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ECOLOGICAL INTERACTIONS AMONG THREE SPECIES OF EUPHORBIA AND THEIR INSECT VISITORS IN THE AMERICAN SOUTHWEST.

The City University of New York, Ph.D., 1975
Biology

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ECOLOGICAL INTERACTIONS AMONG THREE SPECIES OF EUPHORBIA AND THEIR INSECT VISITORS IN THE AMERICAN SOUTHWEST

by

JOAN G. EHRENFELD

A dissertation submitted to the Graduate Faculty
in Biology in partial fulfillment of the requirements
for the degree of Doctor of Philosophy,
The City University of New York.

1975

This manuscript has been read and accepted for the Executive Committee in Biology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

May 22, 1975
Date

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ABSTRACT

ECOLOGICAL INTERACTIONS AMONG THREE SPECIES OF *EUPHORBIA* AND THEIR INSECT VISITORS IN THE AMERICAN SOUTHWEST

by

Joan G. Ehrenfeld

Advisor: Dr. Jerome G. Rozen, Jr.

The interactions of three species of *Euphorbia* subgenus *Chamaesyce* and the insects, particularly the bees, that visit their cyathia have been examined, and the extent of bee-plant coadaptation has been evaluated. The plants are common elements of the ruderal vegetation in southeastern Arizona and adjacent New Mexico. Most of the species of bees are oligolectic on *Euphorbia*; that is, they are dependent on *Euphorbia* for all of their food.

The plants - *E. albomarginata*, *E. capitellata* and *E. hyssopifolia* - were all found to be proterogynous and self-compatible, but were variably capable of pollinating themselves. *E. albomarginata* is obligately dependent on insect visitors for pollination, *E. capitellata* requires insect visitation for maximum seed set but is capable of limited self-pollination, and *E. hyssopifolia* can reproduce without any insect visitation. These differences in pollination biology are paralleled by differences in the abundance and diversity of insects collected on the cyathia, and by differences in the size of the petaloid appendages, glands, and anthers. Two hundred twenty species of insects, principally bees, wasps and flies, were found feeding on the cyathia of the three species; the bees are the most effective pollinators, and, at most sites, are the most abundant visitors. However, the plants have not evolved specific adaptations to foster bee visitation, nor are they dependent on these insects; they are evidently adapted to reproduce via visits from any kind of insect, or to do without them entirely.

The foraging behavior of the seven most common species of bees was analyzed in order to determine their flexibility in dealing with variations in food availability on different food-plants. Forty elements of foraging behavior were identified, and were compared in those bees foraging on *E. albomarginata* and *E. capitellata*. I found that 1) the variation in foraging behavior among the species of bees is primarily based on intrinsic or species-specific influences, and not behavioral plasticity related to food-plant biology, 2) bees oligolectic on *Euphorbia* do not differ in their behavioral adaptations to their food-plants from the polylectic bees that feed on a variety of plant species, and 3) the extensive differences in all aspects of foraging behavior among the bee species suggests that there is no "optimal foraging strategy" for collecting pollen and nectar from *Euphorbia*.

Thus, although some of the bees have evolved physiological ties to their food-plants (i.e., oligolecty), their foraging behavior reveals no further levels of coadaptation. Moreover, the adaptations of Euphorbia to bee visitors are, if anything, even weaker.

The hypothesis that coexisting species of bees are competing for limited food resources was examined by comparing the ratio of bee density to food density (measured as the density of open, full anthers) at four sites and at three times of day. The density of bees per unit of food declined during the day, indicating that there is uncollected pollen present at the end of the foraging period. The data from the peak foraging period (10 A.M. - 2 P.M.) at each site were adjusted for the relative abundance of each bee species and for their relative sizes (that is, pollen gathering capacity); a Kruskal-Wallis test demonstrated that three of the four sites had statistically similar values of bee density/food density. These results imply that competitive interactions for limiting quantities of food are present, but are weaker in effect than the selective pressures that produce an early cessation of foraging.

ACKNOWLEDGMENTS

I am deeply indebted to Dr. Jerome G. Rozen, Jr., American Museum of Natural History, for initially suggesting that the *Euphorbia*-bee association might prove interesting, for his support and advice throughout the project, and for his painstaking and thorough reviews of the many manuscripts associated with this thesis.

Drs. Peter Chabora, Joseph Grossfield, and Jess Hanks, City University of New York, advised me on all aspects of the research and writing. Dr. Robert Cruden, University of Iowa, Dr. E. G. Linsley, University of California, and Dr. Robbin Thorp, University of California, kindly reviewed the research proposal and provided many valuable comments. Drs. George and Kathleen Eickwort, Cornell University, read and improved Chapters 6 and 7. Drs. Howard Levene and F. E. Warburton, Columbia University, spent generous amounts of time guiding my use of statistical techniques. I am grateful to Dr. Norman Pullman, City College of New York, for providing both assistance with the SOUPAC programs and computer time for running them. Dr. G. Jelenkovic and Mr. Earl Bowerman, Rutgers University, permitted me the use of their fluorescent microscope, and greatly assisted me with the observations. Dr. George Eickwort identified the specimens of *Dialictus*, and Dr. Paul Timberlake identified the specimens of *Perdita* and *Exomalopsis*. Mr. Vincent Roth made available to me the facilities of the Southwestern Research Station, and was generous with his time and energy in helping me with equipment.

I am grateful for the following sources of financial support: Sigma Xi Grants-in-Aid of Research (1972, 1973); The Theodore Roosevelt Memorial Fund of the American Museum of Natural History (1972); City University of New York, travel funds (1973); N.S.F. Grant GB 32193 (to Dr. J. G. Rozen, Jr.).

Above all, I am grateful to my husband, David, for his unwavering support and enthusiasm through the vicissitudes of graduate study, for his endurance in the Arizona desert, and for his exceptional critical aid with both the substance and the presentation of the thesis.

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CHAPTER 1.

INTRODUCTION

The common species of Euphorbia subgenus Chamesyce that grow in the desert scrub and grassland associations of southeastern Arizona are notable for the large number of bee and other insect visitors attracted to their blossoms. The American southwest is also notable for the large number of species of bees that are highly restricted in their choice of plant food. A number of these species of bees are entirely dependent for their food supply on Euphorbia. This paper is an investigation of the nature of the ecological interactions that occur between these two groups of organisms, and is an attempt to determine the extent of interdependence between them.

The specific problems that I have investigated can be grouped into two categories, each of which is directed towards elucidating the effect of one of the groups of organisms on the biology of the other. With respect to the plants, I report the results of a study of the reproductive biology of three species of Euphorbia, including the ability of each plant species to pollinate itself and to produce seed when self-pollinated, the relative importance of insects and wind as pollinators, the identity of insect visitors and their movements and feeding behavior on the cyathia. The hypothesis that the cyathium ("flower") of Euphorbia is an adaptation for insect pollination is evaluated. With respect to the bees and other insects, I examine the ways in which the Euphorbia food source is harvested and shared by the different taxa, particularly the bees. Data on the foraging patterns of the bees are examined for evidence that differences in behavior permit differential utilization of resources and therefore reduce competition; these data are also considered in the light of current theories of energetic efficiency in feeding behavior. The ratio of foraging bee density to food density is used to evaluate the importance of food as a limiting factor for bee populations. In conclusion, I assess the extent of interdependence and interaction among the groups.

Pollination biology has traditionally been an autecological discipline, emphasizing both the description of floral mechanisms for attracting insects (e.g., Faegri and van der Pilj, 1971; Macior, 1970; Proctor and Yeo, 1973), and the description and enumeration of insect visitors to particular plants (e.g., Beattie, 1971; Dodson and Frymire, 1961; Linsley and Cazier, 1963; Muller, 1883). Attention has been most commonly directed towards showy, complex flowers such as members of the Scrophulariaceae and Orchidaceae. Indeed, much of what is known of the pollination biology of small simple flowers was obtained by the first comprehensive workers in this field - Knuth (1909), and Muller (1883). Recently, the autecological approach has been extended to include physiological investigations (Heinrich, 1970), chemical analyses of plant attractants (Dodson, 1970), and detailed studies of pollinator behavior (Cruden, 1970; Macior, 1967);

these recent studies have been reviewed by Baker and Hurd (1968).

There has been, however, some emphasis on synecological questions in the botanical literature. Botanists have often used pollination studies to help decipher the genetic structure of plant populations (Bateman, 1947; Levin and Kerster, 1967; Kiang, 1972), and pollinator activity has been particularly well studied as a factor in the population genetics of plant breeding for agricultural purposes (e.g., Free, 1970). Botanists have also used pollination information to study evolution in plants (e.g., Baker, 1960; Grant, 1949; Grant and Grant, 1965). Plant competition for pollinator attention has been mathematically modelled (Levin and Anderson, 1970; Straw, 1972) and studied in natural populations (Mosquin, 1971). Thus, a population approach to the effects of pollinators on plant ecology and evolution has been well established. However, the converse effects of the pollen and nectar food sources on the ecology and evolution of pollinators have been studied much less extensively. In particular, there has been very little quantitative work on the importance of plant food as a limiting resource to pollinators, and the concommitant importance of competition among pollinators in determining community structure and change. Finally, problems of the pollinator-plant system as a whole are just beginning to be phrased and studied in particular ecosystems. For example, although the effects of plant spacing on pollinator behavior have been studied (Levin and Kerster, 1969; Manning, 1956), and the effects of pollinator behavior on plant density have been modelled (Levin and Kerster, 1970), there has been little consideration of the reciprocal effects within a system.

Ultimately, studies of ecological and evolutionary interaction between plants and pollinators must approach an estimate of the extent of coevolution among the organisms involved. The degree of coadaptation seen between *Ficus* and *Blastophaga* (Ramirez, 1974) is much greater than that seen between apomictic Compositae and the wide range of insects that visit them. Relationships can range from the mutual determination of distribution and survival, through unreciprocated dependence of one group on the other, to independence of both groups. Baker and Hurd (1968) have identified some of the patterns of interaction and coevolution, and have stressed the need for further study and definition of these patterns. However, the emphasis in the general ecological literature on social bees (*Apis* and *Bombus*) and on complex flowers has resulted in a somewhat lopsided impression of the coadaptation of flowers and pollinators. Restoring the balance might make pollination biology a major contributor to ecological and evolutionary theory, rather than an extensive description of an evolutionary principle.

The Plants

Euphorbia is one of the largest genera of angiosperms; it contains about 1500 species and is cosmopolitan in distribution (Good, 1964). It is characterized by a unique floral device, termed a cyathium, which is an inflorescence composed of many male flowers and one terminal female flower. Each flower consists simply of the sexual parts (in the case of the male flowers, a single stamen), and lacks calyx and corolla. They are tightly clustered within an involucre of five united bracts. At each junction of the bracts, there is a gland, which may have an expanded, petal-like appendage. Thus, the cyathium resembles a flat, simple flower, with the typically white gland appendages substituting for petals and surrounding the central stamens and pistil. The cyathium ranges in diameter from less than 1 mm to nearly a centimeter. The plants vary in growth form from the well-known cactus-like succulents found in Africa through mesic shrubs and trees to prostrate herbaceous weeds growing in sidewalk cracks. Although there has been much discussion of the need to separate the genus into more manageable units (e.g., Richardson, 1968; Webster, 1967; Wheeler, 1941, 1943), the intergradation of characters among the species has so far confounded all attempts at dismantling the group.

Despite the ubiquity and diversity of Euphorbia, there has been little attention paid to its reproductive biology, and even less to the functioning of its unusual floral device. The few studies of embryology and reproduction, conducted on species scattered throughout the genus, have demonstrated a wide variety of sexual systems ranging from obligate outcrossing in E. cyparissias (Meunscher, 1936) to apomixis by means of adventive embryony in E. dulcis and others (Carano, 1926; Davis, 1966). The early students of pollination biology (Knuth, 1909;

Muller, 1883) observed a diverse group of insects visiting a few common species, but the importance of insects to the reproductive biology of the plants has remained obscure. The observations of insect visitation in conjunction with the conspicuousness of the petaloid appendages and glands in some species, have supported a general assumption that the cyathium is an adaptation to insect pollination (e.g., Cronquist, 1968; Stebbins, 1950). However, the extremely small size of the cyathia of many species, and the weedy nature of many species raises the question whether insect pollination is widespread in the group.

The species studied here belong to the subgenus *Chamaesyce.* This section is distinguished by the opposite, inequilateral leaves, and by the branching habit of the plants: the main axis aborts after the first pair of true leaves appear, and all subsequent growth is attributable to axillary buds. The subgenus includes about 250 species, the majority of which are American. Many of the species occur in waste places, along roadsides, in poor sandy soil, and thus can qualify as ruderals or weeds (Baker and Stebbins, 1965). The three species investigated here, *E. albomarginata* T. & G., *E. capitellata* Engelm. and *E. hyssopifolia* L. all grow abundantly along roadsides in the desert grassland association in the southwest. *E. albomarginata* and *E. capitellata* are common throughout the southwest, extending as far north as northern Arizona. *E. hyssopifolia* is abundant throughout Central America, and reaches the northern limit of its distribution in southern Arizona (Wheeler, 1941). *E. albomarginata* is a prostrate plant that forms dense, low mats along roadsides, near culverts, on road and railroad embankments and other low hills, and along arroyos and other sources of intermittent moisture. *E. capitellata* is an erect to decumbent herb, on which the cyathia are tightly packed in heads. It grows in the same habitats as *E. albomarginata*, and often the two species form mixed populations. These two species tend to grow in patches separate from surrounding vegetation. *E. hyssopifolia* is an erect species, and is most often found intermixed with grasses and other herbs along roadsides. Its cyathia are considerably smaller than in the two preceeding species, and are loosely clumped in groups of three to eight cyathia. All three species are overwintering to perennial, and all flower in the first season.

The Bees

The feeding ecology of many non-social bees is remarkable for the small number of food-plant species on which each bee species depends. Bees that throughout their geographical range rely on one or a few closely related species of plants for the pollen on which both the larvae and the adults feed are termed oligolectic (Linsley, 1958). The term "polylectic" is applied to bee species whose members make use of a variety of plants for pollen; the breadth of their taste preferences ranges from species that visit only a small proportion of the plants in bloom to those that forage on virtually any plant species that is presenting pollen. Linsley (1958) states that the majority of bee species are oligolectic, and this is particularly true of members of certain families of bees. The genera *Andrena* and *Perdita*, in the Andrenidae, contain over 1200 and 700 species respectively, most of which are oligolectic. The other genera of the family are much smaller, but also contain a large percentage of oligolectic species. In contradistinction to the Andrenidae, the Halictidae contain several genera (*Halictus*, *Dialictus*, *Lasioglossum*) with very large numbers of species, few of which are oligolectic. Oligolecty is also common among the Colletidae and Anthophoridae. Restriction in the diversity of plants visited for nectar is much less common; bees that visit few plant species for pollen may visit a wider variety of plants for nectar.

This study is concerned with the behavioral ecology of the seven most common species of bees that visit *Euphorbia* in southeastern Arizona. Five of these are oligoleges of *Euphorbia*, and two utilize other plants as well. Table 1 lists all the bee species that have been found foraging on *Euphorbia* during this study, and identifies the common species described in detail below. The common species are illustrated in Figure 1.

The feeding ecology of most solitary bees is intricately related to other aspects of their life-histories. Nesting sites of the smaller solitary bees are often close to or intermixed with populations of the food-plants; this is true of *Heterosarus nanulus*, *Nomadopsis* *helianthi*, *Perdita minima*, *Perdita obscurella*, and *Calliopsis squamifera*. Most of the panurgine bees nest gregariously (Rozen, 1967) and thus the plant population may cover considerably more area than the nesting site. The large, polylectic species, however, often nest at a greater distance from the food plant, and this is probably the case for *E*. sp. A. Many bee species use the pollen plant flowers as the site of mating; two of the species studied here (*H*. *nanulus* and *P*. *obscurella*) do this. Others mate on the ground at the nesting site, so that newly emerged females are mated as they leave their burrows. The relationship between mating site location, oligolecty, and speciation has been more extensively discussed in Rozen (1958). The seasonal activity of oligolectic bees usually coincides with the period of bloom of the host plant (Linsley, 1958); however, cases are occasionally reported in which oligoleges rely on plants at the end of their blooming season or at the end of the pollen dehiscence phase of the host flower (Linsley et al., 1964). Although the plants studied here probably bloom continuously throughout the spring and summer, the period of maximum bloom and maximum plant density (August to September) coincides with the period of bee activity, and this period of biological activity is tied to the occurrence of the summer rains in July.

The number of generations produced each season varies among the species. Based on evidence from intensive field studies (Rozen, 1958; Shinn, 1967), it seems likely that *C*. *squamifera* and *N*. *helianthi* have two generations per season. I have observed P. obscurella mating from early August to early October; bees mating late in the season are probably a second generation. P. minima has been collected in southeastern Arizona only in August and the first week in September, and thus it is likely to be univoltine. No information on voltinism is available for D. perparvus or E. sp. A. Larvae overwinter in their cells in a quiescent or diapause condition.

The prevalence of oligolecty among bees has provoked some speculation concerning the selective forces involved in the evolution of the trait. Most investigators believe that competition for limited food resources has generated the tendency towards highly specialized feeding behavior (e.g., Cruden, 1972; Hurd and Linsley, 1967; Michener, 1954; Robertson, 1914; Thorp, 1969). Lovell (1914), however, suggested that there is a surplus of flower food, and that bees specialize so as to avoid wasting time and labor. Although the limiting nature of food resources has thus been questioned since 1914, little of the work on the feeding ecology of bees has helped to resolve the matter.

Although the behavior of bees has become an important adjunct to classical taxonomic studies (e.g., Michener, 1974; Sakagami and Michener, 1962), the actions of a foraging bee, on and off flowers, has rarely been considered from an ethological perspective. Foraging behavior of bees on flowers has usually been treated briefly, and has often been restricted to description of the food plants, daily and seasonal phenology, and the length of foraging trips. The work done to date however, is thus insufficient to permit comparisons among taxa. Analysis and comparisons of the motions that comprise foraging in a number of species of bees feeding on the same plants are likely to yield information useful for evaluating the relative contributions of learned plastic responses to floral morphology and of inherited, stereotyped movements to the overall foraging behavior of each species.

Voucher specimens of all bee species have been deposited in the collection of the American Museum of Natural History.

Study Sites

Study sites were located along U.S. Route 80 and intersecting dirt roads in southeastern Arizona and southwestern New Mexico (Fig. 2). The sites at Apache, 11, 13 and 18 miles southwest of Apache (A, 11 SWA, 13SWA, and 18SWA in Fig. 2) consisted of plant populations situated on level or slightly sloping ground in the area between the side of the road and a parallel railroad embankment about 50 m away (Fig. 3). At the site 1 mile east of Apache (1EA), E. albomarginata bordered the edge of a flat dirt road extending across the valley floor. The plant population studied at 12 miles north of Rodeo (12NR) grew in a strip about 2 m wide between the side of Route 80 and the bordering Larrea scrub community. Only at the 9WSWA site (9 miles west-southwest of Apache) was the plant population distant from the road; in this case the plants were growing on the side of an ancient cinder cone (peak elevation about 100 feet above the surrounding desert floor).

The biotic and physical characteristics of each site are listed in Table 2. The soils at all sites except 9WSWA are alluvial deposits of sand, silt and gravel, and are in general hard packed below the surface dust. At 9WSWA, the soil is of basaltic origin. The sites at and south of Apache, Arizona, are in the San Bernardino valley; they are in general cool desert, with an average annual temperature between 47°F. and 59°F., (Buol, 1966) and belong to the grassland biome in the lower Sonoran Life Zone. Rainfall from July to September averages 9.15 inches (data from U. S. Weather Bureau statistics from Apache and Douglas, Arizona). The site at 12NR is located in the San Simon valley, which is classified by Buol (1966) as a thermic region (average annual temperature greater than 59°F.), and is surrounded by a Larrea association type of desert scrub biome. Rainfall in this region averages 5.31 inches for this period (data from U. S. Weather Bureau statistics for Rodeo, N.M. and San Simon, Arizona). According to Lowe (1964), the vegetation of this part of Arizona is characterized by a mosaic of desertscrub and grassland associations, with changes between associations occurring over very short spaces. As can be seen in Table 2, most of the bee species occurred in at least two soil or biome types. Although the occurrence of precipitation during the summer is predictable, it can vary widely in amount and location, because it occurs in thunderstorms. One area can receive several inches during a few days, while a site a mile away remains dry. In this sense, the rainfall on a particular population is highly unpredictable and variable from year to year.

These temporal and spatial fluctuations in environmental conditions are mirrored in the instability of the vegetation from year to year. The sites listed in Table 2, and others in the vicinity that were observed casually from 1971 to 1973 all underwent far-reaching changes in the composition and size of the herbaceous plant populations from year to year. For example, in 1971, at 13SWA, the three species of *Euphorbia* were abundant, and covered most of the ground between tussocks of grass. In 1972, *E. hyssopifolia* was rare, and the other two species of *Euphorbia* were mixed with dense stands of *Lepidium* and *Eriogonum*. In 1973, *Lepidium* and *Eriogonum* were rare, *Euphorbia* was largely dying, and the most common plant was *Heterotheca* sp. Again, at 11SWA, during 1972 a population of *E. capitellata* was found in which the plants were large and vigorous, and had probably survived there for several years. In 1973, I could not find a single individual of this species; the ground that had been covered with it was bare of vegetation. However, the contiguous population of *E. hyssopifolia* that was studied there in 1972 was still vigorous in 1973. Thus, the only aspect of the local vegetation in an area that is certain is the unpredictability of its composition.

TABLE 1. Bees collected at all study sites on three species of *Euphorbia*. Common = many individuals seen at minimum of two sites; Occasional = some individuals seen at only one site and/or during only one season; Rare = small numbers seen on only one occasion.

Family, Subfamily	Species	Dependence on *Euphorbia*	Abundance
Colletidae	*Colletes* sp.	unknown	occasional
Colletinae			
Andrenidae,	*Calliopsis* (*Perissander*) *anomoptera* Michener	oligolectic	occasional
Panurginae	(*Calliopsis*) *squamifera* Timberlake*	oligolectic	common
	(*Perissander*) *rogeri* Shinn	oligolectic	occasional
	Heterosarus nanulus (Timberlake)*	oligolectic	common
	Nomadopsis (*Micronomadopsis*) *helianthi* Swenk and Cockerell*	oligolectic	common
	Perdita (*Epimacrotera*) *biguttata* Timberlake	oligolectic	rare
	(*Perdita*) *chihuahua* Timberlake	oligolectic	occasional
	(*Perdita*) *confusa* Timberlake	polylectic	occasional

TABLE 1. Continued.

Family, Subfamily	Species	Dependence on Euphorbia	Abundance
	(Macroterella) mellea Timberlake	oligolectic	rare
	(Perditella) minima Cockerell*	oligolectic	common
	(Perdita) obscurella Timberlake*	oligolectic	common
Halictidae,			
Halictinae	Dialictus clarissimus (Ellis)	polylectic	rare
	clematisellus (Cockerell)	polylectic	occasional
	hudsoniellus (Cockerell)	polylectic	rare
	hunteri (Crawford)	polylectic	rare
	perparvus (Ellis)*	polylectic	common
	pruinosiformis (Crawford)	polylectic	rare
	tegulariformis (Crawford)	polylectic	occasional
	sp. 4	polylectic	rare
	sp. 7	polylectic	occasional

TABLE 1. Continued.

Family, Subfamily	Species	Dependence on *Euphorbia*	Abundance
	sp. 10	polylectic	rare
	Halictus ligatus Say	polylectic	rare
	tripartitus Cockerell	polylectic	rare
	Evylaeus pectoraloides (Cockerell)	polylectic	rare
	Agapostemon sp.	polylectic	rare
Anthophoridae,	*Exomalopsis* (*Anthophorisca*) sp. A* $^{+}$	polylectic ?	common
Anthophorinae	(Phanomalopsis) sp. B^{+}	polylectic ?	occasional
	(*Phanomalopsis*) *solani* Cockerell	polylectic ?	rare
Xylocopinae	*Ceratina* sp.	unknown	occasional

* Common species included in behavioral studies.

+ Descriptions in preparation by P. Timberlake.

TABLE 2. Biotic and physical characteristics of the study sites.

Site	Plants	Bees	Years Studied	Elevation (ft)	Dominant Vegetation
12NR	*E. albomarginata*	*N. helianthi**	1973	3980	*Larrea*, *Guttierezia*
		P. minima			
		*D. perparvus**			
		D. hudsoniellus			
Apache	*E. albomarginata*	*P. minima**	1972	4382	*Acacia*, *Lepidium*
		P. obscurella			
1EA	*E. albomarginata*	*P. minima**	1973	4340	*Lepidium*, *Yucca*, grasses
		*P. obscurella**			
		N. helianthi			
		*D. perparvus**			
		Colletes sp.			
		Ceratina sp.			

TABLE 2. Continued.

Site	Plants	Bees	Years Studied	Elevation (ft.)	Dominant Vegetation
9WSWA	*E. capitellata*	*H. nanulus**	1973	4840	*Aplopappus*, *Aster*, grasses
		*E. consobrina**			
		N. helianthi			
		C. squamifera			
		Colletes sp.			
11SWA	*E. hyssopifolia*	*H. nanulus**	1972	4620	*Aster*, *Heterotheca*, *Eriogonum*, grasses
	E. capitellata	*D. perparvus**	1973		
	E. albomarginata	*E. consobrina**			
		P. obscurella			
13SWA	*E. albomarginata*	*H. nanulus**	1972	4580	*Lepidium*, *Eriogonum*, *Acacia*, *Applopappus*, grasses
	E. capitellata	*C. squamifera*			
	E. hyssopifolia	*N. helianthi*			
		P. minima			
		*P. obscurella**			

TABLE 2. Continued

Site	Plants	Bees	Years Studied	Elevation (ft.)	Dominant Vegetation
		D. perparvus			
		_E. consobrina_*			
18SWA	_E. albomarginata_	_H. nanulus_*	1973	4500	_Applopappus_, _Aster_, _Crotalaria_, _Amaranthus_, _Franseria_, _grasses_
	E. capitellata	_C. squamifera_*			
	E. hyssopifolia	_P. minima_			
		_P. obscurella_*			
		_E. consobrina_*			
		C. rogeri			
		Colletes sp.			

* Most abundant species at each site.

Figure Captions

Chapter 1

Fig. 1. Species of bees commonly visiting *Euphorbia spp.* in southeastern Arizona. Pm = *Perdita minima*; Po = *Perdita obscurella*; Hn = *Heterosarus nanulus*; Dp = *Dialictus perparvus*; Cs = *Calliopsis squamifera*; Nh = *Nomadopsis helianthi*; Ea = *E.* sp. A.

Fig. 2 Location of study sites in southern Arizona and New Mexico. See text for definitions of site names.

Fig. 3 Typical aspect of desert grassland at sites located south of Apache, Arizona.

FIGURE 1

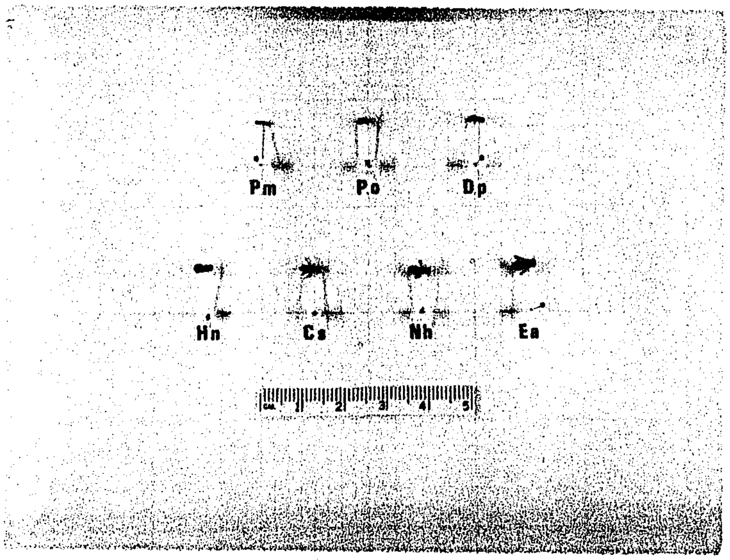
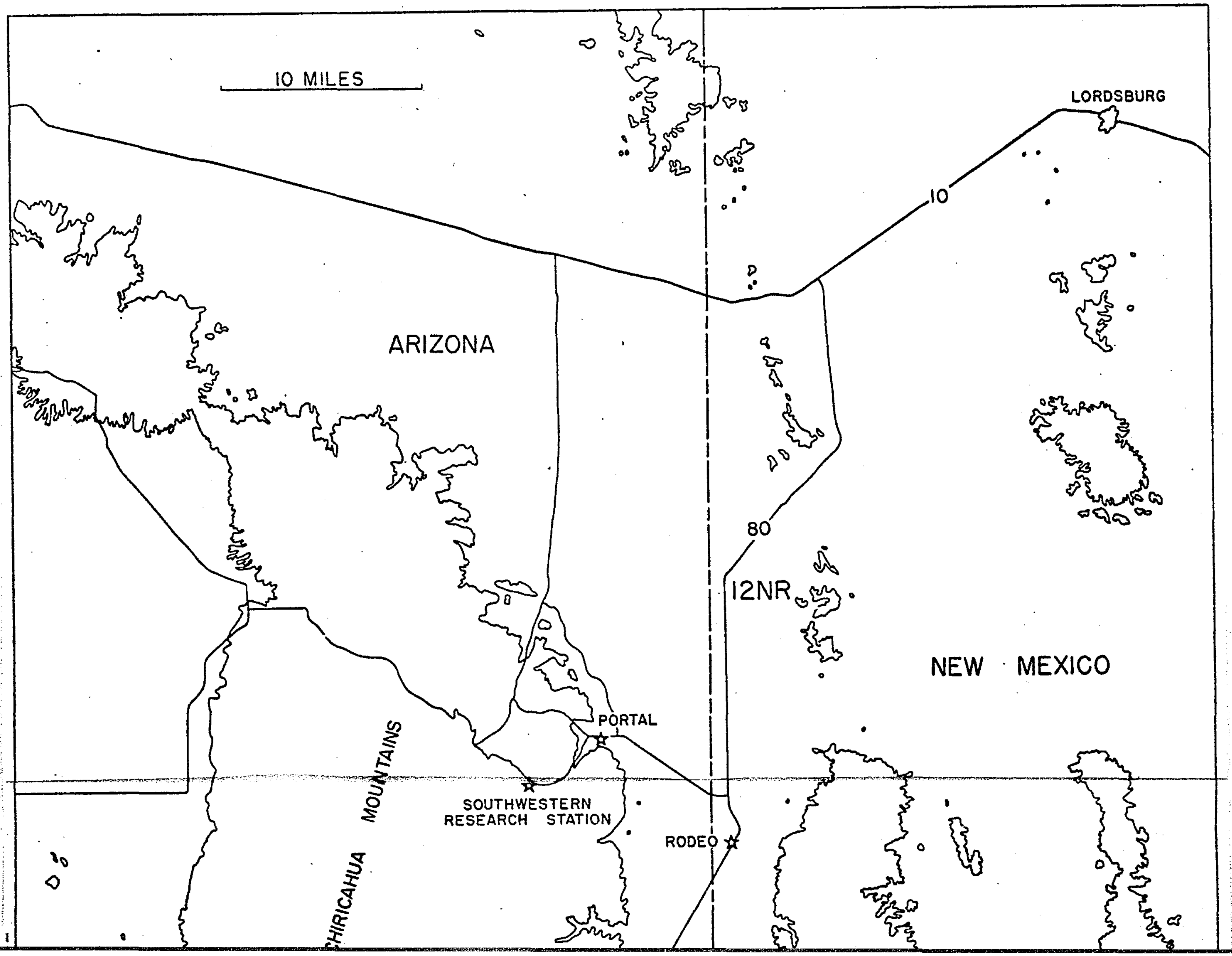

Pm
Po
Dp
Hn
Cs
Nh
Ea
cm 1 2 3 4 5

FIGURE 2


10 MILES
LORDSBURG
10
ARIZONA
80
12NR
NEW MEXICO
PORTAL
SOUTHWESTERN RESEARCH STATION
RODEO
CHIRICAHUA MOUNTAINS

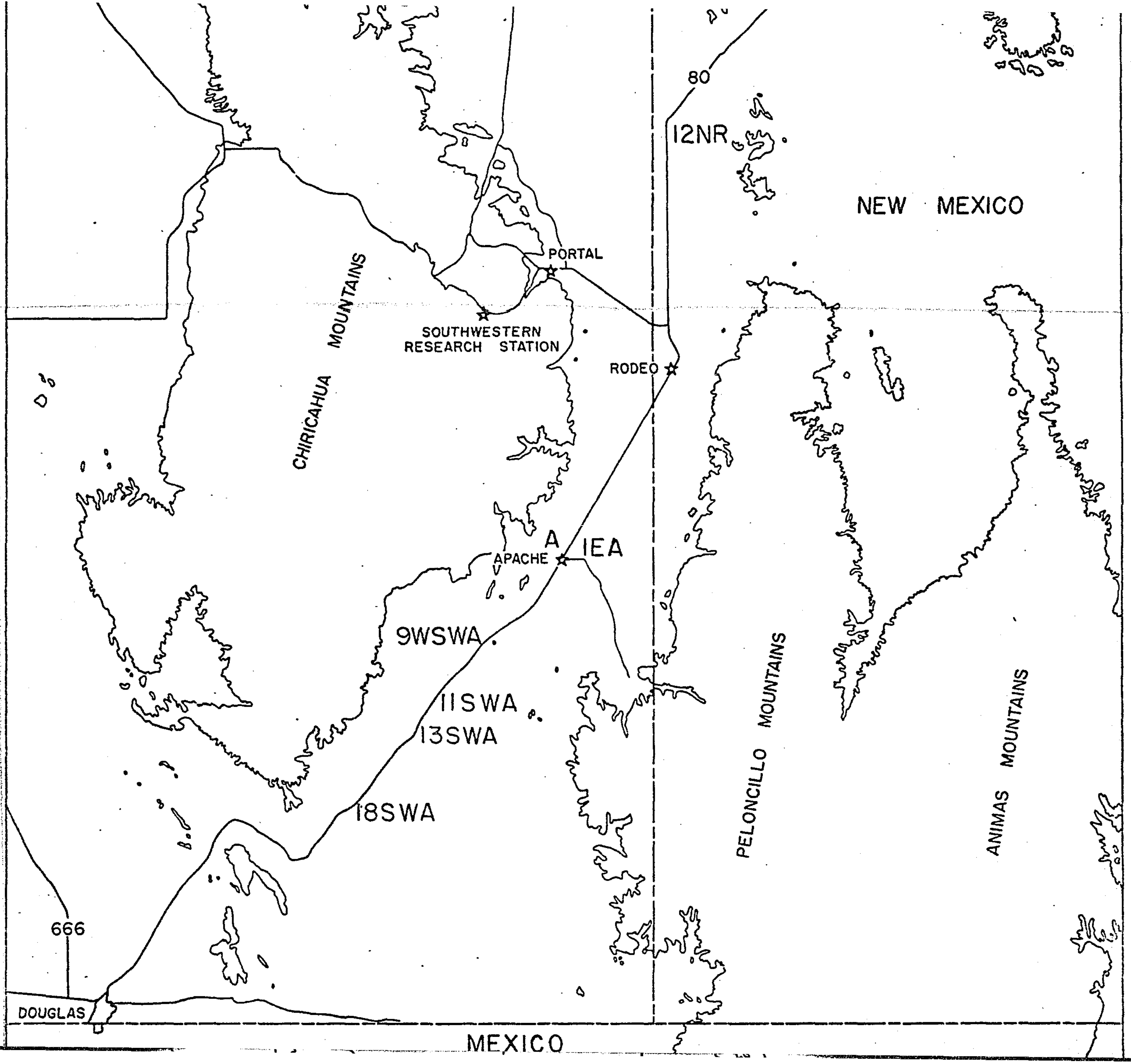
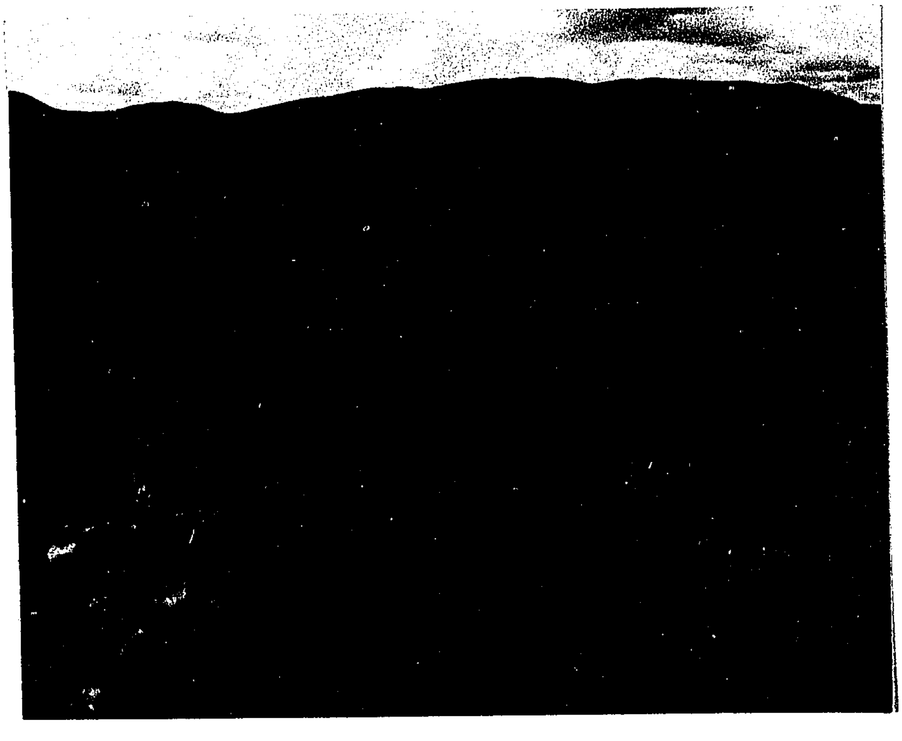

80
12NR
NEW MEXICO
PORTAL
CHIRICAHUA MOUNTAINS
SOUTHWESTERN RESEARCH STATION
RODEO
A
IEA
APACHE
V
9WSWA
11SWA
13SWA
18SWA
PELONCILLO MOUNTAINS
ANIMAS MOUNTAINS
666
DOUGLAS
MEXICO

FIGURE 3



CHAPTER 2

METHODS

Reproductive Biology of Three Species of Euphorbia subgenus Chamaesyce

The plants were studied at the sites described in Table 2, and also in an insect-proof greenhouse on the grounds of the Southwestern Research Station near Portal, Arizona.

During August and September 1972, I placed insect-proof cages of muslin over plants in the field. This method proved impractical with two of the species (*E. albomarginata* and *E. capitellata*) because the plants produced only vegetative growth and few flowers, and because many of the cages (and plants) were destroyed by cattle. The third species (*E. hyssopifolia*) flowered satisfactorily, and resulting seed set in the absence of pollinating agents is reported below.

Because of the partial failure of the muslin cages, an insect-free greenhouse was used to study the breeding system and reliance on insects of all three species. Healthy, flowering plants from each locality were transplanted in pots in their own soil during the beginning of August, 1973, and maintained in the greenhouse. Individual buds were marked on each plant as they appeared, and their development was followed daily until the capsules were mature. Between ten and twenty cyathia on each plant were studied. Because of the rapid transition between the decumbent capsule stage and dehiscence, it was not possible to harvest all capsules produced by marked flowers. Harvested capsules were placed in glassine envelopes and later examined for the number of seeds produced per capsule. Thus the measure of seed set as percent of maximum possible seed set (three seeds per capsule for all capsules) is an estimate of the reproductive performance of marked flowers.

In preliminary studies, I found that seeds with large embryos and copious endosperm were 100% viable when tested by the method of Porter et al. (1947), and seeds with shriveled embryos, or lacking in endosperm, were inviable. I therefore counted as good seed only those seeds with large embryos and endosperm in measures of seed set.

The following treatments were applied to cyathia on the greenhouse plants: they were not touched throughout their development; they were self-pollinated by hand; they were crossed manually with pollen from individuals of the same species taken from different localities; they were pollinated manually with pollen from other species. I discovered, shortly after beginning the greenhouse studies, that in _E. hyssopifolia_ the female-stage cyathia were so small and concealed and the number of stamens per male cyathium so low that manual pollination was highly impractical. I therefore studied only untreated cyathia of this species. Capsule set was measured from cyathia that reached the female stage after at least 1 week in the greenhouse, preventing inclusion in the sample of cyathia pollinated by agents outside the greenhouse.

Pollen tube growth was studied using the technique of Dionne and Spicer (1958). Time between pollination and fixation in the greenhouse was varied from 30 min to 24 hr, hydrolysis time was varied from 5 min to 2 hr, and staining time was varied from 1 min to 30 min. Stigmas were collected from female cyathia in the field, and examined for the presence of both pollen and pollen tubes. In 1974, stigmas of cyathia collected in the field in 1973 and preserved in FAA were washed in distilled water, stained with aniline blue in 0.1 M K_3PO_4, and examined under a fluorescent microscope for evidence of pollen tubes.

Slides coated with methyl-green stained glycerin jelly were set out near the plants in the greenhouse in order to estimate the amount of wind and vibration-induced pollen dispersal.

Measurements of cyathial size were made through a dissecting microscope on FAA preserved material. The data in Table 3 were collected for _E. albomarginata_ and _E. capitellata_ in the field as part of the studies reported in Chapter 7; the information for _E. hyssopifolia_ was obtained from FAA preserved material.

Insect Visitors to _Euphorbia_

The objectives of my study of insect visitors to _Euphorbia_ were to record the diversity of insect visitors to each plant species, and to assess their effectiveness as pollinators. Insect abundance was categorized for major groups as "common", "occasional", or "rare". Insect sampling was conducted principally during 1973 at the five sites indicated in Table 2. Samples were taken throughout the day in order that the diurnal sequence of each visitor class could be established. All insects coming to Euphorbia flowers in a series of randomly chosen 1 m^2 quadrats (situated as described below), were observed during 10 min periods. Approximately 40 such samples were taken at each site. During half the samples, the presence and number of each kind of visitor were noted; during the alternate samples, all insects seen feeding on the flowers were collected either with a net (wasps, flies), in a small plastic vial (bugs, small beetles, minute wasps and flies), or with an aspirator (ants). The catch from each sample was kept separately; speciments were handled so as to minimize loss or transfer of pollen. They were examined at the end of the day for the presence and location of Euphorbia pollen on the body. Body pollen was classified as "rare" (less than ten grains), "occasional" (between 10 and 50 grains), and "dense" (more than 100 grains), and the proportion of specimens with no body pollen was recorded. During the observation samples, the mode of locomotion between flowers was recorded as "flying", "walking", or "stationary". Ten or fewer specimens of each species were examined for gut pollen. They were preserved in Kahle's fluid in the field, and later dissected in aniline blue in lactophenol.

I combined these data to give an index of the ability of the insects to pollinate the flowers. The insect families were grouped on the basis of their size and importance among the visitors, and for each group a "pollinator index" was calculated. I assigned values of 3, 2, and 1 to the body pollen designations dense, occasional and rare respectively, to the abundance categories common, moderate and rare, and likewise to the movement categories walking, flying, and stationary. In the cases where two modes of locomotion were frequently observed, the higher index number was used. I let the values -3, -2, and -1 represent the proportion of specimens within each group that had no body pollen (high proportion scored as -3). The body pollen classes "head", "venter", thoracic pleura", and "legs" were included, since pollen on these parts of the body are effective in pollinating flowers. The pollinator index, then, was the sum of these values, the maximum value of 17 resulting from a designation of "3" in each positive category and "-1" in the negative category. It is probably oversimplistic to assume that all the elements of this index have equal weight in determining the pollinating potential of an insect. However, this approach facilitates an estimation, based on qualitative data for several traits, of the insects' impact on the plant populations. A similar method for comparing the pollinating ability of groups of insects has been used by Bohart et al. (1970) and Bohart and Nye (1960).

Since the identity of each visitor at the species level was not deemed of crucial importance to the results, no attempt was made to have the specimens identified by experts. I identified all mounted specimens to the family level, as classified in Borror and DeLong (1971), and then divided the specimens within each family into species groups on the basis of visual inspection. Thus, the number of species listed for each family may not be precise. I was conservative in assigning individuals to different groups, and thus errors are likely to be on the side of underestimates.

The possibility of wind dispersal of pollen was investigated by sampling on glycerin jelly-coated slides the wind-borne pollen in the vicinity of the plants. Two-thirds of the surface of a microscope slide was coated with methyl green-stained jelly each day, and placed in a shelter near the plants. The shelter was constructed from a large horizontal can containing a slide holder. Two such devices were placed near plants and at right angles to each other at each site during 1972 and 1973, and the slides replaced daily. The slides were then inspected microscopically for the presence and abundance of Euphorbia pollen.

During the night of September 10-11, 1973, I visited each of the sites south of Apache several times during the period from 9:00 P.M. to 6:30 A.M. in order to check for nocturnal and matinal visitors. Plants were inspected by flashlight and light from the full moon for insect presence and behavior.

Temperature was recorded at half-hour intervals during each day of field work. The thermometer was placed within a plant in the sun, in order to record the temperature experienced by foraging bees.

Bee Behavior on Euphorbia

The foraging behavior of the seven common species of bees was examined in order to document the differences and similarities of the species in their utilization of a common resource. Observations were made of bees foraging on *E. albomarginata* and *E. capitellata* at all of the sites listed in Table 2. Individual bees were observed for as long as possible while foraging, and a continuous verbal description of their behavior was recorded with a portable tape recorder. Observation distances varied slightly with species, from a distance of approximately two feet to as close as three inches. I observed no change in the behavior of a bee as I approached from a distance of several feet to several inches away, and so I am confident that my presence did not alter the behavior of the bees. Information recorded included the sequence of arrivals and departures from flowers and the foraging behavior during flower visits. Observed components of foraging behavior included: posture and movements on flowers, nectar collection, pollen-eating, pollen collection, scopal packing, and intra-specific interactions. In the case of *E. capitellata*, whose flowers are clustered into tight heads (see Chapter 3), the heads were treated as single flowers during recording. During the summer of 1972, seven or eight bees of each species were captured after one minute of observation in order to verify the accuracy of my identification of flying bees. During 1973, the places on the plant(s) at which an observation commenced and finished were noted, and the distance between them measured immediately after the observation ended. In addition, the shape of the area covered by the bee was recorded.

The behavioral events were timed by a stopwatch during transcription of the tapes. Events taking less than 0.5 sec were too rapid for accurate verbal description, and so they were recorded as "<.5 sec" and arbitrarily included in the statistical analyses as 0.4 sec. The following data were calculated for each observation, and subjected to statistical analysis: mean time per flight between flowers, mean time spent per flower visit, proportion of flower visits within the same plant, percent of total observation time spent foraging on flowers, extrapolated foraging rate in flowers per minute, temporal patterning of flower visits and flights, frequency of encounters of observed bee with conspecifics, predominant movement shape, and area covered. The data for each species were grouped according to the plant species the bee was foraging on; the few observations in which a bee visited both plant species were omitted from the quantitative analyses.

The data on time per flower visit, time per flight between flowers, percentage of observation time spent foraging, and extrapolated rate of foraging were logarithmically transformed, because the original data were not normally distributed. Two-way analyses of variance were used to detect the importance of the two factors (bee

✓

species and plant species) in the pattern of foraging behavior; these tests were followed by multiple t-tests between all possible combinations of bee and plant species. The variance inherent in the use of average values for variates in the anovas was considered to be included in the error mean square terms. This method of analysis permitted the comparisons of each bee with each of the others and with itself on the different plant species. Both sets of analyses were performed by computer, using the SOUPAC statistical program package in the IBM 360 computer of the City University of New York.

The degree of pollen specialization was assessed by analysis of the scopal loads of specimens both collected during the course of this study and specimens collected over a wider geographical area in the collection of the American Museum of Natural History. Pollen loads were studied by scraping the pollen ball, or most of the pollen of the scopae, onto a slide, and covering the pollen with a drop of methyl green aqueous solution. Five hundred grains were counted on each slide, and the proportion of *Euphorbia* pollen calculated. It was not possible to distinguish the pollen of the three species of *Euphorbia*.

Bee Populations in Relation to Their Food

Because these organisms could not be brought into the laboratory for critical experiments on competition, and because of the impracticality of caging and controlling wild populations, another approach to the problem of competition among bees for pollen was undertaken. Each population of bees and plants was treated as a single observation of bee density as a function of food density. The food density varied from site to site, mimicking the laboratory or field cage situation in which food is presented in variable amounts by the experimenter. I assumed that food density was the independent variable, and bee density was the dependent variable. I then looked for a relationship between bee density and food density indicating that food was a limiting factor for bees. Although such a relationship does not prove that competition is occurring, it does establish the necessary condition for competitive interaction.

These studies were conducted during 1973 at the 1EA, 9WSWA, 18SWA and 12NR sites. At each site, a transect was established across the plant population. Populations growing along a roadside were just slightly wider than 1 m, and thus the location of the transect was completely determined by the one-dimensional distribution of the plants. At the 9WSWA site, it was evident that the plant population consisted of a patchwork of dense and sparse areas; I therefore set out four transects of ten quadrats each, two in each kind of patch. The boundaries of the patches were easily determined by inspection. Four series of random numbers were established by throwing one die, and the numbers were used to measure the distance in feet (units of 30.5 cm) between square meter quadrats. Forty quadrats were marked in this manner along each transect.

Food density was measured as the product of plant density, flower density per plant and anther number per flower. The flowers of these species are long-lived (about a month duration), produce nectar daily throughout this period, and mature one to several new anthers each morning (See Chapter 3), and new flowers are continually appearing on the plants throughout the flowering season. Thus, an estimate of the food abundance taken at one point in time is a good measure of the food available each day throughout the season. *Euphorbia albomarginata* plants were sampled by 1) counting the number of mats per quadrat, 2) measuring the maximum and minimum diameters of each mat, and calculating the area of the resulting ellipse, and 3) taking three counts of the number of cyathia per 4 in^2 (25.8 cm^2) per mat if possible, and one such count if the mat was small. *Euphorbia capitellata* plants were sampled by: 1) counting the number of plants per quadrat, 2) recording the number of "heads" per plant, and 3) determining the number of cyathia per head from two randomly selected heads per quadrat. In both species, the anther density was estimated by randomly dividing the quadrats that contained at least one plant into three groups; at 10:00 A.M., 12:30 P.M., and 3:00 P.M., one such group was examined by taking ten flowers from up to five plants per quadrat. The number of anthers that were full of pollen was recorded for each flower. The sampling regime was repeated three times, so that each group of quadrats was sampled at each of the three times of day; in this way at least 600 flowers from 60 plants were sampled for each time of day. Bee density was assessed during the general insect visitor survey described above. During the observational samples, the number of female foraging bees was recorded by species. The method follows those used by Linsley et al. (1963a,1964), and Macior (1968) to study bee populations, and is based on the concept of "number observed per unit effort" discussed by Southwood (1966). It is thus a relative, rather than an absolute measure of bee density. The samples were taken in subdivisions of the quadrats, because one meter square proved to be too large an area to watch consistently and accurately. Bees were sampled in one-eighth meter square units on *E. albomarginata*, and in one-sixteenth meter square units on *E. capitellata*. Values obtained on the latter species were doubled so that all measures of bee density were in the form of "number of bees per 10 min per 1/8 m^2."

In analyzing the data obtained from this study, I decided it would be useful to include a factor that took into account the different pollen-collecting capabilities of the bees that result from their different sizes. I used the scopal load volume to index the pollen-carrying capacity. Since all species but *D. perparvus* pack the pollen into a mass that closely approximates an oblate spheroid, I measured the axis of the spheroid and calculated the resulting volume. For *D. perparvus* I calculated the volume as if it were a cone surrounding the femora. I then compared each species' scopal volume with the largest bee (*E.* sp. A) by computing the ratio "*Exomalopsis* scopal volume/species *a* scopal volume." The bee density figures were divided by this factor to produce the number of "*Exomalopsis* equivalents," i.e., a translation of the observed bee density into the density of *Exomalopsis* that would collect an equivalent amount of pollen.

Details of the statistical procedures employed in analyzing these data are given in Chapter 7.

CHAPTER 3

REPRODUCTIVE BIOLOGY OF THREE SPECIES OF EUPHORBIA SUBGENUS CHAMAESYCE

Cyathial Development

Because the development and maturation of the cyathia are quite similar among the three species studied, a single description will be given. The five basic stages are illustrated in Fig. 4. During the bud stage, the pistil first appears above the rim of the cyathium. The petaloid appendages and glands are small, and are appressed to the involucre. No nectar is produced by the glands, and pollen placed on the stigma does not germinate. The female stage of the cyathium begins when the pistil is fully exserted above the cyathium. The stigma lobes separate, and eventually come to be slightly recurved; this growth marks the onset of stigma receptivity. There is no change in morphology of the stigma tips that is observable during the maturation process. The appendages are now perpendicular to the central axis of the cyathium, and the glands begin secreting nectar. A transition stage then occurs between the female and male phases. The pedicel of the female flower elongates so that the ovary is pushed out of the cyathium. Pollen is able to germinate throughout this stage, and the stigma lobes remain recurved. Occasionally anthers (male flowers) mature during this stage. The cyathium attains its mature size by the end of this period. The male stage begins when the pedicel of the female flower reflexes so that the ovary rests on the outside of the cyathial involucre. The stigma lobes wither, often becoming straight in the process. The ovary completes its maturation during this stage, which ranges from 7 to 25 days. Each day, a number of anthers mature (Table 3). The pedicel of the male flower elongates throughout the morning, so that the anther, the filament, and eventually the pedicel appear above the rim of the cyathium. The anther begins to dehisce when the temperature reaches about 34°C. The anther walls move apart slowly throughout the morning and early afternoon, so that fresh pollen is still being extruded as late as 2:00 P.M. (Standard Time). During midafternoon (2:00 P.M. to 4:00 P.M.) an abscission layer between the pedicel and filament becomes active; the filament and anthers desiccate and fall off at the slightest motion of the plant. Thus, few old anthers were seen on cyathia after 4:00 P.M. in the field; however, they commonly remained on the greenhouse plants until the plants were handled.

The fruit stage begins when the pedicel of the female flower straightens so that the ovary is held vertically above the cyathium. Anther production has usually, but not always, ceased by this stage; nectar, however, continues to be produced. The seed capsule desiccates during the day, and then dehisces explosively, scattering the seeds for several feet. The process of dehiscence has been described in greater detail by Schneck (1887).

This basic pattern of floral biology interacts with the growth and structure of each species in ways that affect the reproductive biology of the plants, as follows:

E. albomarginata: The growth form of this species is prostrate; a tendency to branch at most nodes produces a solid mat that ranges to over a meter in diameter. Cyathial buds arise in the leaf axils at all points along the stems, in conjunction with new branches. Buds and branches usually appear singly at the nodes, and they arise at each node, on the opposite side, when the first cyathium is in the male stage. The net result of this growth pattern is a mat of cyathia in which young and old cyathia are closely juxtaposed but lie in the same plane (Fig. 5). An ability to root at the nodes allows individual plants to spread extensively by vegetative means.

In this species, cyathia become easily visible during the early female stage. Anther maturation during the transition stage is uncommon, and the stamens grow at an angle that leaves a space at least equal to the anther width between the extruded pollen and the stigma. Thus, self-pollination is very unlikely in the absence of an agent that knocks the anthers against the stigma. The duration of the female and transition stages combined is dependent on the occurrence of pollination; in self-pollinated cyathia 5.9 (n=53; s.e.=0.37) days elapsed between the start of the female stage and the end of the transition stage, whereas in plants not pollinated by hand, this period took 8.1 days (n=60; s.e.=0.43) ($P < .001$). Pollination-dependent growth of the female flower's pedicel was mentioned by Lyon (1898) for *E. corollata*.

E. capitellata: This species grows as a low herb with branches erect to decumbent. Both this species and *E. albomarginata* tend to form dense pure stands (on average 33 plants per m^2 for *E. capitellata*) and grow sparsely when intermixed with other vegetation. Plant density can reach 100 plants per m^2. There is no vegetative propagation. The cyathia are borne in dense cymose glomerules which form the attractive unit and in which the cyathia are strongly overlapping (Fig. 6). The two sites at which this species was studied averaged 12.8 (n=76; s.e.=0.64) cyathia per "head" and 20.3 (n=55; s.e.=1.19) cyathia per "head"; at both sites an average of 25% of the cyathia of each head were in the female stage. The difference between the sites is probably due to drier, less favorable conditions at the site with smaller heads. Anthers grow both vertically above the cyathia and laterally, parallel to or protruding between and slightly below the petaloid appendages. The lateral anthers were sometimes observed to pollinate female-stage cyathia growing directly beneath them. In addition, anthers matured more often during the transition stage in this species than in *E. albomarginata*. Thus, self-pollination can more easily occur in this species than in *E. albomarginata*.

E. hyssopifolia: This species grows as an erect plant, most often intermixed with grasses and other herbs. The cyathia develop in a compound dichasium arrangement in which the stalk supporting each terminal cyathium gives rise to two opposite cyathia with subtending leaves, each of which in turn becomes the terminal cyathium of its stalk, which repeats the process. Variable rates of elongation of the stalks permit the grouping of cyathia into loose clusters of three to seven or eight cyathia (Fig. 7). The cyathia remain very small and tightly enclosed by the developing leaves during the bud and female stages, so that they are not easily observed until the transition stage. The stigma lobes become more strongly recurved than in either of the two preceding species. Anther maturation during the transition stage occurs more commonly than in the preceeding two species, and thus anther contact with the stigma is more likely.

All three species are overwintering to perennial, and all three flower in the first season. *Euphorbia albomarginata* and *E. capitellata* bloom from early spring to late fall; *E. hyssopifolia* blooms from August through late fall (Kearney and Peebles, 1960).

Breeding Biology

The results of the greenhouse experiments on reproductive system are given in Table 4. A cyathium was considered to have set seed if at least one viable seed was produced. Because initial observations showed that self-pollinated plants produced large capsules and because pollen tube growth of self pollen and outcross pollen was not distinguishable, I decided to concentrate the limited plant materials and available time on the ability of the plants to pollinate themselves unassisted by pollen vectors. Occasionally, the female flower withered and died during the female stage, so that no exserted capsule was produced; these cyathia sometimes continued through the male stage, and sometimes died at the end of the female stage. They are included in Table 4 in the column labelled "No. Dead Ovary".

E. albomarginata appears largely incapable of setting seed without a pollinating agent, but pollination within an individual results in seed production. The difference in proportion of cyathia setting seed between the "selfed" and "untouched" categories is significant at $P < .001$. *E. hyssopifolia* clearly requires no external agent to ensure seed set. Although the difference in seed set between the "selfed" and "untouched" categories in *E. capitellata* plants was significant ($P < .01$), the proportionate seed set of untouched plants (31%) was considerably higher than the proportion in *E. albomarginata* (18%). I attribute the seed set by these untreated plants to be caused by self-pollination resulting from the factors described above, namely: 1) persistence of old anthers after dehiscence, 2) the greater number of anthers per cyathium in this species, 3) the close proximity of male-stage and female-stage cyathia, and 4) the lateral growth of some anthers, which permits contact with stigmas of smaller female cyathia. The importance of the first two factors was illustrated by the number of anthers observed on glycerin jelly coated slides placed under the plants in the greenhouse. Slides beneath *E. capitellata* plants had an average of 11.8 anthers (n=12), as opposed to 2.8 under *E. hyssopifolia* (n=10) and 0.3 adjacent to *E. albomarginata* (n=11).

Because of the importance of these old anthers, cyathia were chosen for study that were solitary in the leaf axils, or in heads of no more than three blossoms. Much of the variability of the overall results was accounted for by between-plant effects; on one untreated plant, only three of twenty-two observed cyathia produced any seed, and on another untreated plant, twelve of nineteen observed cyathia produced seed. No reason for this between-plant variability is apparent.

The staining method of Dionne and Spicer (1958) stained only the pollen grain and that portion of the pollen tube outside the stigma. No combination of fixation, hydrolysis and staining times or gentle squashing of preparations succeeded in making pollen tubes clearly visible within the styles. The appearance of pollen tubes stained by this method is shown in Fig. 8. The tubes were readily discernible, however, with aniline blue under fluorescent light, despite the long period of fixation in FAA. The occurrence of germinated pollen grains on variously treated cyathia is reported in Table 5. Results from fluorescent microscopy indicated that pollen tubes could be found in the style whenever germinated pollen grains were seen in the light microscope; therefore I feel that the results from the light microscopy give an accurate picture of the pollination biology of the species.

As can be seen in Table 5, the proportion of stigmas with no adhering pollen is remarkable large. The absence of germinated grains on manually pollinated cyathia was unrelated to the amount of time that elapsed between pollination and fixation. Samples fixed 30 min after pollination had the same proportion of styles without germinated pollen as did samples fixed 24 hr after pollination. Germinated pollen and pollen tubes were readily apparent, however, in transition-stage cyathia; thus rapid pollen grain and tube degeneration is not likely to have caused these results. In order to confirm the observed frequency of unpollinated stigmas in the field, I checked three random samples of _E. albomarginata_ stigmas with a 15X hand lens and found the proportion of unpollinated stigmas to be 37%, 50% and 58%.

The pollen germination results together with the greenhouse studies demonstrate that the _Euphorbia_ species studied here are all self-compatible, but self-pollinating to various degrees. In _E. albomarginata_ and _E. capitellata_, the low proportion of pollinated stigmas in field and greenhouse samples corresponds well with the low percentage seed set observed in both locations. In _E. hyssopifolia_, however, there is a large disparity between the low pollination success and the high percentage seed set. In addition, while studying pollen tube growth with the fluorescent microscope, I observed that some of the stigmas that had no pollen or pollen tubes came from female stage cyathia that already had large, well-developed ovules. This suggests that _E. hyssopifolia_ may be apomictic. The evidence for this hypothesis is circumstantial, and therefore further embryological investigation of this species is indicated.

Table 6 gives the cyathial dimensions of each species, for purposes of comparing the prominence of insect attractants among the species. Nectar is produced continuously during the day in all species, and so gland size is used as a measure of nectar production. The species that is capable of setting a near-maximum number of seeds through self-mediated pollination - _E_. _hyssopifolia_ - has much smaller cyathial dimensions than do the other two species. It produces less pollen per anther, and offers visiting insects less nectar, less conspicuous visual cues, and less space for alighting and resting. Thus, _E_. _hyssopifolia_ clearly has fewer adaptations for insect visitation than do the species that require insect visitors for pollination.

Summary

_E_. _albomarginata_, _E_. _capitellata_ and _E_. _hyssopifolia_ all follow a proterogynous pattern of development in which the female flower of the cyathium is receptive for about a week, and is then exserted from the involucre. Anthers dehisce during the following two to four weeks. Nectar is produced throughout both stages of cyathial development, and thus each cyathium produces food for insect consumption over a period of about a month.

All three species are self-compatible, but they differ in their dependence on insects for reproduction. _E_. _albomarginata_ is entirely dependent on insect vectors for pollination, _E_. _capitellata_ can produce a small amount of seed via self-mediated pollination, and reproduction in *E. hyssopifolia* is independent of the presence of pollen vectors.

TABLE 3. Number of anthers maturing each day per male-stage cyathium in three species of _Euphorbia_.

Species	N	Average	Percent of cyathia with given number of anthers					
		Number	0	1	2	3	4	5+
albomarginata	1119	0. 6	64. 0	20. 5	8. 9	5. 5	1. 1	0. 0
capitellata	997	1. 1	54. 2	16. 3	10. 4	8. 5	6. 0	4. 6
hyssopifolia	158	0. 6	58. 2	25. 4	12. 6	3. 8	0. 0	0. 0

TABLE 4. Breeding behavior of three species of _Euphorbia_. Except as noted treatments refer to greenhouse plants. Sample size for % seed set of greenhouse plants, as explained in the text, is given in parentheses.

Species	Treatment	No. Cyathia	No. Setting Seed	No. Dead Ovary	% Seed Set
albomarginata	selfed	86	40	22	47.6 (14)
	untouched	78	14	15	58.3 (6)
	X _capitellata_				
	pollen	20	4	0	30.0 (3)
	field collected				
	capsules	68	--	--	68.6
capitellata	selfed	49	30	0	47.0 (17)
	untouched	64	20	0	30.6 (25)
	X _albomarginata_				
	pollen	36	17	0	22.6 (28)

TABLE 4. Continued.

Species	Treatment	No. Cyathia	No. Setting Seed	No. Dead Ovary	% Seed Set
	field-collected capsules	501	--	--	61.9
<u>hyssopifolia</u>	untouched	107	91	5	87.0 (46)
	field-caged plants	317	267	--	--
	field-collected capsules	57	--	--	91.8

TABLE 5. Pollen tube development on stigmas of three species of Euphorbia. Trials under various conditions of fixing times, etc. have been lumped for each category.

Species	Stigma Treatment	Total No. Stigmas	Stigmas with Germinated Pollen	Stigmas with Ungerminated Pollen	Stigmas with no Pollen
albomarginata	manually selfed	91	47	13	31
	X capitellata pollen	20	17	2	1
	field-collected	226	107	2	117
capitellata	manually selfed	24	19	3	2
	X albomarginata pollen	6	4	0	2
	field collected	204	99	16	88
hyssopifolia	greenhouse, untouched	50	27	22	21
	manually selfed	10	9	0	1
	field collected	27	7	0	20

TABLE 6. Dimensions (in mm.) of cyathial structures important to insect visitation for three species of *Euphorbia*. Figures in parentheses give sample size and standard error, respectively.

Species	Anther Length	Anther Width	Gland Length	Gland Width	Petal Length	Petal Width	Cyathial Length
albomarginata	0.34	0.31	0.72	0.38	1.18	0.60	1.7
	(40;0.005)	(40;0.004)	(15;0.038)	(15;0.021)	(15;0.113)	(15;0.069)	(15;0.041)
capitellata	0.29	0.26	0.25	0.29	1.13	0.68	1.8
	(40;0.001)	(40;0.001)	(15;0.015)	(15;0.009)	(15;0.051)	(15;0.034)	(15;0.080)
hyssopifolia	0.23	0.20	0.24	0.16	0.48	0.26	1.1
	(42;0.006)	(42;0.005)	(14;0.015)	(14;0.012)	(14;0.033)	(14;0.044)	(15;0.037)

Figure Captions

Chapter 3

Fig. 4 Developmental stages of the *Euphorbia* cyathium. A, bud stage; B, female stage; C, transition stage; D, male stage; E, fruit stage after capsule dehiscence.

Fig. 5 *E*. *albomarginata*, stem. X 3.5.

Fig. 6 *E*. *capitellata*, head. X 4.8.

Fig. 7 *E*. *hyssopifolia*, inflorescence. X 4.4.

Fig. 8 *E*. *capitellata*, germinated pollen grains. X 340.

FIGURE 4

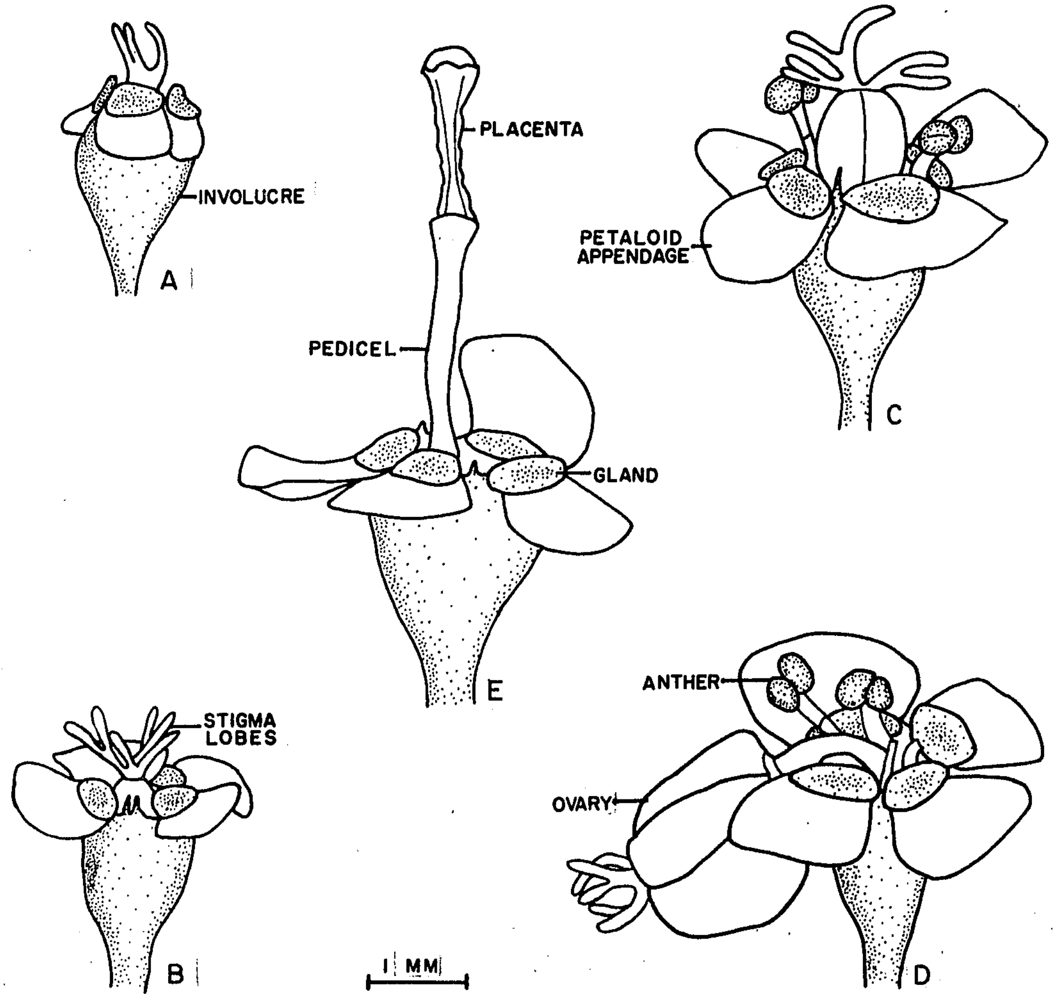

INVOLUCRE
A
PLACENTA
PEDICEL
GLAND
E
PETALOID
APPENDAGE
C
STIGMA
LOBES
B
1 MM
ANTHER
OVARY
D

FIGURE 5

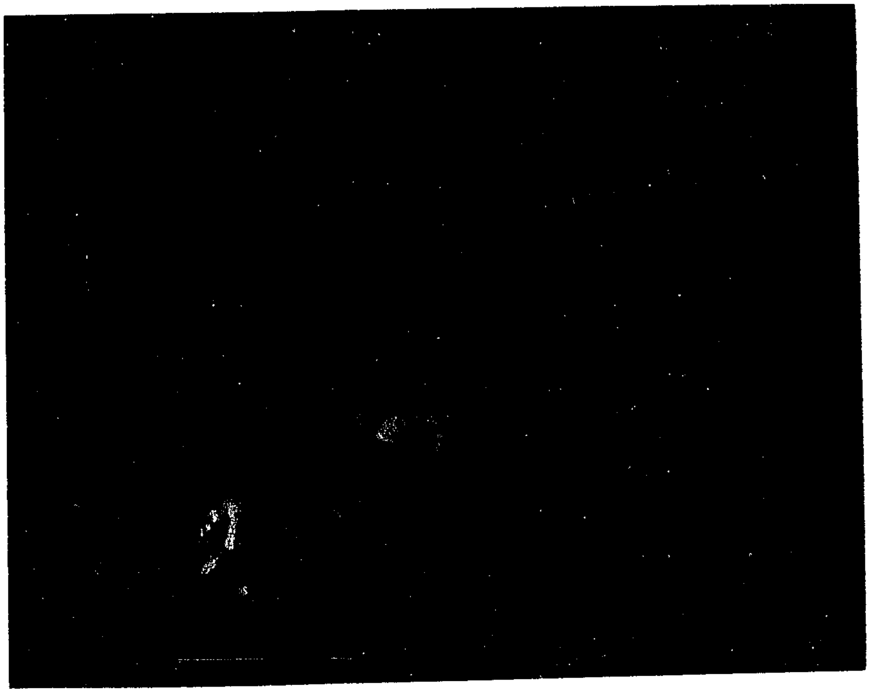


FIGURE 6

FIGURE 7

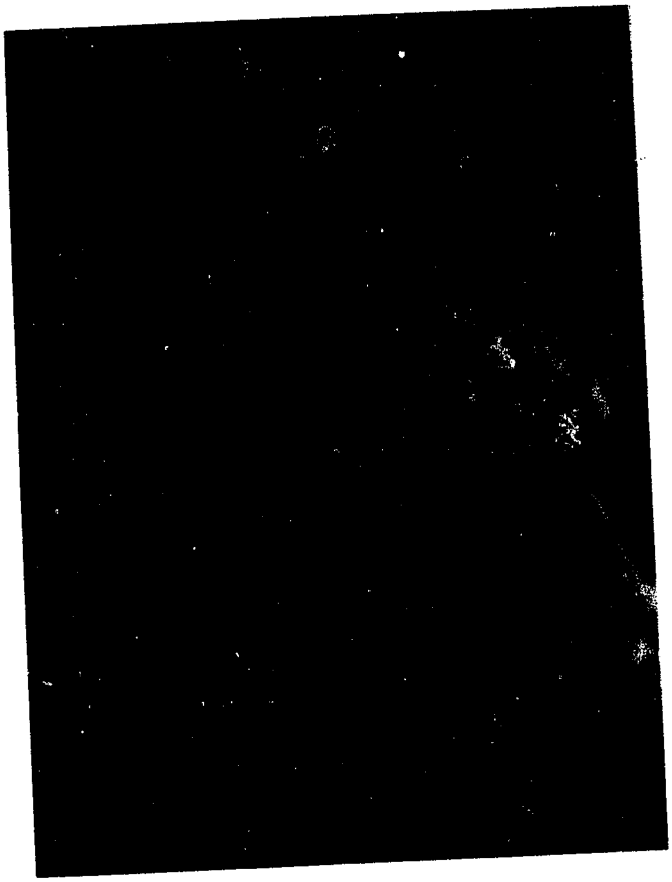


FIGURE 8

CHAPTER 4

INSECT VISITORS TO EUPHORBIA

The plant-pollinator relationships of the three species of Euphorbia studied here are variations on the theme of "promiscuous" flowers being pollinated by means of "mess and soil" behavior of insects (Faegri and van der Pijl, 1971). The term "promiscuous" has been used by Faegri and van der Pijl (1971) to describe flowers that are serviced by a wide variety of pollinating animals; pollination resulting from nonspecific insect motion (as opposed to insect behavior specific to a given flower) has likewise been termed "mess and soil". All three species exploit a diverse, diurnally active insect fauna for both self- and cross-pollination. None of the species relies on a particular insect taxon, and none requires insect behavior more complex than locomotion and extension of the mouthparts. Nevertheless, substantial differences exist among the species in the composition of the insect visitor fauna and the reliance of the plants on the insects for pollination.

Composition of Insect Fauna

The insect visitors are listed in Table 7. The total number of insect species found foraging on these three species is immense, but the numbers per plant species are very unequally distributed. More than three times as many kinds of insects found E. albomarginata to be an attractive food source as were attracted to E. capitellata or E. hyssopifolia. Moreover, the taxonomic composition of the visitor groups to each species differed dramatically, as is illustrated in Fig. 9.

E. albomarginata is visited by a wide variety of Hymenoptera; as can be seen from Table 7, there was only one family (Eurytomidae) in this order in the total collection that was unrepresented on this plant. The apterous groups (ants, mutillids) were only observed on this plant; they rarely climbed up the erect species. They accounted for the entire insect fauna seen on E. albomarginata during the night. The Diptera, although of lower diversity than the Hymenoptera and of approximately equivalent importance to all three species (Fig. 9), were represented by more species on E. albomarginata than on the others. In families represented by numerous species (e.g., Sphecidae, Tachinidae), the majority of the species were collected on E. albomarginata. Even among the Coleoptera, a group of minor importance to E. albomarginata, there were more species found than on either of the other two plants. Unlike the other two plant species, E. albomarginata suffered little predation by bugs.

E. capitellata attracted a much less diverse fauna in which the visitor groups were more evenly distributed. However, a few of the species (four bee species and five beetle species) accounted for most of the visitor abundance. The paucity of Hymenoptera is rather puzzling. The cyathia of this species and E. albomarginata are very similar in size and shape (Chapter 3), and differ only in their distribution on the plants. Since wasps were both more diverse and relatively more important on E. hyssopifolia than on E. capitellata, it seems unlikely that the erect habit of the plant alone could account for the failure of E. capitellata to attract these insects. The differential behavior of wasps toward E. albomarginata and E. capitellata was observed in mixed populations of the plants, and thus the results cannot be attributed to peculiarities of the insect fauna at the study sites. Therefore, it seems most likely that this difference in visitors is related to cyathial distribution and the spatial relationships of petals, nectaries and anthers. A spatial factor may also account for the greater abundance of beetles on E. capitellata than on E. albomarginata. The beetles mostly remain stationary (Table 8), and can reach, without moving, a much greater amount of food on E. capitellata than they can on E. albomarginata.

On both E. capitellata and E. hyssopifolia, Hemiptera account for 25% of the insect visitors. These insects are not feeding from nectaries or anthers, but are feeding from the sap in the involucre and from the developing seeds, and thus indirectly affect the quantity of floral food available to other insects. However, their presence on the flowers makes them potential pollinators and thus of importance to the process of pollination. They are also the only insects to be found on these plants at night.

The only major group of insect visitors to flowers not found on Euphorbia was Lepidoptera. Neither diurnal butterflies nor noctural moths were ever seen visiting the flowers.

Since no attempt was made to precisely quantify the abundance of each kind of insect, it is not possible to compute the richness and evenness components of visitor species diversity for each plant. Nevertheless, the relative determinations of abundance gained during the 10-minute observation samples permit some comparisons among the species. Figure 10 illustrates the relative abundances during the day of each insect order at the four sites. The numbers of individuals of each order were pooled for each hour of the day, and then expressed as the percentage of the total number of insect visitors during the hour. The data are plotted at the midpoint of the hour. It can be seen by comparison of Figs. 9 and 10 that the bees, for example, were far more important in density than in species richness. Unevenness in species abundance was particularly marked on E. capitellata; five species of beetles accounted for the high percentage of Coleoptera at the 9WSWA site, and the more numerous species of wasps and flies were individually quite uncommon. Fig. 10 also shows that the faunisitic composition differs from site to site. Wasps were much less important than flies at 12NR but were similar to the flies in abundance at 1EA. Similar intersite differences are apparent for beetles and flies at 18SWA and 9WSWA.

Insect visitors to *E. hyssopifolia* were qualitatively and quantitatively different from those to the other two species of *Euphorbia*. On *E. hyssopifolia*, both the insect species (Fig. 9) and insect individuals (Fig. 10) are more equitably apportioned among the principal groups. Although bees contributed a high proportion of the total visitors during the mid-morning, the nature of their visits to *E. hyssopifolia* was quite different from their visits to the other two species of *Euphorbia*. On the latter, the bees foraged for several minutes within the small area under observation, and then moved to other individuals of *Euphorbia*. On the former, bees alighted briefly on one or two cyathia, and then disappeared from sight. Only at a part of the Apache site (in 1972) where no species of *Euphorbia* other than *E. hyssopifolia* were growing were bees (mostly *P. minima*) seen to forage extensively on this plant. At other places at Apache, where *E. albomarginata* formed large mats, no bees could be found on *E. hyssopifolia*.

Casual observation at a variety of other plant populations in the San Simon and San Bernardino valleys extend the impression that the insect fauna size and composition is highly variable among sites. At some *E. albomarginata* populations, very few flying insects were seen during several days of observation in good weather, and ants accounted for the majority of all insect visitors observed. Other sites supported just one species of bee in addition to the ants and a few other kinds of flying insects. Sites of this type were found one mile from the site (lEA) with the greatest diversity of wasps and flies. Thus, the reliance of the plants on different kinds of insects depends in part on the composition of the insect fauna at each site.

Insect Behavior in Relation to Pollination

Table 8 describes the feeding habits, ability to carry pollen on the body, behavior on the flowers, overall abundance, and pollinator potential of the insect visitors. I have grouped the families into classes on the basis of the overall similarity in size and behavior, in the interests of conciseness and because not all data were available for each family. The terms "large" and "small" relate the size of the insect to that of the cyathium; large insects are at least about 6 mm long (bigger than the diameter of a cyathium) and small insects are less than 6 mm long, and can stand on a cyathium with room to spare. The larger insects, except for ants, tend to be more effective pollinators, probably because they cannot avoid contacting both anthers and stigmas as they move. The minute flies and wasps carry very little body pollen, and thus can evidently move among the anthers without brushing against them. The ability of an insect to carry pollen is also affected by its pubescence and integumental sculpturing. The smooth, glabrous ants rarely carried pollen unless they were captured while feeding on anthers.

The most common insects are also the most effective pollinators. In some cases (small Formicidae, Corimelaenidae, large and small Bombyliidae), a high pollinator index is largely attributable to the insects' abundance rather than their ability to carry pollen. Only among the small beetles is a capacity to carry pollen and contact the stigma by appropriate motions coupled with low density. The large insects are undoubtedly capable of feeding on and pollinating a wide variety of flowers other than Euphorbia. As Faegri and van der Pijl (1971) point out, the flies and wasps are irregular and unreliable visitors to flowers, and can be of greatest significance as an alternate means of pollination when bees or other specialized visitors are absent. Flies and wasps, however, are the most common visitors to Euphorbia, both in this study and in previous observations (Kugler, 1970; Muller, 1883).

Overall visitor abundance followed the diurnal change in temperature (Fig. 11). During the night and early morning, no nectar is produced, and no open anthers are available, and although the flowers are incapable of closing, the leaves become appressed to the stem and partially hide the flowers. The only insects seen on the flowers at night are ants, coreid bugs, and occasional tiphiid wasps and predacious beetles. As the temperature rises, flying insects become more common and remain active until the late afternoon. Very few flying insects are seen after about 5:00 P.M. There was no evidence that different groups of insects visit the flowers at different times of day, as has been reported for other kinds of flowers

(Schlising, 1970); the same species are collected in the late afternoon as at the beginning of the day. The flight period of the bees, however, is narrower than the other insects (Fig. 11); although bee abundance peaks at around noon as do the abundance curves for all insects, it declines earlier in the afternoon and falls to low levels by 3:00 P.M. Differences in the total insect abundance curves between localities reflect the differing insect faunas of each site; thus the preponderance of bugs and beetles on E. capitellata at 9WSWA accounts for the lack of the peak in activity that was seen with the flies and wasps at 1EA.

This diurnal activity is geared to the production of food by the flowers. A fresh set of anthers mature each day as the temperature reaches 34°C. to 35°C.; the anthers wither and fall off by late afternoon. Insect activity starts to increase around the time that the anthers begin to dehisce and nectar starts to flow. Bee activity slows down before the anthers are shed (discussed more extensively below), and overall insect activity falls as both pollen and nectar become increasingly unavailable. The diurnal cycle of both food presentation and insect visitation is geared to the weather; on overcast days, the cycle begins at whatever time of day the cloud cover breaks up. When the cloud cover lasts all day, a few anthers open and a few flying insects are seen, but their density remains uniformly low throughout the day.

The insect visitors can be divided into four feeding groups: the nectar feeders (wasps, some flies), pollen feeders (beetles), insects feeding on both pollen and nectar (bees, some flies), and insects feeding on plant sap from floral tissues (phytophagous bugs). In Table 8, those groups that ingest moderate to large quantities of pollen are considered to be pollen or pollen and nectar feeders.

From the data presented above, it is evident that if Euphorbia nectar and pollen constitute a limited and important resource for these insects, then the resulting competition is a general "scramble" with no obvious mechanisms for reducing the competition. In other words, there is no kind of temporal separation that would enable the various species to exploit different subsets of the resource. From the information available on the variability of visitor composition among sites, it seems likely that the community of Euphorbia-visiting insects has no set structure or long-term stability of species memberships. It is hard to see how, under such circumstances of labile inter-species interactions, competition-reducing mechanisms could be expected to arise, and therefore their absence is not surprising.

The oligolectic bees comprise the only group among the insects that derives its entire food economy from these plants. The other insects may adjust their reliance on food from Euphorbia to the relative abundances of all available food sources. Thus, the occurrence of competition on Euphorbia may be affected by the nature of the surrounding vegetation as well as by the insect visitor species composition at each site. Indeed, the observed variability in insect abundance at different sites suggests that the occurrence of competition is patchy in space and time, if it occurs at all.

Wind Dispersal of Pollen

The studies of wind dispersal of pollen demonstrate that some *Euphorbia* pollen is transported by wind (Table 9). The number of grains, however, is very low: there are hundreds of grains of pollen in each anther, and thousands of anthers per square meter (see Chapter 7), and therefore the average number of pollen grains reaching the slide during a twenty-four hour period represents a minute fraction of the total amount of pollen released each day within the plant population. This wind-dispersed pollen is probably unimportant in inter-plant pollination; female-stage flowers are small, and often partly concealed by the subtending leaves and are not morphologically suited to capture pollen grains in air currents. However, wind movements of pollen may play some role in intra-plantpollination, particularly between adjacent male- and female-stage flowers. Thus, insect visitors are the only means of cross-pollination available to these plants.

Summary

A large number of species of insects obtain food from the cyathia of the three species of *Euphorbia*, and in so doing effect both cross- and self-pollination of the plants. The insect species diversity is much greater on *E. albomarginata* (a species entirely dependent on insect visitors) than it is on *E. capitellata* and *E. hyssopifolia* (species that are partially and completely capable of self-pollination, respectively). The bees are probably the most important agents of both self- and cross-pollination in areas where they are abundant, because of their feeding behavior and because of the large amounts of pollen on their bodies. Nevertheless, the fly and wasp faunas are both more diverse, and, at some sites, more numerous. The predominant groups of insects vary among the species of *Euphorbia*. Wasps are attracted to *E. albomarginata*, but rarely visit *E. capitellata*; beetles and bugs are often found on *E. capitellata*, but are found very infrequently on *E. albomarginata*. Insects visit the cyathia of all three species during the day; only a few sedentary coreid bugs are found on the plants at night. Although small amounts of pollen are spread by wind, it is unlikely that wind-dispersed pollen accounts for more than sporadic pollinations among adjacent cyathia.

Table 7. Insect visitors to three species of <u>Euphorbia</u>: taxonomic composition.

Order	Family	No. species on albomarginata	No. species on capitellata	No. species on hyssopifolia	Total Spp. Family
Hymenoptera	Ichneumonidae	2	0	0	2
	Braconidae	3	0	1	4
	Chalcididae	3	0	0	3
	Pteromalidae	2	1	1	3
	Eucharitidae	1	1	0	2
	Eurytomidae	0	0	1	1
	Chrysididae	1	0	0	1
	Bethylidae	1	0	1	2
	Tiphiidae	3	0	1	3
	Mutillidae	5	0	0	5
	Pompilidae	9	1	2	10
	Formicidae	9	1	0	9
	Sphecidae	41	5	3	47
	Colletidae	0	1	0	1
	Halictidae	13	6	3	14
	Andrenidae	11	9	7	12
	Megachilidae	1	0	0	1
	Anthophoridae	6	3	1	6
Diptera	Otitidae	1	0	0	1
	Chamaemyidae	1	0	0	1

TABLE 7. Continued.

Order	Family	No. species on albomarginata	No. species on capitellata	Nospecies on hyssopifolia	Total Spp. Family
	Chloropidae	7	3	2	9
	Platystomatidae	1	0	0	1
	Sciaridae	1	1	0	1
	Pipunculidae	0	1	0	1
	Sepsidae	2	1	0	2
	Therevidae	2	0	0	2
	Syrphidae	3	1	0	4
	Bombyliidae	9	5	3	14
	Sarcophagidae	4	0	0	4
	Tachinidae	11	2	1	12
Coleoptera	Anthicidae	1	0	0	1
	Alleculidae	0	1	0	1
	Carabidae	1	0	0	1
	Cantharidae	1	3	1	3
	Cleridae	0	0	1	1
	Chrysomelidae	4	1	0	5
	Coccinellidae	1	0	2	2
	Dermestidae	0	2	1	3
	Bruchidae	1	0	0	1
	Mordellidae	0	1	0	1

TABLE 7. Continued.

Order	Family	No. species on albomarginata	No. species on capitellata	No. species on hyssopifolia	Total Spp. Family
Hemiptera	Miridae	1	1	1	2
	Corimelaenidae	2	2	3	4
	Reduviidae	0	1	1	2
	Phymatidae	0	1	0	1
	Pentatomidae	0	1	1	1
	Lygaeidae	4	2	0	4
	Coreidae	2	2	1	3
Homoptera	Cicadellidae	4	4	0	6
	Acanalomidae	0	0	1	1
Total number insect species per plant species		175	64	40	

TABLE 8. Characteristics affecting the ability of various kinds of insects to pollinate *Euphorbia*.

Group	Gut	Body Pollen[a]						Predominant			Sample
	Pollen[a]	Head	Venter	Pleura	Dorsum	Legs	None[b]	Movement[c]	Abundance[d]	Index[e]	Size
HYMENOPTERA											
Small Formicidae	++	++	+	0	0	+	+++	W	M	6	23
Large Formicidae	0	+	+	0	0	+	++	W	C	7	30
Small Parasitic Wasps	+	++	0	+	+	+	++	W	R	6	21
Large Wasps	+	+++	++	++	+	+	+	W, F	C	13	52
Small Sphecid Wasps	+	+	+	+	+	+	+++	W	C	7	51
Bees	+++	+++	++	++	+	+++	+	W, F	C	15	19
DIPTERA											
Misc. Small Flies	+	0	0	+	0	+	+++	W, F	M	4	47
Syrphidae	0	+	+	0	0	+	+	S	M	5	6
Lge. Bombyliidae	+++	+	++	+	0	++	++	F, S	C	9	37
Sm. Bombyliidae	+++	0	+	0	0	+	++	F, S	C	5	22

TABLE 8. Continued.

Lge. Tachinidae, Sarcophagidae	+	++	++	++	+	++	+	W, S	C	13	31
Sml. Tachinidae	0	++	+	++	0	++	++	W	C	11	54
COLEOPTERA											
Sm. Beetles	+++	0	++	++	++	+	+	W, S	R	8	8
Alleculidae	+++	0	+	+	0	+	+	S	M	5	11
Cantharidae	+++	+	++	0	0	++	+	W, S	M	9	16
Lge. Beetles	0	0	+	0	+	0	+	W	R	5	2
HETEROPTERA											
Corimelaenidae	0	+	++	0	0	++	++	S, W	C	9	45
Sm. Hemiptera	0	+	+	0	0	+	++	S	M	4	22
Cicadellidae	0	0	0	0	0	0	+++	S	M	0	24
Coreidae	0	0	+	0	++	+	+	S, W	M	6	13
Other lge. bugs	0	+	+	0	+	+	++	W, S	M	6	19

TABLE 8. Continued.

[a] 0 = none; + = 1 -10 grains; ++ = 10 - 50 grains; +++ = 50 grains.

[b] +, ++, +++ = low, moderate, high proportion of specimens with no body pollen.

[c] W = Walking; F = Flying; S = Stationary.

[d] C = Common; M = Moderate Density; R = Rare.

[e] See Chapter 2 for method of calculation.

TABLE 9. Wind dispersal of pollen of three species of *Euphorbia*.

Locality, Year	Plant Species	Mean Number *Euphorbia* Grains	Mean % of Total Pollen Grains on Slide	No. Slides Examined
13SWA, 1972	*E. albomarginata* & *E. capitellata*	18.8	8.1	19
	E. hyssopifolia	42.6	14.2	7
18SWA, 1973	*E. capitellata*	39.3	12.1	7
9WSWA, 1973	*E. capitellata*	63.3	32.4	9
1EA, 1973	*E. albomarginata*	14.5	15.9	8
12NR, 1973	*E. albomarginata*	41.4	35.3	8

Figure Captions

Chapter 4

Fig. 9	Percentage of insect species collected in each major group of insect visitors for three species of *Euphorbia*.
Fig. 10	Insect visitor composition during the day at each site. The percentage of total individuals belonging to each insect order is plotted at the midpoint of the time interval. The data collected for *E. hyssopifolia* at different sites are pooled and presented in one graph. Time of day is Mountain Standard Time. Plant species observed at each site: A = *E. albomarginata*; C = *E. capitellata*; H = *E. hyssopifolia*.
Fig. 11	Total insect activity, bee activity and temperature changes during the day at each site.

FIGURE 9

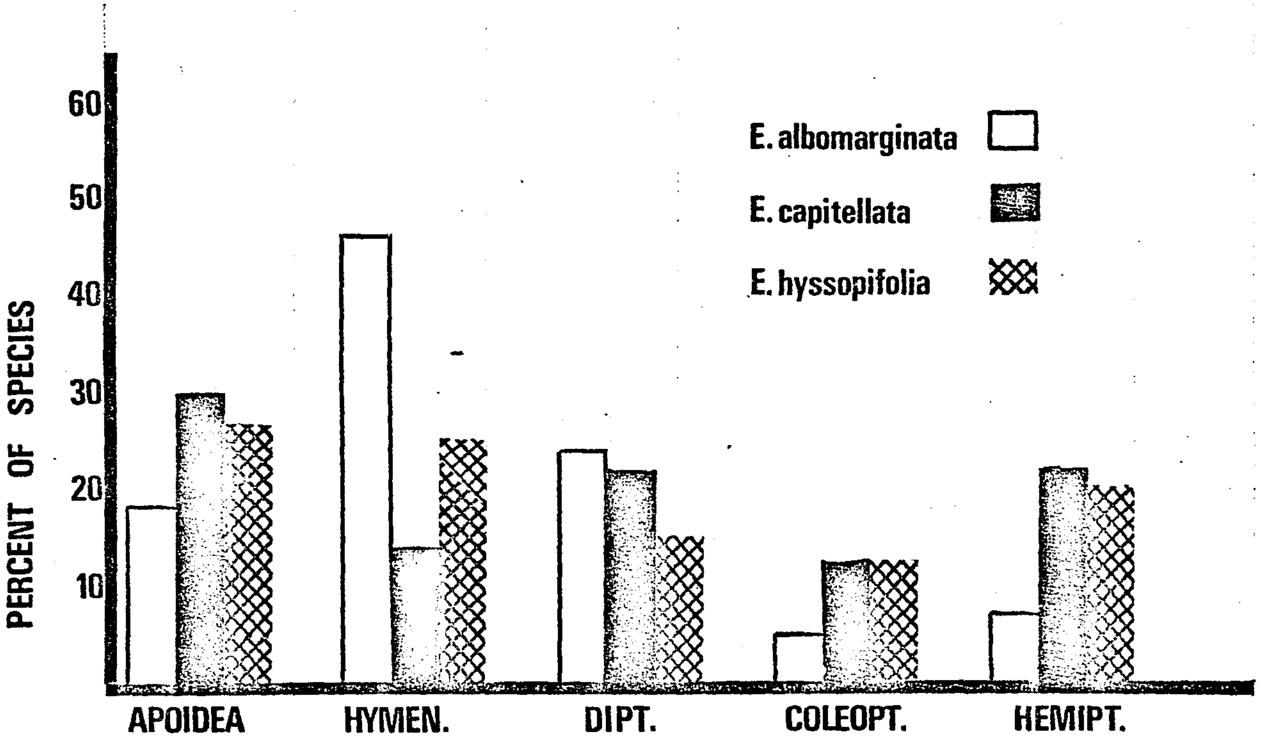
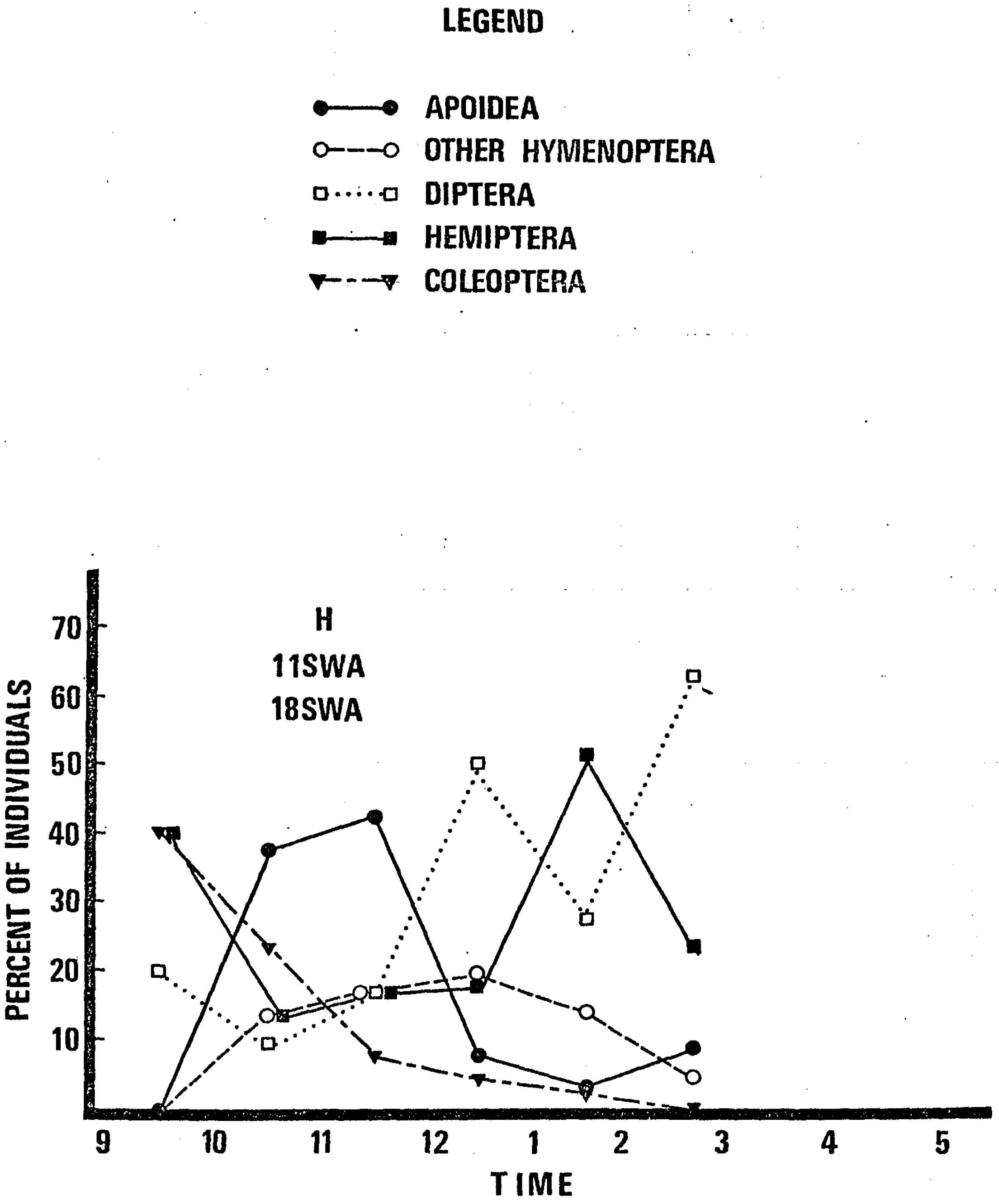
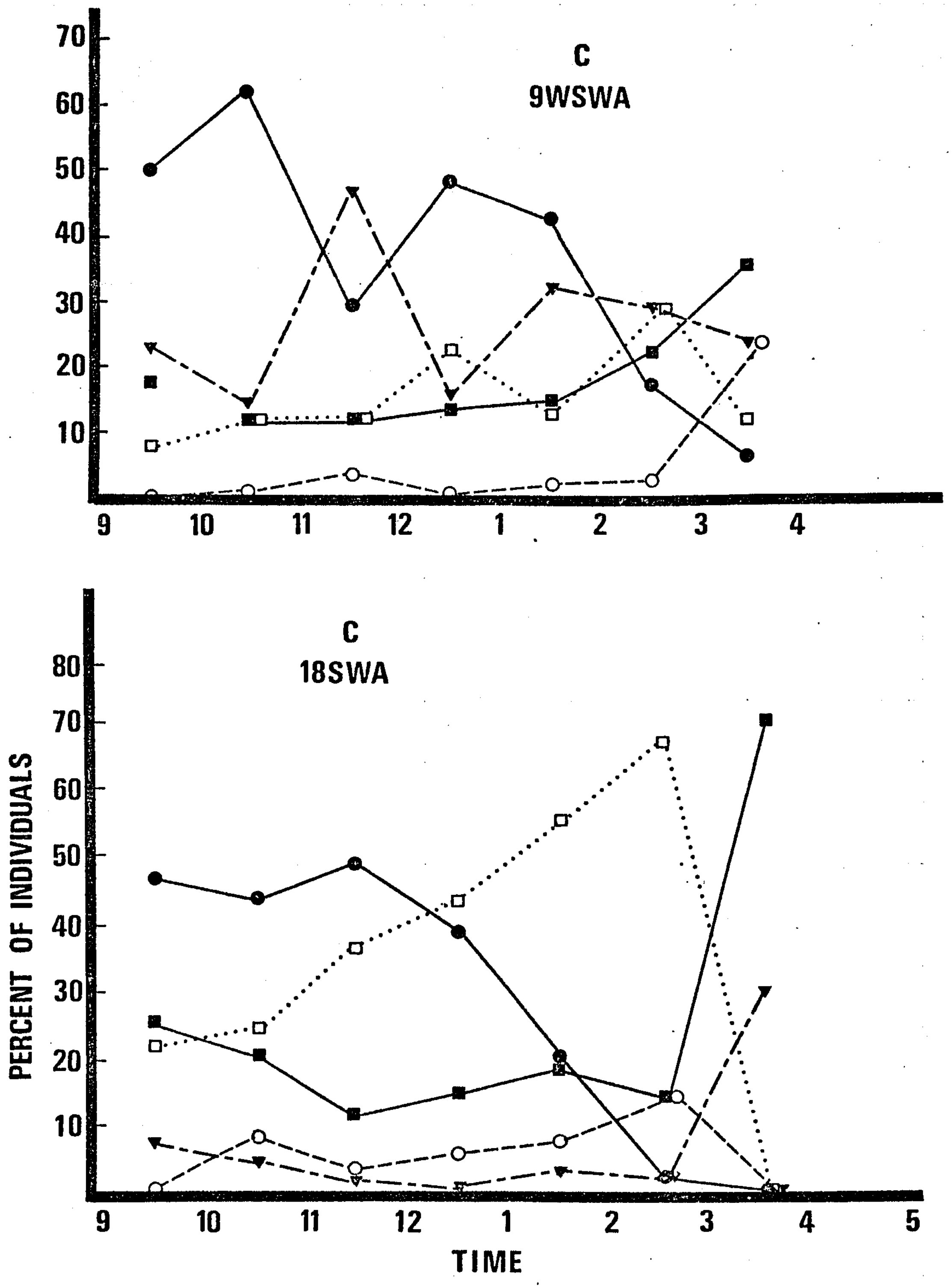

PERCENT OF SPECIES
60
50
40
30
20
10
E. albomarginata
E. capitellata
E. hyssopifolia
APOIDEA
HYMEN.
DIPT.
COLEOPT.
HEMIPT.

FIGURE 10


LEGEND
APOIDEA
OTHER HYMENOPTERA
DIPTERA
HEMIPTERA
COLEOPTERA
H
11SWA
18SWA
PERCENT OF INDIVIDUALS
70
60
50
40
30
20
10
9
10
11
12
1
2
3
4
5
TIME


C
9WSWA
70
60
50
40
30
20
10
9
10
11
12
1
2
3
4
C
18SWA
PERCENT OF INDIVIDUALS
80
70
60
50
40
30
20
10
9
10
11
12
1
2
3
4
5
TIME

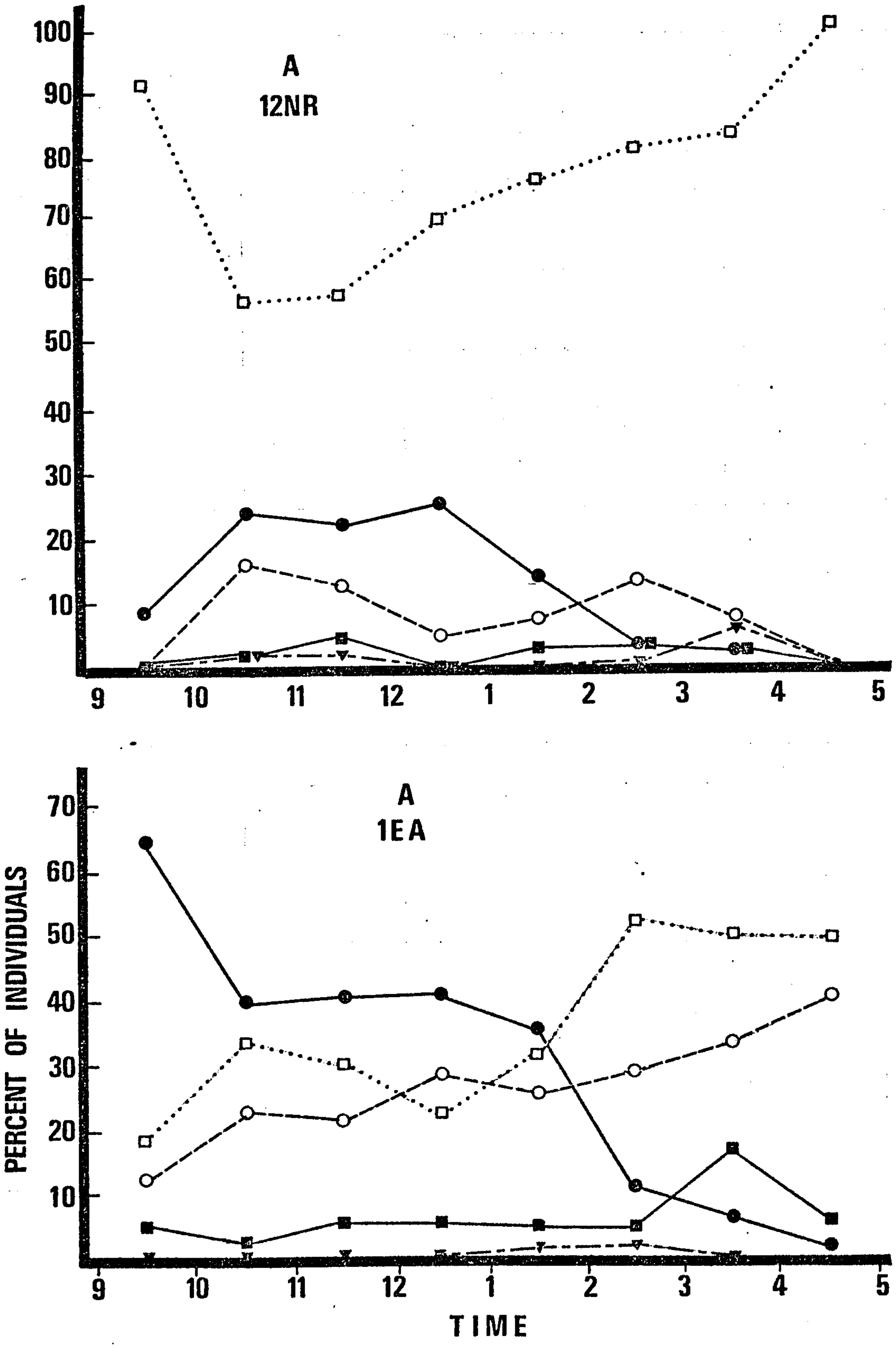
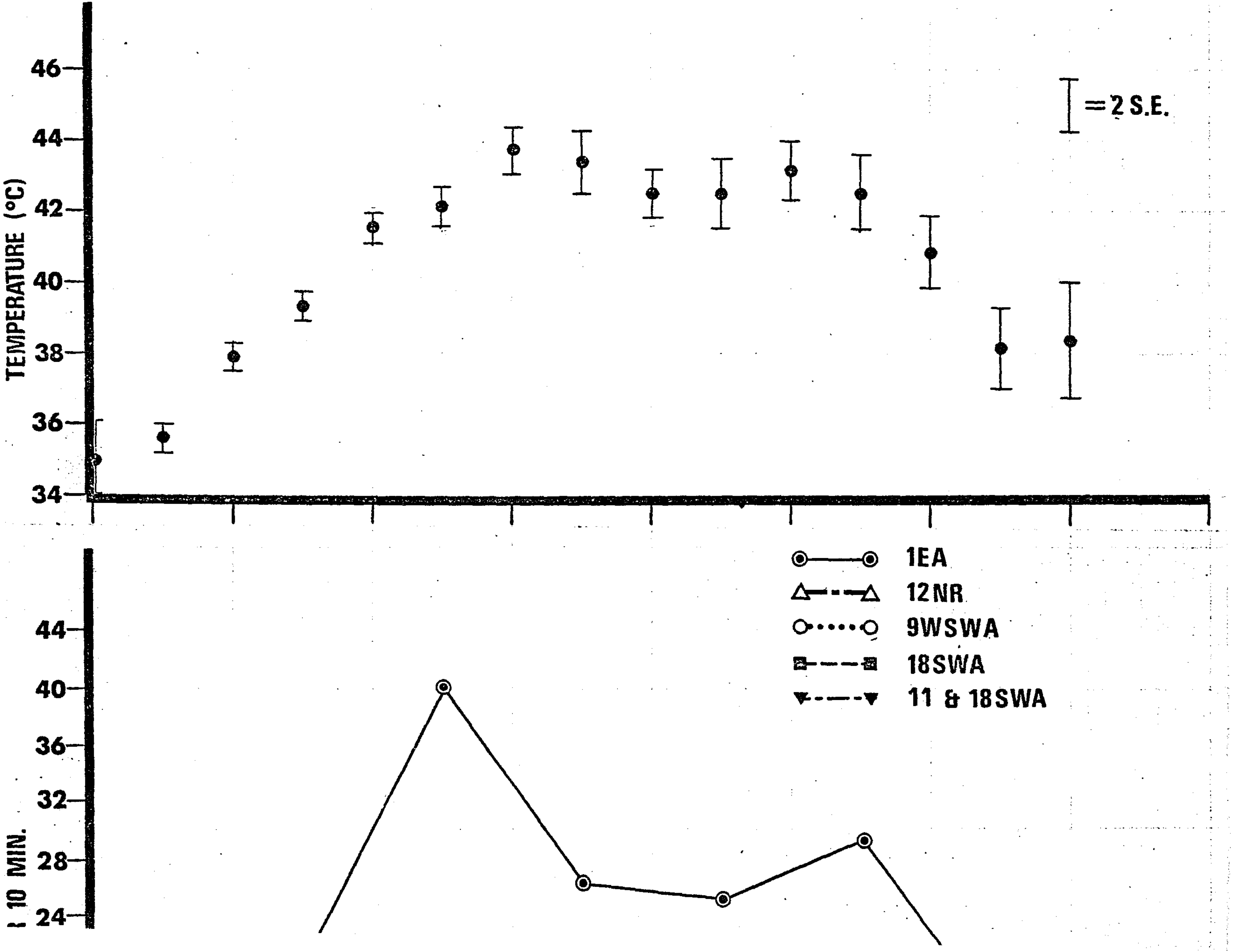
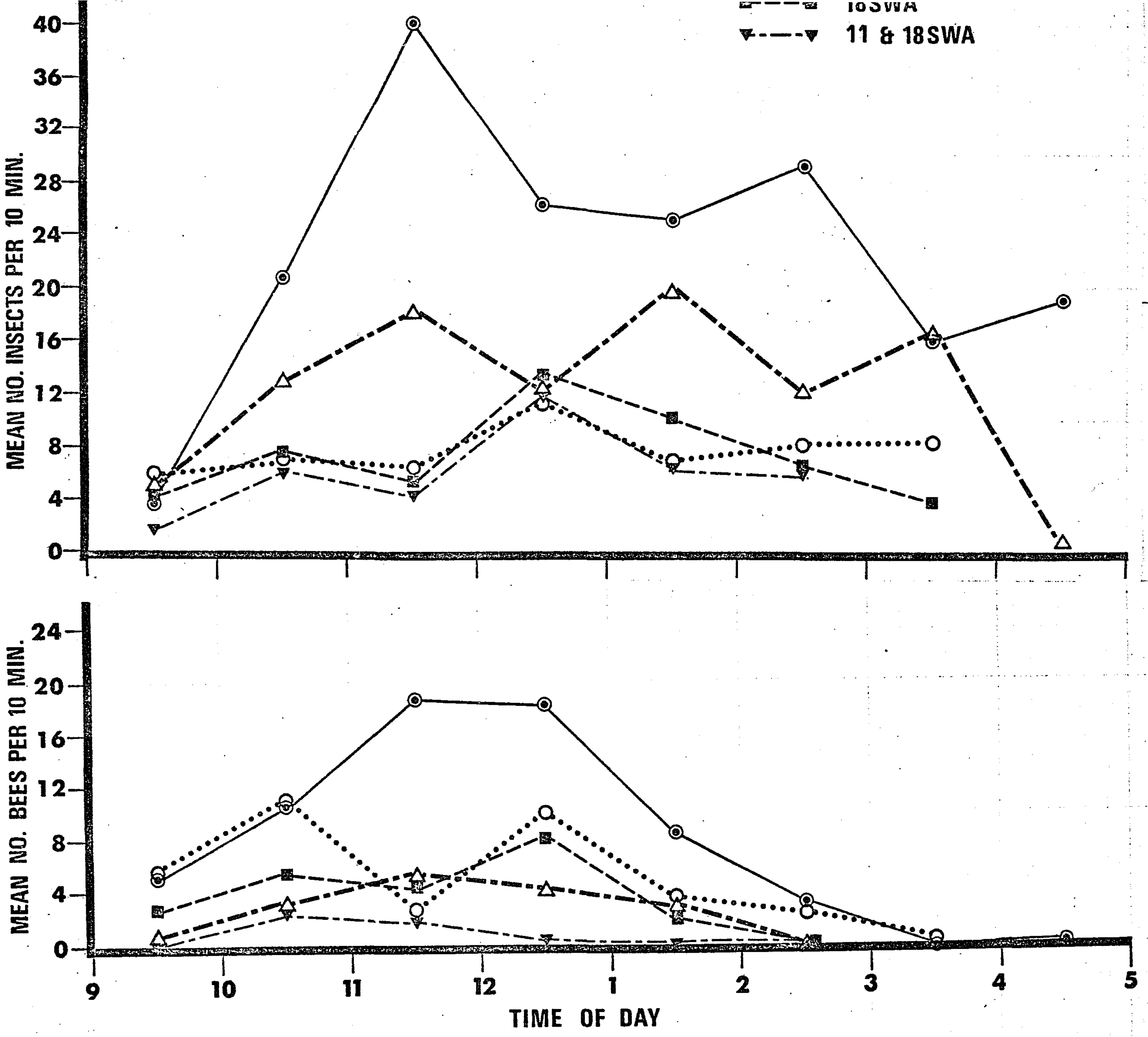

A
12NR
100
90
80
70
60
50
40
30
20
10
9
10
11
12
1
2
3
4
5
A
1EA
PERCENT OF INDIVIDUALS
70
60
50
40
30
20
10
9
10
11
12
1
2
3
4
5
TIME

FIGURE 11



TEMPERATURE (°C)
46
44
42
40
38
36
34
= 2 S.E.
1EA
12NR
9WSWA
18SWA
11 & 18SWA
44
40
36
32
28
24
10 MIN.


18SWA
11 & 18SWA
MEAN NO. INSECTS PER 10 MIN.
40
36
32
28
24
20
16
12
8
4
0
MEAN NO. BEES PER 10 MIN.
24
20
16
12
8
4
0
9
10
11
12
1
2
3
4
5
TIME OF DAY

CHAPTER 5

FORAGING BEHAVIOR: QUALITATIVE AND SPATIAL ASPECTS

In this chapter I present an ethological analysis of the foraging behavior of the seven common species of bees that subsist on Euphorbia. The body movements and behavior patterns that underlie the collection and ingestion of pollen and nectar, and the emplacement of pollen in the scopae are described, and the behaviors of the species are compared with each other. In this way, it is possible to identify elements of behavior that are common to all of the species, and to determine if variations in behavior follow the patterns of taxonomic affinity among the bees.

Table 10 gives sampling information for each bee species. Individual observations of foraging varied from ten seconds to six minutes. In all cases, the total observation time was ample to disclose the full repetory of species specific foraging behavior. Since individual elements of behavior were generally of the order of 1 second duration, total observation times for each species provided a very large sample size for every behavioral category. Characteristics of foraging behavior were remarkably constant from observation to observation within species.

Table 11 gives background information on the bees in this study. The length of the females, measured from the vertex (dorsal part of the head) to the tip of the pygidium (posterior portion of the last metasomal segment) gives a measure of the relative size of the various species. The andrenid bees all moisten their scopal pollen with nectar as it is packed. The structure and density of the hairs that constitute the scopa are related to the moistness of the pollen; species that pack dry pollen have long, thin, plumose hairs, and those that pack wet pollen have stout, curved, hairs with only a few, short, branches. The females of all the species studied ingest large quantities of pollen.

The data on foraging behavior is presented in two parts in the text, and in two tables. In the first section of the text, I describe the behavioral elements that are involved in foraging for pollen and nectar on the flowers of Euphorbia. The manner in which the elements are expressed in each species of bee is given in Tables 12 and 13; the former lists those behaviors that were found to be invariant among the species, and the latter presents the behavior of each species of bee for the elements that were variably expressed. The section of text following the general description only supplies information not included in the tables.

General Description of Foraging Behavior

A foraging female bee traverses an area of variable size and shape. She alights on flowers to feed, and moves to adjacent flowers by walking, hopping, or simply turning in place. She flies after visiting one to several flowers, either to alight again on the same or closely adjacent flowers (*P. minima*) or to proceed to a different plant or a distant portion of the same plant (*N. helianthi*), (Table 13, "Tendency to visit adjacent flowers"). In some species (e.g., *H. nanulus*), the female hovers briefly in front of each flower before landing, oscillating slowly from side to side while hovering, and then either lands or flies to another flower and repeats the movement. None of the species studied here forage on entirely overcast days. On most sunny days, however, occasional cumulus clouds hide the sun for 5 to 10 min, and the species vary in their response (Table 13, "Foraging during transient cloudiness"). Some (e.g., *C. sqamifera*) sit motionless on vegetation on the ground, while others (e.g., *P. minima*) continue foraging. Throughout the day, visits to flowers are occasionally interrupted by brief stops (Table 13, "Grooming pauses"), on rocks, leaves, or the ground. During these stops, the bee can 1) engage in grooming behavior of any part of the body, 2) perform the rubbing together of the hindlegs described below, and/or 3) remain motionless. Females of a few of the species, notably *H. nanulus*, infrequently embark on long, non-foraging flights, during which they alternately fly for several feet and alight briefly on the ground, rocks, or vegetation for periods of 20 to 30 sec or more. They often then resume foraging. None of the bees that took such flights entered their nests subsequently, and bees that I observed entering nests showed no such behavior. Thus, although it is possible that the individuals I saw had "lost" their nests, the resumption of foraging indicates that this was probably not the case.

All flowers that are visited are probed for nectar with the proboscis, but pollen ingestion and pollen collection occur sporadically. A series of consecutive flower visits during which pollen and nectar are both gathered will alternate with a series of visits during which nectar alone is obtained. The length of the exclusive nectar gathering periods varies from several seconds to several minutes.

During the predominantly pollen-gathering phases of foraging, bees of all species could be seen to walk over or pass by flowers with conspicuously full anthers. There was no obvious relationship between the amount of extruded pollen visible and the behavior of a bee passing by that flower. On each visited flower, pollen ingestion may occur independently of pollen collection for scopal deposition. In eating pollen, the mandibles are applied to the pollen exuded from the anther, and the pollen is pushed into the hypopharynx.

The bees can assume three different postures on the flowers, each posture having associated with it certain motions. In the "angled" position, the bee tilts so that the side of the head, mesosoma ("thorax" of a bee), and metasoma ("abdomen" of a bee), are touching the petal, and the proboscis makes a 45° angle with both petal and anther (Fig. 12). Maintaining this position, the bee walks in a circle around the flower, probing each gland for nectar (Table 13, "circle" motion). In the "astride" position, the bee stands across the top of the flower, with its head positioned over a gland (Fig. 13). In this posture it may rotate, visiting each gland in turn. These postures and motions deposit large quantities of pollen on the stigma. In the "vertical" position, the bee shifts so that she is perpendicular to a petal. Her body is continuously supported by the hindlegs, and sometimes by the midlegs, and the metasoma is braced against the edge of the petal (Fig. 14), and either hangs vertically or is curled up under it. The vertical position enables the bee to lean forward and gather pollen directly from the anther using its foretarsi and foretibiae, and sometimes its mandibles. In any of the three postures, the bee may feed at only one nectary or anther, without moving (Table 13, "stationary"). The final motion listed in Table 13 is the "run", described in detail in the section on E. sp. A. The species vary in the extent to which they alter their posture in switching from nectar to pollen collection. (Table 13, "Difference: in posture, pollen vs. nectar collection"); for example, both species of Perdita collect nectar in the angled and astride positions, and collect pollen principally in the vertical position. The species also vary in the completeness with which the resources of a given flower are extracted. P. minima invariably investigates every anther on a flower; H. nanulus does so rarely, if ever.

The sequence of leg movements responsible for pollen collection and scopal packing are common to all the species, but the movements vary in their speed, their timing, and the manner in which the legs are brought into contact with other parts of the body.

The foretarsi and foretibiae, sometimes aided by the mandibles, remove pollen from the anthers. Each foreleg is then rubbed against the tibia and tarsus of the midleg of the same side, in such a way as to transfer the pollen from the foreleg to the inner and posterior sides of the midleg. The midlegs next touch the hindlegs, effecting a transfer of pollen to the scopae. The midleg moves back and forth between foreleg and hindleg (Table 13, "antero-posterior hit"), but may also have a sideways rubbing motion across the surface of the scopal load (Table 13, "lateral rub"). As the midleg and hindleg come together, the midleg is flexed so that a comb of short hairs on the basal posterior surface of each femur brushes the scopa. In some species (e.g., N. helianthi), this sequence of motions is so rapid that each leg's movements appear as a vibration; in other species (P. obscurella, D. perparvus) the movements are slow enough to be easily resolved. Some species move the legs of each pair at the same time (Table 13, "together"); other move them alternately. Other body parts can be involved: the face (frons and clypeus) can be systematically scraped by the forelegs before they touch the midlegs (Table 13, "Face cleaning during pollen collection"); long plumose hairs on the ventral surface of the head and mesosoma may accumulate pollen and then be combed by the foretarsi as they pass from anther to midlegs (e.g., both species of Perdita). Finally, in some species the whole body shakes from side to side as pollen is collected (Table 13, "Body vibration").

Scopal packing is variably integrated into the behavioral sequence of each species. Some bees (e.g., *N. helianthi*) perform the entire leg movement sequence one or a few times on each flower and thus move pollen into the scopae more or less continuously. Others (e.g., *P. obscurella*) gather pollen with the forelegs on several flowers before transferring it to the scopae; scopal packing is thus intermittent. The pollen packing leg movements can occur either in flight or on the flower.

The scopal load is consolidated and shaped by the rubbing together of the hindlegs beneath the metasoma. The tibial and tarsal segments of each hindleg are alternately rubbed across the corresponding segments of the other leg. This movement, like scopal packing, can occur either in flight or at rest. A few species (e.g., *H. nanulus*) jerk the metasoma up and down several times during this hindleg rub.

Intraspecific interactions on the flowers were observed in all the species. Both mating and encounters between females were seen in some species (e.g., *P. obscurella*), whereas only female-female interactions occurred in others. During inter-female interactions in all species, the two bees grapple at right angles to each other, and each bends her metasoma under the other. The two bees may fall off the flower on which the encounter occurred. Their contact lasts less than 0.5 sec. The tendency of the bee that was initially on the flower to leave after such an encounter varies among the species (Table 13, "Number of displacements of original bee"). The tendency of females to interact with each other is indicated in Table 13 as the "Av. number of interactions/minute" (this figure does not include matings as interactions). Mating behavior is described in more detail below for those species in which it was observed on the flowers.

In all species except *P. obscurella*, interactions resulted from the random encounter of two individuals (interaction frequency followed a Poisson distribution). In other words, females neither sought for nor avoided each other, but grappled whenever they chanced to meet.

Species Descriptions

P. minima

This species foraged primarily on *E. albomarginata*; although *E. capitellata* was common at several of the study sites, it was visited very rarely.

The pollen-gathering behavior of this species and the following species, *P. obscurella*, are highly distinctive. The bee assumes the vertical position, as in Fig. 12, leans forward, and extracts the pollen from each open anther on the flower. The use of the mandibles enables the bee to gather both extruded pollen and pollen just inside the rim of the anther. Pollen ingestion most likely occurs at this point. Body vibration accompanies the investigation of each anther. Occasionally, body vibration is observed when the bee is angled between the anthers and the petals; this movement is probably associated with pollen collection from anthers situated closer to the level of the petals. The procoxae and prosternum, which are densely covered with long, plumose erect hairs, become heavily dusted with pollen during both this pollen collecting behavior and during movements over the flowers in the "astride" position.

After anther visitation, the bee resumes her vertical posture on the petal, and commences to transfer the collected pollen from the face, prosternum and forelegs to the scopae. Facial cleaning movements are repeated several times between each contact of the foreleg and midleg. The sequence of movements from face-scraping to midleg-hindleg rubbing may be repeated several times, and the bee may remain engaged in this behavior for up to a minute.

The pollen load is shaped by the motion of the midlegs over the scopae into an approximately oblate spheroidal mass. The long axis of the mass is at a 20° angle to the tibia, so that rounded masses of pollen protrude interiorly from the anterior proximal and exteriorly from the anterior distal parts of the tibia. It is probably that the liquid used to wet the pollen is added during this sequence of motions, being deposited on the forelegs during the face cleaning and then passed backwards with the pollen.

No mating was observed, although males were common.

P. obscurella

The postures, body movements and leg movements of P. obscurella are indistinguishable from those of P. minima. The scopae are filled with pollen while the bee sits on the flowers in the manner described for P. minima. On one occasion, however, scopal packing during flight was seen. This packing was accomplished by similar movements of the midlegs against the hindlegs, but no conspicuous brushing of the face was observed.

The major difference between the two species of Perdita is the occurrence of frequent intraspecies interactions on flowers in P. obscurella. Females are mated while they feed on flowers, and a single female may accept several mates. One female was observed to separate from a male to which she was joined, and mate with another two minutes later. Pairs remain in copulo for at least as long as my longest observation (6 min). No courtship behavior is evident; a male rapidly approaches the female from behind, immediately grasps her with his legs, curls the tip of his metasoma under the tip of hers, and engages his genitalia. Often the female is knocked off the flower by this attack, but she returns to the flower immediately and continues foraging. The male maintains an almost vertical position above the female, and grasps her with the hind and midlegs. His antennae point forward, and may occasionally touch her head, but they do not move in a conspicuous or regular way. He may shake his body from side to side throughout copulation, and both partners shake violently during disengagement. Mated pairs are frequently "attacked" by other bees, both male and female, and are sometimes knocked off the flower. During these encounters, the attacker bee and the mated female curl their abdomens about each other. I never observed such an encounter to result in the separation of a mated pair.

Female-female interactions between unmated bees are also more common than in *P. minima*. The encounters did not occur randomly (departure of interaction frequency distribution from Poisson significant at $P < 0.005$). This finding implies that under some conditions individuals (both male and female) actively seek for each other, and at other times, they avoid each other. The result is an excess of both observations with no encounters, and observations with many encounters. The factors governing these behavioral changes are unknown.

H. nanulus

The most salient aspect of the foraging pattern of this species is the amount of flight in which the females engage (discussed further in Chapter 6). The bee usually flies for several seconds when travelling between heads on *E. capitellata*, even when the heads are adjacent, and less commonly it hops or walks between contiguous heads. Although *H. nanulus* covers considerably more area per unit time than most of the other species, it tends to circle about the area repeatedly, visiting the same flowers on *E. albomarginata* and the same heads on *E. capitellata*. It was more frequently observed on *E. capitellata*; on this plant, it would visit several flowers within a head with minimal movements between the flowers. On several occasions, it was observed to fly rapidly over patches of *E. albomarginata* that lay between *E. capitellata* plants and resume foraging on *E. capitellata*.

Pollen gathering seems to be accomplished by walking over anthers, and removing the pollen that adheres to the pubescence on the forelegs and midlegs and on the venter of the metasoma. There is no digging from the anthers with the forelegs as in the two species of Perdita. From the similarity in shape of the scopal load to that of Perdita, I infer that the midlegs scrape laterally across the hindlegs, as well as the observed antero-posterior movement. Although brushing of the face with the forelegs was observed, no movement of pollen was associated with it and thus it appears to be pure grooming behavior.

Intraspecific encounters - both between females and between males and females - are more pronounced in this species than in any other. No differences in behavior were noted between inter-female and male-female encounters, and both were less than a second in duration. Because of the rapidity of the events and the tendency of pairs to fall to the ground, I do not know if males succeeded in copulating with the females. However, matings of brief duration are not uncommon among bees, and these interactions probably have a sexual function (Rozen, pers. comm.).

C. squamifera

This species forages in a manner different from all the preceeding species. Females fly moderately rapidly over the flowers, stopping briefly at many of them. I observed no systematic turning around the flower; thus, it does not seem to search every gland for nectar. The bee rapidly brushed the forelegs over the anthers two or three times, accumulating pollen on the hairs of the forelegs, and then passes it backwards by means of midleg and hindleg motions similar to those already described. During pollen collecting bouts, this sequence occurs on every flower visited. Some bees were seen collecting only nectar; no leg movements other than walking motions were observed at these times. After foraging bouts of 30 to 60 sec, the bee rapidly flies around the plant, either leaving or returning to the same place to resume foraging. Scopal packing movements are seen during these flights. Although some use of the mouthparts on anthers was observed, I could not determine whether they were being used for pollen collection or just pollen ingestion.

Although males were abundant, interactions between males and females were rare, and copulation was never seen. On two occasions, a male approached a foraging female; he hovered briefly directly behind and slightly above her, while she elevated her body on extended legs, and flicked her metasoma up and down several times. Her behavior was apparently a rejection signal, since the male flew off rapidly.

N. helianthi

The foraging behavior of this species is very similar to that of C. squamifera. It is characterized by the same alternation of brief stops on flowers and equally brief flights to nearby flowers. During these brief flights between nearby flowers, the bees produce a loud, high-pitched buzz that was not heard with any of the other species. It is not known if this sound accompanied other kinds of flight by N. helianthi. Scopal packing generally occurs during slow flights over the plants, during which the midlegs rub against the hindlegs. From the frequency with which pollen was observed on the midlegs during pollen collecting bouts, it seems likely that pollen is accumulated there from the foreleg scraping, and then periodically deposited in the scopae.

Although males were commonly observed, no mating attempts were seen.

The pollen carried by N. helianthi changes in color from bright yellow to dark orange after it is deposited in the scopae. Fresh (yellow) pollen appears as a light dusting on the anterior dorsal surfaces of the pollen load; the color change evidently occurs shortly after deposition, since yellow pollen is never seen on other parts of the pollen ball. This change is unique among the species studied, and is probably attributable to some effect of the liquid with which the pollen is mixed during packing.

D. perparvus

This species spends less time in flying between flowers than any other studied, preferring to walk instead. When in flight, individuals of D. perparvus are easily distinguished from members of the other genera of bees visiting Euphorbia because of their jittery, erratic movements.

The foraging behavior of this species combines elements similar to several of the preceeding bees. *D. perparvus* is the only bee, in addition to the two species of *Perdita*, to utilize the vertical posture. Unlike the vertical posture of *Perdita*, however, the metasoma is curled around so that the pygidium touches the undersurface of the petal, and the mesosoma and head are bent forward over the upper surface of the flower, bringing the mandibles and/or forelegs in contact with the anthers. Pollen gathering may occur in either the astride or vertical posture, and is accomplished by a *Nomadopsis* - like scraping motion of the forelegs. This motion is not as rapid as in the latter. In both postures, the mandibles are applied to the anthers, and pollen accumulates on the face.

E. sp. A.

E. sp. A forages mostly on *E*. *capitellata*; only rarely did it visit *E*. *albomarginata*. In foraging, it either circles around an area, repeatedly visiting the same heads, or it flies in a linear path, stopping on occasional plants but passing over others without stopping. The latter behavior is significantly more common. Between flights, it traverses each head in a curious gait that is midway between running and flying. Even during the longest flower visits, it rarely stops moving. In the few times when it is stationary, it engages in grooming of the face, mouthparts and forelegs; this behavior does not result in pollen transfer.

Pollen is gathered on each visit to a head by a very rapid brushing of the forelegs over the head as the bee runs. The pollen adheres to dense, short combs of hair on the profemora and protibiae. It appears to be passed backwards to the midlegs and then to the hindlegs at each movement of the forelegs. This combination of pollen collection and transfer with locomotion is undoubtedly responsible for the clumsy and uneven appearance of the gait of E. sp A; the use of the wings while it runs probably helps it keep its balance.

Another feature of the running behavior is a frequent and simultaneous raising and lowering of both hindlegs. In the raised position, the legs are extended vertically above the mesosoma, where they remain for a variable period of time, up to several seconds. This behavior was seen in most but not all observations of foraging. The function of the leg-raising behavior is obscure; however, the observed facts that 1) although males were abundant, no male-female interactions of any kind were seen, and 2) pollen accumulated in the scopa during periods of the lowered position, suggest that this behavior is somehow associated with scopal packing, and not sexual display. However, the variability in the occurrence of the motion during pollen collection is difficult to understand if it is a necessary part of the pollen collecting sequence. A similar behavior has been described for Protandrena, an unrelated species of bee (Rozen, 1967).

At the end of a foraging bout, E. sp. A flies back and forth several times over the plants from which it has been foraging, rapidly rises to a height of five or six feet, and flies off in a straight line, presumably towards its nest.

On three or four occasions, bees were seen foraging on _E. albomarginata_. The basic pattern was similar to that seen on _E. capitellata_, but the running-flying motion was more rapid.

Interspecific Comparisons

In order to study the patterns of resemblance among the seven species in these aspects of foraging behavior, the percentage similarity of each pair of species was computed (Table 14). These figures were obtained by studying the data in Table 13 for each pair of species; the number of characters for which the pair showed the same behavior was determined, and then converted to a percentage of the total number of characters involved (25). In Fig. 15, the pattern of greater-than-average similarity is shown.

In general, the relationships seen in Fig. 15 parallel the taxonomy of the bee species involved. Among the panugines genera, the patterns of similarity reflect the concepts of phylogenetic affinity that have been advanced on morphological grounds (Rozen, pers. comm.). _C. squamifera_ and _N. helianthi_ resemble each other more closely than either resembles _H. nanulus_, and the two species of _Perdita_ form a group apart from the other panugines. The position of _E._ sp. A in a different family is reflected in its lack of strong resemblance to members of two unrelated families.

Summary

The foraging behavior of bees can be divided into groups of behavioral elements concerning movements among flowers within the plant population, the acquisition, ingestion and transport of pollen and nectar, and the interactions on the flowers of conspecifics. Analysis of the foraging behavior of each of the seven species of bees studied here discloses the following patterns: 1) certain behavioral elements, notably those concerning the manipulation of pollen, do not vary in form among the species; 2) other elements, a majority of those described, are characterized by several qualitatively different states among the bees; 3) some of the species of bees studied here have behavioral patterns unique to themselves (e.g., the leg-raising behavior of E. sp. A); 4) the patterns of similarity in foraging behavior among the species follow lines of taxonomic affiliation. This finding raises the possibility that foraging behavior can be profitably used as adjunct to taxonomic investigations.

TABLE 10. Sample sizes for each bee species.

Bee	Number Observations	Total length observation time (min)	Mean observation time per individual (min)
P. minima	70	106.2	1.5
P. obscurella	64	63.1	1.0
H. nanulus	89	114.8	1.3
C. squamifera	49	47.3	0.9
N. helianthi	59	60.3	1.0
D. perparvus	42	35.3	0.8
E. sp. A	62	81.3	1.3

TABLE 11. Morphological characteristics of each bee species.

Bee	Average Length, mm (N)	Scopal Pollen	Scopal Location	Scopal Hairs
P. minima	2.7 (11)	moist	anterior surface, hind tibiae	mod. dense; short; thick; simple
P. obscurella	3.3 (7)	moist	anterior surface, hind tibiae	mod. dense; short; thick; simple to short branches
H. nanulus	4.3 (16)	moist	anterior surface, hind tibiae and basitarsi	mod. dense; long; thick; short branches
C. squamifera	4.9 (5)	moist	anterior and distal posterior surfaces, tibiae; anterior surface, basitarsi	mod. dense; long; thick; simple or short branches
N. helianthi	5.6 (10)	moist	anterior and distal posterior surfaces, hind tibiae; anterior surface, basitarsi	mod. dense to dense; long; thick to thin; long to short branches.

TABLE 11. Continued.

Bee	Average Length, mm (N)	Scopal Pollen	Scopal Location	Scopal Hairs
D. perparvus	3.9 (11)	dry	hind coxae, femora, tibiae; venter of abdomen	mod. dense; long; thin; highly plumose.
E. sp. A.	5.2 (10)	dry	entire hind tibiae, basitarsi	very dense; long; thick to thin; highly plumose

TABLE 12. Behaviors common to all bees foraging on two species of Euphorbia. In this and the succeeding table, the elements described in the general section on foraging behavior have been clustered into six aspects of foraging behavior.

Aspect of Foraging	Common Element of Behavior
General organization of foraging behavior	Occurrence of grooming pauses
Feeding	Nectar collection on every flower visited
	Pollen collection on some, but not all flowers visited.
	Use of mandibles for ingesting pollen.
Behavior on flowers	None
Pollen Collection	Use of forelegs to extract pollen.
	Transfer of pollen from forelegs to midlegs to hindlegs.
	No pollen collection on some visits to flowers with full anthers.
Scopal Packing	Occurrence of hindleg rub.
Intraspecific Interactions	Occurrence of female-female interactions.

TABLE 13. Elements of the foraging behavior of seven species of bees visiting *Euphorbia*. See "General Description" for discussion of each element.

Behavior	*P. minima*	*P. obscurella*	*H. nanulus*	*C. squamifera*	*N. helianthi*	*D. perparvus*	*E. sp. A*
	General Organization of Foraging Behavior						
Tendency to visit Adjacent, Nonadj. fls.	A	A	N	N	N	A	A
Foraging during transient cloudiness: Continues, Stops.	C	S	S	S	S	C	C
Grooming pauses: Rare, Moderate, Frequent	M	M	F	M	M	R	R
Long non-foraging flights: Yes, No.	N	N	Y	N	Y	Y	N
Hover flight in front of fl before landing: Often, Sometimes, Never.	N	N	O	S	S	N	O
Av. foraging area per observation (m^2)	0.33	0.26	1.96	0.86	0.70	0.35	4.30

TABLE 13. Continued.

Behavior	*P. Minima*	*P. obscurella*	*H. nanulus*	*C. squamifera*	*N. helianthi*	*D. perparvus*	*E. sp. A*
Usual shape of area covered: Circle, Line.	C	C	C	C	C	C	L
				Feeding			
Pollen eating: with Pollen collecting; Separately.	P	P	S	P	S	P	P
				Behavior on Flowers			
Posture on fls: Astride, Angled, Vertical.	As, An, V	As, An, V	As	As	As	As, V	As
Difference in posture, pollen vs. nectar collection: Yes, No.	Y	Y	N	N	N	N	N
Motion on fl: Circle, Rotate, Run, Stationary.	C, Ro, S	C, Ro, S	S	S	S	C, Ro, S	Ru
Collect from all anthers of each fl: Always, Sometimes, Never.	A	S	N	S	S	A	N

TABLE 13. Continued

Behavior	*P. minima*	*P. obscurella*	*H. nanulus*	*C. squamifera*	*N. helianthi*	*D. perparvus*	*E. sp.* A
Body vibration: Yes, No.	Y	Y	N	N	N	N	N
			Pollen Collection				
Motion of paired legs: Together, Alternate.	T	T	A	A	A	A	A
Involvement of head and mesosomal venter in pollen collection: Yes, No.	Y	Y	N	N	Y	Y	N
Face cleaning during pollen collection: Yes, No.	Y	Y	N	N	N	N	N
Use of mandibles to collect pollen: Yes, No.	Y	Y	Y	Y?	N	Y	N
Movement of midlegs against hindlegs: lateral Rub, antero-posterior Hit.	R	R	R	R	R	H	H

TABLE 13. Continued

Behavior	P. *minima*	P. *obscurella*	H. *nanulus*	C. *squamifera*	N. *helianthi*	D. *perparvus*	E. *sp. A*
Speed of leg movements: Moderate, Fast.	M	M	F	F	F	M	F
			Scopal Packing				
Performance of hindleg rub: on Flower, in Flight, Both.	Flo	Flo	B	B	B	Flo	B
Metasomal motion with hindleg rub: Yes, No.	N	N	Y	Y	Y	N	Y
Temporal pattern of scopal packing Intermittent, Continuous.	I	I	C	C	C	I	I
Scopal packing: on Flower, in Air, Both.	F	F	A	B	B	F	B
			Intraspecific Interaction				
Mating on fls: Yes, No.	N	Y	N? +	N	N	N	N

TABLE 13. Continued.

Behavior	P. minima	P. obscurella	H. nanulus	C. squamifera	N. helianthi	D. perparvus	E. sp. A
Average number interactions per min.	.11	.38	.20	.11	.09	.09	.04
Number displacements of original bee on fl/total number interactions.	7/11	7/26	18/22	2/5	4/5	0/3	0/3

+ See species descriptions for explanation.

TABLE 14. Percentage similarity of all pairs of species for the behavioral elements listed in Table 13. See text for method of computation.

	P. minima	*P. obscurella*	*H. nanulus*	*C. squamifera*	*N. helianthi*	*D. perparvus*	*E. sp. A*
P. minima	--						
P. obscurella	80						
H. nanulus	20	24	--				
C. squamifera	36	36	72	--			
N. helianthi	28	28	72	84	--		
D. perparvus	64	56	32	36	36	--	
E. sp. A	24	20	44	52	44	48	--

$\bar{X} = 45$

Figure Captions

Chapter 5

Fig. 12 A female *P. obscurella* in the angled position on a male-stage cyathium of *E. albomarginata*.

Fig. 13 A female *N. helianthi* in the astride position on cyathia of *E. albomarginata*. The scopal load is in contact with the stigma of a female-stage cyathium.

Fig. 14 A female *P. minima* in the vertical position on a cyathium of *E. albomarginata*. This individual is passing pollen from the forelegs to the midlegs preparatory to depositing the pollen in the scopae.

Fig. 15 Species relationships of greater-than-average percentage similarity: qualitative aspects of foraging behavior. Data from Table 14. Cs = *C. squamifera*; Dp = *D. perparvus*; Ea = *E.* sp. A; Hn = *H. nanulus*; Nh = *N. helianthi*; Pm = *P. minima*; Po = *P. obscurella*.

FIGURE 12

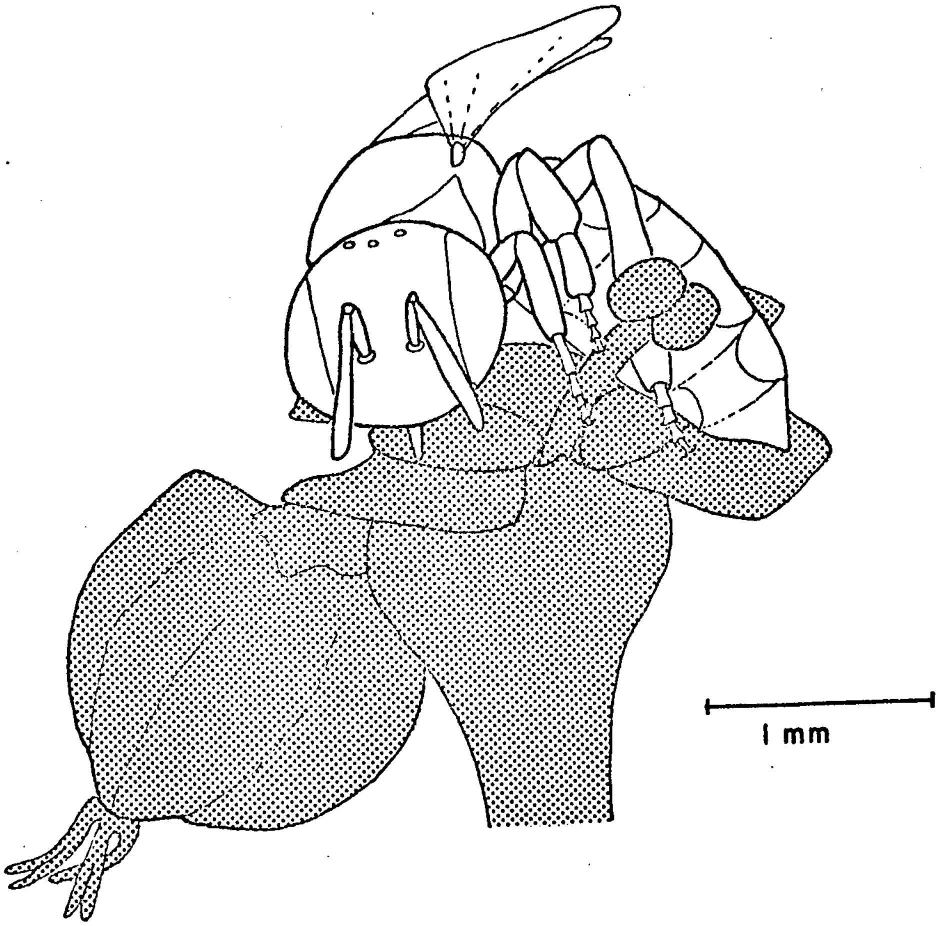

1 mm

FIGURE 13

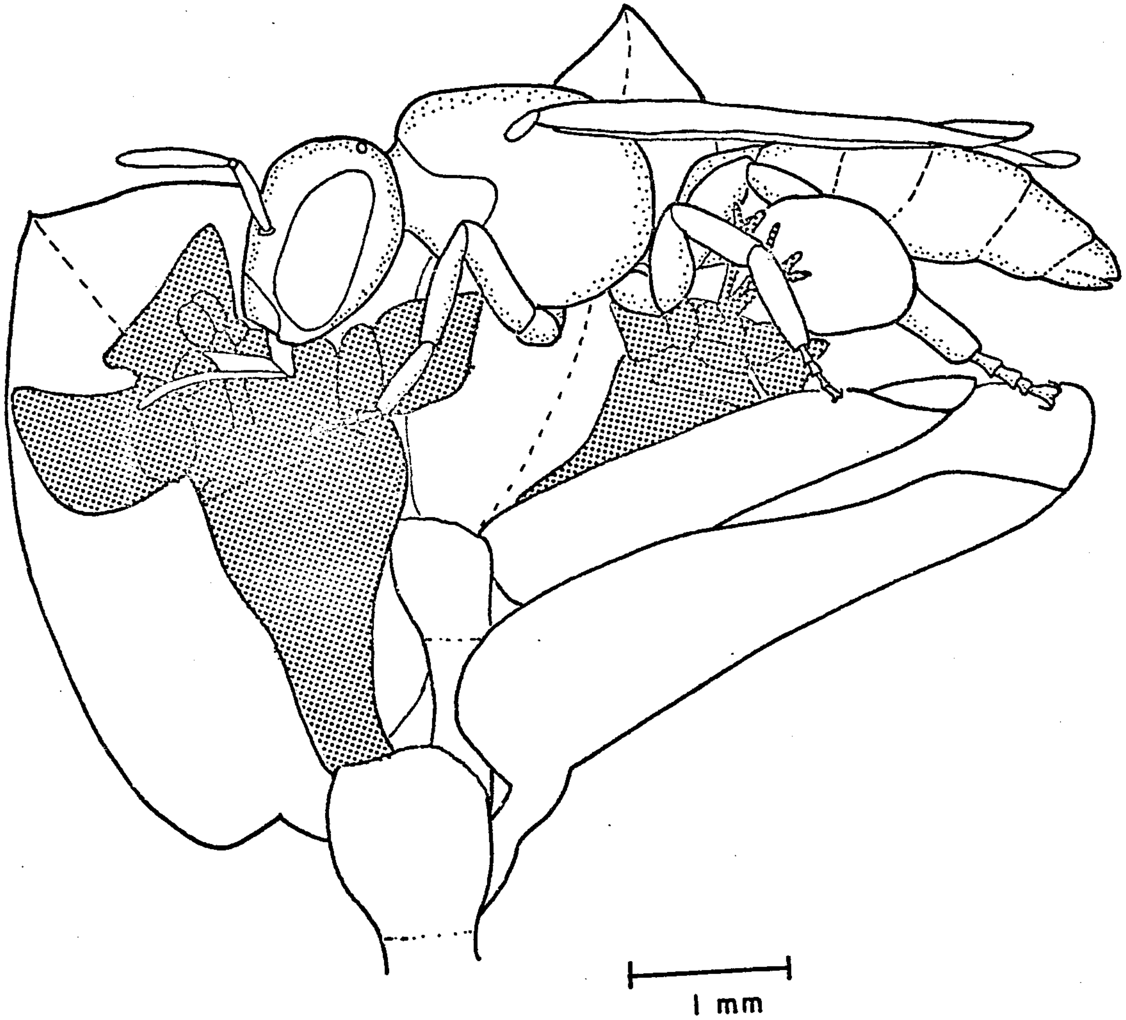

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FIGURE 14

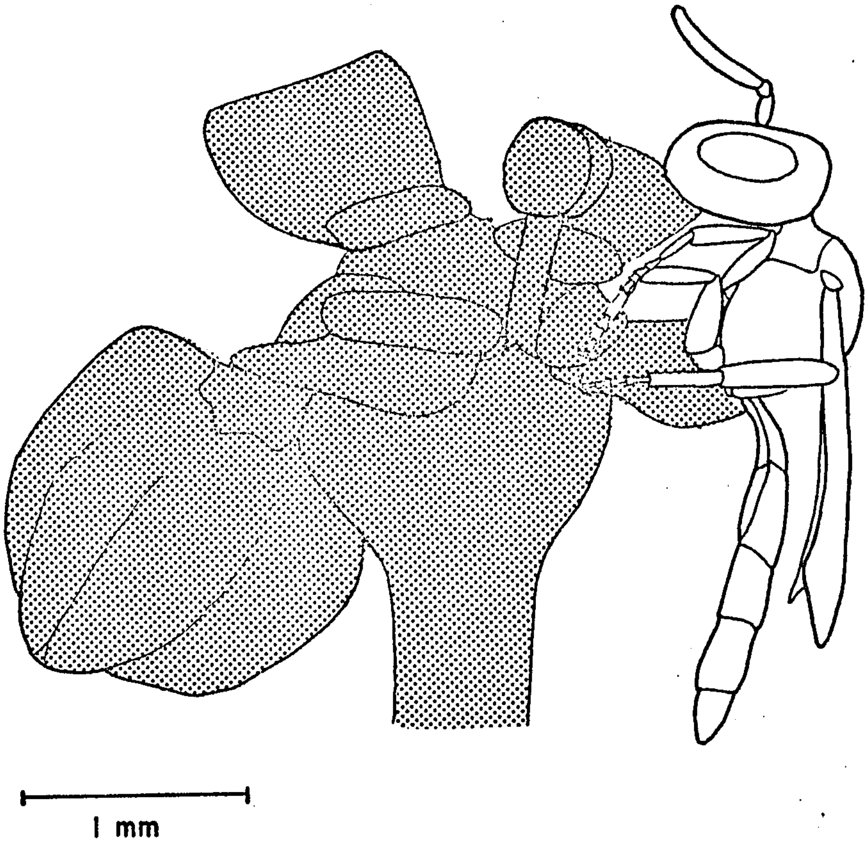
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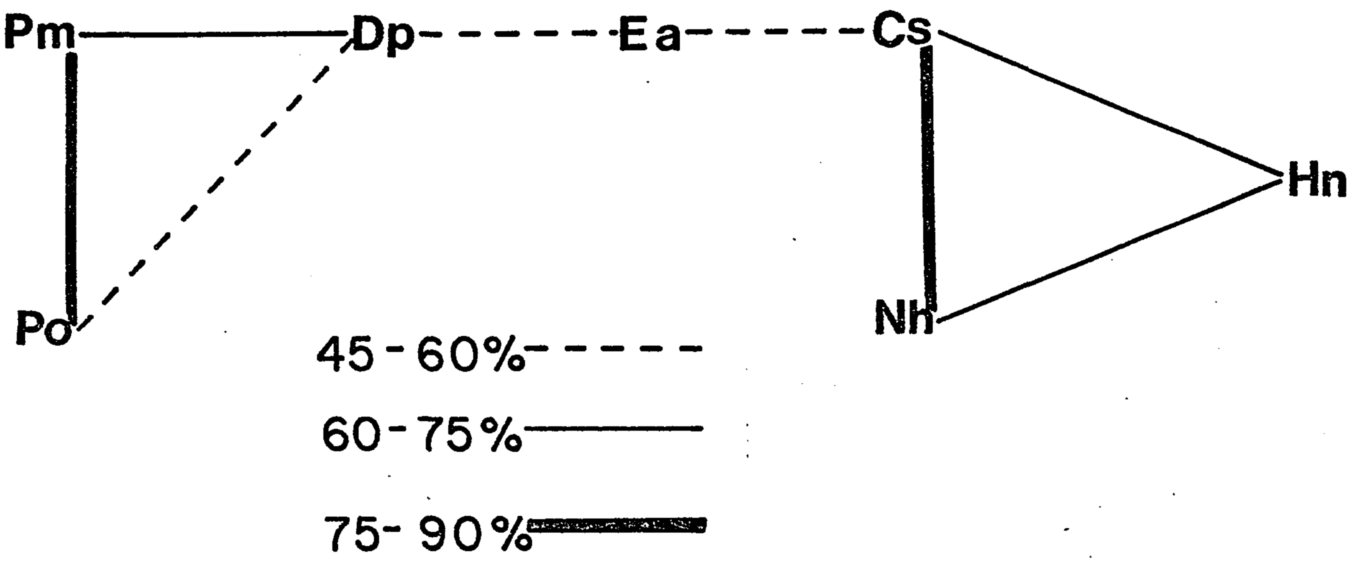
FIGURE 15



Pm
Dp
Ea
Cs
Hn
Po
Nh
45-60%
60-75%
75-90%

CHAPTER 6

FORAGING BEHAVIOR OF BEES: TEMPORAL ASPECTS

In the previous chapter the movements used by the bees to gather pollen and nectar from the flowers and spatial attributes such as the foraging area size and shape were shown to differ greatly among the species. In this section, aspects of the timing and sequence of the movements that constitute foraging behavior are examined. The bee species are compared with each other in order to determine the importance of species-specific components of behavior and the extent to which the bees respond behaviorally to the differences in the biology of two of the plant species.

Pollen Constancy of Bees

Table 15 demonstrates that the species studied are indeed foraging solely on *Euphorbia*. Grant (1950) has defined those bees that collect a single kind of pollen during each foraging trip, but utilize many kinds of pollen during their lives, as exhibiting "constancy" with respect to their food sources. Although *D. perparvus* is reported to be polylectic (Moldkenke, 1973; Eickwort, pers. comm.) it clearly is constant on *Euphorbia* during a given pollen-collecting trip. *Exomalopsis* sp. A generally also shows a high degree of constancy to *Euphorbia*; the decrease in the percentage of *Euphorbia* pollen compared to the other species was caused by two individuals with mixed loads of pollen. Since no other sources of information for this species are available to me, I cannot definitively describe this species as oligolectic or polylectic; however, the presence of some individuals not constant to *Euphorbia* strongly suggest catholic pollen preferences. Most of the species of *Exomalopsis* that have been studied so far are polylectic (Rozen, pers. comm.), and so it is likely that this species will prove so when better studied. Specimens of the panurgine species in the collection of the American Museum of Natural History from localities other than those studied by me were checked for the presence of *Euphorbia* pollen; the data were pooled with the data from the other specimens in Table 6. One individual of *P. obscurella* carrying unidentified pollen, and four individuals of *N. helianthi* carrying *Lepidium* pollen were found; the rest carried only *Euphorbia* pollen. Only three or four grains of foreign pollen were found in the scopae of the rest of the panurgine specimens, and this pollen was from the same plant species that contributed most of the wind-borne pollen discussed in Chapter 4. Thus, it is likely that the foreign pollen grains were contaminants blown onto *Euphorbia* plants and there picked up by the bees. Extensive collecting of bees on all other plants in flower at each site did not produce a single female collecting pollen on plants other than *Euphorbia*. Thus, the museum specimens carrying pure loads of non-*Euphorbia* pollen most likely represent rare instances of departure from oligolecty on *Euphorbia*. The occasional occurrence of individuals or populations of an oligolectic species collecting foreign pollen has been described and discussed in detail by Cruden (1972) and Thorp (1969). They concur in the opinion that these events usually represent plastic behavior during periods of extreme stress, and do not vitiate the concept of oligolecty. Thus, the panurgine bees are oligolectic in the sense of utilizing only *Euphorbia* at my study sites, at localities throughout their geographical ranges, and at localities reported in the literature (Rozen, 1958; Shinn, 1967; Timberlake, 1956, 1964a, 1964b).

The sample sizes upon which the following analyses are based are shown in Table 16. It was not possible to include in this study bees foraging on *E. hyssopifolia* because of the very small number of bees that were seen on this plant.

The two plants on which foraging was extensively observed - *E. albomarginata* and *E. capitellata* - differ in their growth form and in the arrangement of their cyathia. On *E. albomarginata*, the cyathia are distributed more or less uniformly over the surface of a mat, and thus within a mat, there is no clumping of the bees' food sources. On *E. capitellata*, units of ten to twenty cyathia grow in dense heads (Fig. 6); several to many such heads are scattered over the erect, short branches of each plant. On *E. capitellata*, then, floral food occurs in dense clumps, and each clump (that is, head), has ten to twenty times as much food as do the separate cyathia of *E. albomarginata*. Bees feeding on *E. capitellata* can thus, with minimal body motion, obtain food from several cyathia, whereas bees feeding on *E. albo-*

marginata must fly, hop or walk when the food of one cyathium is exhausted. However, the distance that a bee must travel between heads on E. capitellata is much greater than the distance she must cover between cyathia on E. albomarginata. In this chapter, the term "flower visit" refers to the act of feeding from a unit of floral food: in the case of E. albomarginata, this is one cyathium, and in the case of E. capitellata, this is one head.

During a foraging sequence, a female bee intermingles two categories of behavior: she stops at flowers and collects food, and she moves between flowers. In moving between flowers, she can walk or hop between adjacent flowers, or she can fly. "Flights" are defined as occasions when the bee rises off the surface of the plant and remains airborne for at least 0.3 sec; during "hops", the bee remains at the level of the flowers, and the movement takes less than 0.3 sec. Because of the rapidity of the hops, it was not possible to measure their duration, and thus to subject them to analyses comparable to those of flower visits and flights. Consecutive flower visits are defined as those in which the movement between flowers is only by walking and hopping, as described above. The amount of time spent in each behavioral category and the arrangement and relative frequency of each category are reflections of the way in which each bee spends the time she has available for feeding. Therefore, intra- and inter-species comparisons can illuminate the variability of such patterns to be found among organisms using similar resources.

Flight Behavior

Three aspects of flight behavior can be distinguished for analysis: the frequency with which flight is begun, the length of time spent aloft once flight has commenced, and the sequence in which flights are interpolated between flower visits. These aspects will be considered in turn.

Flight Frequency

The proportion of flights that characterized each bee-plant combination was studied by tabulating for each observation the number of visited flowers and the number of flights. These numbers were summed within each bee-plant category, thereby giving a total number of movements and permitting the calculation of the proportion of each movement class. The proportion of flights - i.e., flight frequency - (flights/flights plus flower visits) is given in Table 16; it measures the tendency of the bees to initiate flight while foraging. The equality of the frequencies for each bee species on the two plants was tested by a one-tailed t-test for percentages (Sokal and Rohlf, 1966). Only two bees - *P. obscurella* ($P = 0.031$) and *H. nanulus* ($P = 0.004$) - respond differentially to the two plants by altering the number of flights relative to the number of flower visits. In both cases, the clumping of the food on *E. capitellata* is associated with a greater frequency of flights. The heads on this plant are rarely close enough to permit walking from one to another, whereas walking and hopping between cyathia on *E. albomarginata* is easy. Therefore, one would expect a higher frequency of flights in bees foraging on E. capitellata. The other three species, however, did not alter their tendency to fly when foraging on different plants. Differences among the bees were tested separately for each plant by means of the X^2 test for frequencies in Snedecor (1956). On each plant, two of the bee species differed significantly from the other four in flight frequency. The uniformity of the values for most of the species on both plants is noteworthy; the tendency to begin flight remains about the same regardless of size differences, behavioral variation, or taxonomic affiliation.

Sequence of Flights and Flower Visits

The flight frequency that characterizes each bee-plant combination does not necessarily determine how flights and flower visits are alternated during a foraging bout. If, after a flower visit, a bee "decides", on a random basis, whether to walk to an adjacent flower or to fly, the observed number of consecutive flower visits between flights will be set by the bee's inherent tendency to fly (i. e., flight frequency), and will approximate a geometric distribution (Warburton, pers. comm.), However, if she superimposes on the basic flight frequency a tendency to order her activities in a specific way, the distribution of numbers of consecutive flower visits between flights will depart from the predicted geometric distribution.

A comparison of the expected and observed distributions of this quantity for each bee-plant category is given in Fig. 16. Expected values were calculated for up to fifteen consecutive flower visit sequences; because long sequences were relatively rare, all categories above six consecutive visits were lumped in the graphs. Departure from the geometric distribution, and thus from the random alternation of flower visits and flights, was tested by a X^2 goodness-of-fit test. In all the bee-plant combinations except *P. obscurella* on *E. capitellata*, the observed pattern of consecutive flower visits departed from a random distribution with a probability of less than 0.005; in the latter case, the departure was significant at $\alpha = 0.05$. Thus, no species organizes its foraging behavior by randomly interspersing flights and flower visits; all species show a greater tendency than expected to alternate flights and visits to a single flower.

The bees vary, however, in their tendencies to forage on many flowers uninterruptedly; that is, with some bees, the observed numbers of fifteen and more consecutive flower visits were markedly greater than expected. On *E. albomarginata,* only *H. nanulus* and *P. minima* failed to show this kind of behavior, but on *E. capitellata*, only one species (*E.* sp. A) did forage in long unbroken sequences. The arrangement of flowers in a continuous flat layer in *E. albomarinata* evidently permits the bees to move from flower to flower without intervening flights, whereas the separated heads on *E. capitellata* make frequent flights more difficult to dispense with. The frequency of long foraging bouts by *E.* sp. A on *E. capitellata* can be accounted for by the peculiar semi-flying run (described in Chapter 5), which

3

enables the bee to pass between neighboring heads without change of pace.

H. nanulus stands out in these data as foraging in a fundamentally different pattern from the others. On E. albomarginata (Fig. 16), this species principally makes single stops, and distributes longer sequences of visits almost uniformly among the next larger categories. It very rarely initiates long uninterrupted sequences; the longest observed series was eight flowers. On E. capitellata, H. nanulus makes almost nothing but single head stops. This bee exhibits, then, a strikingly regular alternation of movements. The other bees distribute their flower visits in a form more closely resembling the shape of the geometric distribution, and differing from it principally in the predominance of a single flower stops.

In summary, several conclusions can be drawn from the data on consecutive flower visits. 1) The difference in growth form between the two plant species influences the organization of foraging behavior in some, but not all of the bee species. 2) Species-specific behavioral characteristics (e.g., the running gait of E. sp. A, the regularity of movement of H. nanulus) can overshadow the importance of the plant morphology in determining the pattern of foraging behavior. 3) The number of flowers visited in sequence does not appear to be a random variable, and, in fact, the universality of single flower stops among the bees in this study suggests that this behavior may be a general property of their foraging behavior.

The Average Duration of Flights

The average duration of flights is also listed in Table 16. The average time per flight calculated for each observation was ln-transformed; this operation permitted the use of parametric statistical tests in studying the sources of variation observed in the duration of flight. A Model I, two-way anova (analysis of variance), for unequal and disproportionate sample sizes (bee species and plant species as factors) was performed in order to assess the relative importance of 1) species-specific aspects of bee behavior, 2) modification of bees' behavior with respect to plant biology, and 3) idiosyncratic interaction between the bee species and the food plants in producing the observed variations. Since the computer program required all cells to be complete, I could not include the data for *P. minima* and *E.* sp. A, because these bees were each found foraging on only one of the two plant species. Results of the anova are given in Table 18 (together with the results of similar analyses of other characters discussed below). In order to ascertain which bee-plant combinations contributed to the significant effects of the factors in the anova, all possible comparisons among the twelve bee-plant combinations were made, on an *a priori* basis, by t-tests (also run by computer). Results of the t-tests are given in Fig. 17A. F values in this and subsequent anovas were accepted as significant if their values could be attributed to chance alone with a probability of less than 5%. The significance level for the multiple t-tests was set at $P < 0.02$, in order to reduce the chance of a Type I error among the large number of comparisons.

A comparison of flight frequency and flight duration (Table 16) reveals little relationship between the two variables. P. minima, and P. obscurella (on E. capitellata) fly more frequently than the other bee species, but they are not distinguished by extreme length or brevity of flight. Indeed, Fig. 17A demonstrates that on E. capitellata, P. obscurella does not differ significantly in flight duration from any other bee. Only in H. nanulus is the tendency to initiate flight coupled with a tendency to remain in flight; this species had both the highest flight frequencies and the longest flight times of all species on both plants.

The bee species factor significantly contributes to variation in flight duration. It is evident from Fig. 17A that the results of the statistical tests are principally attributable to the behavior of H. nanulus and P. minima. On E. albomarginata, these two species of bee differed from the others regardless of size, taxonomic affinity, or similarity of foraging movements (Chapter 5). Thus, except for these two species, flight duration is a relatively constant quantity.

Variation in flight duration attributable to the plants' growth forms was of marginal significance. In the anova, the plant species factor contributed significantly to variation at the 5% level. This result was associated with a difference in the mean duration of flights (in the two plants) by C. squamifera that was also significant at the 5% level, and thus not reported in Fig. 17A. I conclude from these results that the time spent on each flight is not usually altered by most bee species in response to variations in the food plants. In other words, once a bee has begun to fly, she tends to stay in the air for a period of time whose length is set by factors other than the distance between flowers.

Behavior on Flowers

Variability in the time that is spent by a bee on each flower can be related to the variation in the amount of food available from the flowers. Prior visitation by bees or other insects, the age of the flower, and time since anther dehiscence, and the presence of plant predators or other sources of plant injury or stress will all modify the amount of food available from each flower. (Chapters 3 and 7 describe the variation in the quantity of available pollen; Vansell (1940) has identified factors affecting nectar production in other species of *Euphorbia*.) Imposed on this variation in food level among the flowers of each plant species are the effects of the differences in size and arrangement of cyathia among related species. The size of the anthers and nectaries, and the number of anthers per cyathium, were reported in Tables 3 and 6, and the differences in growth form germane to this investigation were described at the beginning of this chapter. Since food (nectar and/or pollen) is collected continuously by a bee during a flower visit, variation in the quantity of time alloted by a bee to each flower reflects its flexibility in dealing with the range of food levels encountered.

Two aspects of the time spent per flower are discussed in this section. 1) Frequency histograms of the time spent on a flower by the individuals of each bee species are used to examine the responses of the bees to the variation encountered on each species of plant. 2) Comparisons of the mean length of time spent on a flower are used to detect: a. changes in behavior from one plant species to the other, and b. variation among the bees on each species of plant.

Frequency Histograms

The frequency histograms of time spent on a flower are shown in Fig. 18. The data from all individuals of a bee-plant category were pooled in constructing this figure, so the sample sizes in the figure are for the total number of flower visits. The flower visit times (measured with an accuracy of 0.1 sec; see Chapter 2) are grouped into classes of 0.3 sec.

Two patterns of response can be discerned from the data in Fig. 18, namely: 1) each species of bee has a characteristic range over which it varies the time expended on a flower, and 2) within this range, most, but not all, of the bee species modify the variability of this behavior in going from one plant species to another. These two facets of variation in the length of flower visits are readily illustrated by comparing the graphs for *N. helianthi*, and *D. perparvus*. On both plants, *N. helianthi* alters its behavior from flower to flower far less than does *D. perparvus*; nevertheless, in both species of bees, there is an increase in the dispersion of flower visit times on *E. capitellata*, as compared to *E. albomarginata*.

The spread of flower visit times that typifies each species of bee can be related to some of the qualitative aspects of foraging described in Chapter 5. Changes of body posture on the flowers, the rapidity of leg movements, the examination by the bee of each anther and nectary, all affect the time required to extract the food from the flowers. *P. obscurella*, *P. minima*, and *D. perparvus* all assume the vertical posture for pollen foraging, but collect nectar in the astride or angled positions, and they examine all the anthers of each flower before passing to another. The flexibility engendered by this behavior pattern is reflected in the extreme range of values observed for these bees; *P. minima* was seen to spend less than 0.5 sec on a flower, and also, on a few occasions, a minute on a single cyathium of *E. albomarginata*. Thus, these bees have the capacity to adjust the time spent per flower to the quantity (and perhaps quality) of the resources found there. On the other hand, *N. helianthi* brushes its forelegs over the anthers so rapidly that the movements appear like a blur; it only forages astride the flowers, and rarely inspects all the nectaries and open anthers at each stop. Its foraging behavior is thus fairly constant, regardless of the variations it encounters from flower to flower. The implication of these observations is that *N. helianthi* (and the other species that forage like it) does not collect all the available food from each flower, but that the species of *Perdita* (and others like them) probably do obtain most or all of the food at each flower visit.

Mean Duration of Flower Visits

The average value of time spent on each flower was calculated for each observation of a foraging bee, and the means in each bee-plant category (after transformation to their natural logarithms) were contrasted with each other in a two-way anova and in multiple t-tests (as described above for flight duration). The results of the analyses are given in Tables 17 and 18, and Fig. 17B.

Four of the five species that foraged on both plants lengthen the time spent per flower on *E. capitellata* over that on *E. albomarginata* (Fig. 17B, lower left-hand quadrant). This increase is undoubtedly related to the greater amount of food present on a head of *E. capitellata* than on the single cyathium of *E. albomarginata*. This result is similar to that obtained in the study of the distribution of flower times. Thus, most, but not all of the bee species, can modify both the range and average value of the amount of time spent on a flower on different species of plant.

The behavioral plasticity in time spent per flower occurs within the context of significant differences among the species. Some bees (for example, *P. obscurella*) stay for a relatively long time on each flower, just as others (for example, *N. helianthi* and *C. squamifera*) barely stay at all. The pervasiveness of inter-species differences are apparent in Fig. 17B (upper left and lower right quandrants).

The results of the foregoing analyses of the behavior in flight and on flowers can be summarized as follows:

1. Each bee species, except _C_. _squamifera_, modifies both the range and average amount of time devoted to gathering food from a flower as it goes between different species of plants.

2. None of the species of bees alter the duration of flights between flowers on the two plants.

3. However, some species, but not all, modify the frequency with which they undertake flight, and rearrange the sequence of flower visits and flights when foraging on different species of plants.

4. The time spent on a flower is a much more sensitive indicator of interspecific differences in foraging behavior than is time spent per flight or the frequency of flights.

5. The only characteristic of foraging behavior that appears uniformly in all bees is the tendency to alternate flights with visits to single flowers. Otherwise, no two species of bee forage in the same way on either species of plant.

Foraging Performance

The various aspects of foraging pattern discussed so far interact with each other in determining two measures of overall foraging performance, namely, the percentage of the total observation time of each individual that is spent on flowers, and the extrapolated foraging rate in number of flowers per minute. Both measures are affected by the time spent per flower, the time spent per flight, and the distributions of these events discussed above; the measures also reflect the tendency of the bees to interact with each other, and to alight on leaves, rocks, etc. as described in Chapter 5. Both measures were studied as were the time per flower and the time per flight; that is, two-way anovas on the ln-transformed values for each observed bee were used to identify the significant sources of variation (Tables 17 and 18), and multiple t-tests pinpointed the bee-plant combinations responsible for the variation (Figs. 17C and D).

Percentage of Time Spent Foraging

This quantity, calculated for each observation as "100 (time spent on each flower/total length of observation time (sec))," is a measure of the efficiency with which each bee uses its foraging time. Since it was not possible to measure caloric (or other nutrient) intakes and expenditures, it was not possible to study variations in energetic efficiency. However, these bees need time to construct nests and cells, prepare the provisions, prevent the entry of parasites and predators, mate, and travel from the nest to the food plants, and so the efficient use of the time devoted to foraging must be at least as important as the efficient use of calories.

It might be expected that the influence of plant biology would outweigh differences among the bee species in the percentage of time spent on flowers, and that there would be less interspecific divergence in this character. These expectations are based on the following reasons: 1) It is generally assumed that natural selection maximizes the food intake per unit time in the interests of efficiency (Cody, 1974; Emlen, 1966; Pulliam, 1974). 2) Because there is more food to be gained on a head of *E. capitellata* than on a cyathium of *E. albomarginata*, one would expect the proportion of time spent on flowers of *E. capitellata* to be greater than on *E. albomarginata* (less flight should be necessary to gather an equivalent amount of food per unit time). 3) Inasmuch as food is being acquired while the bee is on a flower, the proportion of time spent on flowers could be expected to be maximized by all bee species, resulting in few significant differences among them. This approach to the analysis of optimal behavior - a search for similarity or convergence among organisms that are allegedly using some resource in an optimal fashion - is analogous to that proposed by Cody (1974).

The results reported in Tables 17 and 18 and Fig. 17C do not conform to these expectations. No species alters the proportion of its total foraging time that is devoted to food acquisition, when foraging on different plant species (Fig. 17C, lower left-hand quadrant; Table 18, plant species factor in the anova). In other words, no bee "takes advantage" of the clumping of food on the heads of *E. capitellata* to increase the proportion of its foraging time that results in food acquisition. Rather, each bee species devotes a characteristic proportion of its foraging time to being on flowers, regardless of plant. This behavioral constancy is particularly well marked in

_P_. _obscurella_ and _H_. _nanulus_. Thus, the bees show patterns of response diametrically opposed to those expected on the assumption that food intake per unit time is maximized by natural selection.

A more direct comparison of the relative amounts of time spent travelling between flowers and obtaining food from flowers can be made by calculating the ratio "% of time spent foraging/% of time spent travelling." The percentage of time spent travelling is 100 - % foraging time; it includes the time spent flying, hopping and walking, time spent sitting on rocks, etc. and grooming, and time spent interacting with other individuals. The ratios are tabulated in Table 17. The ratio is comparable to the "pursuit/search" ratio used by ecologists studying the foraging ecology of animals with varied diets (MacArthur and Pianka, 1966; Schoener, 1971). While it is clear that all bees spend a greater proportion of their time extracting food from flowers than searching for flowers to visit, it is equally clear that the magnitude of the ratio varies greatly among the species. The species with the highest ratio - _D_. _perparvus_ - is a polylege, and, the one with the lowest ratio - _H_. _nanulus_ - is an oligolege of _Euphorbia_. By this criterion, then, the polylectic bee is more efficient in using its foraging time on _Euphorbia_ than is a bee that has evolved a strict dependence on these plants. This finding is certainly contrary to the general assumption that a "jack-of-all-trades is master of none." The other polylege, _E_. sp. A, is one of the least efficient species. Thus, there seems to be no correlation between food plant specificity and the relative efficiency with which bees organize the elements of their foraging time. (It may well be, of course, that the oligoleges can metabolize *Euphorbia* pollen much more efficiently than the polyleges, and thus use their resources more completely; efficiency of this kind, however, would not be expected to promote inefficient foraging patterns. It is also possible that the oligoleges obtain more food from each flower per unit effort or time than do the polyleges. However, *D. perparvus* collects food from every anther and nectary on each cyathium, whereas *H. nanulus, N. helianthi* and *C. squamifera* do not, and so this possibility is also unlikely.) Furthermore, closely related species (e.g., *P. obscurella* and *P. minima*) are more similar to each other than are unrelated species, and even among the oligolectic species in the Andrenidae, there is no uniformity in the value of the ratio. Thus, the evidence does not support the hypothesis that selection for optimal foraging behavior has favored similarity or convergence among bees dependent upon the same resource.

Foraging Rate

The foraging rate varies with both plant species and bee species, and is affected by the particular response of each bee species to the two plants (interaction effect, Table 18). The data in Tables 17 and 18 and in Fig. 17D demonstrated that all bees responded to the plant differences by having greater rates of foraging on *E. albomarginata* than on *E. capitellata*. However, the foraging rates of the bees vary greatly on each plant species; on *E. albomarginata, N. helianthi* forages more than twice as rapidly as *H. nanulus*, and on *E. capitellata*, *E.* sp. A forages almost four times as fast as *P. obscurella*.

The foraging rate is inversely correlated with the average time spent per flower ($\tau = 0.82$; $P < 0.001$; Kendall coefficient of rank correlation), but is uncorrelated with flight duration, flight frequency, or the percentage of time spent on flowers (Kendall coefficients of rank correlation nonsignificant). That is, the shorter the flower visit, the more flowers can be visited per unit time, regardless of the duration or frequency of flying. Foraging rate, then, reflects the same influences as does mean duration of flower visit, and, in particular, is sensitive to qualitative differences in foraging behavior. The behavioral traits previously related to variation in the time spent per flower (body postures, rapidity of leg movements, investigation of all food sources on a cyathium) thus also affect the foraging rate. For example, the rapid brushing movements of *N. helianthi* accompany the highest observed foraging rate; the vertical posture, meticulous examination of anthers, and lengthy scopal packing behavior of *P. obscurella* are associated with the lowest foraging rate.

Movements Between Plants

In moving from flower to flower, a bee eventually moves from one plant to another. Variation among the bee species in the amount of movement between plants not only measures their relative abilities to cross-pollinate the plants, but also reflects species-specific patterns of motion. Because of the difficulty of following bees between the well-separated mats of *E. albomarginata*, no quantitative data on the proportion of movements between plants could be obtained for this plant. The small *E. capitellata* plants growing in dense stands permitted ready identification of moves within and between plants.

The average percentage of moves within a plant for each bee species is presented in Table 19. For this analysis, a "move" was considered to be any motion (walk, hop or flight) that caused a bee to go from one flower to another; total moves thus equals the total number of flowers visited minus one. As with the preceeding variables, the percentage of moves in which a bee went to a flower on the same plant as the preceeding flower (i.e., within plant moves) was calculated for each observation, and a one-way Model I anova performed on the arcsine-transformed data. The observed value of F (4.779) was greater than that expected by chance alone ($P < 0.001$) and thus individuals of each bee species move from plant to plant with significantly different frequencies. Differences among species were determined by a Student-Newman-Keuls test; this analysis demonstrated three groups of nonsignificantly different species (Table 19). Species that do not co-occur in any of the groups can be considered to differ in their frequency of moves within plants. By this criterion it can be seen that *P. obscurella* has a significantly greater tendency to forage on a single plant than does *C. squamifera* of *E.* sp. A and *H. nanulus* also visits flowers on a given plant more often than does *E.* sp. A.

These data again demonstrate the strong influence of species-specific behavior on foraging patterns. The relatively high proportion of movements between plants seen in *E.* sp. A is probably related to its proclivity for flying in a straight line, rather than circling about a small area (Chapter 5). The size of the area covered per unit time by a bee (Chapter 5) is not closely related to its ability to visit many plants during that time; *H. nanulus*, which covers the greatest area of any of the panurgine bees, does less moving between plants than any other bee except *P. obscurella*. Flights that are long in duration do not necessarily cover large distances. The species with the largest percentage of time spent on flowers (*D. perparvus*) did not have the lowest frequency of between-plant moves. This situation evidently results from a high proportion of long-distance flights. *P. obscurella*, on the other hand, tends to both stay on heads for a long time, and move short distances between adjacent heads. Its movement between plants is largely a result of the close juxtaposition of separate plants in the dense patches of *E. capitellata*.

Interspecific Comparisons

The information presented in the foregoing section has been summarized in Table 20. In this table, every species is compared with the others by means of the percentage similarity of each pair. Percentage similarity was computed as the number of behavioral traits for which the pair did not differ, divided by the total number of traits considered. In cases in which both species of a pair foraged on both species of plants, they were compared with each other twice for each trait (once for each plant). Since only bees foraging on the same plant were compared, *P. minima* and *E.* sp. A were not compared with each other. The results are more clearly illustrated in Fig. 19, in which the species have been placed in groups of similarities greater than the average value for all species pairs.

The species do not segregate into groups corresponding to their taxonomic affinities. The two congeners (*P. minima* and *P. obscurella*) are more different from each other than some species pairs representing different families (e.g., *P. obscurella* and *D. perparvus*), and *H. nanulus* forages in a pattern unlike either most other panurgine bees or members of unrelated families. Nor do the species segregate according to size; *D. perparvus* closely resembles one of the small bees (*P. obscurella*), but not the other (*P. minima*). This result is strikingly different from that obtained in the analysis of the qualitative aspects of foraging behavior (Chapter 5). In that analysis (see Fig. 15), the species grouping obtained on the basis of qualitative characteristics of foraging behavior closely followed the conventional taxonomic relationships of the species.

Thus, this investigation shows that temporal aspects of foraging behavior - the amount of time devoted to the main events of foraging, and the sequence in which those events occur - form in each bee species a unique complex of traits. No two species of bees forage in the same way on a given species of plant, and species pairs that tend to have similar patterns of behavior need not be closely related. The diversity of foraging "styles" that evidently have coexisted for a long time makes dubious the proposition that there is an "optimal" way of gathering Euphorbia pollen and nectar towards which the species of bees have converged.

Summary

The comparative analysis of foraging behavior begun in Chapter 5 has been extended to the analysis of the timing and sequence of the two main categories of foraging - visits to flowers and movements between flowers. In this investigation, the behavior of each bee was studied on each of two species of Euphorbia; this approach facilitated an estimation of the capacity of the bees to modify their behavior in response to differences in the distribution of flowers on the plants. The analysis yielded the following results: 1) variation among the bee species in the timing and sequence of foraging events is as extensive as it was in the qualitative traits; 2) the behavior of each species of bee on the flowers is changed when it feeds on plants with differing growth forms; 3) flight behavior is relatively insensitive to changes in the distribution of flowers; 4) although all the bees spend a greater proportion of their time feeding on flowers than moving between flowers, the wide variation in the ratio of these two behaviors implies that there has been no convergence toward one "optimal" use of foraging time; and, 5) the pattern of variation among the species of bees does not correspond to their taxonomic affiliations.

TABLE 15. Scopal load contents of seven species of bees foraging on *Euphorbia* plants. 500 grains counted per scopal load.

Species	Total N	No. Specimens with no *Euphorbia* pollen	Mean % *Euphorbia* pollen, remainder of specimens
P. minima	10	0	99.1
P. obscurella	13	1	99.0
H. nanulus	12	0	99.3
N. helianthi	19	4	99.6
C. squamifera	8	0	99.0
D. perparvus	10	0	99.5
E. consobrina	18	1	85.6

TABLE 16. Flight characteristics of bees foraging on *Euphorbia*. Asterisk denotes differences significant at P 0.05 in flight frequency.

Bee Species	Number of Observations	Mean Flight Duration (sec)	Total No. Movements Counted	Flight Frequency	Differences Among Bees
		Behavior on E. albomarginata			
P. minima	63	1.28	2488	0.33	*
P. obscurella	49	0.94	1292	0.28	
H. nanulus	15	2.00	574	0.36	*
N. helianthi	51	0.95	2883	0.26	
C. squamifera	37	1.20	1337	0.25	
D. perparvus	22	0.98	672	0.27	
		Behavior on E. capitellata			
P. obscurella	12	1.36	95	0.38	*
H. nanulus	63	1.86	1802	0.44	*
N. helianthi	6	1.19	319	0.30	
C. squamifera	12	1.65	268	0.25	

TABLE 16. Continued.

Bee Species	Number of Observations	Mean Flight Duration (sec)	Total No. Movements Counted	Flight Frequency	Differences Among Bees
D. perparvus	19	1.14	271	0.27	
E. sp. A	58	1.57	3029	0.28	

TABLE 17. Temporal aspects of foraging behavior of bees visiting two species of *Euphorbia*. 95% confidence interval for each mean is given in parentheses. A = *E. albomarginata*; C = *E. capitellata*.

Bee species	Plant	Mean Time per Flower (sec)	Mean % Foraging Time	Mean Foraging Rate (fls/min)	"Pursuit/Search" Ratio
P. minima	A	2.66	76.2	17.3	3.39
		(2.35-3.01)	(72.9-79.6)	(15.6-19.2)	
P. obscurella	A	2.31	79.0	21.0	4.13
		(2.08-2.57)	(74.4-83.9)	(18.9-27.5)	
	C	6.45	81.1	7.5	4.58
		(2.59-6.88)	(72.7-90.2)	(5.01-11.3)	
H. nanulus	A	1.73	57.7	20.2	1.41
		(1.50-2.98)	(51.1-65.2)	(16.5-25.0)	
	C	2.51	57.1	14.1	1.51
		(2.21-2.85)	(52.3-62.5)	(12.6-15.8)	
N. helianthi	A	0.95	70.9	44.7	2.57
		(0.89-1.02)	(67.5-74.7)	(41.1-48.5)	

TABLE 17. Continued.

Bee Species	Plant	Mean Time per Flower (sec)	Mean % Foraging Time	Mean Foraging Rate (fls/min)	"Pursuit/Search" Ratio
N. helianthi	C	1.74	73.6	25.8	2.87
		(1.53-1.98)	(64.8-83.7)	(22.8-29.1)	
C. squamifera	A	1.40	73.6	31.7	2.97
		(1.31-1.51)	(69.0-78.4)	(28.7-35.0)	
	C	1.56	59.5	23.0	1.77
		(1.21-2.01)	(44.8-78.8)	(26.5-32.9)	
D. perparvus	A	1.91	85.6	26.9	6.01
		(1.68-2.19)	(64.8-113.)	(23.6-30.7)	
	C	4.20	82.3	11.3	5.16
		(3.21-5.56)	(74.6-90.8)	(8.97-14.1)	
E. consobrina	C	1.40	63.5	27.1	1.91
		(1.28-1.53)	(55.0-68.3)	(23.9-30.6)	

TABLE 18. Results of two-way anovas of four aspects of foraging behavior of bees. Mean squares are those of the ln-transformed data.

Source of Variation	df	Mean Square	F	Significance
		Mean time spent per flower		
bee species	4	7.2185	45.1566	$P < 0.001$
plant species	1	14.9280	93.3864	$P < 0.001$
interaction	4	1.1554	7.2279	$P < 0.001$
error	276	0.1599		
		Mean flight duration		
bee species	4	2.3172	7.2317	$P < 0.001$
plant species	1	1.8303	5.7121	$P < 0.05$
interaction	4	0.2517	0.7854	NS
error	276	0.3204		
		Mean % foraging time		
bee species	4	79.525	13.0443	$P < 0.001$
plant species	1	6.8204	1.1187	NS
interaction	4	8.8607	1.4534	NS
error	276	6.0965		
		Foraging rate, flowers per min		
bee species	4	5.4415	35.7409	$P < 0.001$
plant species	1	16.833	110.5624	$P < 0.001$
interaction	4	0.8257	5.4236	$P < 0.001$
error	276	0.1522		

TABLE 19. Percentage of movements within plants of bees foraging on *E. capitellata*.

Bee species	N	% movements within plants	95% Confidence Interval	Nonsignificantly Different Groups
P. obscurella	12	96.0	85.5 - 99.9	
H. nanulus	63	83.3	76.6 - 89.1	
D. perparvus	19	79.4	68.1 - 88.8	
N. helianthi	6	76.5	58.5 - 90.8	
C. squamifera	11	67.3	40.1 - 89.4	
E. sp. A	58	66.8	59.5 - 73.9	

TABLE 20. Percentage similarity of all pairs of species in the temporal aspects of their foraging behavior. Species abbreviations as in Fig. 17.

	Hn	Dp	Po	Nh	Cs	Pm	Ea
H. nanulus	--						
D. perparvus	23.1	--			$\overline{X}$ = 44.2		
P. obscurella	38.5	84.6	--				
N. helianthi	23.1	53.8	53.8	--			
C. squamifera	30.8	61.5	53.8	76.9	--		
P. minima	50.0	0.0	30.0	16.7	30.0	--	
_E._ sp. A	28.6	42.8	14.3	85.7	85.7	--	--

Figure Captions

Chapter 6

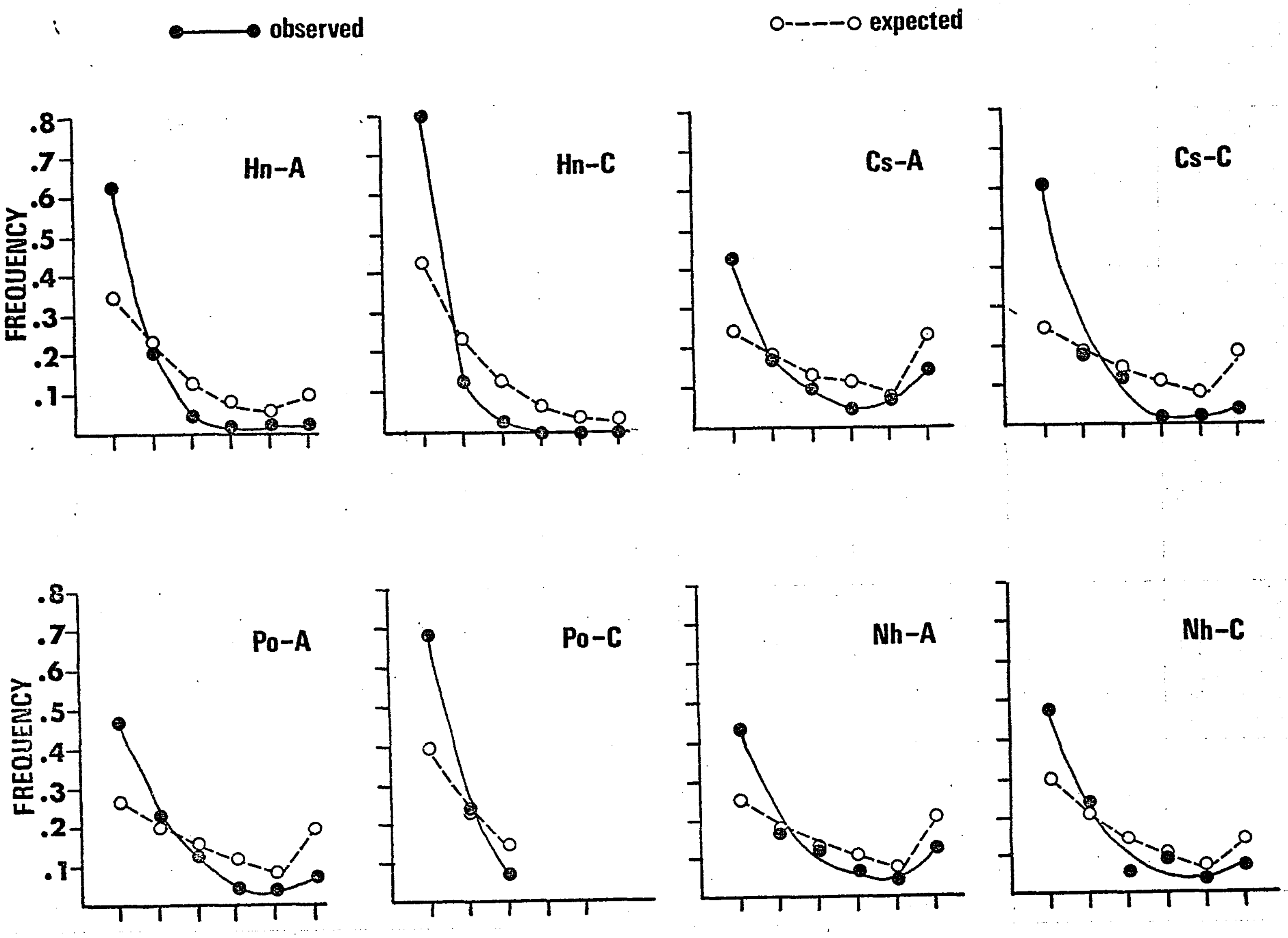
Fig. 16 Frequency distributions of the number of consecutive flower visits between flights for each combination of bee species and plant species. Expected values derived from geometric distribution based on flight frequencies in Table 16. A = *E. albomarginata*; C = *E. capitellata*; Cs = *C. squamifera*; Dp = *D. perparvus*; Ea = *E.* sp. A; Hn = *H. nanulus*; Nh = *N. helianthi*; Pm = *P. minima*; Po = *P. obscurella*.

Fig. 17 Results of multiple t-tests for four aspects of foraging behavior, comparing pairs of bee-plant combinations. A darkened square indicates the pair differed significantly at P 0.02. Abbreviations as in Fig. 16.

Fig. 18 Frequency histograms of the time spent on each flower for each bee-plant combination. Sample size is the number of observed flower visits summed over all individuals. Abbreviations as in Fig. 16.

Fig. 19 Species relationships of greater than average percentage similarity: temporal aspects of foraging behavior. Data from Table 20. Abbreviations as in Fig. 16.

FIGURE 16


observed
expected
FREQUENCY
.8
.7
.6
.5
.4
.3
.2
.1
Hn-A
Hn-C
Cs-A
Cs-C
Po-A
Po-C
Nh-A
Nh-C

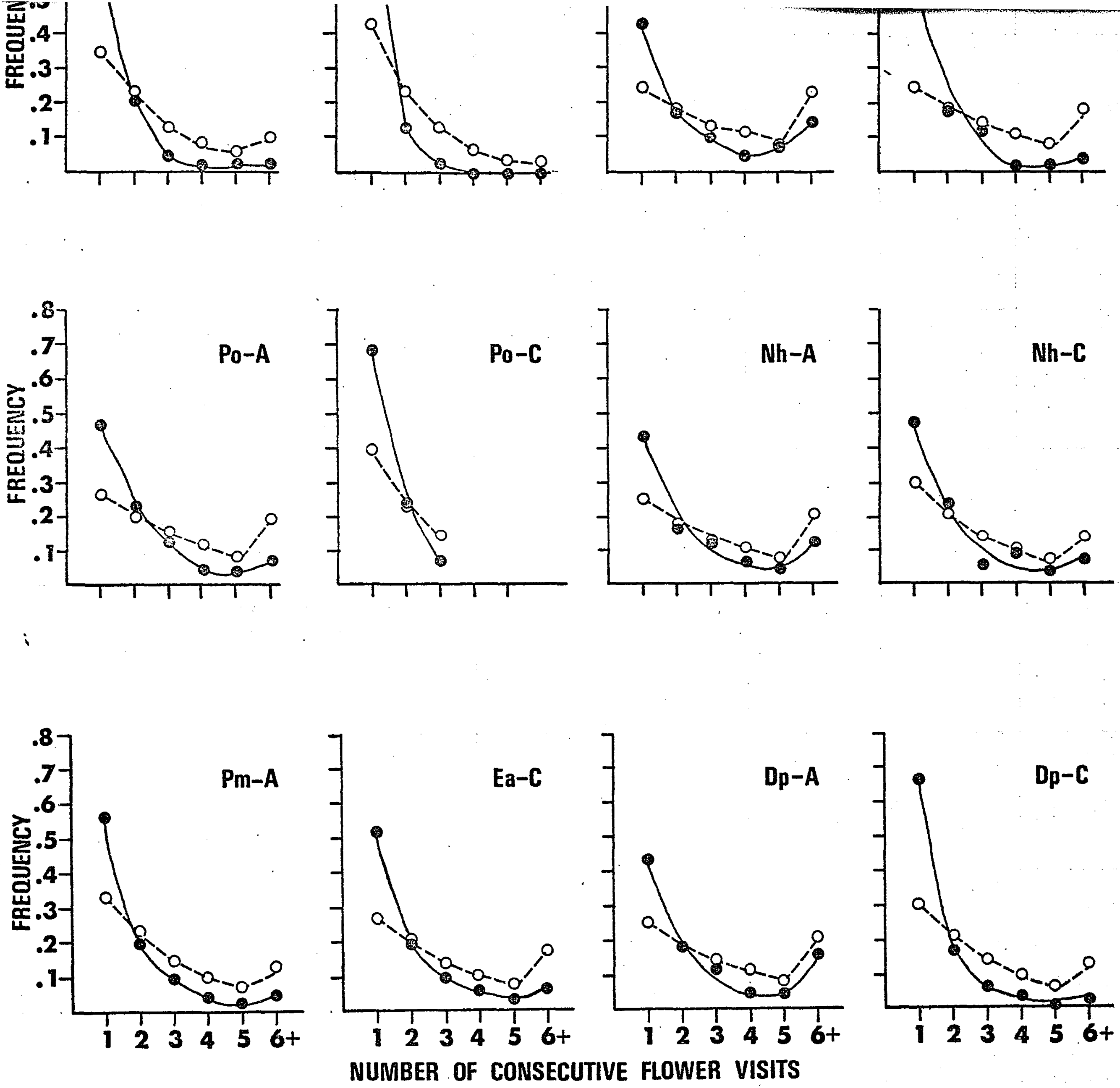
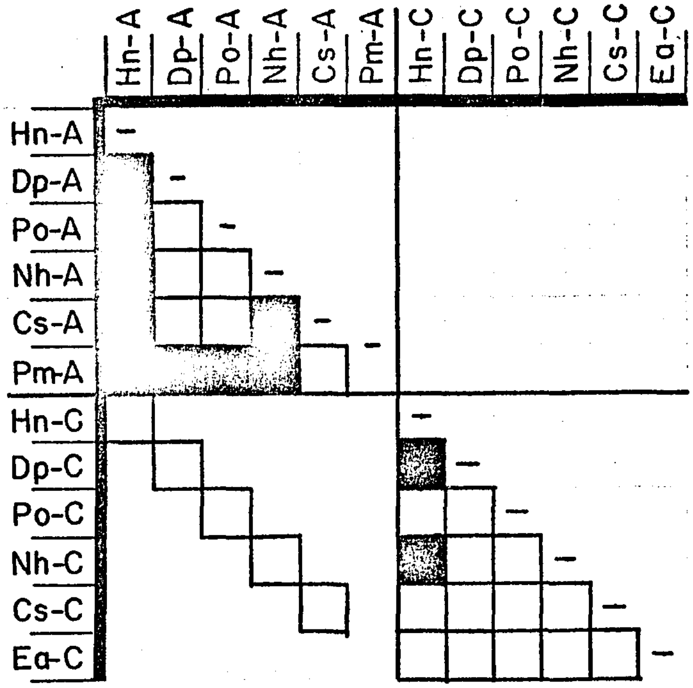
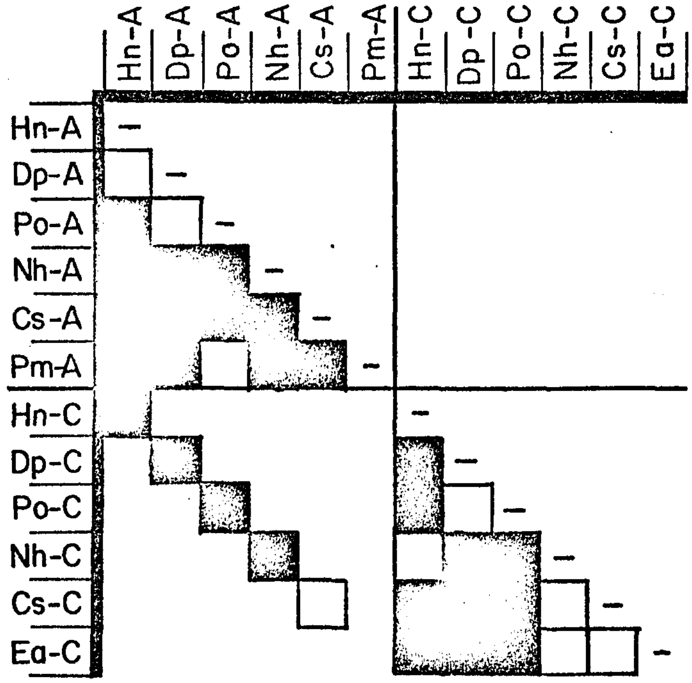

FREQUENCY
.8
.7
.6
.5
.4
.3
.2
.1
Po-A
Po-C
Nh-A
Nh-C
Pm-A
Ea-C
Dp-A
Dp-C
1 2 3 4 5 6+
NUMBER OF CONSECUTIVE FLOWER VISITS

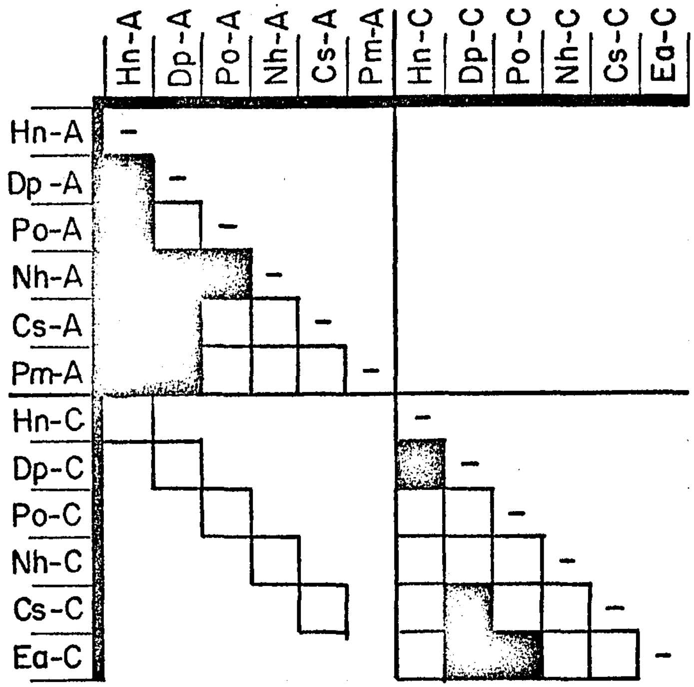
FIGURE 17



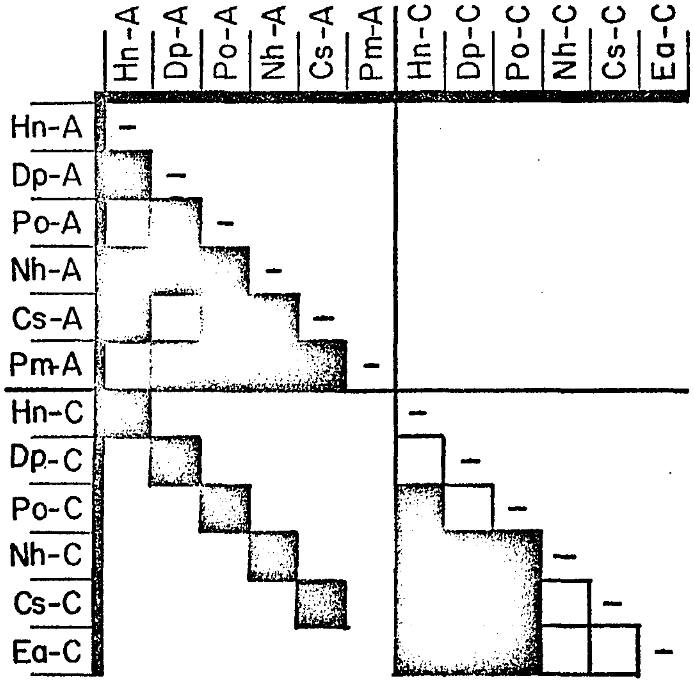
(A) FLIGHT TIME



(B) FLOWER VISIT TIME

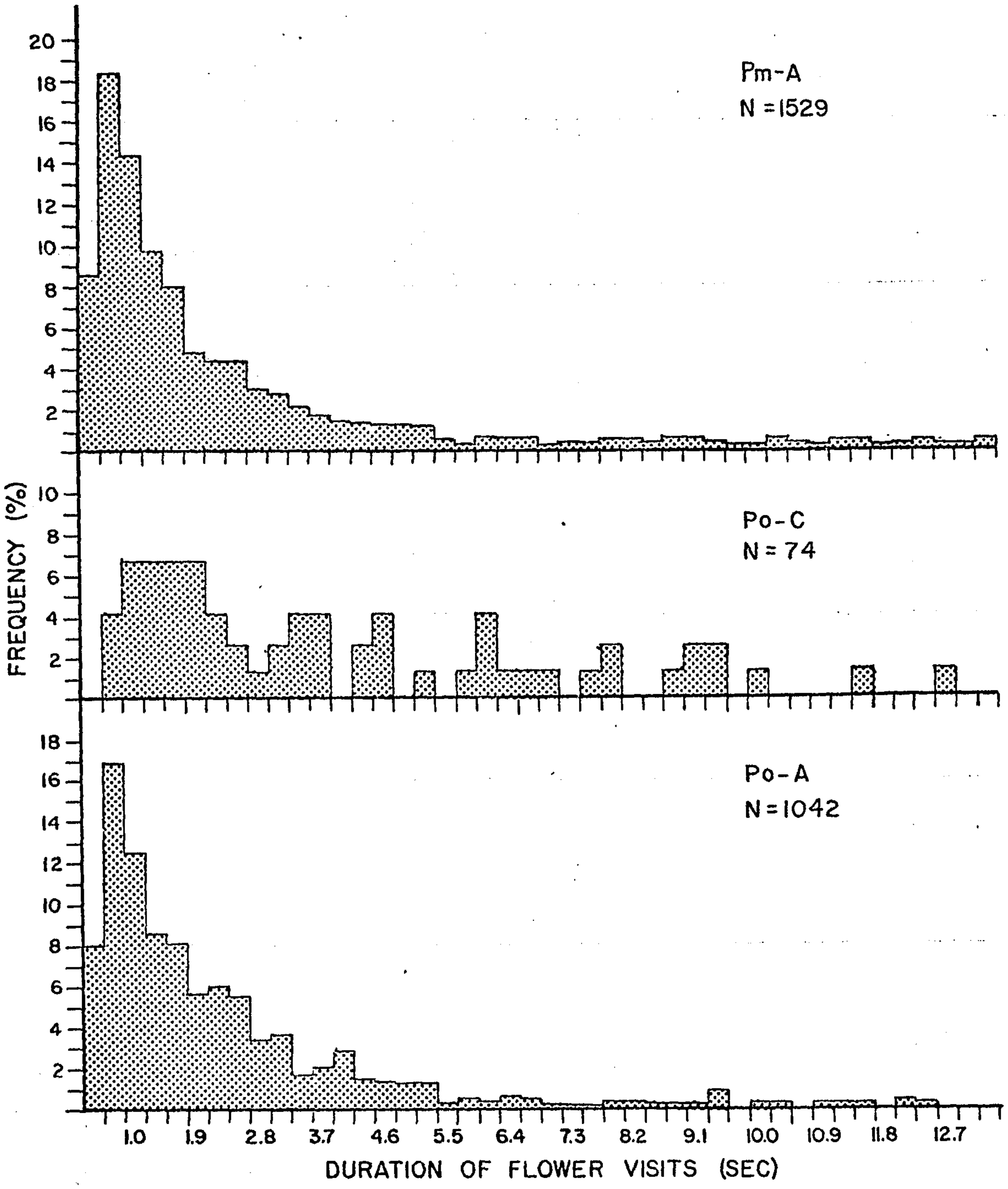


(C) % TIME ON FLOWERS

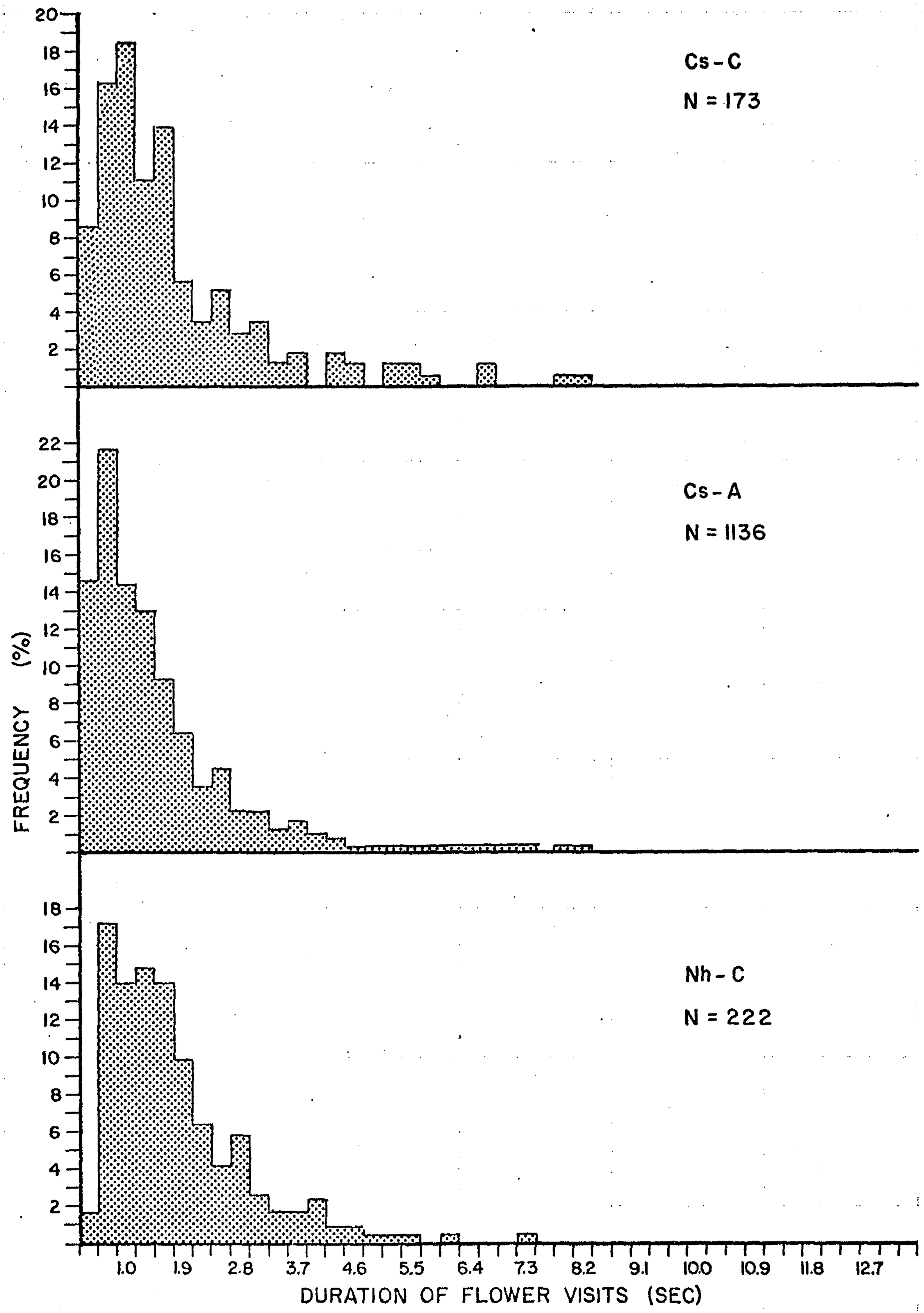


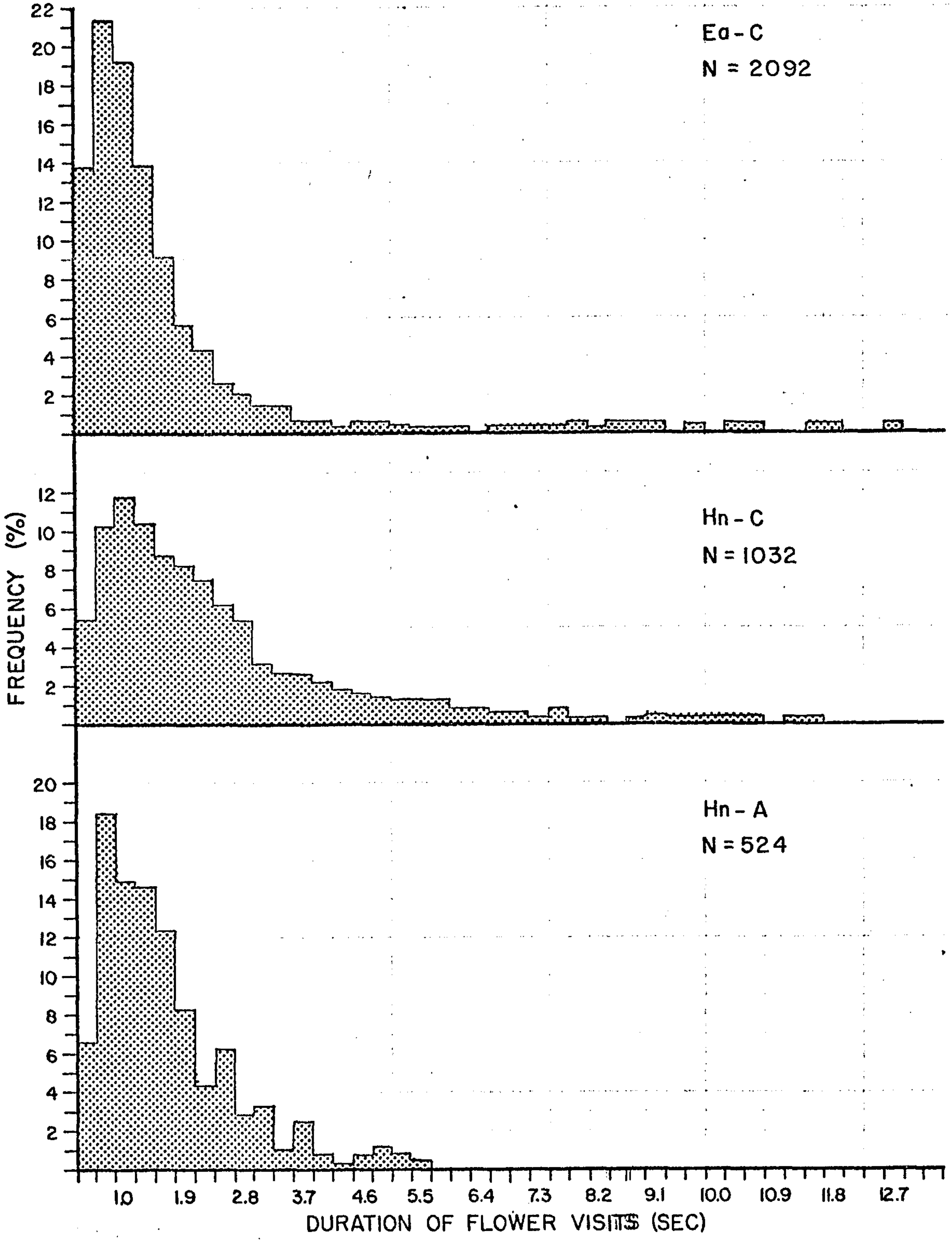
(D) FORAGING RATE (FLS/MIN)

FIGURE 18



Pm-A
N = 1529
Po-C
N = 74
Po-A
N = 1042
FREQUENCY (%)
20
18
16
14
12
10
8
6
4
2
1.0
1.9
2.8
3.7
4.6
5.5
6.4
7.3
8.2
9.1
10.0
10.9
11.8
12.7
DURATION OF FLOWER VISITS (SEC)


Cs - C
N = 173
Cs - A
N = 1136
Nh - C
N = 222
FREQUENCY (%)
20
18
16
14
12
10
8
6
4
2
22
20
18
16
14
12
10
8
6
4
2
18
16
14
12
10
8
6
4
2
1.0
1.9
2.8
3.7
4.6
5.5
6.4
7.3
8.2
9.1
10.0
10.9
11.8
12.7
DURATION OF FLOWER VISITS (SEC)


Ea - C
N = 2092
Hn - C
N = 1032
Hn - A
N = 524
FREQUENCY (%)
22
20
18
16
14
12
10
8
6
4
2
12
10
8
6
4
2
20
18
16
14
12
10
8
6
4
2
1.0
1.9
2.8
3.7
4.6
5.5
6.4
7.3
8.2
9.1
10.0
10.9
11.8
12.7
DURATION OF FLOWER VISITS (SEC)

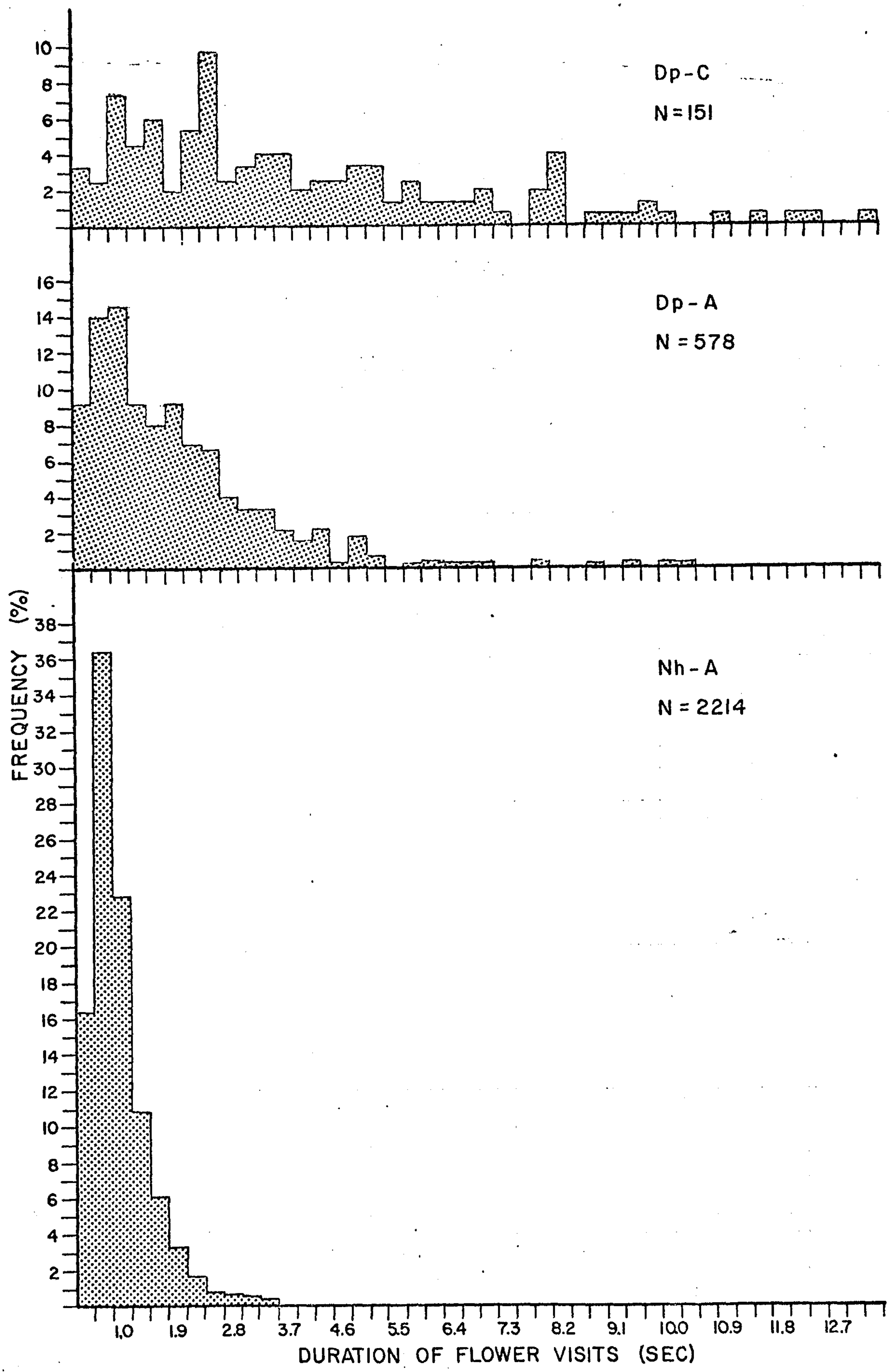
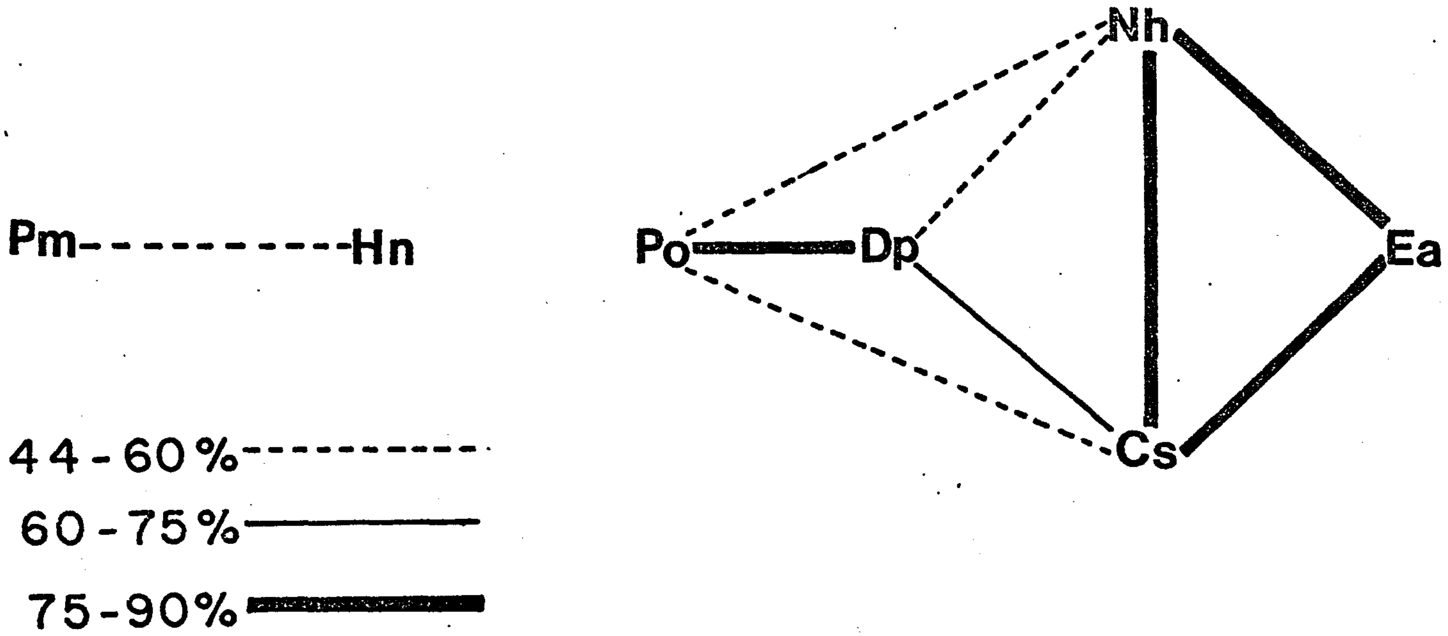

Dp-C
N=151
Dp-A
N = 578
Nh-A
N = 2214
FREQUENCY (%)
10
8
6
4
2
16
14
12
38
36
34
32
30
28
26
24
22
20
18
1.0
1.9
2.8
3.7
4.6
5.5
6.4
7.3
8.2
9.1
10.0
10.9
11.8
12.7
DURATION OF FLOWER VISITS (SEC)

FIGURE 19


Pm
Hn
Po
Dp
Nh
Cs
Ea
44-60%
60-75%
75-90%

CHAPTER 7

BEE POPULATIONS IN RELATION TO THEIR FOOD

The twin problems of the role of food as a limiting resource for bees and the presence of competition for food among co-occuring bee species have been examined by a number of investigators using a variety of approaches (see discussion below). In this chapter, I examine these problems in the Euphorbia - bee association: 1) by studying the daily activity of each bee species, in order to assess the possibility of temporal separation among the bee species, and 2) by quantifying the relationship between bee population density and available food density at four sites.

Diurnal Cycle of Bee Activity

Fig. 20 illustrates the activity of each bee species during the course of the day. The results of this study indicate that minimal resource partitioning is possible by means of temporal separation. Considering the length of time during which pollen is extruded (Chapter 3), temporal separation might be possible if one species foraged in mid-morning, and another in early afternoon. However, no such pattern is apparent at any of the localities. No foraging bees were seen at any site before 9:00 A.M.; bees started appearing with increasing frequency from 9:15 to 9:30, and were moderately abundant by 10:00. Most of the bee species have a peak abundance between approximately 10:30 A.M. and 1 P.M. Differences of one hour between peak abundances are ecologically trivial because the depleted anthers will not have replenished the extruded pollen in that time. There are two partial exceptions to the general pattern. At 12NR, D. perparvus reaches its peak abundance at about 10:30 A.M., as the other species become more abundant. It is possible that D. perparvus can avoid competition by foraging before the other species begin to fly; it is also possible that its greater efficiency (as measured by the % of foraging time spent on flowers: see Chapter 6) compensates for the smaller amount of food available between 9 A.M. and 10 A.M. (see below). E. sp. A begins foraging earlier than H. nanulus at both 9WSWA and 18WSA. However, it maintains high densities throughout the morning, and both species cease foraging at about the same time. Considering the low efficiency of this species and the low food density, this slight difference in foraging time probably gives E. sp. A only a small proportion of its total daily pollen in the absence of competitors.

The reduction in density observed at 9WSWA between 11:00 A.M. and 12:00 M. (Fig. 20) is paradoxical. The number of samples taken during this interval (7) was comparable to the sample sizes of the neighboring time intervals, and so the observation probably is real, and not an artifact of a small sample size. High densities of bees were observed during the preceeding 10:50 - 11:00 sample and the subsequent 12:00 - 12:10 sample, and moderate numbers of bees were present during the 11:15 - 11:25 sample. Very few bees, however, were seen during the rest of the hour period. These observations make unlikely the possibility that the bees are responding to changes in the polarization of light at midday (Chabora, pers. comm.). The significance, if any, of the dip in the graphs is thus obscure.

Bee Density in Relation to Food Density

Tables 21, 22, 23 and 24 present the data used in the second part of this study; namely, the relationship of bee density to food density. From these figures the ratio "number of foraging female bees per 10 minutes per 1/8 m^2/number of open, full anthers per m^2" was obtained for each site-time category as described in Chapter 2. Fig. 21 shows the data of Table 24 in graphical form. The weakest link in the chain of figures leading to the ratio of bees to food is the bee density estimates. As can be seen from the reported standard errors, the variability in the observations at a given locality and time was large; it can be attributed in part to sampling error, in part to inherent variability in the appearance of bees from day to day, and in part to variability in the density of the bees at different points within the plant population. Since sampling for each locality-time category was accomplished over several days and on randomly selected quadrats, the latter two factors were important. The large amount of sampling necessary for this study and the short duration of the bees' flight season (August and September) made the temporal constraints on the number of samples per locality-time category severe and unavoidable.

The final ratio of bees/food produces only one observation per locality-time category, and thus these figures are difficult to analyze statistically by the techniques of analysis of variance. Therefore, the data were analyzed qualitatively (Figs. 21 and 22) and by nonparametric methods.

Two hypotheses were examined with these data. First, if bees are competing for limited food resources, one would expect the daily allotment of food produced by the plants to be completely utilized, and so the ratio of bees/food should remain approximately constant during the day. Secondly, if the sizes of the bee populations are determined by the amount of food available, the ratio of the two should be the same from site to site; larger bee populations should be associated with larger plant population.

Several results concerning the first hypothesis are apparent from the data in Tables 21, 23 and 24, and Figure 21. The diurnal changes in both bee and food density are very similar - a rapid rise between 9 and 10 A.M., little change in either bees or food until early afternoon, and a rapid fall to low levels by 3 P.M. However, because of the very large number of flowers per unit area (Table 22), even very low numbers of anthers per flower result in appreciable amounts of food per square meter (Table 23). The result, as can be seen in Fig. 21, is a sharp decrease in the ratio by 3 to 4 P.M. The equivalently small amounts of food available at 9 A.M. (at 1EA and 9WSWA) supported relatively large bee populations, and in fact the early morning samples gave the highest relative number of bees per unit food of all observations. Thus, Fig. 21 shows that the diurnal changes in the ratio do not mirror the time-course of food availability (Table 23), and although the absolute number of foraging bees increases during the morning, the number relative to available food declines.

The only site at which the ratio of bees to available food was constant throughout the day was 12NR. This site supported a constant low level of bees during the peak foraging times (Table 21 and Fig. 20), and, as seen above, the two common species (*D. perparvus* and *N. helianthi*) differed in the time of their peak activity. Although the ratio at 3 P.M. does decrease slightly, the results at this site conform more closely to the expected set of numbers than those from any other site.

The second hypothesis is studied in Fig. 22. In this figure, the bee density has been plotted as a function of food density irrespective of time of day. The points show a general positive relationship, which was further tested by calculation of a Spearman rank coefficient of correlation. The coefficient was significant at $P<0.05$ ($r_s = 0.485$; $n = 14$). This result indicates, therefore, that the density of the foraging bee populations does reflect the density of the food populations.

Despite the statistical significance of the correlation, the points in Fig. 22 are highly scattered, particularly in the region of low food values. Since it seemed likely that the abovementioned diurnal changes in the ratio were responsible for this scatter, and that the observed variability in bee density was not properly taken into account in the foregoing analysis, I reanalyzed the data by considering only those observations made during the period of peak abundance (10 A.M. to 2 P.M.). By calculating a bee/food ratio for each bee density observation made during this time period, the variability in these figures could be taken into account in the statistical analysis. Each variate was computed using a value of anther availability derived from the pooled data of the 10:00 A.M. and 12:30 P.M. samples, and a summary of these data is given in Table 25. The sites were compared by the Kruskal-Wallis test. The null hypothesis (all samples derived from one statistical population) corresponded to the biological hypothesis being tested; namely, all bee populations will have the same ratio of bee density to available food because the limit on bee population growth is set by the quantity of food.

By this method of analysis, I found that the sites were significantly heterogenous ($H = 33.959$; $P < 0.005$). Since inspection of the data showed that the 1EA site was aberrant compared to the rest, I recalculated the test statistic for 12NR, 18SWA and 9WSWA. For this group of sites the null hypothesis could also be rejected

($H = 17.189$; $P < 0.005$). In this case, 12NR evidently has a smaller level of bees per food than do the other two sites. Thus, the sites have disparate numbers of bees living per unit of pollen food.

Since the bees differ greatly in size, it is possible that these observed differences in bee density as a function of food density could be attributed to the varying amount of pollen that can be collected by individuals of each species. That is, a large number of _P_. _minima_ would be equivalent to a small number of _E_. sp. A in the amount of pollen removed from the plants per unit time. In order to correct for this possible source of error, I recalculated the values for bee density, using the "_Exomalopsis_-equivalent" described in Chapter 2. These conversion factors are listed in Table 26. The figures for bee density and bees per food corresponding to those of Tables 21 and 24 are given in Table 27, and the averages of the individual observations between 10 A.M. and 2 P.M. corrected for species composition and relative abundance are given in Table 25. As can be seen from Table 27, the correction for pollen-carrying ability did not affect either the ranking of the sites with respect to bee density, or daily variation in the ratio. Thus, the 9WSWA site supported the largest absolute number of bees despite the fact that the species at this site collected the largest amounts of pollen per bee.

The analysis of the pooled data from the period of peak abundance gave different results, however. Although the four sites together were still statistically heterogenous ($H = 23.520$; $P < 0.005$), with the omission of the 1EA site from the analysis the null hypothesis could be accepted ($H = 1.983$; $P > 0.5$). Thus, three of the four sites appear to support similar quantities of bees relative to the amount of food present at each site, when the relative abundance and size of each species at each site is taken into account.

The results of this series of analyses give only scant support to a hypothesis that food is the principal controlling factor of bee populations. The general decline in the ratio of bee density to food availability during the day suggests that factors other than the need to gather food govern the diurnal activity patterns of bees. Even after correction for scopal size and relative species abundance, one site supported a significantly different density of bees per unit food than did the others. Thus, it seems reasonable to conclude that other factors are at least as important as food limitation in the determination of bee population size.

Summary

In this chapter, I have sought for evidence that the bees are competing for pollen from *Euphorbia*. The investigation was in two parts, as follows: 1) A study of the daily activity period of each species of bee revealed virtually no differences that would permit coexisting species of bees to forage on separate portions of the pollen resources. Thus, there is no evidence that competitive pressures have generated nonoverlapping foraging periods. 2) The relative density of bees supported by varying levels of food abundance was studied at four sites and three times of day. Fewer bees forage per unit food density in the afternoon than forage in the morning; this finding suggests that a) not all the available pollen is harvested by the bees, and b) no species of bee has sufficient difficulty finding adequate pollen (because of the presence of competitors) that it has to collect pollen late in the day. On the basis of data from just the midday period, only two of the four sites support similar densities of bees per unit food density. However, when the data are adjusted for the relative abundance and relative pollen-carrying capacity of each bee species, three of the four sites have comparable values of "bee density/food density." This result supports the hypothesis that some, but not all populations of *Euphorbia*-dependent bees are food-limited.

TABLE 21. Total foraging bee density: observed numbers at four sites and times of day. Numbers in parentheses are sample size and standard error, respectively.

Site	9 - 10 A.M.	10 - 11 A.M.	12:30 - 1:30 P.M.	3 - 4 P.M.
	Total number of bees per 1/8 m^2 per 10 minutes			
1EA	5.5	11.0	11.4	1.3
	(2; 2.5)	(2; 1.5)	(10; 2.1)	(4; 1.0)
12NR		3.4	3.6	0.3
		(5; 1.1)	(10; 0.8)	(3; 0.3)
9WSWA	12.0	21.6	16.5	1.0
	(5; 6.0)	(11; 2.4)	(11; 2.5)	(2; 1.0)
18SWA		11.0	5.1	0.0
		(4; 2.1)	(7; 2.8)	(3; 0.0)

TABLE 22. Characteristics of the plant populations at each locality used in calculating food density. Figures in parentheses are sample size and standard error, respectively.

Site	Plant Species	Plant Density (#/m^2)	Mean Plant Size[a]	No. Flowers Per Unit[b]	No. Flowers Per m^2
1EA	*albomarginata*	1.2	428.9	1.79	767.78
		(40; 0.26)	(40; 113.52)	(45; 0.17)	
12NR	*albomarginata*	4.3	1413.8	1.02	1442.10
		(40; 0.49)	(40; 205.02)	(97; 0.07)	
9WSWA	*capitellata*	24.5	3.04	20.3	1511.90
		(40; 3.0)	(40; 0.4)	(55; 1.2)	
18SWA	*capitellata*	34.0	4.83	12.8	2099.84
		(40; 7.57)	(40; 1.17)	(76; 0.6)	

[a] *E. albomarginata*: area, cm^2; *E. capitellata*: mean number of heads per plant.

[b] *E. albomarginata*: cyathia per cm^2; *E. capitellata*: cyathia per head.

TABLE 23. Available pollen food, in numbers of open full anthers, at different times of day at each site. Numbers in parentheses are sample size and standard error, respectively.

Site	9 - 10 A.M.	10 - 11 A.M.	12:30 - 1:30 P.M.	3 - 4 P.M.
		mean number of anthers per flower		
1EA	0.089	0.457	0.384	0.109
	(406; 0.017)	(611, 0.033)	(565; 0.031)	(579; 0.016)
12NR		0.767	0.758	0.100
		(600; 0.040)	(595; 0.040)	(600; 0.016)
9WSWA	0.417	1.335	1.237	0.082
	(350; 0.046)	(570; 0.077)	(581; 0.077)	(600; 0.017)
18SWA		0.494	0.721	0.170
		(629; 0.047)	(595; 0.054)	(599; 0.021)
		mean number of anthers per m^2		
1EA	68.30	350.88	294.83	83.69
12NR		1106.09	1093.11	144.21
9WSWA	631.41	2021.43	1873.04	124.16
17SWA		1037.32	1513.99	356.97

TABLE 24. Total foraging bee density: numbers in relation to food density. Each datum is the ratio of total observed density of bees per 10 min to the mean number of anthers per m^2.

Site	9 - 10 A.M.	10 - 11 A.M.	12:30 - 1:30 P.M.	3 -4 P.M.
1EA	0.0805	0.0313	0.0387	0.0160
12NR		0.0031	0.0033	0.0021
9WSWA	0.0190	0.0105	0.0086	0.0081
18SWA		0.0106	0.0040	0.0

TABLE 25. Mean ratio of bee density to food density during the peak abundance period (10 A.M. .to 2 P.M.) for observed numbers of bees, and numbers adjusted for species composition and scopal size.

Site	N	Observed, Mean Ratio	S.E.	Adjusted, Mean Ratio	S.E.
1EA	16	0.0408	0.0052	0.0067	0.0007
12NR	20	0.0046	0.0010	0.0017	0.0003
9WSWA	29	0.0080	0.0012	0.0023	0.0004
18SWA	18	0.0072	0.0015	0.0015	0.0003

TABLE 26. "*Exomalopsis*-equivalent" conversion factors used in correcting for pollen-carrying capacity of each bee species.

Bee Species	Scopal Volume (mm^3)	Conversion Factor
P. minima	0.080	7.56
D. perparvus	0.080	7.56
P. obscurella	0.123	4.92
H. nanulus	0.142	4.26
C. squamifera	0.245	2.47
N. helianthi	0.446	1.36
E. sp A	0.605	1.00

TABLE 27. Total foraging bee density and bee density in relation to food density, corrected for species composition and pollen-carrying capacity. Sample sizes are as in Table 21.

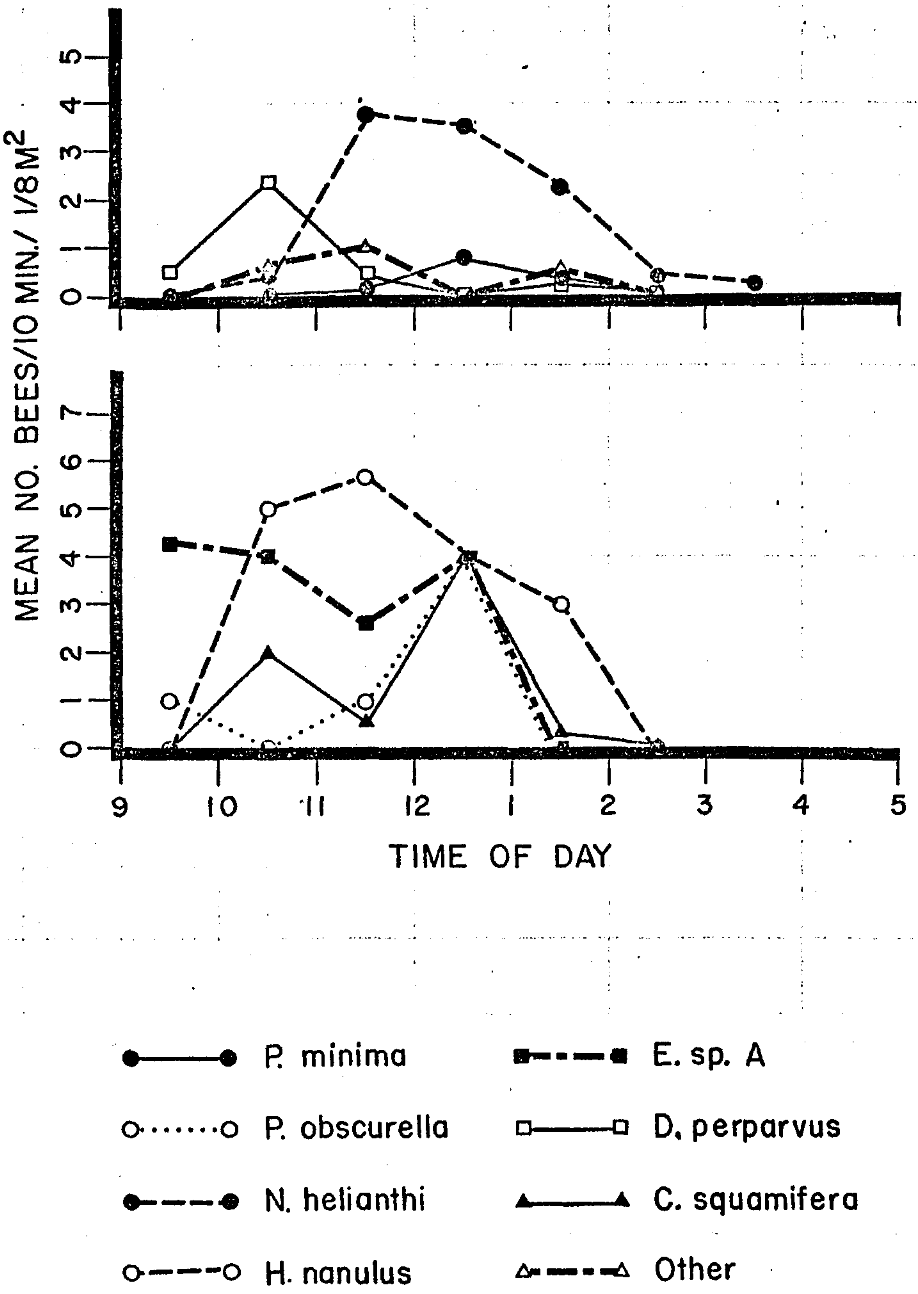
Site	9 - 10 A.M.	10 - 11 A.M.	12:30 - 1:30 P.M.	3 - 4 P.M.
	total number of bees per 1/8 m^2 per 10 minutes			
1EA	0.98	2.00	1.87	0.17
12NR		0.69	2.18	0.18
9WSWA	10.16	14.56	7.37	0.40
18SWA		5.83	1.81	0.0
	bee density/anther density			
1EA	0.0143	0.0057	0.0063	0.0020
12NR		0.0006	0.0020	0.0013
9WSWA	0.0161	0.0072	0.0039	0.0032
18SWA		0.0056	0.0120	0.0

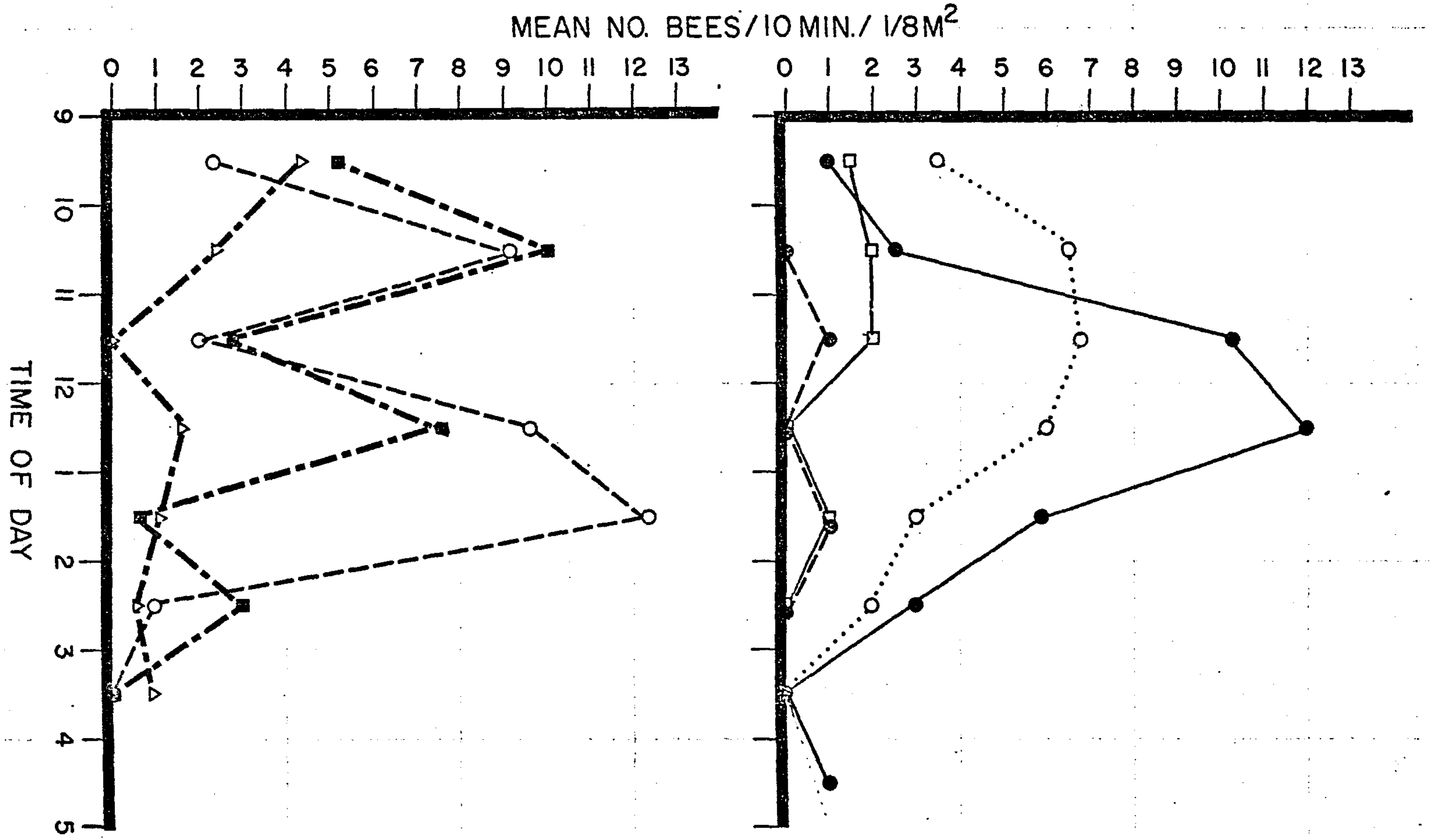
Figure Captions

Chapter 7

Fig. 20	Daily activity pattern of bees foraging on *Euphorbia* at four sites. Data have been averaged for each hour period, and are plotted at the midpoint of the hour.
Fig. 21	Daily time-course of the ratio of bee density to food density. Data are from Table 24, and are plotted at the midpoints of the anther sampling time periods.
Fig. 22	Correlation between bee density and food density measured in number of open, full anthers per square meter.

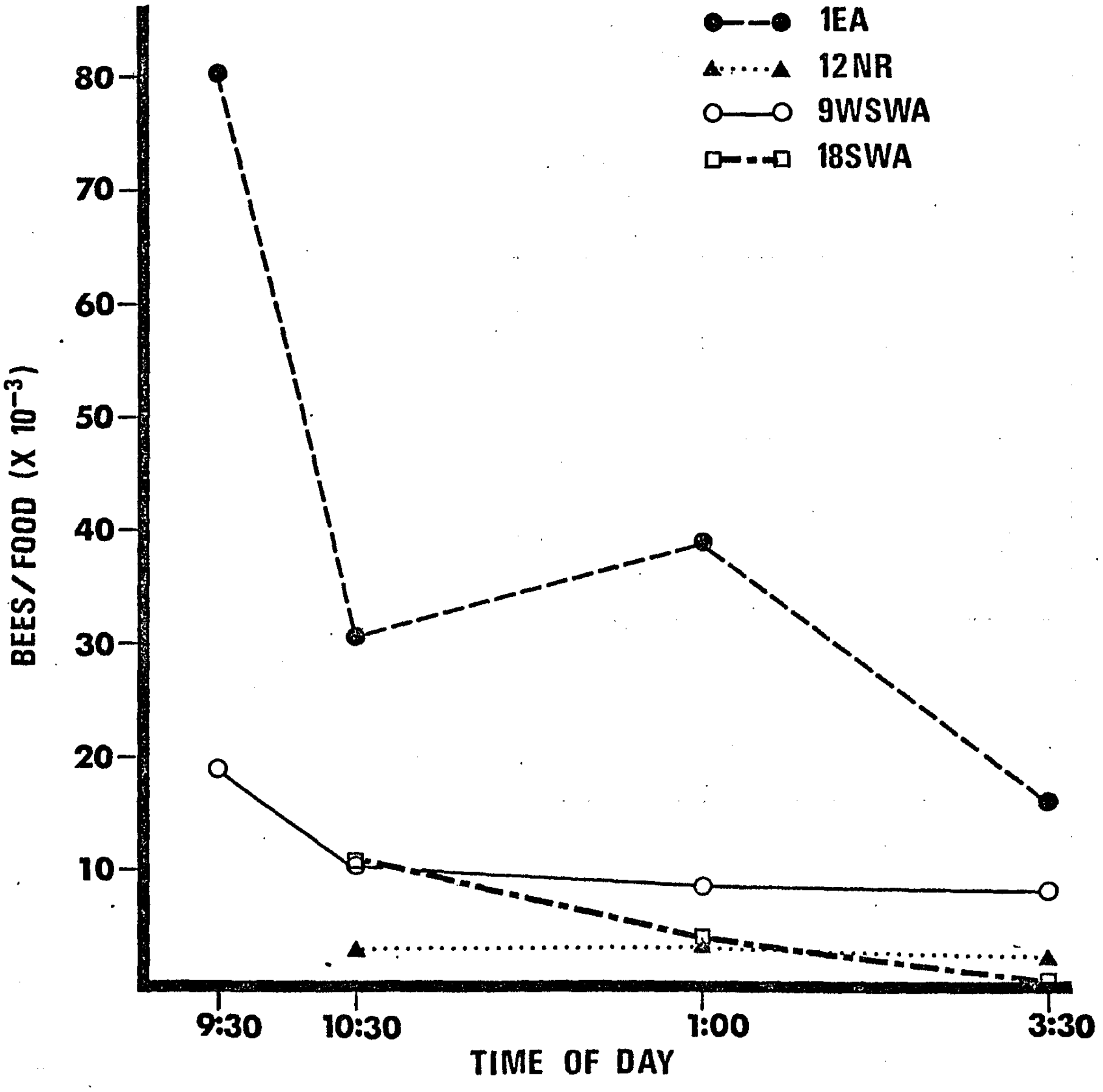
FIGURE 20


MEAN NO. BEES/10 MIN./ 1/8M²
0
1
2
3
4
5
0
1
2
3
4
5
6
7
9
10
11
12
1
2
3
4
5
TIME OF DAY
P. minima
P. obscurella
N. helianthi
H. nanulus
E. sp. A
D. perparvus
C. squamifera
Other



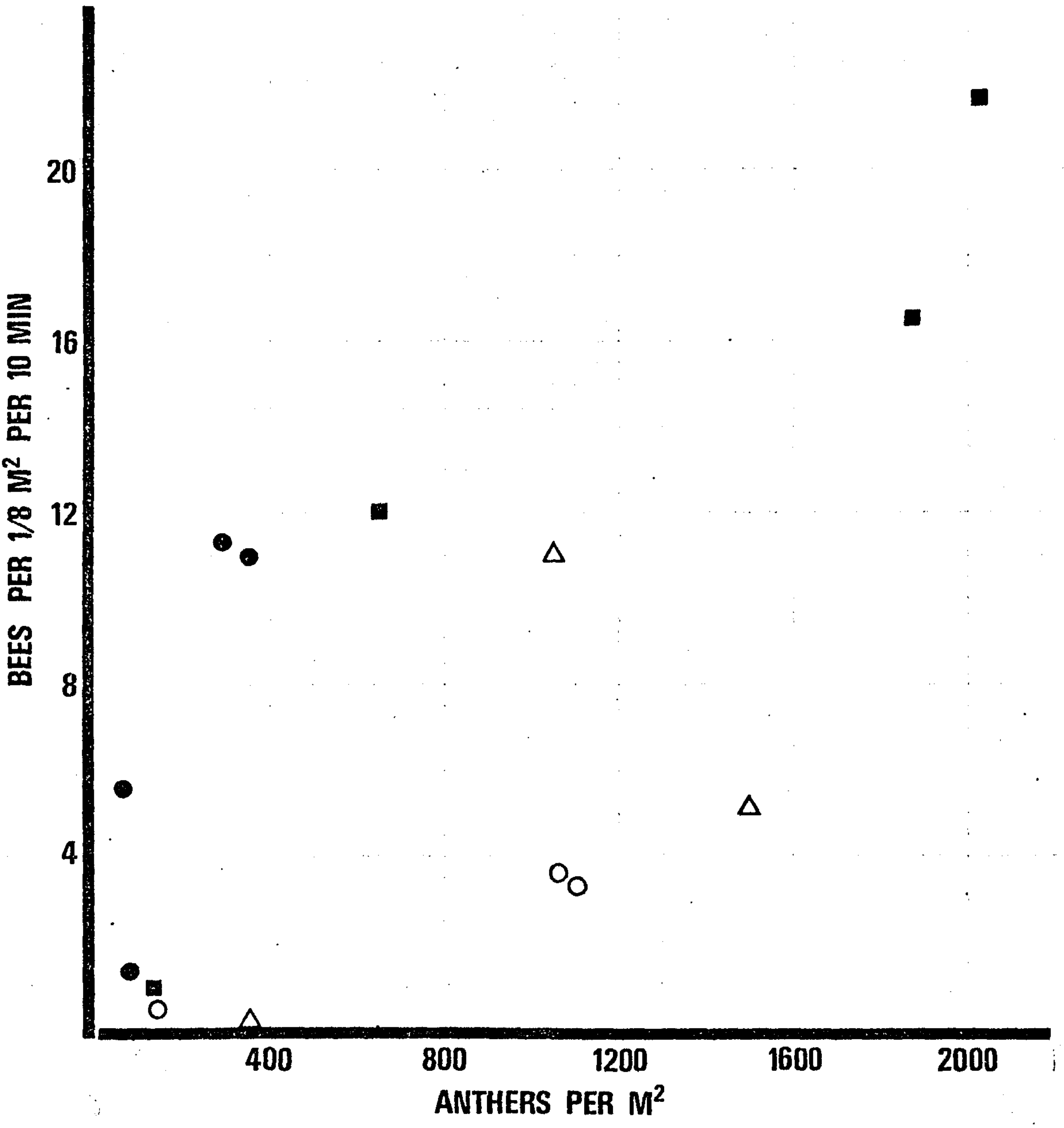
MEAN NO. BEES/10 MIN./ 1/8M^2
0 1 2 3 4 5 6 7 8 9 10 11 12 13
0 1 2 3 4 5 6 7 8 9 10 11 12 13
TIME OF DAY
9
10
11
12
1
2
3
4
5

FIGURE 21



1EA
12NR
9WSWA
18SWA
BEES/FOOD (X 10^{-3})
80
70
60
50
40
30
20
10
9:30
10:30
1:00
3:30
TIME OF DAY

FIGURE 22


BEES PER 1/8 M² PER 10 MIN
20
16
12
8
4
400
800
1200
1600
2000
ANTHERS PER M²

CHAPTER 8

DISCUSSION

In this discussion of interactions between *Euphorbia* and its insect visitors, four topics will be considered, as follows: 1) the role played by pollinating insects in the biology of the plants, 2) the significance of variation in the foraging behavior of bees, 3) the importance of *Euphorbia* as a limiting factor in bee populations, and the presence of competition among the bees feeding on these plants, and 4) the effects of the interactions on the evolution and ecology of the plants and the insects.

The Role of Insects in the Biology of the Plants

The reproductive biology of *Euphorbia albomarginata* and *Euphorbia capitellata* has been shown to be inextricably linked to the activities of the insects that are induced to land on the cyathia. There are two basic mechanisms of insect pollination. First, pollination can occur as a result of the walking movements of the common insects over the surface of the cyathia; pollen adheres to the legs, ventral surfaces of the head, thorax and abdomen, and the sides of the thorax, and is deposited on the next stigma traversed by the insect. The placement of pollen on an insect's body is partly a function of the insects's size and partly a function of its movement. Second, all insects, and particularly those insects that spend much of their time motionless on flowers (Heteroptera and some Coleoptera), can pollinate by jostling the cyathia when they move from one to another, and causing anthers to touch stigmas. Hovering insects, such as bombyliid flies, are least effectual because they rarely contact the sexual parts of the cyathia and the movements of their probosces on the glands do not disturb the cyathia sufficiently to cause self-pollination. In view of the fact that Euphorbia pollen does become airborne and is moved around by wind, it is conceivable that the air currents produced by the wing motions of these flies suffice to blow pollen from anthers to nearby stigmas.

The large predacious bugs, insects which do not derive their living directly from the plants, can cause pollination by jostling, and thus probably are more effective as pollinators than are some of the insects, such as hover-flies, which as adults derive much of their food from the plants. The parasitoid wasps feed both directly from the plants (taking nectar), and also use the plants as a site for searching for prey. Many of the wasps, for example, belonging to the genus Solierella (Larridae), characteristically hunt for prey on Euphorbia spp. (Williams, 1950). It is likely that other species of wasps also use the Euphorbia plants simultaneously as a source of food for themselves and a site for the location of prey for their larvae. Thus, these species of Euphorbia are not only relying on - and supporting - a large population of herbivorous insects that pollinate as they feed, but also are being pollinated by insects one step up the food chain.

Previous studies of insect visitors to Euphorbia have uniformly implicated a diverse group of small flies, beetles, and wasps as pollinators (Muller, 1883; Proctor and Yeo, 1973). These lists were compiled from studies with species of Euphorbia lacking the petaloid appendages. My observations corroborate these observations, and extend them to species that have conspicuous white petaloid appendages. According to Muller (1883), bees are found visiting the European species when the plant populations are sufficiently dense; this observation was repeated for E. albomarginata by Krombein (1961). These herbaceous euphorbs, then, must rely primarily on flies and wasps, and enjoy the advantages of bee visitation only in exceptional geographic areas or individual populations. It may be that E. albomarginata and E. capitellata overcome the behavioral disadvantages of flies and wasps by offering large amounts of food in a small area, and thus enticing the insects to feed at numerous flowers on each visit. E. hyssopifolia can afford to attract few insects because of its ability to pollinate itself. Many of the visitors are effective as pollinators, but the plants clearly have no closely evolved relationship with or dependence on any of the visitors. Thus the cyathium functions as a promiscuous floral device in attracting insects and relies on "mess and soil" insect behavior (Faegri and van der Piji, 1971) to be pollinated. The cyathium also functions variably in promoting self-pollination to the extent that male flowers mature during the transition stage. The data presented here suggest that the insect-attracting function is of only facultative importance to individual plants, and that it tends to disappear as the size of the cyathium, and particularly the size of the petaloid appendages, decreases. This is particularly evident in the case of _E. hyssopifolia_, which combines the lowest rate of insect visitation with the highest percent seed set in the field.

Knuth's (1909) generalization concerning the relationship of flat blossoms to diverse, numerous and unspecialized floral visitors is generally true of these species. However, the great differences in insect diversity among the plant species studied here indicate that factors in addition to flower shape control the number and variety of insect visitors to particular species. It is not clear, for example, why _E. capitellata_ received relatively little attention from non-apoid Hymenoptera and Diptera, since there is little apparent difference in reproductive structures between this species and _E. albomarginata_, except for arrangement of the cyathia into dense heads, the smaller glands, and the more numerous stamens. The disproportionate attention from beetles is perhaps related to the greater number and the higher concentration of anthers on the heads, since beetles are known to respond to pollen attractants (Faegri and van der Piji, 1971). However, gland size, petal size, and the juxtaposition of cyathia seem more important than anther number in accounting for the difference in insect visitation between _E. hyssopifolia_ and the other two species. Therefore, slight differences in the arrangement and nature of the attractants, plant growth form, and probably other factors as yet unidentified significantly affect the visitor diversity of a particular type of floral device. Bell (1971) described similar restrictions and variations in insect visitors to promiscuous flowers in the Umbelliferae.

The cyathia of these species are markedly proterogynous, an adaptation that presumably prevents pollination within a cyathium. However, the cyathial density per plant, and the tendency for visiting insects to repeatedly visit the same portions of a single plant (see Chapter 5) greatly reduce the effectiveness of this trait in promoting outcrossing. Mulligan (1972) reported that of nine autogamous weed species, seven were proterogynous. Faegri and van der Pijl (1971) suggested that proterogynous flowers might be more prone to be associated with autogamy than would proterandry, because a slight prolongation of the female phase would bring both sexual systems together. Such a mechanism was indeed found to operate in E. albomarginata, but in general, self-pollination follows from the massing of many flowers of different developmental stages on the same plant. It can only be presumed that the evolutionary advantages of occasional outcrossing provides the selective force that maintains the proterogynous pattern of development.

The various kinds of insects differ in their likelihood of causing outcrossing. The variability observed among the species of bees alone in frequency of movements between E. capitellata plants (Chapter 6) is probably equally pervasive among the various groups of insects listed in Table 7. In general, however, large insects (particularly wasps and flies) and those that predominantly fly or move rapidly between cyathia are likely to carry pollen between plants.

Although no attempt was made to measure the rate of outcrossing in these species, it is possible to compare the probable amounts of outbreeding in the three species on the basis of their biology. Euphorbia hyssopifolia attracts relatively few species of insects, many of which (the Heteroptera) are highly sedentary, and is evidently largely self-pollinating; these factors undoubtedly result in a very low rate of outcrossing. The visitors to E. capitellata include a sedentary group (the Coleoptera) and a mobile group (the Apoidea). I have estimated that an average of 22% of the bees' movements are between different E. capitellata plants (this figure is an average for all bee species; see Chapter 6). The amount of outcrossing effected by bees may be countered by the self-pollination of which this species is evidently capable. Nevertheless, E. capitellata clearly has more extensive outbreeding than does E. hyssopifolia, because of the frequency and nature of the bee visits. E. albomarginata attracts the greatest density and variety of mobile insects, but the large size of individual plants, the high density of cyathia per plant, and the efficacy of vegetative propagation in spreading one individual plant over a large area must reduce the potential of the insect fauna for outcrossing. Among the bees, probably over 80% of all movements are within a mat and consequently result in self-pollination. (The method of observation prevented accurate assessment of movements between large mats.) Thus, the species with the greatest dependence on insect visitors (*E. albomarginata*) probably has a considerably lower outcrossing rate than does a species (*E. capitellata*) with a partial ability to pollinate itself.

All three species of *Euphorbia* succeed in producing very large numbers of seeds. As noted above, *E. albomarginata* and *E. capitellata* grow so as to maintain extremely dense populations of cyathia (1532 to 2892/m^2 and 1512 to 2100/m^2 respectively (Chapter 7)). Although the average seed set for these species was between 60% and 70%, the sites were highly variable, ranging from 20% to 80%. Poor seed set is presumably attributable to unfavorable environmental conditions; these data were collected during an unusually dry season, when the plants were under considerable physiological stress. Even under conditions of low percentage seed set, the absolute number of seeds produced by the combined long flowering season and high density of cyathia is enormous. With an average of 2000 cyathia/m^2, an average seed set of 50% (1.5 seeds per cyathium), a population covering about 50 m^2 (comparable to the smaller of those sites studied), and a peak flowering season of two months, about 300,000 seeds are released in each population. This ability to produce enormous numbers of seeds under adverse conditions surely is a major factor in the success of the plants.

All three species are typical of colonizing species, in that they are usually found growing in disturbed areas (in southeastern Arizona, they are most common in overgrazed grasslands, along roadsides that are frequently mowed, scraped, traversed by heavy machinery, etc.), and they disappear as other vegetation moves in. Dense stands rarely include individuals of other species of plants. The reproductive biology described in this paper is in accordance with that described for other weedy plants (Baker, 1965), in that reliance is placed on enormous seed set, a long flowering season, rapid growth, and production of seed by small seedlings. This combination of characteristics promotes both the genetic variation necessary for survival from year to year, and the genetic uniformity favoring rapid colonization of each locality during a year (Allard, 1965). Thus, these species meet many of the criteria set out by Baker (1965) for the "ideal weed".

Casual observation of other weedy species in *Chamaesyce* (*E. maculata* and *E. Preslii*), which have cyathia considerably smaller than those studied here, suggests that high seed set can be coupled with the virtual absence of insect visitors. According to recent taxonomic treatments (Webster, 1967; Wheeler, 1941; Richardson, 1968), many, if not most species in the subgenus grow as weeds in waste places, and many (63% of those considered by Wheeler) have petaloid appendages smaller than *E. albomarginata*. This suggest that self-pollination is widespread in this subgenus. Investigation of a larger sample of species will be necessary to establish the prevalence of self-pollination in the groups and the importance of this reproductive pattern to the weediness of so many of its species.

In conclusion, the reproductive patterns of these three species are differently organized, but the end result - copious seed set - is the same. *E. albomarginata* has a reproductive system that gives it great flexibility; such a wide variety of insects visit the plants that all populations can rely on at least some visitors. Also, the long period of stigmatic receptivity ensures that even with very low rates of visitation, most cyathia will at least be self-pollinated. *E. capitellata* maintains an equivalent flexibility, in spite of reduced insect visitor diversity and abundance, because it has a greater capacity for self-pollination. *E. hyssopifolia* has substituted self-pollination for reliance on insects altogether; it would be interesting to determine if it has sacrificed some genetic variability because of the much lower rate of outcrossing.

Variability in Foraging Behavior

The patterns of difference and similarity among the bees can be used to analyze the following topics: 1) What kinds of behavior are common to all the bees, and which behavioral elements vary among the species? Does foraging behavior provide appropriate material for ethological analysis? 2) How flexible is the foraging behavior of bees? Can individual bees adjust their behavior when they forage on different species of plants? 3) Is there an "optimal" way of obtaining food from Euphorbia that is evident from the data on these species of bees? Has selection for efficiency had any effect on the evolution of bees' feeding behavior? 4) Can behavioral variation among the bees foster competitive coexistence? These topics will be considered in turn.

Ethological Aspects of Bee Foraging Behavior

Table 12 summarized those qualitative behaviors that were performed by all of the bee species, regardless of food plant. In general, the leg movements used to extract pollen, pass it posteriorly, and pack it into the scopae are similar among widely different groups of bees. In addition to those bees studied here, other that have been reported to collect and manipulate pollen in this way include Agapostemon spp., on a variety of flowers (Roberts, 1969), Megachile brevis Say on Psoralea, Rhus, and Gutierrezia (Michener, 1953), Apis mellifera L. on a variety of plants (Parker, 1926), Dialictus imitatus on Rhus and Plantago (Michener and Wille, 1961), Andrena chalybaea (Cresson) on Camissonia, and several other Andrena species on Agoseris (Thorp, 1969), and Nomia melanderi Cockerell on alfalfa (Bohart, 1958). Thus, this sequence of leg movements is common to species with scopae of plumose hairs on the femora (Agapostemon, Dialictus), scopae of plumose hairs on the tibiae and basitarsi (Exomalopsis), scopae of relatively sparse, simple hairs on the tibiae and basitarsi (Andrena chalybaea, panurgine bees), and scopae of plumose hairs on the abdominal venter (*Megachile*). This sequence occurs on flowers of diverse morphology - flat, open blossoms (*Euphorbia*), cup-shaped blossoms (*Camissonia*), composite heads (*Agoseris*, *Gutierrezia*), and flag-shaped blossoms (*Psoralea*), and brush type blossoms arranged in spikes (*Plantago*). A few examples of bees which differ partly or completely from this behavior sequence have been described; they include *Proteriades*, which extracts pollen from *Cryptantha* using curled bristles on the galeae and labial palps, but uses the common leg movements for transfer of pollen and scopal packing (Timberlake and Michener, 1950), *Hoplitis anthocopoides* (Schenck) on *Echium vulgare* (Eickwort, 1973) and *Megachile umatillensis* Mitchell on *Oenothera* (Bohart and Youssef, 1972) which gather the anthers together with the hindlegs and push them against the abdominal scopal hairs, *Ptiloglossa*, *Bombus*, and others which extract pollen from flowers with tubular anthers (such as *Cassia* and *Solanum*) by biting the base of the anther and vibrating the wings in order to shake the pollen out onto the abdominal venter (Wille, 1963).

These scanty records of exceptions to the standard behavioral sequence suggest that one extrinsic factor, highly unusual anther morphology, and one intrinsic factor, occurrence of the scopal hairs on the abdomen (i.e., in the Megachilidae and Fideliidae) are the major causes of exceptional behavior, when it occurs. More extensive data may of course expand the number of factors that cause a departure from the common sequence.

The occurrence, but not the timing, of the hindleg rub beneath the abdomen is also common to many species. In addition to all of the bees studied here, Agapostemon (Roberts, 1969) performs this movement; however, little attention has been paid by investigators to this behavior, and the extent of its occurrence is unknown.

Thus, the evidence available to date suggests that the leg motions associated with pollen acquisition and manipulation are primitive features of bee behavior, and, by implication, departures from these behaviors represent derived conditions. Obviously, considerably more work on a greater variety of bee species will be needed to substantiate this hypothesis. A detailed investigation of foraging behavior amont the Megachilidae might be particularly informative, since this family has shown considerable variability in the leg movements associated with pollen collecting.

In addition to the leg movements used for pollen gathering, several of the aspects of temporal sequence studied above can be added to the list of behavioral elements common to all of the bees in this study. All bees tend to fly after visiting a single flower about 50% of the time, a frequency considerably greater than that expected by chance alone. Thus, the non-random arrangement of the basic elements of foraging - flower visits and flights between flowers - may be a general characteristic of bees foraging on plants with aggregated flowers. Secondly, all bees spend a greater proportion of their time visiting flowers than flying between flowers. Thirdly, all bees foraging on E. capitellata make over half their moves to flowers of the same plant. (This is also certainly true for the bees foraging on E. albomarginata, even though the precise relative frequency of such behavior was not measured.)

The class of behaviors that are variable among the species is much larger than the class of behaviors common to all of the bees. These traits include not only those listed in Table 13, but also all of the aspects of temporal organization of foraging discussed in Chapter 6. A number of behaviors that are performed by all species are seen at varying frequences or rates in the different species (e.g., grooming pauses, frequencies of movements between plants).

Many of the behavioral elements that are listed in the "variable" category of Table 13 have strong ecological effects on insect-plant interactions and interspecies interactions. For example, adherence of pollen to the face and venter, posture of the bee on the flower, type of motion of the bee and tendency to visit adjacent flowers determine the effectiveness of the bee as a pollinator, and as an agent of outcrossing versus selfing. Characters such as rapidity of leg movements, reactions to passing clouds, percentage of time foraging, distance covered, frequency of and intraspecies interactions may contribute to the competitive abilities of each species (see below). (These ecologically significant behaviors tend, in addition, to be the most variable within bee species on different plants (Michener, 1953) and under different conditions of plant density (Manning, 1956). Differences in bee posture and motion, in particular, account for most of this intraspecies variability.

The variable behaviors are likely to be useful in taxonomic and ethological analyses. In Chapter 5 it was shown that the patterns of species similarity in qualitative aspects of behavior resemble the patterns of taxonomic relationship currently accepted. In addition to patterns of overall similarity, particular behaviors may prove to be important characters for the purposes of classification. For example, parallel leg movements, body vibration, lengthy pollen packing movements in the vertical position, and involvement of the prosterna and procoxae were seen only in the two species of *Perdita*. *H. nanulus*, *N. helianthi* and *C. squamifera* resembled each other in packing the scopae during flight, in gathering pollen while stationary and astride the flowers, in the hover flight before landing, and in an intermediate-sized foraging area. *Calliopsis* and *Nomadopsis* are thought to be closely related on morphological grounds (Rozen, 1951, 1958), and further investigation may demonstrate that they share foraging behaviors not generally common to panurgines. Although the overall similarity of species with respect to the temporal aspects of foraging (Chapter 6) does not reflect taxonomic relationship, particular aspects of timing and sequence in foraging behavior may also be distinctive of some species. For example, the nearly regular alternation of flower visits and flights in *H. nanulus* set this species apart from the others so clearly that foraging individuals could be correctly identified by the observer on the basis of this behavior alone. Thus, the elements of foraging behavior described here show a sufficient range of variability among the species that in the future, more extensive analysis of foraging behaviors may prove as useful to the study of bee systematics as have studies of nest architecture among bees (Michener, 1974; Sakagami and Michener, 1962).

Flexibility of Individuals in Response to Plant Variation

All of the species studied modify only two aspects of their foraging behavior when they switch from uniform mats of cyathia (*E. albomarginata*) to discrete clumps of cyathia (*E. capitellata*); bees visit fewer heads per minute than they do solitary cyathia, and they spend more variable amounts of time per head than they do per cyathium. These results are not surprising, since more food is available on a head than on a single cyathium, and the heads are more variable in size than is a cyathium. The mean duration of flower visits, and all aspects of flight behavior, however, generally were not changed in response to plant differences. No bee species, then, was as flexible in dealing with varied plant morphology as might have been expected.

Species-specific influences evidently account for much more of the observed variability in bee foraging behavior than do resource-related influences. Although my results concern behavioral variation on plants which differ in the arrangement of similar flowers (cyathia), the limited data in the literature, discussed above, suggest that few traits other than body posture, body motion, and foraging rate (flowers/min) vary within a species of bee on plants of very different morphology. If this conclusion is confirmed in future studies of bee foraging behavior, it will imply that intrinsic factors can be more pervasive in determining patterns of foraging behavior than factors related to the nature of the food. In view of this possibility, species-specific aspects of behavior should be taken into account in any investigation of foraging "strategies".

"Optimal" Foraging Behavior of Bees

The features that were general among the bees studied are sharply at variance with the hypothesis that foraging behavior is molded by selection for maximum efficiency (Emlen, 1966; MacArthur and Pianka, 1966; Schoener, 1971). Firstly, bees tend to return repeatedly to the same flowers and/or heads over the course of several minutes, even though much or all the nectar and pollen is gathered on the first visit. This implies that the "decision" of a bee to alight on a flower and commence foraging is not necessarily dependent on a prior assessment of the resources to be gained from that flower. It is possible, of course, that small amounts of pollen and nectar, not visible to the human observer, remain after the first visit, and are "worth" the time and energy expended when the bee returns two, three, four or more times; but this is difficult to believe. Secondly, some of the flowers that have highly conspicuous pollen and nectar are often skipped during a pollen-collecting run, even though they may be directly in the path of the bee.

Further evidence against the efficiency hypothesis comes from two behaviors that are variable among the species. The bees vary in the completeness of their foraging efforts on a given flower; P. minima and D. perparvus gather pollen from every anther, but H. nanulus and E. sp. A forage on only some of the anthers of each flower. It is hard to understand why the latter species should not spend the slightly increased time necessary to obtain all the food possible per stop on a flower, unless this kind of efficiency has less evolutionary importance than other factors. The relationship between the relative proportions of time spent foraging and flying, and the ratio of "pursuit/search" was examined in Chapter 6. It was shown there that contrary to expectation, the species-specific effect was of much greater importance in explaining variation in the ratio than was the plant factor. If maximization of foraging efficiency is a prime factor in bee evolution, one might expect to find that search time has been minimized. It is curious, therefore, that among the Euphorbia - visiting bees, organisms of approximately the same size have responded to an identical food density and distribution with such different time-allocation "strategies". For example, H. nanulus spends considerably more time in flight than C. squamifera, when both are foraging on E. albomarginata. Pulliam (1974) predicts that search time will decrease with increasingly clumped food distribution. Although the heads of E. capitellata would appear to offer just such an opportunity to decrease search time per unit food intake, no species of bee studied here responds in the predicted way.

It seems, then, that the behavior of these animals has been selected for something other than short-term efficiency, and not just to "maximize the net caloric intake per individual of that species per unit time" (Emlen, 1966). One possible explanation might be that rapid movement and the continuous alternation of movement and immobility results in lower predation than that which would accompany the more lengthy flower visits necessary to extract completely the available resources. As Pulliam (1974) points out, maximum feeding efficiency measured in calories per unit time does not necessarily lead to maximum fitness. It is more likely that a variety of selective forces, perhaps outweighing caloric efficiency in importance, have affected the evolution of foraging behavior. The repeated visits to flowers may be inefficient in the short term; yet they may be highly efficient in delimiting and maintaining a feeding area that is highly profitable each day. The behavior of Exomalopsis as it ends foraging is very similar to the orientation flights performed by bees leaving nests, and suggests that at least this species returns to the same foraging area repeatedly. Thorp (1969) has found that A. chalybaea repeatedly returns to the same small foraging area over a period of days, and Linsley et al. (1959) has found the same to be true of some, but not all, of the species of Andrena associated with Ranunculus.

The various mathematical models of feeding efficiency all predict that specialization in the choice of food will increase as the overall abundance of all food sources increases, (see discussion in Pulliam, 1974); it is thus possible that considerations of efficiency are more important in the evolution of oligolecty, itself, than in the evolution of the behavioral elements of foraging. Individuals of many polylectic species (e.g., *Apis*, *Bombus*, *Lasioglossum* *s.* *l.*, *Megachile*) are often highly "constant" in their foraging behavior (Darwin, 1891; Free, 1966; Grant, 1950; Hurd and Michener, 1955). Each bee will collect pollen loads from only one species of plant on each foraging trip, and often visit only one species of plant for several days or longer, although the species as a whole utilizes a large number of plant species. The strongly clumped distribution of most herbaceous plant species (Greig-Smith, 1964) may have interacted with an overall abundance of food in such a way that fidelity to similar patches of vegetation has been maximally efficient. Darwin (pp. 418-438, 1891) suggested that both the flower constancy of *Apis* workers, and the nectar-robbing behavior of *Bombus* are adaptations for minimizing foraging time, and pointed out that both of these behaviors are seen only in dense plant populations. He thus originated the hypothesis that the highly restrictive feeding habits of bees are related to considerations of efficiency. If this indeed was (and is) a guiding factor in the evolution of bee foraging behavior, it would make oligolecty (a species characteristic) and constancy (an individual or population characteristic) different evolutionary responses to the same selection pressures exerted by the nature of the food source and the premium on efficient use of time.

Behavior in Relation to Partitioning of Food Resources

Finally, the relevance of the documented differences in behavior to resource partitioning and the avoidance of competition must be evaluated. On the basis of a combination of qualitative, spatial and temporal aspects of foraging, two basic methods of gathering flower food from *Euphorbia* can be discerned. 1) The small species - *P. minima*, *P. obscurella*, and *D. perparvus* - tend to move between adjacent flowers, extract all available resources from each flower, spend the longer times per flower, and do not cease foraging when clouds momentarily obscure the sun. 2) The larger species move rapidly over the flowers, brushing loose pollen into their scopae; they cover larger areas at a greater rate, cease foraging during temporary shade. These groups could be called "diggers" and "brushers" respectively. The length of the filaments and pedicels of the male flowers of each cyathium, and the angle which they form with the petaloid appendages are variable in both *E. capitellata* and *E. albomarginata*; since I observed that the "diggers" but not the "brushers" were capable of obtaining food from partly concealed or unusually placed anthers, behavioral separation seems at least possible. Within each group, there is additional differentiation of species on the bases of the groups of traits discussed above. The aggregate effect of the various behavioral differences documented above is that each bee will alight on a different proportion of flowers, differently arranged, per unit area and time. Insofar as these pattern and foraging method variants tend to bring coexisting species into contact with previously unvisited anthers they are, at least theoretically, capable of reducing competition.

Competition and Food Limitation in Bee Populations

Recognition of the factors that regulate the size of a population of bees has been a complex and difficult task, because of the lack of techniques for field and laboratory study of all but a few economically important species. As a result, much of the current understanding of the population dynamics of solitary bees is based on qualitative observations of population changes, and inferences based on ecological theory. One of the principal hypotheses resulting from these sources of information is that pollen (and perhaps nectar) is present in short supply, and that therefore bee population size is limited by the availability of food. It follows from this hypothesis that bees that feed on the same plants at the same time must be competing.

In order to assess the hypothesis that bee populations are limited by the food supply, and that coexisting species are therefore competing with each other, it is necessary to examine the evidence that has been advanced to support the hypothesis, the validity of this evidence, and the evidence that other limiting factors are at least as important in bee population ecology. The arguments for the presence of competitive interactions among species of bees include both field observations and logical inference. These arguments will be examined in turn.

Field Studies of Food Utilization and Competition Among Coexisting Species of Bees

The presence of numerous species of bees utilizing the same plant at the same time has often been taken as presumptive evidence of interspecific competition among bees. This type of argument for the hypothesis of competion is encountered in monographic studies of groups of bees (e.g., in *Calliopsis*, Shinn, 1967), as well as in observational studies of bee communities (e.g., Linsley et al., 1973).

In some studies, data have been collected that purport to show ecological differentiation with respect to food gathering. Foremost among these have been differences in the daily time of onset of foraging and concommittant differences in the daily times of peak abundance (Linsley et al., 1959, 1963 a, b; Schlising, 1970; Thorp, 1969). Variation in daily foraging time can only lead to reduction of competition if 1) fresh pollen is exuded more or less constantly while the flowers are open, and/or 2) the bee species vary in their behavior in such a way that pollen available to some species is not available to others, or 3) interference behavior, in which one species is actively excluded from the flowers by another species, is common. Unfortunately, little data bearing on these points is available. Linsley et al.

(1959, 1963 a, b; 1973) describes some behavioral differences among the oligoleges of *Ranunculus* and *Oenothera* that might support the second point above. Although territorial behavior has been described for some male bees (e.g., *Protoxaea gloriosa* (Fox), Cazier and Linsley, 1963; *Calliopsis andreniformis* Smith, Shinn, 1967), I have been able to find in the literature only one instance of feeding areas defended by females, particularly against unrelated bees. In this case, foraging *Trigona* actively defended food sources (Johnson and Hubbell, 1974); however, these social,polylectic bees are so different ecologically from the solitary, oligolectic bees under consideration that the revelvance of their findings to other bee species is questionable. Despite the numerous interactions I witnessed on *Euphorbia* among conspecifics (Chapter 5), I saw no interactions between bees of different species. In summary, there is insufficient information available to evaluate the suggestion that variation in daily foraging time can lead to a reduction of competitive pressures.

Linsley et al. (1959) and Thorp (1969) have demonstrated some differences in seasonal phenology. On *Ranunculus*, for example, the numerous oligoleges and polyleges begin their active seasons at different times ranging over a period of four to five weeks; at any one time, however, there are several bee species relying on the same plant population for food.

Linsley and Cazier (1970) have described a situation in which competitive exclusion from a food source seems to have occurred.

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Ptiloglossa jonesi Timberlake normally forages on *Solanum elaeagnifolium*, despite the presence of several other bee species foraging on the same plant. At a site where *P. arizonensis* Timberlake was utilizing *S. elaeagnifolium*, however, *P. jonesi* flew over the plant population to a more distant population of an unrelated plant species. Since *P. jonesi* was found foraging on *S. elaeagnifolium* wherever *P. arizonensis* was absent, but not where it was present, it seemed most likely that it was being excluded from the plant by the latter species.

I have described above how the species of bees foraging on *Euphorbia* can be divided into two behavioral groups which collect different portions of the available pollen; "diggers" remove extruded and some unextruded pollen from all the anthers of a cyathium, and stay within small foraging areas, and "brushers" acquire loose, extruded pollen by rapid scraping over some of the anthers of a cyathium, and travel over larger foraging areas. The existence of these two groups presents at least the possibility that behavioral differentiation allows the species at a given site to subdivide the pollen resources. A comparison of the data in Table 2 concerning the composition of bee species at each site with the behavioral categoriesyields only limited support for the hypothesis that the differentiation of the behavioral groups contributes to partitioning of resources. The most abundant species at three of the sites (1EA, 9WSWA, and 18SWA, *E. capitellata* plants) were all from the same behavioral group; at 1EA, all were diggers, and at the other two, all were brushers. The two most abundant species at each of the other sites (12NR and on E. albomarginata at 18SWA) were one digger and one brusher. Thus, the behavioral dichotomy between the two groups seems irrelevant to the bee community structure.

Numerous investigators have observed that the anthers of a variety of flowers studied are devoid of pollen by the end of the daily foraging period (e.g., Knerer and MacKay, 1969; Thorp, 1969), and they have cited this fact as evidence of food limitation. Mosquin (1971), in a more complete study, systematically observed, but did not quantify, the amounts of pollen and nectar resources available each day in a temperate zone meadow during an entire season. He found that pollen and nectar were completely consumed during the spring, but during the summer they were more plentifully produced than could be used by the flower-visiting insects. My studies of available pollen in Euphorbia (Chapter 7) indicate that precise measurement of the densities of empty and full anthers at the end of the day may reveal the presence of more substantial amounts of food than might be suspected from casual inspection. Therefore, it is difficult to evaluate the significance of many of the observations of empty anthers found in the literature.

The investigation reported in Chapter 7, in which available pollen has been quantified and related to the density of bees that are surviving on it, provides a more objective test of the food-limitation hypothesis than has heretofor been presented. The results of the study are seemingly contradictory; on the one hand, some pollen is evidently available and uncollected at the end of the foraging period, and on the other hand, when species composition and relative size are taken into account, three of the four sites support equivalent densities of bees relative to the available food. These results can be reconciled in the following way. It is likely that most solitary bees provision only one cell each day (Bohart, 1958; Lind, 1968; Roberts, pers. comm.). Furthermore, cells that are not completely provisioned by the end of the day are thought to be abandoned, and a new one started. This observation necessitates the assumption that as yet unidentified selection pressures favor the early cessation of pollen foraging over the completion of provisioning late in the day. If pollen is not abundant, population size will decrease because of a high frequency of empty cells, or because adults produced from small pollen balls are less viable and less fertile. Thus, the size of a bee species' population can respond to changes in food (pollen) availability, although some pollen remains uncollected. Varley et al. (1974, pp. 22-25) point out that competition, like all density-dependent processes, can act over a range of intensities that variably affect the fate of the population. Mild competition will promote a stable population size, according to their analysis, and could be reconciled with the existence of strong selective forces, such as those that evidently prevent mid-afternoon foraging. Thus, my data support the hypothesis that competition among coexisting species of bees utilizing the same food plants is mild in its effects on population size.

Thus the field evidence for the existence of competitive interactions among bees largely consists of 1) many cases in which several species of bees rely on one plant population at the same time, 2) observations of behavioral differentiation which do not clearly foster the ecological separation of coexisting species, and 3) my finding that although the bees feeding on *Euphorbia* are evidently competing for limited food, the effects of this competition are probably not severe.

Theoretical Problems with the Hypothesis of Competition

As I have indicated above, it is generally assumed that food is a limiting quantity for bees, and that therefore bees feeding on the same plant are competing with each other (Cruden, 1972; Linsley, 1958; Michener, 1954; Robertson, 1914). This assumption is based on the following reasoning: according to current ecological theory, specialization of an animal's use of food (or other resource) is an evolutionary response to competition, which serves to minimize the negative effects of the interaction. Therefore, an observed case of extreme food specialization (i.e., oligolecty) is likely to be the end product of competition for food. It is further assumed that although oligolecty may reduce competition within a community, it does not necessarily eliminate it entirely. The existence of competition between two or more species implies that the resource at stake is present in limiting quantities for all. If oligolectic bees are competing for food, then food can be presumed to be a limiting resource. This reasoning is not logically rigorous in that the truth of the latter portion of the inference "if competition occurs then specialization will evolve" does not necessarily imply the truth of the former. Thus there is no necessary relationship between specialization and competition, unless the existence of competition is established independently.

Sale (1974) has pointed out that extensive niche overlap may signal either high- or low-intensity competition. Pianka (1974), who also pointed out this fact, proposed that niche overlap is inversely related to intensity of competition, and is related to the number of competing species, as well as the number and kind of resources that are in short supply among them. Therefore, the presence of numerous species of bees relying on a particular plant population at the same time implies a low level of competitive interaction, if it implies anything.

Emlen (1966) has suggested that a difference of the frequency of each food item found in nature from its frequency in an animal's diet is indicative of abundant food. According to this formulation, oligolecty, or flower-constant behavior in bees would imply unlimited food sources, if it can be assumed that all plant species in flower at a given locality constitute the available food. Although it can be argued that for oligolectic bees, physiological constraints make this assumption untenable, it is clearly true for members of such genera as *Apis*, *Bombus*, *Agapostemon*, some *Megachile* and some *Lasioglossum*, whose populations use a vast array of plant sources. The degree of constancy exhibited by individual forager of these species can be very high (Batra, 1966; Eickwort and Eickwort, 1969, 1971; Free, 1966; Grant, 1950; Michener, 1953), and thus if Emlen's formulation is correct, it would be likely that food is not limiting to these bees. One final observation is germane to this discussion; namely, in a number of studies of oligolectic bees (e.g., Linsley et al., 1963a; Thorp, 1969; Hurd and Linsley, 1964) at a give site only one of several similar, congeneric food plants is visited by the bees, while the others go untouched. At a different site, the relative preferences among the various plant species may be reversed. Since physiological intolerances seem more unlikely in these circumstances, this seems to be another legitimate case of noncongruence of the proportionate representation of food items in nature and in the diet.

Thus, the evidence from both field and theory makes a contradictory case for the hypothesis that competition and food limitation are major features of the biology of solitary, oligolectic bees. There is some good evidence favoring the hypothesis: a few documented cases of competitive exclusion, the observations of anthers emptied of pollen, and my data on the ratio of bee density to food density. There are also some reasons to doubt the hypothesis: the correlation proposed in the literature between high niche overlap and low-intensity competition, the suggested association of abundant supplies of food with highly selective feeding behavior, and the absence of behavioral differentiation that clearly allows species to utilize different portions of the available food. This confusing state of affairs can be resolved by taking into account three factors.

First, it is likely that the abundance of food varies from year to year independently of the bees. During favorable years, competition would be minimal, whereas during lean years, competition would be widespread and more intense. Such fluctuations in plant population size are common in desert ecosystems (see description of study sites, Chapter 1; Epling et al., 1960). This variation could easily produce erratic evidence of competitive interactions.

Second, the morphology of the food plant may affect the frequency of competitive interactions. Plants which flower profusely and make large quantities of pollen and nectar easily obtainable from each flower have been aptly termed "cornucopian" by Mosquin (1971). These kinds of plants are more likely to provide food in excess of the bees' requirements than are plants which grow in small populations and produce small amounts of food per flower. Taraxacum officinale is a typical cornucopian plant; Primula sp. exemplies the non-cornucopian type.

Third, I suggest that few populations of bees maintain an equilibrium size over long periods of time, but instead, experience shifts between rapid, uncontrolled growth and fluctuations about an equilibrium population size. In other words, it is likely that at least those bees that live in arid regions are subject to relatively frequent alternations in the occurrence and intensity of density-independent and density-dependent controlling forces. If this is the case, then competition among bees could be expected to be erratic in occurrence and intensity, and evolution of competition-reducing behaviors (among oligoleges on a given plant) might be forestalled. There is some evidence to support this hypothesis. A number of papers have ascribed important roles to density-independent factors: disruption from man's activities (Shinn, 1967; personal observations), weather (Linsley, 1952; 1958), the appearance and disappearance of plant populations for reasons unrelated to the bees (Eickwort, 1973; Michener, 1953; personal observations, see description of study sites, Chapter 1). Bees inhabiting arid or semi-arid regions, or early successional stages in temperate ecosystems, would be particularly likely to experience these sources of density-independent mortality. There are some reports (Linsley, 1958) of long-term persistence of particular populations; others found that sites become extinct within a few years of their discovery (Rozen, 1963). There is evidence that at least some species of bees can disperse widely (Eickwort, 1973; Linsley et al., 1959; Michener, 1953), a character necessary for survival if populations are likely to suffer sudden destruction. Finally, the available data for the other principal density-dependent factor - predation and parasitism

- display as wide a range of significance in population control as does the evidence for competition. In Megachile umatillensis (Bohart and Youssef, 1972), predation and parasitism cause the mortality of only about 3% of the population. Among the bees studied by Danks (1971) predators and parasites within the nest destroyed 34% of the egg-to-pupa population, and Linsley (1952) cites a case of near extinction of the host bee population (Diadasia bituberculata Cresson) because of parasitism. If density-independent controlling factors are moderately frequent, and yet some bee populations reach equilibrium size, then the observed variation in the apparent food limitation of bees would be precisely that expected.

Koch (1974) has recently demonstrated that in theory, the alternation of density-independent and density-dependent regulation of population growth in competing species can foster stable coexistence. If my suggestion concerning the sporadic nature of competition among solitary bees is correct, his model might help explain the coexistence of large numbers of bee species utilizing the same food plants at the same time.

I conclude that the intensity of competition among bees and the concommitant degree of limitation of population size by food shortages will depend on the kind of flower providing the food, the age and developmental history of the particular population, and the random occurrence of density-independent events.

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Ecological Interactions between *Euphorbia* and Its Insect Visitors

In considering the nature of the interactions between *Euphorbia* and its insect visitors, the adaptations of individuals of each species to the other species should be distinguished from the responses of whole populations, since adaptation or coadaptation on the level of the individual may be independent of the mutual responses of populations. The interrelations that have been portrayed here between the insects and the plants are indicative of only general, nonspecific evolutionary adaptations on the part of the individuals of each group to the others, and include few instances of effects on the population biologies of the participants.

Interactions Affecting the Traits of Individuals

In the plants, the evolution of the size of the petaloid appendages, glands, and anthers is related to the extent of their dependence upon insects for pollination, but there is no evidence that these species of *Euphorbia* have evolved in such a way as to exploit a particular group of insects. Indeed, although the various types of visitors differ greatly in their ability to pollinate, and in their likelihood of promoting outcrossing, there is no evidence to suggest that the plants have evolved so as to favor more effective visitors and exclude ineffective ones. Thus, adaptation of the plants to the pollinators evidently consists of changes in cyathial dimension and development promoting dependence on insects in general or independence via self-pollination.

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The plants seem to have had little effect on the evolution of the insect visitors to the cyathia (except for the bees; see below). Because of the tremendous diversity of insects collected, it is impossible to generalize about the impact of the association with Euphorbia on the life-histories and ecologies of each kind of insect. However, some, like the predacious bugs, the widely foraging ant species, and the flies and wasps which are tied to animal sources for larval food, are clearly neither likely to experience Euphorbia as a limited food resource, nor are strongly tied to these plants morphologically or physiologically. Others, like the oligolectic bees, some wasps (for example those in the genus Solierella mentioned above), the species of bees and bombyliid flies parasitic upon the bees in this study, at the least are specially adapted to locate these plants and to nest and reproduce under the physical conditions found with the plant. In general, the insect fauna of Euphorbia forms a "concourse" in the terminology of Elton (1966), a grouping distinguished by its temporary nature. The size of the concourse, at least on E. albomarginata, must be in part due to the flat, open form of the cyathium, and to the fact that food presentation occurs during the most common activity period for insects; no special adaptations of foraging behavior or foraging times are required. Thus, the plants have not clearly caused any evolutionary modifications in most of the insects that visit them.

The biology of individual bees oligolectic on Euphorbia, however, has clearly been affected by the plants. Closely related

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congeners of each of the panurgine bees listed in Table 1, that feed on *Euphorbia*, have unusually small mouthparts, whereas bees within the same subgenus or species group that feed on plants with larger flowers generally have larger mouthparts. This pattern suggest that small mouthpart size is an adaptation evolved for feeding on *Euphorbia*. These bees are all among the smallest of their respective genera, but is not clear that small size is an adaptation evolved with respect to *Euphorbia*. In all of the genera, there are other species, foraging on unrelated plants, that are as small or smaller than the bees oligolectic on *Euphorbia*; for example, according to size data for *Nomadopsis* given in Rozen (1958), 31% (11) of the species are as small as *N. helianthi* (as are 50% of the species in subgenus *Micronomadopsis*, to which *N. helianthi* belongs). Whatever the mechanism is that maintains oligolecty (genetic control and possibly preimaginal conditioning), it has been tuned in these bees to *Euphorbia*. Foraging behavior, however, does not display further evidence of adaptation of these bees to their sole food source. No aspect of foraging behavior separated the oligoleges from the polyleges, which are presumably adapted for foraging on a variety of flowers, and no behavior that could be peculiar to this bee-plant association was obvious.

Interactions among Populations

On the population level, these species of *Euphorbia* seem to have experienced little evolutionary or ecological effects from their pollinators. The geographical distributions of the three species are independent of the distributions of the bees (the most effective pollinators and agents of outcrossing), and certainly are unrelated to the distributions of the myriad other insects which frequent the plants. As seen above, the local distribution of populations of the three species is equally unaffected by the composition of the resident insect fauna; the number and identity of the visitors varies greatly from one plant population to another. The success and persistance of the plants under such varied conditions of insect visitiation suggests that insect pollinators are rarely a limiting resource for the two species that require them. The most likely impact of insect visitation on the population biology of the plants is on the genetic population structure; the size of the panmictic population (Grant, 1971), the amount of inbreeding that occurs, and the resultant effects on intra- and inter-population genetic variability could be strongly influenced by the composition and size of the insect fauna. Further investigations will be required to clarify this last point.

Although modification of population phenomena are more pronounced in the oligolectic bees that visit Euphorbia than in any other group, the ties between the plants and the bees are general and weak. The bees are obligately dependent on the presence of Euphorbia for existence, but can make use of a variety of species of Euphorbia in addition to those studied here. (This statement is based on flower record data in Rozen, (1958), Shinn (1967), and Timberlake (1956, 1964a, 1964b), and on the recorded presence of populations of some of these species outside the range of the species of Euphorbia studied here.) Thus, the bees are free to range over much of the southwest, since Euphorbia is diverse and abundant throughout the region, and the known limits of their distributions must be attributable to other factors. The dynamics of each bee population may, in addition, be modified by the nature of the host plant population. I have discussed above the reasons for believing that limitation of the bees' populations by inadequate quantities of food does occur, but the effects (principally the onset of competition among the bees) are mild, and not present in every population.

Thus, interactions among these organisms have been lopsided in direction and intensity, with the result that the elements of the Euphorbia-insect complex vary from very loosely to very tightly coupled. E. albomarginata and E. capitellata are (more or less) obligately dependent on insect visitation, but are not tightly bound to any one species, and E. hyssopifolia probably derives some benefit from insect visitors but is not obligately dependent on them. Conversely, most of the insect visitors derive benefit from the plants, but only a few are obligately, or even principally, dependent on them for food.

Baker and Hurd (1968) divided insect-plant interactions into categories based on the pattern of interaction over evolutionary time; these categories are mutually continuous modification, concurrent stepwise change, and reciprocating stepwise change. This study demonstrates that in any of these categories, the interacting groups can affect each other with unequal force, and it suggest two refinements of this conceptual framework for the study of coevolution. First, interacting groups can affect each other with unequal force, resulting in unequal amounts of evolutionary change in the participants. Second, evolved modifications of individuals may or may not be accompanied by changes in the population biology of the species.

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