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Patchiness in the Dispersion of Nectar Resources: Evidence for Hot and Cold Spots

John M. Pleasants* and Michael Zimmerman[1]
Department of Biology, Washington University St. Louis, Missouri 63130 USA

Summary. The dispersion pattern of resources can have a significant effect on foraging behavior. We examined the dispersion pattern of standing crop of nectar in a population of *Delphinium nelsonii.* The nectar content of flowers was measured for subject inflorescences and their two nearest neighbors. Inflorescences were divided into those which had some nectar (hot plants) and those which had none (cold plants). Tests for independence showed that subject plants and their neighbors were likely to have the same "temperature", indicating that resources were patchy. The implications of this pattern for the foraging movements of bumblebees are discussed.

Introduction

Optimal use of patchy environments by foragers has been studied from both a theoretical (MacArthur and Pianka, 1966; Schoener, 1971; Tullock, 1971; Charnov, 1976) and an empirical (Krebs et al., 1974, 1978; Gill and Wolf, 1977) point of view. Resources are often found to be arranged in a nonrandom or patchy manner (Gibb, 1958; Wiens, 1976; Reichman and Oberstein, 1977) and consumer utilization patterns in such situations have been investigated for a wide range of organisms. In many cases foragers have been shown to "meander" in a fairly constant direction until a high quality patch is encountered. At the point of discovery the organism begins to increase its rate of turning which tends to keep it within the patch. This "area-restricted searching" (Tinbergen et al., 1967) is very commonly found in insects searching for hosts or food items (Laing, 1937, 1938; Mitchell, 1963; Chandler, 1969; Richerson and Borden, 1972), in fish (Beukema, 1968; Kleerekoper et al., 1970), and birds (Cody, 1971, 1974; Smith, 1971, 1974a, b).

Several researchers have observed the movement patterns of foraging pollinators, either for the purpose of studying optimal foraging strategies (Pyke, 1978; Zimmerman, 1979) or assessing the extent of pollen and gene flow in a population

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[1] Department of Biology, College of William and Mary, Williamsburg, Virginia 23185 USA

* The order of authorship was determined by the flip of a coin

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(Levin et al., 1971). In no case has the spatial dispersion pattern of the nectar resources used by these pollinators been characterized. Knowing whether resources are patchy or not is crucial to understanding observed instances of area-restricted foraging behavior and for biulding models of optimal foraging behavior. The present study is an attempt to characterize the nectar dispersion pattern for a population of *Delphinium nelsonii* Greene (Ranunculaceae) by measuring the standing crop of nectar for individual plants. This species was chosen because extensive information on the foraging behavior of bumblebees on it is available (Pyke, 1978). We discuss the implications of this dispersion pattern for pollinator foraging.

Methods

The fieldwork was conducted during July, 1978 in a meadow at Kebler Pass (elevation 3,048 m) in the Gunnison National Forest, 11 km west of Crested Butte, Colorado. This meadow contained a fairly dense, non-clumped population of *Delphinium nelsonii D. nelsonii* has a vertical inflorescence with 3–5 flowers open at any one time. It is visited primarily by *Bombus flavifrons* and *B. appositus* and in 1978 it was also visited by the unusually abundant sphinx moth, *Hyles lineata*. Sampling of the *D. nelsonii* population was done at four times: 1600 h, July 18; 1130 h, July 22; 1030 h, July 24; and 0830 h, July 29. For each sampling period a transect was run through a portion of the meadow and all individuals of *D. nelsonii* within 0.5 meters of this transect line were considered to be subject plants. Approximately 100 subject plants were included in each sample. For each subject plant the nectar content of each of the bottom three open flowers was measured by slitting the two nectar spurs and removing the nectar with a 5 μl capillary tube. The height of the nectar in the tube was measured in millimeters and recorded. After measuring the nectar content of the flowers of a subject plant, the nectar content of the three bottommost flowers on each of its two nearest neighbors was measured. Plants were considered to be neighbors only if they were within 0.5 meters of the subject plant.

To determine whether subject plants with a certain amount of nectar had near neighbors with a similar amount of nectar, plants were divided into two classes: those which had no measureable nectar in any of their flowers (cold plants) and those which had nectar in at least one of the flowers (hot plants). The results of the nearest neighbor analysis were cast in a 2×2 contingency table where each cell gives the number of times a hot plant or cold plant was observed to have *at least one* hot neighbor (i.e. the two nearest neighbors were either both hot or one was hot and one was cold) or two cold neighbors. The 2×2 table for each time period was tested for independence using a Chi square test corrected for continuity.

Results and Discussion

The results of the nearest neighbor analysis are shown in Table 1. For the first three sample periods the test for independence was statistically significant and for the last just barely non-significant. Therefore we reject the null hypothesis that the resource quality of subject plants and the quality of their nearest neighbors are independent. The probability of finding another hot plant near a hot plant is greater than expected if plants were randomly arranged with respect to quality. Conversely, the probability that a cold plant has cold nearest neighbors is higher than expected.

The fact that hot spots and cold spots exist for this population should have major implications for the behavior of foraging bumblebees. We assume, as do all models of optimal foraging, that bees forage so as to maximize their

Table 1. Relationship between the reward value of subject plants and their neighbors

	sample periods 0830 h		1030 h		1130 h		1600 h	
	subject plants							
	hot	cold	hot	cold	hot	cold	hot	cold
Two nearest neighbors:								
hot and hot or hot and cold	54	25	63	25	61	21	63	21
cold and cold	6	14	6	9	6	11	4	6
	$\chi^2=8.29$		$\chi^2=4.44$		$\chi^2=8.13$		$\chi^2=3.77$	
	$p<0.01$		$p<0.05$		$p<0.01$		$p\simeq 0.06$	

net energy intake rate. Thus we would expect bees to behave in a manner which maximizes their changes of finding hot plants and minimizes their changes of finding cold plants. If a bee has just found a hot plant, the results in Table 1 indicate that the probability of encountering a hot plant on the next visit is higher if the bee flies a short distance to a near neighbor than if it flies a longer distance to some other plant. But if a bee has just found a cold plant we would expect it to fly a longer distance to the next plant to avoid visiting near neighbors which have a higher probability of also being cold. These long moves, which involve bypassing plants, provide a means of distinguishing between an underlying resource distribution which is patchy and one which is non-patchy. If plants were randomly distributed with respect to quality we would expect only short moves since bees should go to near neighbors to minimize interplant flight costs. A second component of area-restricted searching we would expect bees to employ is a greater degree of turning after encountering a hot plant.

Both these predictions are supported by the observed behavior of bumblebees on *D. nelsonii* and on *Acontium columbianum* (Ranunculaceae) which has a similar type of inflorescence. For these two species the number of flowers visited on an inflorescence can be used as an indicator of a plant's reward value. Bees visit more flowers on an inflorescence when there is a larger amount of nectar in the flowers (Pyke, unpub. data). In support of the first prediction, the mean distance between successively visited inflorescences increases as the number of flowers visited per inflorescence (reward value) decreases (Pyke, 1978; Fig. 5; Price and Waser, unpub. data). In support of the second prediction, the bee's angle of departure (difference between the direction of arrival to and departure from a plant) increase as the number of flowers visited per inflorescence (reward value) increases (Pyke, 1978; Fig. 4a, b).

Pyke's Fig. 4 and 5 show a sytematic change in bee behavior for each of his reward classes. This implies that bees are able to discern finer categories of plant reward value than simply hot and cold. It also suggests that besides hot and cold spots there are also warm and cool spots. From the frequency distribution of subject plants with different amounts of nectar, (Fig. 1) it is clear that a variety of plant reward values exist. Sample sizes were not sufficiently

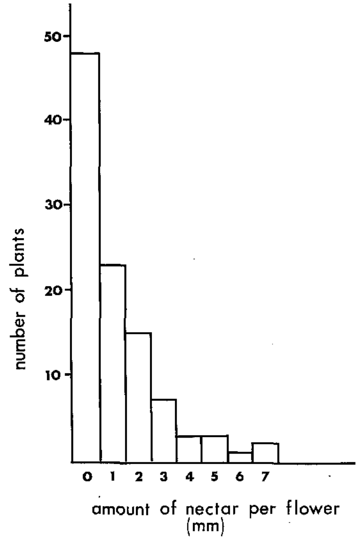

Fig. 1. Frequency distribution of subject plant reward values. This distribution is from the 1130 sample, July 22. The distribution for other time periods is similar. Amounts of nectar are measured in millimeters; 1 mm = 0.066 μl. The mean amount of nectar per flower per plant is: 1.6 mm, 0830; 1.3 mm, 1030; 1.4 mm, 1130; 1.5 mm, 1600

large to investigate the existence of differences in patch quality by further subdividing plant reward values for a multiway independence test. However, we have examined this indirectly by testing for independence using other criteria for distinguishing between hot and cold plants. When hot plants are defined as having more than $\bar{x}$ amount of nectar the results of the statistical analysis are similar to those obtained from the data in Table 1. A number of values of $\bar{x}$ were used. This holds for cases where a plant's "temperature" is based on the *average* amount of nectar per flower. It also holds for cases where a plant's "temperature" is based on the amount of nectar present in the flower with the most nectar. The fact that this latter criterion also works is significant because the flower with the most nectar is important in determining bumblebee foraging movements. This flower is almost always at the bottom part of the inflorescence (unpub. data) and is the first flower visited by a foraging bumblebee (Pyke, 1978). In addition, a bumblebee's decision to visit the next higher flower on an inflorescence depends on the quantity of reward obtained at the previous flower (Pyke, unpub. data). As a result, bumblebees often base their assessment of a plant's reward value on the few flowers visited.

Until now we have treated the resource distribution in the *D. nelsonii* population as a given and discussed the expected and observed foraging patterns of bees with regard to this distribution. But what is the underlying cause of this distribution? Why do hot and cold spots exist? Two elements of the resource dispersion pattern must be explained: (1) the variation in patch quality, and (2) the existence of patches themselves. The explanation for (1) has to do with the probabilistic aspects of foraging. For a given number of bees foraging on a given number of plants, there will be a frequency distribution of lengths of time between successive visits to a plant. At any point in time there will be plants which have recently been visited and thus have little nectar renewed. There will also be plants which have not recently been visited and have more accumulated nectar. This accounts for the distribution seen in Fig. 1. With regard to (2), when successive visits by a bee are to near neighbors, which often is the case (Levin and Kerster, 1969a, b; Pyke, 1978), the status of plants in a localized area become linked. Thus patches with similar reward value are created. Furthermore, bees will leave a patch if the amount of nectar obtained from the first plant encountered is insufficient. Thus patches with low or intermediate reward value will not be completely harvested when visited, meaning that they will be of higher quality on a subsequent visit. This will promote a greater range of patch qualities. Other factors could contibute to the integrity of patches. If the substrate for these plants is composed of a mosaic of edaphic conditions, then plants growing under similar conditions could have similar nectar production rates. Also, since in this system neighboring plants are genetically related (Price and Waser, 1979), patches of plants with similar nectar production rates could result. Similarity in nectar production rate makes it more likely that a group of plants will have a similar standing crop of nectar.

It is important to point out that patches, or spots, are discussed here are not discrete entities. Hot and cold spots cannot be recognized as conspicuous clumps of plants. Perhaps it would be more appropriate to talk about the nectar topography of a meadow, with contour lines representing plants with similar amounts of nectar. Such a topography would be constantly changing over time as the actions of bees reduce hills to valleys and as nectar renewal slowly turns valleys into hills.

How widespread is the resource dispersion pattern found in this system? The only other appropriate study of pollinator movements also shows that pollinator foraging behavior changes with a plant's reward value, implying an underlying patchy distribution. Gill and Wolf (1977) found that sunbirds (*Nectarinia spp.*) exhibited two types of behavior at inflorescences of *Leonotis nepetiflora* (Lamiaceae). Sunbirds would either visit a few flowers and then leave (reject) or visit all the flowers on an inflorescence (acept). The flowers on rejected inflorescences were found to have less nectar than those on accepted ones. Significantly, sunbirds flew farther to the next inflorescence after an inflorescence was rejected than after it was accepted. This suggests that sunbirds recognized hot and cold spots. Clearly more studies characterizing both the resource dispersion pattern and pollinator foraging movements are needed before generalizations can be made about resource patchiness and area-restricted foraging.

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References

Beukema, J.J.: Predation by the three spined stickleback (*Gasterosteus aculeatus*). Behaviour **31**, 1–126 (1968)

Chandler, A.E.F.: Locomotory behavior of first instar larvae of aphidophagous Syrphidae (Diptera) after contact with aphids. Anim. Behav. **17**, 673–678 (1969)

Charnov, E.L.: Optimal foraging: The marginal value theorem. Theor. Pop. Biol. **9**, 129–136 (1976)

Cody, M.L.: Finch flocks in the Mohave Desert. Theor. Pop. Biol. **2**, 142–158 (1971)

Cody, M.L.: Optimization in ecology. Science **183**, 1156–1164 (1974)

Gibb, J.: Predation by tits and squirrels on the eucosmid *Enarmonia conicolama* (Heyl.). J. Anim. Ecol. **27**, 375–396 (1958)

Kleerekoper, H., Timms, A.M., Westlake, G.F., Davy, F.B., Malar, T., Anderson, V.M.: An analysis of locomotor behaviour of goldfish (*Carassius auratus*). Anim. Behav. **18**, 317–330 (1970)

Krebs, J.R., Ryan, J.C., Charnov, E.L.: Hunting by expectation or optimal foraging? A study of patch use by chickadees. Anim. Behav. **22**, 953–964 (1974)

Krebs, J.R., Kacelnik, A., Taylor, P.: Test of optimal sampling by foraging great tits. Nature **275**, 27–31 (1978)

Laing, J.: Host finding of insect parasites. I. Observations on the finding of hosts by *Alysia manducator, Mormoniella vitripennis* and *Trichogramma evanescens*. J. Anim. Ecol. **6**, 298–317 (1937)

Laing, J.: Host finding by insect parasites. II. The chance of *Trichogramma evanescens* finding its hosts. J. Exp. Biol. **15**, 281–302 (1938)

Levin, D.A., Kerster, N.W.: Density-dependent gene dispersal in *Liatris*. Amer. Natur **103**, 61–74 (1969a)

Levin, D.A., Kerster, N.W.: The dependence of bee-mediated pollen and gene dispersal upon plant density. Evolution **23**, 560–571 (1969b)

Levin, D.A., Kerster, N.W., Niedzlek, M.: Pollinator flight directionality and its effect on pollen flow. Evolution **25**, 113–118 (1971)

MacArthur, R.H., Pianka, E.: On optimal use of a patchy environment. Amer. Natur. **100**, 603–608 (1966)

Mitchell, B.: Ecology of two carabid beetles, *Bembidion lampros* (Herbst) and *Trechus quadristriatus* (Schrank). I. Life cycles and feeding behavior. J. Anim. Ecol. **32**, 289–299 (1963)

Price, M.V., Waser, N.M: Pollen dispersal and optimal outcrossing in *Delphinium nelsonii*, A montane wildflower. Nature **277**, 294–297 (1979)

Pyke, G.H.: Optimal foraging: Movement patterns of bumblebees between inflorescences. Theor. Pop. Biol. **13**, 72–98 (1978)

Reichman, O.J., Oberstein, D.: Selection of seed distribution types by *Dipodomys merriami* and *Perognathus amplus*. Ecology **58**, 636–643 (1977)

Richerson, J.V., Borden, J.H.: Host finding behavior of *Coeloides brunneri* (Hymenoptera: Braconidae). Can. Entomol. **104**, 1235–1250 (1972)

Schoener, T.W.: Theory of feeding strategies. Ann. Rev. Ecol. Syst. **2**, 369–404 (1971)

Smith, J.N.M.: The food searching behavior of two European thrushes: I. Description and analysis of search path. Behaviour **48**, 276–302 (1974a)

Smith, J.N.M.: The food searching behavior of two European thrushes: II. The adaptiveness of the search patterns. Behaviour **49**, 1–61 (1974b)

Tinbergen, N., Impekoven, M., Franck, D.: An experiment on spacing-out as a defense against predation. Behaviour **28**, 307–320 (1967)

Tullock, G.: The coal tit as a careful shopper. Amer. Natur. **105**, 77–80 (1971)

Weins, J.A.: Population responses to patchy environments. Ann. Rev. Ecol. Syst. **7**, 81–120 (1976)

Zimmerman, M.: Optimal foraging: A case for random movements. Oecologia (Berl.), in press (1979)

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