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**Effects of black mustard population size
on the taxonomic composition of pollinators**

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Abstract In plant species that are pollinated by a variety of animal species, spatial and temporal variability in the taxonomic composition of those pollinators may cause spatial and temporal variability in selection on floral traits. While temporal variation in pollinator composition has been widely reported, spatial variability, particularly on a local scale, has been studied less frequently; nevertheless, available evidence suggests that local spatial variability may be a widespread feature of plant-pollinator interactions. In addition, the causes of this spatial variability are poorly known. This study was undertaken to quantify variability in the taxonomic composition of pollinators visiting local populations of black mustard, *Brassica nigra*, and to determine some of the causes of this variability. Simultaneous observations were conducted in seven pairs of black mustard populations. The members of each pair were in close spatial proximity but differed in number of plants. Larger plant populations were visited by significantly greater numbers of honey bees and significantly fewer small bees than small populations on a per-plant basis. There was also a trend toward greater syrphid fly visitation in small populations. The increased numbers of honey bees at large plant populations is probably due to their ability to recruit long distances to the most rewarding plant populations. The lower number of small bees at large plant populations may be due to competition from honey bees and/or spreading a constant number of small bees over the larger number of plants in large populations.

Key words Spatial variability · Pollinator assemblage · Population size · Black mustard · *Brassica nigra*

Introduction

Biologists have long believed that animal pollinators are the primary cause of natural selection on floral traits (Darwin 1877). Most studies of selection on floral morphology have examined selection caused by only one species of pollinator (e.g., Campbell 1989; Galen 1989). Many plants, however, are visited by an array of pollinator species. If these pollinator species differ in size, morphology, or behavior, they may exert different selection pressures on floral traits (Galen et al. 1987; Stanton 1987; Herrera 1989; Schemske and Horvitz 1989; Eckhart 1991; Stanton et al. 1991; Eckhart 1992). Furthermore, if the taxonomic composition of pollinators varies spatially or temporally, then this could give rise to spatial or temporal variation in selection on floral morphology (Schemske and Horvitz 1989).

Temporal variation in the composition of pollinator assemblages has been well-documented, including both variation within a single season (Paige and Whitham 1985; Herrera 1988; Wolfe and Barrett 1988; Ashman and Stanton 1991; Eckhart 1992; Cane and Payne 1993) and across years (Herrera 1988; Wolfe and Barrett 1988; Schemske and Horvitz 1989; Horvitz and Schemske 1990; Eckhart 1992; Cane and Payne 1993). Spatial variation in the overall frequency of visitation has also been demonstrated repeatedly (e.g., Thomson 1981; Feinsinger et al. 1982; Klinkhamer et al. 1989). Spatial variation in the *taxonomic composition* of pollinators has been less well documented, but several studies have shown significant variability on a local scale (Johnson and Hubbell 1975; Sih and Baltus 1987; Spears 1987; Herrera 1988; Schemske and Horvitz 1989; Sowig 1989; Horvitz and Schemske 1990; Eckhart 1992; Jennersten and Nilsson 1993; Aizen and Feinsinger 1994). In many cases the causes of the temporal or spatial variability are unknown, but some studies have suggested that plant population size affects the composition of pollinators visiting that population (Johnson and Hubbell 1975; Schaffer et al. 1979; Sih and Baltus 1987; Sowig 1989; Jennersten and Nilsson 1993). In particular, visi-

This paper is dedicated to the memory of George Eickwort

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tation by honey bees seems to increase with increasing plant population size.

We used a novel approach to test the hypothesis that plant population size affects the taxonomic composition of pollinators. We determined the composition of pollinators visiting a number of nearby paired plant populations differing in size. By performing simultaneous observations in paired populations, we were able to control for temporal variability in visitation, which may have confounded results of earlier studies. In addition, multiple regression analysis was used to control for the effects of other variables that are correlated with population size.

Materials and methods

Plant populations

Black mustard (*Brassica nigra*, Brassicaceae) is a widespread annual weed introduced to North America that occurs in disturbed areas. Black mustard plants have numerous terminal inflorescences of yellow, hermaphroditic, self-incompatible flowers (J. Conner, unpublished data).

Eleven populations of black mustard in Champaign Co., Illinois were used in this study (Fig. 1). Ten of these populations were naturally occurring; the other (PT) was planted using seeds collected from a natural population the previous year. Seven pairs of populations were selected, with the two members of each pair differing in size but in close proximity to each other (Table 1). In all pairs but one, the large population had more than twice as many plants as the small population (Table 1); in most cases the size difference was much greater. The one exception, the IPL population, was a patch of plants within a larger diffuse population, so that the number of plants listed for IPL probably underestimates the number perceived by the pollinators.

Populations were defined as discrete patches of plants, with few or no black mustard plants in between them. In three pairs (YWH-YWL, SCS-SCL, and IPS-IPL) there were some widely scattered black mustard plants between populations. The YWL population was paired with each of three nearby smaller populations; thus, these comparisons are not completely independent of each other. After the vast majority of plants had ceased flowering in the large I74 population (approximately 16,000 plants), a patch of 48 later-flowering plants remained along the edge of the original population. This subpopulation was treated as a separate small population (I74S), and was paired with a later-flowering large population (UA).

To estimate plant number in each large population, all plants were counted in twenty 1-m² plots that were randomly selected from a grid or transect. The mean of these 20 counts within each population was multiplied by the total area covered by the population to estimate the total number of black mustard plants present. In small populations, all of the plants were counted.

Observations

In small populations all of the plants were numbered. In large populations, grids or transects were laid out (see above) and plants at 1 m intervals were numbered. From these numbered individuals, plants were chosen randomly without replacement for observation. Most of the observations in each pair of populations were made simultaneously by a pair of observers to control for such factors as weather, date, and time of day; therefore, any visitation differences found were due to population differences only. Observation periods lasted for 30 min per plant. During these periods, observers recorded the taxonomic group of each insect visitor (i.e., honey bee, small fly, syrphid fly) as it landed on a plant. While the latter two

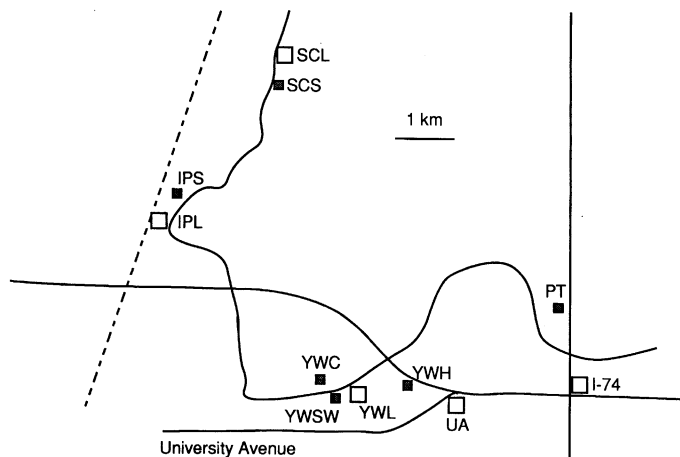


Fig. 1 Map of the study area in Urbana, Illinois, showing the 11 populations of black mustard used. Small populations are denoted by small shaded squares, and large populations by large open squares

categories contain several species (samples of visitors were collected at each site; see Results), insects were lumped into categories because they could not be identified to species on the wing and because individual species in these categories were not abundant enough for statistical analysis.

Since the insects were not individually marked, an insect that left the plant and then returned later to the same plant would be recorded as visiting twice. Therefore, these observations provide overall rates of insect visitation *per plant* over 30 min periods. The number of flowers probed by pollinators on a given visit was not recorded because often there was more than one pollinator at a plant simultaneously. The height and the number of open flowers of these focal plants were also recorded. For very large plants, the number of open flowers on five haphazardly chosen inflorescences was counted, and the average of these counts multiplied by the total number of inflorescences to estimate total number of open flowers. Observations were made between 8:00 a.m. and 5:00 p.m. from 7 June 1992 to 5 August 1992, spanning most of the black mustard flowering season.

Because a number of observers participated in pollinator observations, accuracy was checked by having two people make simultaneous but separate observations of the same plant and comparing results. Since honey bee visits were the most easily observed due to the bees' large size and obvious flight patterns, the accuracy check focused on the smaller categories of insect visitors, small bees and flies. For plants having fewer than 1,000 flowers, the mean percentage difference in observed numbers of visits was 5%. For plants having more than 1,000 flowers, the mean percentage difference was 13%. However, only 5% of all plants in this study had more than 1,000 flowers (only 20% had greater than 500 flowers), so observer accuracy was generally high.

Analyses

To determine if the composition of insect visitors differed between the large and small plant populations, a multivariate analog of the paired *t*-test was performed. For each pair of simultaneous observations, the number of visits by each of the three main categories of insects at the large plant population was subtracted from the number of visits by the same insect category at the small population. This operation produced three new variables: the differences between the observation pairs in the numbers of honey bees, small bees, and flies. For all population pairs together and for each population pair separately, Hotelling's *T*² (Harris 1985) was calculated using the three new variables to test the null hypothesis that the composition of insect visitors was the same in the large and small plant population pairs. The three comparisons involving YWL

Table 1 Characteristics of black mustard study populations. Populations are presented in pairs, with the smaller of each pair presented first. Note that the YWL population was paired with three nearby smaller populations [*N* the total number of half-hour observation periods completed for each population (not all of these were simultaneous, so the sample sizes for the paired comparisons are smaller; see Fig. 3)]

Population	Distance between populations	Number of plants	Dates observed	<i>N</i>
PT	1.5 km	45	6/7/92-7/15/92	45
I74		16,000	6/23/92-7/31/92	26
YWH	0.80 km	46	6/30/92-7/16/92	16
YWL		790	6/30/92-7/16/92	34
YWSW	0.33 km	20	6/30/92-7/16/92	18
YWL		790	6/30/92-7/16/92	34
YWC	0.66 km	330	7/1/92-7/14/92	19
YWL		790	6/30/92-7/16/92	34
SCS	0.66 km	80	7/6/92-7/14/92	18
SCL		8,700	7/6/92-7/14/92	18
IPS	0.50 km	23	7/21/92-7/29/92	17
IPL		37	7/21/92-7/29/92	15
I74S	2.50 km	48	8/1/92-8/5/92	15
UA		4,400	7/31/92-8/5/92	15

should not be considered as three completely independent tests, but within each test no assumptions of independence were violated. The results from these three comparisons do not show the same pattern (see Results), so it is clear that the YWL data are not causing major bias.

The paired analysis described above provides a powerful method of detecting differences among populations in visitation, but it does not indicate whether these differences are caused by population size itself or some other characteristic of the population correlated with population size. In particular, plants in larger populations were significantly taller and had more flowers (see Results). To help discover what factors influenced visitation rates by the three main categories of pollinators, the numbers of each category visiting in each observation period were regressed separately on the following independent variables: total number of plants in the population, number of flowers open and the height of the plant observed, the numbers of the other two categories of pollinators recorded, the date and time of the observation, and the air temperature and intensity of solar radiation (MJ/m²).

All observations made at each site were used in this analysis, including observations that were not made simultaneously in each member of a population pair (see Table 1). The observations made at YWL were used only once in this analysis, so there was no lack of independence as there was in the paired analyses. The weather data were hourly records from an Illinois State Water Survey location approximately 4–9 km from the study populations. The number of plants, number of flowers per plant, and the numbers of each category of pollinator visiting were ln transformed to improve normality. All independent variables were then standardized to $\bar{x}=0$ and $SE=1$ to reduce multicollinearity and allow scale-corrected comparisons of slopes.

In the first model, both linear and quadratic (squared) terms were fitted for all the above independent variables. The independent variables were entered in the model in decreasing order of interest (e.g., plant population size and plant characteristics before date, time and weather variables). Using type I (sequential) SS, variables with *P*-values greater than 0.10 were removed from the bottom until the first significant variable was encountered. The reduced model was then re-run and type III SS used for final tests of significance. Since correlations among these independent variables were generally low (only 4% of the correlations were greater than 0.4), removing variables did not have a major effect on the regression slopes of the variables retained. To further check for multicollinearity, variance inflation factors (VIFs; Neter et al. 1985) were calculated for all three final models; all VIFs were less than three, indicating little multicollinearity. Residual plots for all models

were examined, and no serious heteroscedasticity was found. Analyses were performed using JMP (SAS Institute Inc. 1994) and KaleidaGraph (Abelbeck Software 1993) on a Macintosh computer, and SAS (SAS Institute Inc. 1985) on an IBM mainframe.

Results

Plant population characteristics

Populations of *Brassica nigra* studied varied greatly in size, ranging from 20 plants to approximately 16,000 (Table 1). Average plant height was 149 cm, with a range of 40–290 cm. The number of flowers open per plant varied from 15 to more than 2,400; however, the distribution was highly skewed with a median of only 165. Comparing the plants paired across large and small populations for observations, plants in large populations were significantly taller (mean difference 41.2 cm, paired $t=6.9$, 108 *d.f.*, $P<0.0001$) and had significantly more flowers (mean difference 128.7 flowers, paired $t=2.5$, 108 *d.f.*, $P=0.01$) than those in small populations.

Pollinator visitation patterns

The numbers of each category of insect visitor at each population are given in Fig. 2. Overall, the size of the population did not affect the total numbers of all visitors: the average difference between large and small populations in the total numbers of visitors per plant in 30 min across all populations was -0.06 (paired $t=-0.021$, 108 *d.f.*, $P=0.98$). Although several individual pairs of populations showed sizable differences in the total number of visitors (Fig. 2), none of these differences were significant using Bonferroni-corrected paired *t*-tests.

The three main categories of visitors, honey bees (*Apis mellifera*), small native bees, and flies made up

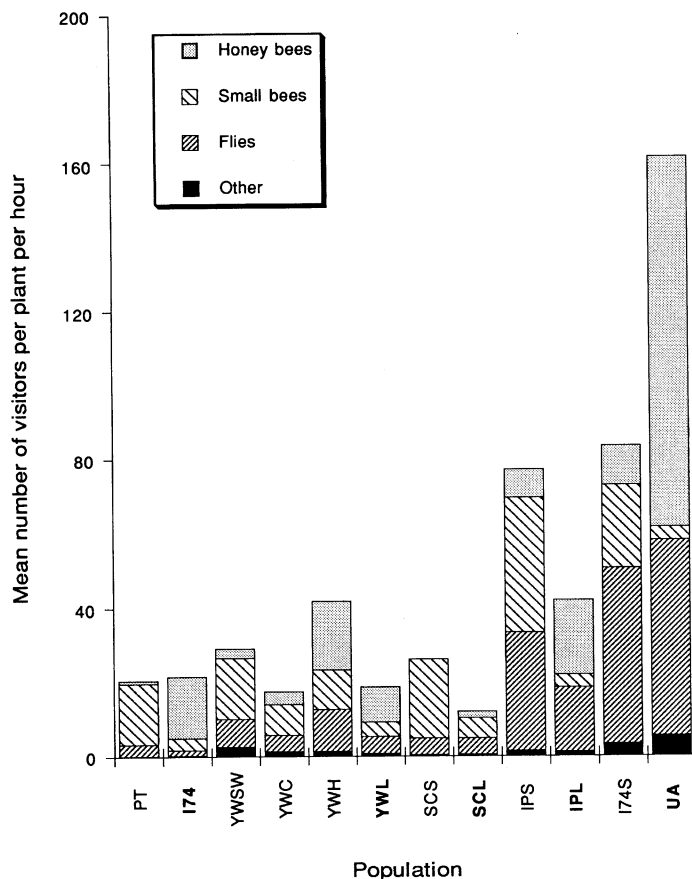


Fig. 2 Number of insects visiting each plant presented on a per-hour basis, averaged over all plants observed in each population. All observations are included (see Table 1). Populations are arranged chronologically, with those observed closest to the beginning of the black mustard flowering season furthest to the left. Large populations are indicated by *boldface letters* on the x-axis. Paired populations are adjacent, with the larger population of each pair to the right of the smaller. YWL is the exception: it was used in three different comparisons, as the large population in comparison with each of the other YW populations. There were no significant differences between the seven pairs of populations in the total numbers of all visitors per plant per 30 min, tested using paired *t*-tests with sequential Bonferroni correction (Rice 1989)

more than 90% of all visitors at all populations. The small bees included *Agapostemon virescens*, *Augochlorrella striata*, *Dialictus imitatus*, *Halictus rubicundus* (Halictidae) and *Heriades carinata* (Megachilidae). Over 95% of the flies were in the family Syrphidae (we could distinguish syrphids from other fly families on the wing), including *Allograpta obliqua*, *Eristalis tenax*, *Syrirta pipiens*, and *Toxomerus* spp. All these insect groups are likely to be effective pollinators of black mustard for several reasons. Insects in these groups contact anthers and stigmas on a high proportion of visits (J. Conner and R. Neumeier, personal observation) and show fidelity to black mustard in these populations (there were typically few other flowering plants in the immediate vicinity). All of the 11 study populations had high seed set, regardless of which insect groups visited them. Finally, these insect groups are known to be generally effective pollinators (e.g., Lindsey 1984). The relative effectiveness of each

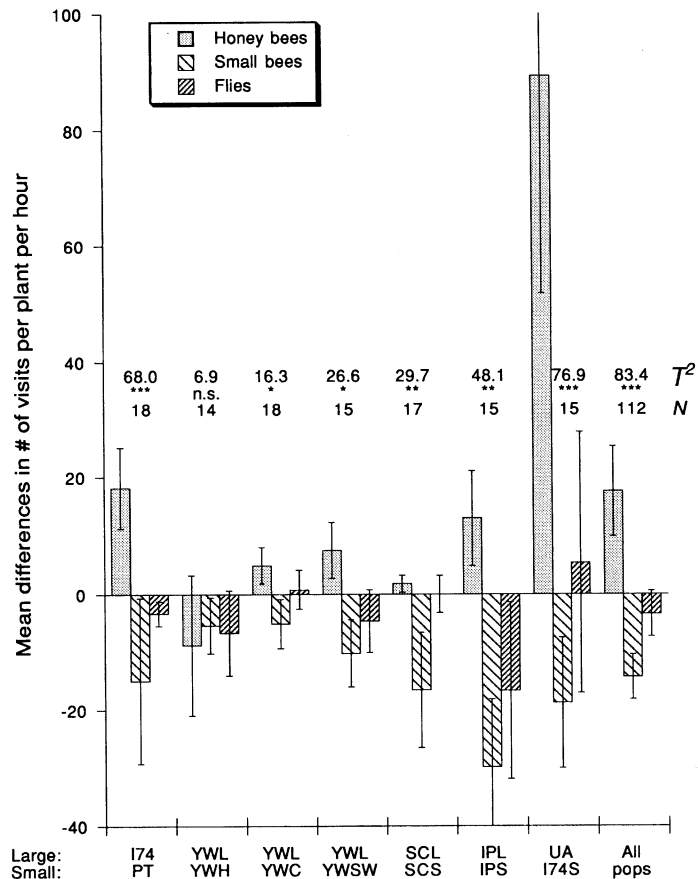


Fig. 3 Mean difference between large and small population pairs in visitation presented on a per-hour basis for each of the three main categories of insect visitors. Hotelling's T^2 with significance levels corrected by sequential Bonferroni are given for each pair of study populations (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$). Error bars are 2x SEM. The sample size (*N*) is the number of simultaneous half-hour observations conducted for each pair of populations. All but one of the population pairs differed significantly in insect visitation, with a greater number of honey bees and a smaller number of small bees observed visiting plants in larger populations on a per-plant basis

of these groups in pollinating black mustard is unknown, however.

While the total numbers of visitors did not differ consistently between large and small black mustard populations, the taxonomic composition of these visitors did differ significantly between pairs of large and small populations in all pairs but one (Fig. 3). The analysis over all populations showed significantly more honey bees and significantly fewer small bees in larger plant populations, and a non-significant trend toward fewer flies in larger populations. This pattern held in analyses of most individual pairs as well. The main exception was the YWL-YWH pair, which did not exhibit a significant overall difference in visitor composition. In addition, there were significantly fewer flies in the larger populations in the I74-PT and IPL-IPS population pairs.

The composition of visitors at the I74 population became similar to that at small populations after most of the I74 plants ceased flowering (I74S): the number of honey bees dropped and the number of small bees in-

Table 2 Results of multiple regressions of per-plant pollinator visitation rates on a variety of environmental variables, to determine causes of variability in visitation. Each column represents the results of a separate multiple regression, with the response variables being the numbers of each of the three main categories of pollinators visiting individual plants over the 30-min observation period ($n=231$ observation periods). Standardized partial regression slopes with their standard errors in parentheses are shown, with total proportion of variability explained by the independent variables and overall significance of each regression model given in the *Total r^2* row

	In no. honey bees	In no. small bees	In no. flies
In no. plants	0.328 (0.064)****	-0.502 (0.083)***	-0.133 (0.058)*
In no. plants ²	- ^a	0.195 (0.082)*	-
In no. flowers	0.556 (0.067)****	0.171 (0.069)*	0.317 (0.060)****
Height	0.123 (0.062)*	-	0.001 (0.052)
In no. honey bees	-	-0.151 (0.073)*	-0.042 (0.068)
In no. small bees	-0.064 (0.063)	-	0.117 (0.054)*
In no. flies	-0.047 (0.079)	0.273 (0.083)***	-
Date	0.323 (0.080)****	-0.183 (0.080)*	0.614 (0.053)****
Date ²	0.243 (0.057)****	-	0.201 (0.039)****
Time of day	-0.098 (0.080)	-0.267 (0.059)****	-
Time of day ²	-0.023 (0.081)	-	-
Temperature	0.044 (0.077)	0.143 (0.068)*	-
Temperature ²	-0.042 (0.044)	-0.122 (0.043)**	-
Solar intensity	0.068 (0.066)	-	-
Solar intensity ²	0.188 (0.063)**	-	-
Total r^2	0.58****	0.37****	0.65****

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$;

^a Dashes indicate variables that were not included in the regression model (see Methods)

creased to levels similar to small populations early in the season.

Variables affecting pollinator visitation

The results of the paired comparisons strongly support the hypothesis that plant population size affects composition of insect visitors. However, the significant differences in plant height and flower number between the paired plants raises the possibility that these variables, rather than plant population size, may have been responsible for the differences. Multiple regression results, however, suggest that population size is a strong determinant of pollinator composition independent of plant height and flower number (Table 2). As predicted from the paired analyses, the number of honey bee visits per plant increased with the number of plants per population while the numbers of small bees and flies declined. The standardized regression slopes mean that an increase of 1 SD in the number of plants at a population was associated with a 33% increase in the number of honey bees and a 50% decrease in the number of small bees (Table 2). Because these are partial regression slopes, they indicate the relationships between the number of pollinators arriving at the plant and population size after the affects of the other included variables are corrected for by the multiple regression.

In contrast to the expectation based on the paired analyses, however, all three categories of pollinators increased significantly as the number of flowers per plant increased. Therefore, the lower number of small bees at larger populations cannot be explained by differences in flower number. The height of the plants within a population had a significant effect on only honey bee visitation, which increased slightly with greater plant height. The quadratic terms for these three variables were significant in only one case, indicating that these relationships are fairly linear.

The numbers of small bees and flies visiting had no direct effect on honey bee visitation, after correcting for

the other variables (Table 2). The number of honey bees present did have a small direct negative effect on small bee visitation, suggesting the possibility of competition. Honey bees had no effect on the number of flies. Small bee and fly visitation seemed to facilitate each other: the numbers of each of these two categories increased with increasing numbers of the other category. Alternatively, both small bees and flies may be responding in the same way to some unmeasured variable.

Date had a substantial effect on the taxonomic composition of the pollinators visiting black mustard, with honey bee and fly visitation increasing strongly and small bee visitation declining slightly in the later part of the flowering season. For both honey bees and flies the linear and the quadratic regression coefficients were strongly positive, indicating a positive relationship with the slope increasing in magnitude as the season progressed. At least some of the reasons for the curvature in these relationships can be seen in Fig. 2: the number of flies visiting increased in all four of the late-season populations, and honey bee visitation increased dramatically at UA. Time of day had a significant effect only on small bee visitation, which declined later in the day (Table 2).

Small bee activity increased with increasing atmospheric temperatures, while the other categories of pollinators were not affected by this variable. In contrast, only honey bees responded to levels of solar radiation, with highest visitation at low and high levels of radiation, and low visitation at intermediate radiation levels after correcting for temperature and time of day (Table 2). This surprising pattern was confirmed using LOWESS plots (Chambers et al. 1983), although the pattern appears to be weak.

Discussion

Our results show great variability in the taxonomic composition of insect pollinators over short distances (medi-

an distance between pairs=660 m). In fact, our study underestimates variability by lumping a number of different species of small bees and flies into single categories. It is likely that further spatial variability occurred within these categories, as local abundances of the different species probably vary due to factors unrelated to the plants (e.g., nest sites for small bees; G. Eickwort, personal communication).

The composition of pollinators varied consistently with population size: honey bees were more abundant per plant at large populations while small bees (and possibly flies) were more abundant at small populations. It is likely that the population size is directly responsible for these differences, because the paired design eliminated temporal variability in visitation, and the multiple regression analyses showed strong effects of population size after other variables were controlled for statistically. It is possible that some unmeasured variable correlated with population size may be the cause of the visitation differences. Experimental manipulation of plant population size on a large scale is the only way to show definitively that population size is the cause of the differences seen.

The increased numbers of honey bees at larger populations is consistent with all previous reports on a wide variety of plant taxa (Schaffer et al. 1979; Sih and Baltus 1987; Sowing 1989; Stanton et al. 1991; Jennersten and Nilsson 1993) and may therefore be a general pattern for plant species that are visited by honey bees. This pattern is almost certainly due to the ability of honey bees to recruit long distances to the most rewarding plant populations (Seeley 1985; Seeley 1989).

An interesting result of our study was that small bees and possibly flies were actually less abundant on a per-plant basis at larger populations. Decreases in visitation rates of a variety of less social or less aggressive pollinator taxa with increasing population sizes of a variety of plant taxa have been reported (Johnson and Hubbell 1974; Schaffer et al. 1979; Sih and Baltus 1987; Jennersten and Nilsson 1993). There are at least two hypotheses to explain the smaller number of certain pollinator taxa at large populations; these hypotheses are not mutually exclusive. First, these pollinators may forage over relatively restricted areas (Morse 1982; Roubik 1989). This would tend to decrease the variance in the total number of these pollinators present in the vicinity of plant populations differing in size. Therefore, large plant populations could have the same absolute number of these taxa present as small populations, but the individual insects would be spread over a greater number of plants. Visits to any given plant in a large population would then occur at a lower frequency than visits to a plant in a smaller population (see Jennersten and Nilsson 1993 for a similar argument).

Alternatively, the presence of a large number of highly social or aggressive taxa may have a direct effect on the visitation of other taxa through competitive interactions (Johnson and Hubbell 1974; Johnson and Hubbell 1975; Roubik 1978; Roubik 1980). This possibility is

supported by the weak negative effect of honey bees on small bees seen in our regressions (Table 2); however, honey bee visitation had no effect on flies. Our observations of insect visitation at the SCL and SCS populations do not support the existence of competitive interactions between honey bees and small bees, however; despite a very small absolute number of honey bees visiting the large population (SCL), there were many fewer visits to plants by small bees at this population relative to the small population (SCS; see Fig. 2). Experimental studies are required to determine the causes of reduced small bee visitation at large plant populations.

The taxonomic composition of the visitors varied over the season, with honey bees and syrphid flies increasing and small bees decreasing as the season progressed. Other studies have reported seasonal variation in the composition of pollinator assemblages (see Introduction). Stanton (1987) also found increases in syrphid fly visitation later in the season. The reasons for the seasonal variation in our study are unknown, but probably include phenology of the insect species involved and phenology of other plant species competing with black mustard for pollinators. The pollinator phenology is likely to be most important for the small bees and syrphid flies, because honey bees are active throughout the flowering season of black mustard. Conversely, the phenology of other plants is likely to be particularly important for honey bees, due to their greater ability to locate and exploit plant populations over large areas.

If the different pollinators cause differential selection on floral traits, then the differences among plant populations in composition of pollinators could lead to genetic differentiation for floral traits among the populations. For floral differentiation to occur, however, the spatial variability in selection would have to be consistent over time. Our results and other observations suggest that this is unlikely. We showed, as have other authors working on other plant species, that there was variation through the season in composition of the pollinator assemblage. In addition, there is likely to be great variability across years in black mustard, as has been shown in other species (see Introduction). Since black mustard is a weedy colonist of disturbed areas, the population sizes of this species are likely to vary widely among years, causing changes in pollinator composition (J. Conner and R. Neumeier, unpublished observations). For these reasons it seems unlikely that our black mustard populations would evolve different floral morphologies in different populations to adapt to the diversity of pollinators (cf. Feinsinger 1983; Herrera 1988; Horvitz and Schemske 1990; Eckhart 1992). Rather, the evolution of plasticity in floral traits (Paige and Whitham 1985) or a generalized flower seems more likely.

In summary, we found clear evidence for spatial and temporal variability in the composition of insects visiting black mustard. The spatial variability was over extremely short distances, and was caused at least in part by differences in plant population size. Future work should focus on the causes of reduced small bee visitation in large

plant patches, and the degree to which the different taxa of pollinators exert different selection on floral morphology.

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