

The mean percentage of open flowers visited per plant differs significantly among phases (Tab. 2). As predicted, during phase II, when plant density was decreased and interplant distances were significantly increased, bees visited a greater percentage of open flowers per plant relative to both controls (Student-Newman-Keuls test; $P < 0.05$). The two controls did not differ significantly from one another (Tab. 1).

The departure decision prediction assumes a positive relationship between interplant distance and bumblebee flight distances. During phase II this assumption was not met. Mean flight distances for phase II were, in fact, significantly shorter than the means for both phases I and III (Tab. 1), implying that bees flew to nearby plants with greater relative frequency during phase II. A k-sample van der Waerden test shows that the means of the frequency distributions of the nearest neighbor status of visited plants (Tab. 1) differ significantly among phases ($W = 8.63$; 2 df; $0.025 > P > 0.01$; $N = 122$). A posteriori tests indicate that the mean nearest neighbor status of visited plants for phase II is significantly smaller than those for both phase I and III. The mean interplant distance for phase II was, however, substantially greater (30.8%) than that for phase III, and may have been large enough to trigger the same response by bees.

Tab. 1. Means and sample sizes for variables measured at Kebler Pass.

	Phase		
	I	II	III
Interplant distance (m)	0.110^{a} N = 170	0.157^{b} N = 82	$0.120^{a,b}$ N = 143
Plant density (no. plants m^{-2})	8.50	4.10	7.15
Flight distance (m)	0.468^{a} N = 65	0.322^{b} N = 39	0.768^{a} N = 21
Nearest neighbor status	7.67^{a} N = 63	3.03^{b} N = 39	7.55^{a} N = 20
Size (no. open flowers/ visited plant)	3.78 N = 60	3.51 N = 45	3.33 N = 24
Percent flowers visited	42.80^{a} N = 60	54.67^{b} N = 45	45.65^{a} N = 24

a. Different superscripts indicate values that differ between phases at $P < 0.05$.
b.

Discussion

Bumblebees, as predicted, adjusted their departure decisions during the experimental period in which plant

Tab. 2. Results of analysis of covariance used to test null hypothesis that the means for percent of open flowers visited per plant do not differ among phases. Plant size (number of open flowers on visited plants) was used as a covariate.

Source of variation	df	SS	MS	F	P
Covariate:					
Plant size	1	0.724	0.724	18.98	0.001
Main effect:					
Phase	2	0.369	0.185	4.84	0.009
Explained	2	1.093	0.364	9.55	0.001
Residual	125	4.770	0.038		
TOTAL	128	5.863	0.046		

density was significantly reduced, and visited increased percentages of blossoms before leaving individual flowering stalks. This result is in contrast to that found by Zimmerman (1981a) who also worked with *B. flavifrons* workers as well as *B. bifarius* workers. Zimmerman (1981a) compared the mean percentage of open flowers that bees visited per plant for two plant populations differing significantly in density. These populations are 8 km apart and differ by 300 m in elevation. Contrary to prediction, the mean percentage of open flowers visited per plant did not differ significantly between the two sites (Zimmerman 1981a). The cause of the difference between these two studies is not entirely clear. Uncontrolled differences between Zimmerman's study sites may have had confounding influences on foraging behavior. Secondly, the mode of resource presentation on *Polemonium foliosissimum* differs substantially from that on *D. nelsonii,* possibly affecting bees' abilities to predict future rewards on a plant. Unlike *D. nelsonii,* resource presentation on *P. foliosissimum* is non-orderly; flowers appear to be scattered randomly over the plants' outer surfaces. Additionally, it is unknown whether the correlation in nectar volumes between adjacent blossoms on a *D. nelsonii* raceme (Pyke 1978b) also occurs on *P. foliosissimum.* These factors may lead to different departure rules for the two plant species.

Although the prediction of the analog of the marginal value theorem was met during the experimental phase of the current study, examination of another aspect of bumblebee behavior suggests that this result may, in fact, be paradoxical. The prediction that bees would visit more flowers per inflorescence under low density conditions stemmed directly from the assumption that under such conditions inter-inflorescence flight costs would be increased relative to high density conditions. Larger movement costs should result in foragers being less inclined to leave patches (Cowie 1977, Zimmerman 1981a). Despite the fact that plant spacing distances were greater during the experimental phase of the present study, bees flew significantly shorter distances during this phase than during control periods. If reduced flight distances indicate lowered inter-inflorescence flight costs (Waddington 1980), the discrete, stochastic analog of the marginal value theorem actually predicts that the number of blossoms visited per stalk should have been lowest during the experimental period. Therefore, because of decreased flight distances, this result implies that bees are not foraging in a manner consistent with the marginal value theorem.

The shortening of flight distances in response to a decrease in plant density is due to the increased frequency with which bumblebees began to move between near neighbors. Bees made the same response to low density stands of *P. foliosissimum* (Zimmerman 1981a). In both cases it appears that changes in plant density triggered a behavioral response that decreased the cost of inter-inflorescence movement. This behavior, although not predicted by the marginal value theorem, appears to increase foraging efficiency, but it is not without cost. Because standing crops of nectar on adjacent *D. nelsonii* plants are positively correlated (Pleasants and Zimmerman 1979, Zimmerman 1981b), visits to nearby neighbors after encountering a low reward inflorescence may yield additional below-average rewards. Thus, the higher flight costs associated with longer moves are often well worth paying. In any case, as pointed out by Zimmerman (1981a), the behavioral flexibility demonstrated by animals strongly implies that those optimal foraging models predicting a shift in any one particular behavior in response to environmental conditions are too simplistic to accurately predict foraging behavior.

It should be pointed out that rates of nectar production and/or volumes of standing crop may have varied among experimental phases. Such a change, however, should not have had a significant effect on bumblebee departure decisions. Ollason (1980) has presented the mathematical verification demonstrating that departure decisions are actually independent of the overall habitat average reward value while Cibula and Zimmerman (unpubl.) have confirmed that under experimental conditions bumblebees on *D. nelsonii* (as well as on *D. barbeyi* and *Aconitum columbianum*) forage in a manner consistent with Ollason's predictions.

The behavioral responses observed in the present study also have some relevance to the manner in which bees assess the costs of foraging. All optimal foraging models assume that animals are constantly comparing their energetic expenditures with their energetic gains and making movement decisions based on the ratio of these two values. The current work raises the possibility that another method exists. Bees may not estimate flight costs directly, but rather use an assessment of plant spacing distances as an index of potential foraging costs. Bumblebee foraging during phase II is consistent with this hypothesis. Upon entering an area of low plant density, bees, in an attempt to decrease their foraging costs, increase their frequency of moves to near neighbors and visit more flowers per inflorescence before departing. It is possible for bees to overcompensate, however, and this is what appears to have happened in phase II. During this period bees increased their utilization of nearest neighbors to such an extent that their absolute flight distances were actually significantly shorter than during either control period. The number of blossoms visited per inflorescence during this time period, however, was consistent with that expected had bees' flight distances been greater than in the control phases. If departure decisions are based on a visual perception of the environment instead of on the actual flight costs incurred, overcompensation can thus lead to sub-optimal foraging. The results of the present study suggest that if bees are basing departure decisions on directly estimated costs, they are not foraging in keeping with predictions of the marginal value theorem. If, on the other hand, bees estimate foraging costs indirectly via plant density, foraging models need to be reformulated to incorporate this behavior. Clearly, tests need to be designed that are capable of distinguishing between these two methods of decision-making if the efficiency of bumblebee foraging and the utility of optimal foraging models are to be evaluated.

Acknowledgements – We are indebted to A. Frucht, R. Gross and J. Pleasants for making needed improvements in an earlier draft of this manuscript. This study was supported by NSF grants DEB 80-04280 and DEB 81-01800 and by a grant from the Society of Sigma Xi. We appreciate their support.

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