The Effect of Nectar Production on Neighborhood Size

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Summary. Bumblebee foraging behavior was observed on two plant species with similar floral and inflorescence structures. One species produces nectar while the other does not. Bees, upon visiting nectar producing flowers tend to empty them of nectar and by frequently moving between close neighbors, create a patchily distributed resource base. Bees maximize their foraging efficiency in such an environment by using an area-restricted searching behavior and flying distances inversely correlated with the quality of reward received. Pollen collecting bumblebees do not create a patchy environment and maximize their foraging efficiency by more consistently moving shorter distances. Pollen collecting bumblebees are significantly more likely to revisit flowers and to visit more flowers per inflorescence than are nectar gathering bumblebees. These differences in foraging behavior increase the neighborhood size for nectar producing species and make it increasingly unlikely that random drift will be a dominant mode of evolution in populations of these species.

Introduction

The degree of panmictia experienced by a population may influence the effect that selective forces have upon it and thus is an important aspect in the biology of that population. Wright (1943, 1946), in his isolation-by-distance model, has demonstrated that the pattern and mode of genetic differentiation within a population is a function of the number of randomly interbreeding individuals within it. This number, neighborhood size, varies as a function of population density and gene dispersal. Neighborhood size is of interest because it can significantly modulate the impact of evolufory pressures impinging on a population. Small neighborhood sizes, for example may lead to inbreeding depression, loss of heterozygosity and may allow random changes in gene frequency to play a major role in evolution. Alternatively, larger neighborhood sizes with increased gene flow can dampen the effects of localized selective forces and lead to increased genetic uniformity within populations.

Plant populations have been the focus of much work dealing with neighborhood sizes because the spatial patterns of plants are fixed and because one can observe pollinator movements and draw conclusions about gene flow. Pollinators often vary their foraging patterns in a predictable fashion as some characteristics of the plant population change. For example, as interplant distances increase, pollinator flight distances also increase (Levin and Kerster 1969a, b), as the number of available flowers on an inflorescence increases, the number of flowers visited on that inflorescence also increases (Pyke 1981; Zimmerman, unpublished data) (but see Zimmerman 1979a, b) and, in a number of species, the length of a foraging movement is inversely related to the quality of the reward received at the last flower visited (Pyke 1978; Pleasants and Zimmerman 1979; Zimmerman 1979a, 1981c). These factors suggest that various plant characteristics can have a significant effect on the degree of panmixia and thus on the neighborhood size of a plant population. In the present paper I will examine one plant characteristic, the presence or absence of nectar production, and will assess its influence on pollinator foraging behavior and thus, indirectly, on neighborhood size.

Although neighborhood sizes have been calculated for a number of plant populations only Schaal (1980) has tracked gene flow; the others (e.g., Kerster and Levin 1968; Beattie and Culver 1979; Schmitt 1980) have based their inferences on the movements of pollinators. Such inferences are questionable, however, because pollen flow is affected by carryover. The longer pollen remains on a forager's body before coming to rest on a stigmatic surface, the less reliable pollinator flight distance becomes as an estimate of actual pollen flow. By using genetic markers in an experimental population of Lupinus texensis (Fabaceae) Schaal (1980) was able to measure gene flow and conclude that neighborhood size was approximately 100 individuals, small enough for differentiation to occur in the absence of selection (Endler 1977). Because Lupinus texensis does not produce nectar (Schaal and Leverich 1980) and because nectar reward has been shown to influence subsequent pollinator movements (Pyke 1978, 1979; Pleasants and Zimmerman 1979; Zimmerman 1979a, 1981c) the present study was undertaken to see if the restricted neighborhood size found in L. texensis might be attributed to its lack of nectar production.

Estimates of neighborhood size were calculated for and bumblebee foraging behavior was observed on two morphologically similar, taxonomically related plant species. The first species, Lupinus amplus does not produce nectar while the second, Thermopsis montana, does. It is predicted that bumblebees, in an attempt to maximize their rate of net energy intake, will forage differently on these two species and that these differences will lead to neighborhood size restriction in the species which does not produce nectar.

The fact that the resources in question, pollen and nectar, are distinct from one another does not complicate the analysis. Regardless of which resource bumblebees are collecting they should be under strong selection pressure to maximize their rate of net energy intake. The predictions of the present paper are that bumblebees will utilize qualitatively different foraging strate-
gies depending upon the resource for which they are foraging and that this difference will have a significant effect on the population biology of the respective plant populations. Although nectar production may be shown to influence neighborhood size, this by no means suggests that pollinator foraging behavior or neighborhood size is directly correlated with the rate of nectar production. In fact, it has been suggested (Ollason 1980; Zimmerman 1981 b) that some aspects of foraging behavior are actually independent of the amount of standing crop of nectar available in a population. It is not reasonable, therefore, to compare two plant populations which differ in their nectar production rates and to expect to find neighborhood size differences. It is hypothesized that differences in this parameter between populations producing and those not producing nectar are due to the different foraging strategies employed by pollinators attempting to maximize their foraging efficiency while collecting discrete resources.

**Methods**

*Lupinus amplus* Greene (Lupine) and *Thermopsis montana* Nutt. (False lupine) (Fabaceae) are herbaceous perennials abundant in the vicinity of Horse Ranch Park, Gunnison National Forest, Colorado. Both species typically bloom from late June until mid July (Pleasants 1977, 1980). Flowers of both species are arranged on racemes of similar size and are visited by a number of species of bumblebees (*Bombus* spp.) as well as by solitary bees (Pleasants 1977, 1980). Bees forage on *T. montana* primarily for nectar while they visit *L. amplus*, which produces no nectar, exclusively for pollen. While the species occasionally grow in adjoining stands, bumblebees very rarely switch between them (personal observation).

A 12 square meter area of *T. montana* was demarcated and 237 flowering stalks were characteristically marked with colored embroidery thread. A similar marking scheme was employed for 216 *L. amplus* stalks in a 6 square meter area at a second site. The location of each stalk was then mapped. The number of open flowers on each *T. montana* stalk was counted and recorded on 24 June 1980 and 29 June 1980 and observations were made daily from 25 June 1980 to 1 July 1980. The number of open flowers on each stalk of *L. amplus* was counted and recorded on 12 July 1980 and 17 July 1980. Nectar measurements were taken from a nearby population of *T. montana* flowers on 5 July 1980. Nectar was removed from the flowers using 5 μ capillary tubes and the height of the nectar in the tube was measured in mm and recorded. All open flowers on each selected stalk were assayed. Standing crop of nectar in all of the flowers on the first and second nearest neighbors of each of the stalks so examined were also measured. The average amount of nectar per flower per stalk was recorded and correlation coefficients between the average nectar per flower on a plant and its first and second nearest neighbor were determined.

Nectar measurements were taken from a population of *T. montana* flowers on 23 June 1981. A single anther was removed from an *L. amplus* flower with a pair of forceps. The anther was then gently touched to a piece of scotch tape. This technique was repeated for 50 plants. Pollen was similarly collected from the first and second nearest neighbor stalks of each of these 50 plants. The number of pollen grains adhering to the tape for each stalk sampled was counted using a binocular dissecting microscope with 40 × magnification. Spearman rank correlation between the number of pollen grains per flower on a plant and both its first and second nearest neighbors was performed. This sampling technique was not meant to estimate the number of pollen grains within an anther but rather to approximate the number of grains on the surface readily accessible to bumblebees. Sampling only one flower per plant was adequate to document nectar patches (cf. Zimmerman 1981 c) so this technique should fairly assess the pattern of pollen dispersion.

**Results and Discussion**

*Thermopsis montana* and *Lupinus amplus* are appropriate subjects for studies of the effects of distinct floral rewards on pollen flow. Except for corolla color (yellow vs blue) flower structure of the two species is similar as are the numbers of blossoms displayed. *T. montana*, with a mean of 6.8 open flowers per stalk did not differ significantly from *L. amplus* which averaged 6.5 open flowers (*t* = 0.84; *P* > 0.40). Floral equivalence of this sort is important since the method of resource presentation can have a significant effect on the foraging behavior of pollinators (Zimmerman 1979 a, b). Thus the foraging patterns of bumblebees on these two species has probably been influenced by the different floral reward each offers.

The percentage of bumblebee moves to each nearest neighbor is presented in Fig. 1. A Kolmogorov-Smirnov two sample test showed these distributions to be significantly different from one another (*P* < 0.005). Bumblebees are more likely to move between...