

POLLINATION RELATIONSHIPS IN SOUTHERN SPANISH MEDITERRANEAN SHRUBLANDS

Table of contents

JAVIER HERRERA

Digitalizado por
Biblioteca Botánica Andaluza

Departamento de Botánica, Facultad de Biología, E-41080 Sevilla, Spain

SUMMARY

(1) Pollination relationships were investigated for fourteen months in a southern Spanish Mediterranean coastal scrub community, composed of thirty plant species, at Reserva Biológica de Donana, Donana National Park.

(2) Flowering encompassed the whole year, as did insect visits to flowers. Distinct seasonal changes, however, in both the number and identity of insect taxa, and in the number of plant species in bloom were apparent: maximum plant and insect richness occurred in spring.

(3) Insect visitors mainly included small beetles, honeybees, small halictid bees, syrphids and bombylids. The overall species richness of the pollinator array was very high (187 taxa).

(4) Plant species with specialized pollination mechanisms were relatively infrequent. Most plants had non-restrictive or small flowers, or both. Species relying on pollen to attract pollinators outweighed those relying on nectar as the main reward.

(5) Joint analysis of flower attributes, blooming phenology and pollination vectors demonstrated that species flowering at about the same time of year tend to have their flowers visited by the same insects, irrespective of floral features.

(6) It is hypothesized that fruit set is more resource- than pollen-limited and that to achieve maximum fruit set most plants have unspecialized pollination relationships. The generalized nature of pollination systems may have been a major factor contributing to the survival and weedy behaviour of many Mediterranean scrub species.

INTRODUCTION

Pollination studies at the community level are seldom undertaken (Kevan 1972; Heithaus 1974, 1979a, b; Arroyo, Primack & Armesto 1982; Bauer 1983). Investigators usually prefer to concentrate on pollination interactions of particular plants with specialized vectors or, at most, to deal with a few related species. Nevertheless, the community approach, with the general view it provides, is specially suitable to detect trends of organization of pollination relationships on a regional scale. The identity and proportions of the major groups of pollinating insects have been reported for many communities, but there is a lack of information on pollination of scrub systems. Some data are available for scrub vegetation in America (Moldenke 1977; Arroyo, Primack & Armesto 1982) while for the Mediterranean Sea area this is largely unknown.

This paper investigates pollination relationships in a Mediterranean scrub community as part of a study carried out at the community level (Herrera 1986, 1987). Our main goals were (i) to determine the identity and relative abundances of pollen vectors, (ii) to detect seasonal changes both in the pollinator and plant communities and (iii) to assess if specific combinations of floral attributes were related to the type of pollinators. Many pollination studies have dealt with competition or facilitation among plants for pollination, and an extensive literature on character displacement is currently available (Waser 1982;

Rathcke 1983; and references therein). Other studies demonstrate competition among pollinators, suggesting that flowers rather than pollinators are limiting (Inouye 1978; Frankie, Opler & Bawa 1976; Roubik 1982, for example). Although the focus of this paper is not on the occurrence of competition for pollination, results reported here may help to understand the interspecific interactions of plants in Mediterranean shrublands.

STUDY AREA AND METHODS

The study was conducted at Reserva Biologica de Donana (37°1'N, 6°33'W), which lies inside Donana National Park (south-western Spain). The Reserve is in a sandy coastal area where Mediterranean scrub constitutes the main and dominant vegetation. A full description of vegetation types in Donana may be found in Rivas-Martinez *et al.* (1980). The climate is of the Mediterranean type, with mild and moderately wet winters. Average precipitation is 537 mm y⁻¹ and mean annual temperature is 16 °C. January is the coolest month (mean temperature 9·8 °C) and July the hottest (24·6 °C). During 1983, when most of this study was done, total rainfall was below average (476 mm).

The study plot (about 4 ha in size) was 2 km away from the coast. From January 1982 to February 1984 the plot was visited weekly. Our sample of woody perennial plants included thirty species, all of which are very common in scrub formations of Donana (Table 1). The Cistaceae have five taxa in three genera, but most families are represented by just one genus with a single species. The main floral features, such as the colour of the corolla, its morphology and sexuality, and the main reward (nectar, pollen, or both) offered to pollinators were noted. The flowering stage of each species was checked every week by counting the number of flowers on marked plants. The dimensions of flowers (length and radius) were measured to the nearest 0·1 mm in samples of twenty flowers. Data on the reproductive biology of the species which are not included in this paper (fruiting levels, pollen production, nectar secreted, seed dispersal systems, fruiting phenologies, etc.) have been published separately (Herrera 1986, 1987). Most analyses below deal with entomophilous taxa, which account for c. 80% of the total species.

Pollinator censuses

To ascertain the number and identity of pollinators, a number of censuses were performed in all but one of the entomophilous species, *Rhamnus lycioides*, because of its poor flowering in 1983. Each census was five minutes long, and during this time all the insects arriving at the flowers in an area of approximately 1 m² were recorded, provided that they touched anthers and stigmas of the flowers. Many- or few-flowered individual plants were selected for insect censusing, in accordance with the flowering stage of each population. The behaviour of insects and the kind of foraging activity (collecting pollen, nectar or both) were also registered. The amount of pollen transported by different pollinators, however, is not considered in this study. Ants which appeared at the flowers were also collected and identified. Their numbers have not been included in the overall number of insect visitors, because they were not considered to be potential or effective pollinators; ants behaved as nectar thieves or robbers (Inouye 1980). On the basis of floral features (scent, colour, flower opening time), nocturnal pollination was likely to occur in *Daphne gnidium*, *Lonicera periclymenum* and *Smilax aspera*. All three were checked for nocturnal visitors using a head lamp with red light, in addition to the census carried out on them during the day.

TABLE 1. Floral features of the scrub species studied. Major flower visitors recorded at entomophilous species, observation effort (OE, in min), and the total number of insects censused are given. The date of flowering peak is indicated by the month-day (e.g. 4-20 indicates April 20). Plant nomenclature follows Tutin *et al.* (1964-1980).

Species (family)	Form ¹	Size ²	Colour ³	Reward ⁴	Major visitors	Date or flowering peak	OE	Number of insects
<i>Amieria velutina</i> (Plumbaginaceae)	r	10.3	p	N-P	Dermestidae, Halictidae, Calliphoridae	4-20	105	291
<i>Asparagus aphyllus</i> (Liliaceae)*	r	7.0	g	N-P	Calliphoridae, Syrphidae, Halictidae	9-6	120	104
<i>Calluna vulgaris</i> (Ericaceae)	st	3.7	p	N-P	Syrphidae, Calliphoridae, Lycaenidae	11-8	160	134
<i>Chamaerops humilis</i> (Palmae)*	a	6.2	y	None	Wind pollinated	4-20		
<i>Cistus libanotis</i> (Cistaceae)	r	29.9	w	P	Dermestidae, Alleculidae, Halictidae	5-4	155	651
<i>Cistus salvifolius</i> (Cistaceae)	r	42.6	w	P	Dasytidae, <i>Apis</i>	4-6	85	290
<i>Corema album</i> (Empetraceae)*	a	4.9	b	None	Wind pollinated	2-23		
<i>Cytisus grandiflorus</i> (Leguminosae)	f	28.9	y	P	<i>Apis</i>	4-6	60	1
<i>Daphne gnidium</i> (Thymelaeaceae)	st	5.0	c	N-P	Moths, Bombyliidae, Lycaenidae, Anthophoridae	8-26	1080	1830
<i>Erica ciliaris</i> (Ericaceae)	t	8.1	p	N	Anthophoridae, Halictidae, Lycaenidae	9-20	235	64
<i>Erica scoparia</i> (Ericaceae)	st	2.6	g	None	Wind pollinated	5-4		
<i>Halimium commutatum</i> (Cistaceae)	r	22.7	y	P	Halictidae, <i>Apis</i>	3-23	165	116
<i>Halimium halimifolium</i> (Cistaceae)	r	31.7	y	P	Alleculidae, Meloidae, Halictidae	5-18	145	164
<i>Helianthemum croceum</i> (Cistaceae)	r	23.9	y	P	Mordellidae, Dasytidae	4-13	60	64
<i>Helichrysum picardii</i> (Compositae)	st	3.7	y	P	Halictidae, Lycaenidae	6-28	150	42
<i>Lavandula stoechas</i> (Labiatae)		9.1	purple	N	<i>Apis</i> , Bombyliidae	3-30	175	210
<i>Lonicera periclymenum</i> (Caprifoliaceae)	t	40.6	c	N	Sphingidae	7-26	930	51
<i>Myrtus communis</i> (Myrtaceae)	r	15.2	w	P	Anthophoridae, Megachilidae	7-19	75	6
<i>Osyris alba</i> (Santalaceae)*	r	4.1	g	N-P	Mordellidae, small flies	4-13	85	65
<i>Osyris quadripartita</i> (Santalaceae)*	r	3.2	g	N-P	Calliphoridae, Tiphiidae, Sphecidae	5-11	295	81
<i>Phillyrea angustifolia</i> (Oleaceae)	st	3.2	w	None	Wind pollinated	3-16		
<i>Pistacia lentiscus</i> (Anacardiaceae)*	a	2.6	y	None	Wind pollinated	3-30		
<i>Rhamnus lycioides</i> (Rhamnaceae)*	r	5.2	g	N-P	Flies	4-6		
<i>Rosmarinus officinalis</i> (Labiatae)	st	13.1	w	N	<i>Apis</i> , Andrenidae, Halictidae	2-23	715	498
<i>Rubus ulmifolius</i> (Rosaceae)	r	30.7	p	N	Andrenidae, Anthophoridae	6-8	210	230
<i>Smilax aspera</i> (Liliaceae)*	r	6.7	w	P	Syrphidae, Calliphoridae	11-22	290	90
<i>Stauracanthus genistoides</i> (Leguminosae)	r	12.3	y	P	<i>Apis</i> , Halictidae	3-2	145	16
<i>Thymus mastichina</i> (Labiatae)*	st	5.2	w	N	Lycaenidae, Nitidulidae	6-14	135	548
<i>Ulex minor</i> (Leguminosae)	f	10.1	y	P	<i>Apis</i>	11-22	215	64
<i>Ulex parviflorus</i> (Leguminosae)	f	12.7	y	P	<i>Apis</i>	1-16	390	43

¹ r, radiate, dish-bowl corollas; st, shortly tubular (tube less than 5 mm long); t, tubular; a, apetalous; f, flag flowers.

² mean maximum dimension of the corolla, in mm. In sexually dimorphic species (*) the average size of morphs is indicated.

p, pink; g, green; y, yellow; w, white; b, brown; c, cream.

⁴ P, pollen; N, nectar; N-P, nectar and pollen.

Marking of bees and beetles suggested that they foraged day after day in the same site (J. Herrera, personal observation). Furthermore, many bees nested in the ground just below the plants they visited. Because most observations were being carried out in a relatively small area, we thought that the systematic collection of insects inside the study plot could affect the natural density and composition of the pollinator array. For various reasons this seemed undesirable and we tried to keep insect collecting to the minimum necessary for their identification and for gathering data on their size, length of mouth parts, etc. This procedure caused field identification at the specific or generic level to be somewhat ambiguous in some groups. Because of this, the number of individuals is reported at the family level. Moths in various families were indistinguishable in the field and their number is reported collectively. It must be noted that neither the taxonomic criteria in delimiting species nor the accuracy in identification need to be equivalent in all four major insect orders. Insects were consistently identified to the species in the following groups: butterflies, bees, sphecids, syrphids and bombylids. Beetles in most families were identified to the genus. Our analyses do not consider insects in orders other than Coleoptera, Diptera, Hymenoptera and Lepidoptera, because they account altogether for more than 99% of the total. Physical features of a few common pollinating insects, such as length and dry weight of the body, and length of mouth parts, were measured in samples of two to ten specimens per species. These species were selected to illustrate the range of variability found among insects visiting the flowers of scrub species.

Censusing time totalled 6220 min distributed through 57 weeks. The time employed each week was 108 ± 9 min (mean \pm S.E.), and it was divided among the plant species currently in bloom. An effort was made to keep the weekly observation time as constant as possible, so that species remaining in flower for a long time accumulated a higher number of censuses than those with short flowering seasons. Observation effort and flowering duration are in fact positively correlated ($r_s = 0.818$, d.f. = 23, $P < 0.001$). Minimum observation effort for any species was 60 min and maximum 1080 min.

Data analysis

In order to establish how plants differed with respect to pollinators, flower features and blooming phenology, cluster analyses were employed. The purpose of these analyses was to determine if a classification of plant species according to pollinators was congruent with another classification of the same set of species based upon flower features, and with another based on flowering time.

A statistical program in the BMDP series (Dixon 1981) entitled P2M was used to perform classification. The program calculates the dissimilarity between every pair of cases (here, plant species) according to a set of variables supplied. The program was run twice, each with a different set of variables. One set included those variables related to flower features (flower size, colour, morphology of the corolla and reward offered; [Table 1](#)). The other set included thirty-eight insect families, the variates being the numbers of insects recorded at the flowers (Appendix). Each run yielded a species-species symmetrical matrix where the 900 elements are values of dissimilarity. A third species-species matrix was computed separately, where the elements are the numbers of weeks between the flowering peaks of each pair of species. These three matrices could have been used to elaborate three cluster diagrams but, instead, we have made use of their elements as variates in three dissimilarity variables: DSMFLO, which is related to flower features; DSMVEC, related to pollinators; and DSMPHE, related to phenology. After being log-transformed to correct for skewness in their distributions, correlations between

TABLE 2. Abundance of the major insect families and orders recorded at the flowers of the studied species.

Order	Family	Number of insects (
Coleoptera	Dermeestidae	1498
	Nitidulidae	404
	Dasytidae	339
	Others	586
	Total	2827 (33·5)
Diptera	Bombyliidae	1057
	Syrphidae	307
	Calliphoridae	252
	Others	165
	Total	1781 (21·1)
Hymenoptera	Apidae	1287
	Halictidae	715
	Anthophoridae	318
	Sphecidae	93
	Others	325
Lepidoptera	Total	2738 (32·4)
	Lycanidae	755
	Moths ¹	222
	Others	86
	Total	1063 (12·6)
Others		33 (0·4)

¹ Including the families Arctiidae, Geometridae, Noctuidae, Phycitidae and Pyraustidae.

DSMFLO, DSMVEC and DSMPHE were investigated. Because the matrices were symmetrical, only those elements on one side of the main diagonal (i.e. 435) can be properly used, and the degrees of freedom for r are 433.

Positive correlation of DSMFLO vs. DSMVEC would indicate congruency between the classifications based upon flower features and that based upon pollination vectors or, in other words, that plants differing very much in flower traits are likely to have very different flower visitors, and vice versa. Positive correlation of DSMPHE vs. DSMVEC would indicate that most pairs of plants with dissimilar flowering phenologies have also dissimilar flower-visiting insects, at least at the family level.

RESULTS

Plants

The most outstanding floral traits of the species are summarized in Table 1. Five species are anemophilous and the remaining twenty-five, considered in the analyses below, are entomophilous. There are two widespread traits in the entomophilous groups. First, radiate or short-tubed corollas predominate. Except for one long-tubed species (*Lonicera periclymenum*) and the legumes (which have flag flowers), most plants have non-restrictive or small corollas, or both. Second, species offering nectar as the main reward to pollinators are scarce. Both Cistaceae and Leguminosae are heavy pollen producers, not nectariferous (Herrera 1985, 1987), and have the largest flowers in the sample. On the other hand, nectar-offering species commonly had small flowers which provided small amounts of sugar nectar on a daily basis (ranging between 2·0 and 0·1 mg of sugar flower⁻¹ 24 h⁻¹; Herrera 1987).

TABLE 3. Physical features of some common pollinators of the scrub flowers.

Species (Family)	Length (mm)		Body dry weight (mg)
	Body	Proboscis	
Coleoptera			
<i>Anthrenus</i> sp. (Dermestidae)	4		1
<i>Lobonyx aeneus</i> (Dasytidae)	6		2
<i>Heliotaurus ruficollis</i> (Alleculidae)	13		26
Diptera			
<i>Bomb_vlius torquatus</i> (Bombyliidae)	10	8	16
<i>Phthiria</i> sp. (Bombyliidae)	5	2	2
<i>Eristalis tenax</i> (Syrphidae)	15	5	36
<i>Lathyrphtalmus quinquelineatus</i> (Syrphidae)	9	3	5
Hymenoptera			
<i>Apis mellifera</i> (Apidae)	13	6	32
<i>Lasioglossum littorale</i> (Halictidae)	6	2	5
<i>Lasioglossum immunitum</i> (Halictidae)	10	3	12
<i>Amegilla fasciata</i> (Anthophoridae)	12	11	36
<i>Ceratina cucurbitina</i> (Anthophoridae)	8	3	5
Lepidoptera			
<i>Plebejus argus</i> (Lycaenidae)	11	7	11
<i>Syntarucus pirithous</i> (Lycaenidae)	10	6	8

TABLE 4. Number of scrub species reaching flowering peak in each season, and number of insect taxa that visited the flowers of the entomophilous group. Winter encompasses January—March; Spring, April—June; Summer, July—September; Autumn, October—December.

Plant species	Winter 8	Spring 14	Summer 5	Autumn 3
Insect taxa				
Coleoptera	8	23	12	0
Diptera	13	13	14	18
Hymenoptera	11	31	32	19
Lepidoptera	7	12	13	7
Total	39	79	71	44

Insects

Some 187 insect taxa were recorded, of which twenty-nine are coleopterans, thirty dipterans, eighty-seven hymenopterans (fifty-six apoidean, thirty-one non-apoidean), and forty-one lepidopterans (Appendix). Forty-six insect families are represented, but only five exceed 5% of total insects, namely Dermestidae, Bombyliidae, Apidae, Halictidae and Lycaenidae (Table 2). Beetles in the families Dermestidae, Nitidulidae and Dasytidae were small insects up to 6 mm long and were often seen foraging and mating at the flat, open flowers of the Cistaceae. Larger and showy beetles such as those in the Alleculidae (Table 3) were far less common. Representatives of the Bombyliidae ranged in size from those in the genus *Phthiria* to those in the genus *Bombylius* (up to 10 mm). They usually had proboscides which were long relative to body size (Table 3). They probed for nectar either in open or tubular flowers. Among the hymenopterans, it is striking that out of 1287 insects in the family Apidae all but one (a bumblebee) were honeybees. Conversely, Halictidae and Anthophoridae had high species richness. Most halictid bees

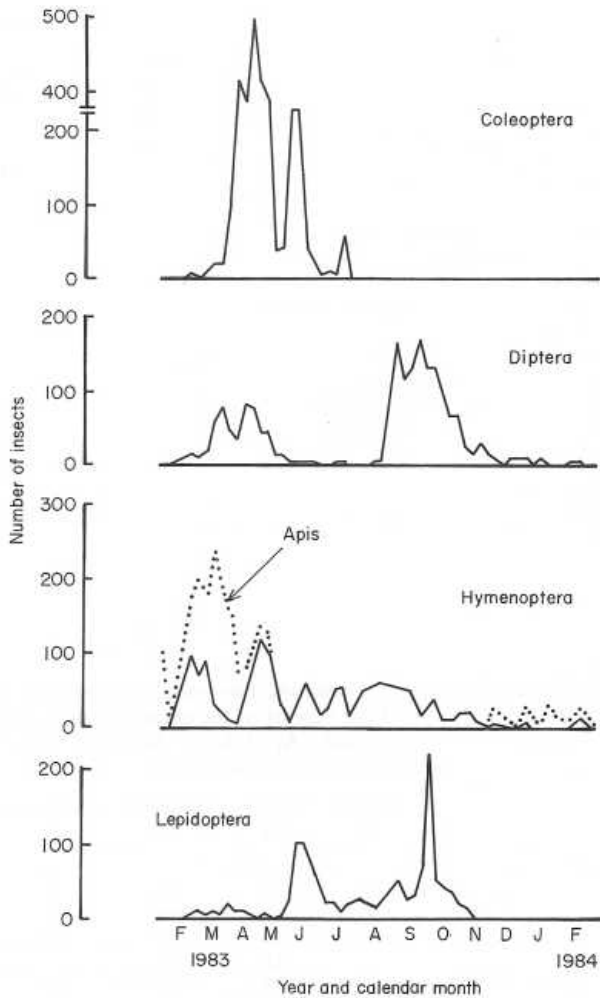


FIG. 1. Number of insects in the four major orders recorded at the flowers of entomophilous scrub species at Reserva Biologica de Donana at weekly intervals.

were small, short-tongued bees in the genus *Lasioglossum*. The Anthophoridae included either small (*Ceratina*) or large (*Anthophora*, *Amegilla*, *Xylocopa*), commonly long-tongued bees (Table 3). The only lepidopteran family strongly represented was Lycaenidae. These were small butterflies, with relatively short proboscides, that foraged for nectar in flowers with open or shortly tubular corollas. Hawkmoths were unimportant in terms of the number of individuals observed.

Seasonality

The plant community showed uninterrupted flowering activity through the year, but most species reached their blooming peaks in spring (Table 4). In a parallel way, insect visits to flowers was also continuous. Maximum insect taxa richness occurred in spring and summer, while winter and autumn had much lower richness (Table 4).

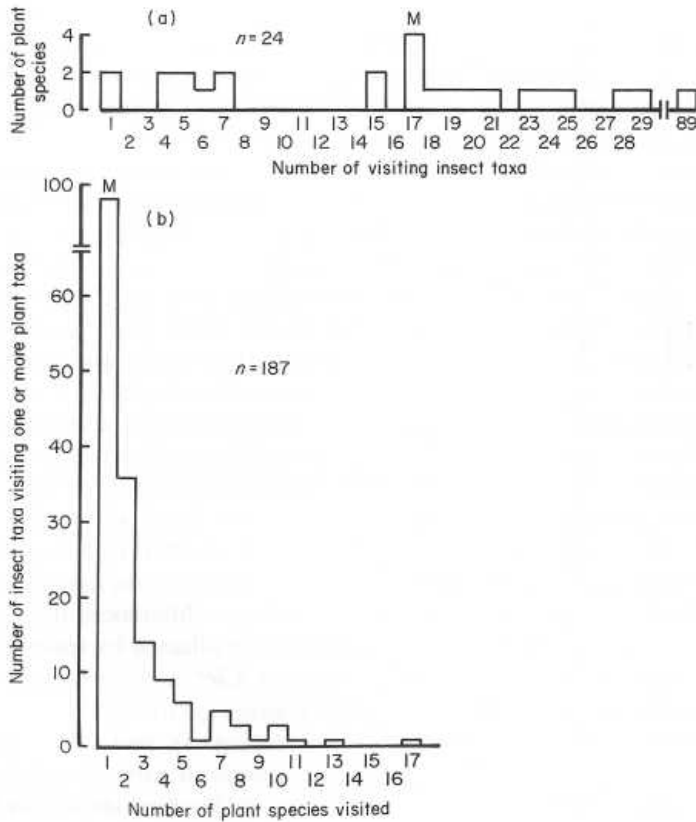


FIG. 2. Distribution of insects among plants and of plants among insects at Reserva Biologica de Doñana from February 1983 to February 1984. M, median value.

There were seasonal changes in the number of insects in the four major orders (Fig. 1). Beetles were nearly absent from flowers in seasons other than spring (April–June), but in this season they appeared in very large numbers. Dipterans were present all through the year but exhibited two marked peaks: the Bombyliidae were responsible for the early spring peak, whereas the Syrphidae and Calliphoridae constituted the late summer–early autumn peak. Maximum numbers of hymenopteran visitors were registered in late winter and spring. From January to May *Apis mellifera* was the most frequent bee at flowers, together with halictids in the genus *Lasioglossum*. Whether the honeybees in our plot came from distant domestic hives or from wild colonies is unknown. Intensive beekeeping is common outside the Biological Reserve. From May to November honeybees were absent, and during that time many solitary bee species, each represented by low numbers of individuals, visited the flowers of the scrub species. Lepidopteran visitors showed a peak in June, caused by the lycaenid *Plebejus argus*, and another peak in September–October caused by another lycaenid, *Syntarucus pithous*, together with moths in various families.

Pollination relationships

Overall, honeybees, halictids, syrphids and caliphorids, together with small beetles and, to a lesser extent, lycaenid butterflies and anthophorid bees were all frequent visitors of

many plant species (Table 1). The legumes were visited by only hymenopterans, mostly *Apis mellifera*. The Cistaceae were favoured by small or large beetles and pollen-collecting solitary bees, while the Labiatae were favoured by hymenopterans and nectar-seeking dipterans and lepidopterans. There is a coarse organization of pollination relationships, which becomes apparent mostly at the family level.

Total numbers of insect taxa for any plant ranged between one and eighty-nine (Fig. 2a). Mean number for all plants is 14.8 ± 3.04 . The number of plant species visited by any insect taxon ranged between one and seventeen (Fig. 2b) and the mean is 2.4 ± 0.28 . Both distributions in Fig. 2 are either strongly skewed or discontinuous, so that the median (i.e. the value that divides the distribution in two halves) may be a more representative measure of location than the mean (Sokal & Rohlf 1981). The median for the first distribution is 17, and for the second is 1. This implies that, while most plants were visited by seventeen or more insect taxa, most insects appeared on the flowers of just one plant species. Thus, pollination relationships departed from a one-to-one interaction, because there were many uncommon visitors which appeared in very low frequencies.

The relationship between observation efforts and the numbers of visitors censused (Table 1) is not straightforward, these variables not being significantly correlated ($r_s = 0.202$, d.f. = 22, $P > 0.2$). For instance, an observation effort totalling 390 min of the flowers of *Ulex parviflorus* yielded forty-three visitors, while *Cistus salvifolius* yielded 290 insects after 85 min. It seems likely that there are intrinsic differences among plants with respect to their attractiveness. Also, visitation rates are affected by seasonal changes of insect abundance: *Cistus salvifolius* flowers in spring, *Ulex parviflorus* in winter.

Undoubtedly, the size of the insect array undergoes seasonal changes. The diversity and the relative composition of the array do likewise (Fig. 1), and this could affect the occurrence or non-occurrence of particular insect groups on particular plants. Although some organization of pollination relationships exists and has been shown, we have tried to ascertain whether flowering phenology plays a major role or not in determining the kind of visitors found on the flowers. We have investigated the importance of flower features in determining the composition of the visitor array of each plant by three dissimilarity variables, named DSMVEC (related to the pollinators of each plant species), DSMFLO (related to flower features) and DSMPHE (related to flowering phenology). The variates of these variables are dissimilarity values in two species-species matrices obtained through cluster analyses and one species-species matrix of phenological dissimilarity (see Methods). DSMFLO and DSMVEC are uncorrelated ($r = -0.034$, $P > 0.5$), while DSMPHE and DSMVEC show a highly significant correlation ($r = 0.211$, $P < 0.001$). Thus, in relation to the time of year in which a scrub species bloomed, flower features played a minor role in the distribution of insects among plants. In other words, a classification of plants according to pollinators is not congruent with another classification of the same set of plants made according to flower characteristics (colour, reward, size, morphology), whereas it is with a classification based on flowering phenologies.

DISCUSSION

Most scrub species studied have small, non-restrictive flowers. In many instances, species offer little or no nectar to pollinators (Herrera 1985, 1987), pollinator attraction being based on pollen. On the other hand, the array of insects is mainly constituted by small beetles, short-tongued solitary bees, flies, etc., all of which have been reported to exhibit

low energetic demands (Heinrich 1975). The results are consistent with the statement made by Heinrich & Raven (1972) that for a pollination system to work properly there must be a trade-off between the reward provided by flowers and the energetic requirements of the pollen vectors. Proportions of pollinating insects reported in this paper closely resemble those reported for other Mediterranean areas (Moldenke 1977) but, unlike Chilean, Californian, South African and Australian shrub communities, bird pollination is absent (Ford 1985).

Both plants and insects showed a markedly seasonal pattern. Peak number of plant species in bloom and of insects at flowers occurred in spring. Nevertheless, many non-anthophilous insects in southern Spain show peak activity in spring as well (Jordano 1984). Thus, simultaneous flower and insect abundance may be due to the fact that general environmental conditions existing during the spring in Mediterranean ecosystems are optimal for both insect and plant physiological activity (Cody & Mooney 1978; Kummerow 1983). The possibility should not be ruled out, however, of past phenological adjustments between particular plants and anthophilous insects.

Lack or relative scarcity of floral specialization in the community studied leads one to envisage it largely as a system of generalists in which species currently in bloom attract insects currently available. This notion is supported by the fact that plants flowering at about the same time of year tend to have their flowers visited by the same insects, as demonstrated by strong positive correlation between dissimilarity of phenology (DSMPHE) and dissimilarity of pollinating insects (DSMVEC). On the other hand, similarity of flower traits does not involve proportional similarity of flower visitors, as demonstrated by lack of correlation between dissimilarity of flower features (DSMFLO) and dissimilarity of pollinating insects. It could be that the features used to measure the differences between two flowers were inappropriate. Nevertheless, colour, size, morphology and reward are all usually employed to reveal most pollination syndromes (van der Pijl 1961; Faegri & van der Pijl 1979). Rather, we think that floral differences among scrub species are not significant enough in most instances to bring about sizeable differences in pollinating insects. Certainly, there were instances of plants whose flowers consistently attracted some kind of pollinators more than others: the Cistaceae were favoured by beetles and pollen-collecting bees; the legume flowers were worked more commonly by hymenopterans; *Lonicera periclymenum*, the only hawkmoth flower (Brantjes 1973), was visited by hawkmoths. Thus, pollination relationships show a pattern in the community, although a rather coarse one.

Bagging experiments not reported in this paper demonstrated that exclusion of pollinators caused seed production to be negligible in most instances (Herrera 1987). On the other hand, percentage fruit set was inversely related to fruit and seed size, so that large-seeded species commonly dispersed by vertebrates have low percentage fruit set, and abiotically-dispersed ones have higher (Herrera 1987). This suggests that the number of seeds released is more resource- than pollen-limited (Bawa & Beach 1981; Stephenson 1981). Offering many small and unspecialized, low-rewarding flowers may be the way by which scrub plants achieve maximum fruit set. Fruit and seed features (perhaps related to dispersal or seedling establishment) may have been more significant in the evolutionary history of Mediterranean scrub plants than pollination mechanisms.

These remarks on pollination relationships only take into account frequent visitors, and some caution is needed. A major shortcoming in our data is that differential effectiveness of particular visitors is not contemplated. We know nothing about their respective flight patterns and relative effectiveness in pollen transfer, and there is no

reason to assume that the importance of a given visitor is just proportional to its abundance (Primack & Silander 1975; Webb & Bawa 1983; Janzen 1985). Results showed that about sixteen insect taxa visited the flowers of any entomophilous species, while only two plant species were on the average visited by a given insect. The reason for such asymmetry was the existence of many rare insect species which contributed only few individuals to the pollinator array. Although skewed frequency distributions of pollinators among plants are common in the pollination assemblages of the world where this has been studied (Heithaus 1974, 1979a; Arroyo, Primack & Armesto 1982), it could be misleading to overlook rare pollinators and to draw conclusions from just the commonest ones. Thus, relative effectiveness of different pollinators demands further study.

According to Boucher, James & Keeler (1982) and Kevan & Baker (1983) pollination relationships should be largely generalized in many plant communities because of the benefits which flexibility in mutualistic interactions may provide. One of the benefits is the possibility of replacement of any member of the mutualist group following environmental changes. The Mediterranean Basin has experienced dramatic changes of climate during the last 3·5 million years caused by glaciations at higher latitudes. Moreover, extant scrub communities are considered to have been built up recently through destruction of the original *Quercus*-dominated, sclerophyllous forests (Pons 1981). Axelrod (1975) pointed out that many Mediterranean scrub taxa were ecologically generalists, since they had successfully surmounted changing environmental conditions. We suggest that the generalized nature of pollination systems may have been, and is today, another major factor contributing to the survival and invasive behaviour of many Mediterranean scrub species.

ACKNOWLEDGMENTS

Funds provided by the Spanish C.A.I.C.Y.T. made possible this study, through a grant to S. Talavera (Departamento de Botanica, Facultad de Biologia, Sevilla). Computer facilities were supplied by the Centro de Calculo, Universidad de Sevilla. I thank C. M. Herrera and R. B. Primack for reading and criticizing an earlier version of the manuscript. The following persons assisted with insect identification: E. Asensio, I.N.I.A., Valladolid (bees); J. Baez and J. Bowden, Departamento de Zoologia, Universidad de La Laguna, Tenerife (beeflies); X. Espadaler, Departamento de Zoologia, Universidad Autonoma, Barcelona (ants); S. F. Gayubo (wasps) and M. A. Marcos (hoverflies), Departamento de Zoologia, Facultad de Biologia, Salamanca; C. M. Herrera and J. A. Amat, Estacion Biologica de Donana, Sevilla (butterflies); A. Vives and J. L. Yela, Instituto Espanol de Entomologia, Madrid (moths); A. Cobos, Estacion Experimental de Zonas Aridas, Almeria (beetles).

REFERENCES

- Arroyo, M. T. K., Primack, R. & Armesto, J. (1982). Community studies in pollination ecology in the high temperate Andes of Central Chile. I. Pollination mechanisms and altitudinal variation. *American Journal of Botany*, **69**, 82-97.
- Axelrod, D. I. (1975). Evolution and biogeography of the Madrean-Tethyan sclerophyll vegetation. *Annals of the Missouri Botanical Garden*, **62**, 284-334.
- Bauer, P. J. (1983). Bumblebee pollination relationships on the Beartooth Plateau Tundra of southern Montana. *American Journal of Botany*, **70**, 134-144.

- Bawa, K. S. & Beach, J. H. (1981). Evolution of sexual systems in flowering plants. *Annals of the Missouri Botanical Garden*, **68**, 254–274.
- Boucher, D. H., James, S. & Keeler, K. H. (1982). The ecology of mutualism. *Annual Review of Ecology and Systematics*, **13**, 315–347.
- Brantjes, N. B. M. (1973). Sphingophilous flowers, function of their scent. *Pollination and Dispersal* (Ed by N. B. M. Brantjes & H. F. Linskens), pp. 27–46. Department of Botany, University of Nijmegen.
- Cody, M. L. & Mooney, H. A. (1978). Convergence versus non-convergence in Mediterranean-climate ecosystems. *Annual Review of Ecology and Systematics*, **9**, 265–321.
- Dixon, W. J. (1981). *Statistical Software*. University of California Press.
- Faegri, K. & van der Pijl, L. (1979). *Principles of Pollination Biology*. Pergamon, Oxford.
- Ford, H. A. (1985). Nectarivory and pollination by birds in southern Australia and Europe. *Oikos*, **44**, 127–131.
- Frankie, G. W., Opler, P. A. & Bawa, K. S. (1976). Foraging behaviour of solitary bees: implications for outcrossing of a neotropical forest tree species. *Journal of Ecology*, **64**, 1049–1057.
- Heinrich, B. (1975). Energetics of pollination. *Annual Review of Ecology and Systematics*, **6**, 139–170.
- Heinrich, B. & Raven, P. H. (1972). Energetics and pollination ecology. *Science*, **176**, 597–602.
- Heithaus, E. R. (1974). The role of plant–pollinator interactions in determining community structure. *Annals of the Missouri Botanical Garden*, **61**, 657–691.
- Heithaus, E. R. (1979a). Community structure of neotropical flower visiting bees and wasps: diversity and phenology. *Ecology*, **60**, 190–202.
- Heithaus, E. R. (1979b). Flower visitation records and resource overlap of bees and wasps in northwest Costa Rica. *Brenesia*, **16**, 9–52.
- Herrera, J. (1985). Nectar secretion patterns in southern Spanish Mediterranean shrublands. *Israel Journal of Botany*, **34**, 47–58.
- Herrera, J. (1986). Flowering and fruiting phenology in the coastal shrublands of Donana, south Spain. *Vegetatio*, **68**, 91–98.
- Herrera, J. (1987). Flower and fruit biology in southern Spanish Mediterranean shrublands. *Annals of the Missouri Botanical Garden*, **74**, 69–78.
- Inouye, D. W. (1978). Resource partitioning in bumblebees: experimental studies of foraging behaviour. *Ecology*, **59**, 672–678.
- Inouye, D. W. (1980). The terminology of floral larceny. *Ecology*, **61**, 1251–1253.
- Janzen, D. H. (1985). The natural history of mutualisms. *The Biology of Mutualism* (Ed by D. H. Boucher), pp. 40–99. Croom Helm, London.
- Jordano, P. (1984). *Relaciones entre plantas y ayes frugivoros en el matorral mediterraneo del area de Donana*. Ph.D. Thesis, Universidad de Sevilla.
- Kevan, P. G. (1972). Insect pollination of high arctic flowers. *Journal of Ecology*, **60**, 831–847.
- Kevan, P. G. & Baker, H. G. (1983). Insects as flower visitors and pollinators. *Annual Review of Entomology*, **28**, 407–453.
- Kummerow, J. (1983). Comparative phenology of Mediterranean-type plant communities. *Mediterranean-Type Ecosystems* (Ed by F. J. Kruger, D. T. Mitchell & J. U. M. Jarvis), pp. 300–317. Springer, Berlin.
- Moldenke, A. R. (1977). Insect–plant relations. *Chile–California Mediterranean Scrub Atlas* (Ed by N. J. W. Thrower & D. E. Bradbury), pp. 199–217. Dowden, Hutchinson and Ross, Stroudsburg, Pennsylvania.
- Pons, A. (1981). The history of Mediterranean shrublands. *Mediterranean-type Ecosystems* (Ed by F. di Castri, D. W. Goodall & R. L. Specht), pp. 131–138. Elsevier, Amsterdam.
- Primack, R. B. & Silander, J. A. (1975). Measuring the relative importance of different pollinators to plants. *Nature*, **255**, 143–144.
- Rathcke, B. (1983). Competition and facilitation among plants for pollination. *Pollination Biology* (Ed by L. A. Real), pp. 305–329. Academic Press, Orlando.
- Rivas-Martínez, S. M., Costa, M., Castroviejo, S. & Valdes, E. (1980). Vegetación de Doñana (Huelva, España). *Lazarro*, **2**, 5–189.
- Roubik, D. W. (1982). The ecological impact of nectar-robbing bees and pollinating hummingbirds on a tropical shrub. *Ecology*, **63**, 354–360.
- Sokal, R. R. & Rohlf, F. J. (1981). *Biometry*. Freeman, San Francisco.
- Stephenson, A. G. (1981). Flower and fruit abortion: proximate causes and ultimate functions. *Annual Review of Ecology and Systematics*, **12**, 253–279.
- Tutin, T. G., Heywood, V. H., Burges, N. A., Moore, D. M., Valentine, D. H., Walters, S. M. & Webb, D. A. (Eds) (1964–1980). *Flora Europaea*. 5 vols. Cambridge University Press, Cambridge.
- van der Pijl, L. (1961). Ecological aspects of flower evolution. II. Zoophilous flower classes. *Evolution*, **15**, 44–59.
- Waser, N. M. (1982). Competition for pollination and floral character differences among sympatric plant species: a review of evidence. *Handbook of Experimental Pollination Biology* (Ed by C. E. Jones & R. J. Little), pp. 277–289. Scientific and Academic Editions, New York.
- Webb, C. J. & Bawa, K. S. (1983). Pollen dispersal by hummingbirds and butterflies: a comparative study of two lowland tropical plants. *Evolution*, **37**, 1258–1270.

(Received 1 April 1987)

APPENDIX

Insect visitors recorded at the flowers of the scrub species. Figures in parentheses following each family name indicate the number of individuals in this family censused; NI, unidentified genus. The names of the plant species visited by each insect taxon are indicated in parentheses in abbreviated form: AV, *Armeria velutina*; AA, *Asparagus aphyllus*; CV, *Calluna vulgaris*; CH, *Chamaerops humilis*; CG, *Cytisus grandiflorus*; DG, *Daphne gnidium*; EC, *Erica ciliaris*; CL, *Cistus libanotis*; CS, *Cistus salvifolius*; HC, *Halimium commutatum*; HH, *Halimium halimifolium*; HEC, *Helianthemum croceum*; HP, *Helichrysum picardii*; LS, *Lavandula stoechas*; LP, *Lonicera periclymenum*; MC, *Myrtus communis*; OA, *Osyris alba*; OQ, *Osyris quadripartita*; PA, *Phillyrea angustifolia*; RO, *Rosmarinus officinalis*; RU, *Rubus ulmifolius*; SA, *Smilax aspera*; SG, *Stauracanthus genistoides*; TM, *Thymus mastichina*; UM, *Ulex minor*; UP, *Ulex pary florus*.

Coleoptera

ALLECULIDAE (56): *Heliotaurus ruficollis* Fabr. (CL, HH); BRUCHIDAE (1): NI (HH); BUPRESTIDAE (9): *Anthaxia parallela* C. et G. (CL), *A. dimidiata* C. Thumb (HH, HC), *Acmaeodera* sp. (HH, HP); CANTHARIDAE (7): *Malthodes* sp. (CS), NI (CS, HH, CL, MC); CERAMBYCIDAE (17): *Nustera distigma* Charpentier (CL, AV), *Deilus* sp. (CS, CL), NI (CS); CETONIIDAE (5): *Palleira femorata* I11 g. (AV), *Tropinota squalida* Scop. (RO, CS); CRYOMELIDAE (62): *Coptocephala unifasciata* Scop. (TM, HH), *C. scopolina* L. (HH); CURCULIONIDAE (2): *Tychius* sp. (AV), NI (CH); DASYTIDAE (339): *Lobonyx aeneus* F. (HC, HEC, CS, CL, HH); DERMESTIDAE (1498): *Anthrenus* sp. (TM, HEC, CS, OA, HP, AV, CL, HH, RU), *Attagenus* sp. (HC); ELATERIDAE (3): *Cardiophorus bipunctatus* Fab. (CL); HELODIDAE (1): NI (CS); MALACHIDAE (9): *Malachius* sp. (HC, CS, CL), NI (CS, CH); MELILIDAE (8): NI (CS, CL); MELOIDAE (70): *Mylabrix* sp. (HH); MELOLONTIDAE (81): *Chasmatopterus* sp. (CL, HH), *Hymenoplia* sp. (AV); MORDELLIDAE (81): *Mordellistena* sp. (CL, HEC, CS, OA, AV); NITIDULIDAE (404): NI (AV, RU, TM, HH); OEDEMERIDAE (1): NI (HH); OTHER FAMILIES (123).

Diptera

BOMBYLIIDAE (1057): *Bombylius argentifrons* Loew (LS), *B. ater* L. (LS, CL), *B. fulvescens* Wied. (LS), *B. torquatus* Loew (LS, RO, HC), *Dischistus senex* Mg. (LS), *Conophorus fuminervis* Dufour (CS, CL), *Lomatia infernalis* Schiner (CL, TM), *Exoprosopa italica* Meigen (HP), *Petrorossia* sp. (MC, DG), *Phthiria* sp. (CL, RU, TM, HP, AA, DG, EC, CV, HH, HC, RO); CALLIPHORIDAE (252): NI (UP, RO, HC, LS, CS, OA, AV, CL, OQ, RU, TM, HP, AA, DG, SA, CV, UM); MUSCIDAE (30): NI (RO, OQ, AA, DG, SA, CV, UM); SYRPHIDAE (307): *Eristalis tenax* L. (RO, HC, LS, AV, OQ, RU, DG, EC, UP, CV), *E. arbustorum* L. (DG), *E. pratorum* Meigen (CS, DG, CV), *Eristalodes taeniops* Wied. (DG, AA, CV), *Episyrphus balteatus* De Geer (DG, SA, CV), *E. auricollis* Meigen (RO, DG, SA, UM), *Chrysotoxum intermedium* Mg. (SA), *Lathyrophthalmus aeneus* Scop. (HC, DG), *L. quinquelineatus* Fabr. (DG, CV), *Melanostoma mellinum* L. (SA), *Metasyrphus corollae* Fabr. (RO, OQ, DG, SA, UM), *Sphaerophoria scripta* L. (CS, TM, HP, DG, CV), *S. rueppelli* Wied. (TM), *Syrirta pipiens* L. (AA), *Paragus tibialis* Tallen (HP), *Volucella elegans* Lw. (DG); TACHINIDAE (17): NI (RO, OA, DG, SA, UP); OTHER FAMILIES (118).

Hymenoptera

Apoidea: ANDRENIDAE (86): *Andrena bicolor* subsp. *nigrosteria* Per. (RO), *A. bimaculata* War. (OQ), *A. assimilis* subsp. *gallica* Schm. (RU), *A. hispania* War. (RO, AV, RU, TM), *A. nigroaenea* Drs. (CL, CS), *A. squalida* Perez (RO, HC), *Andrena* sp. (CS), *Panurgus* sp. (CS); ANTHOPHORIDAE (318): *Amegilla fasciata* F. (DG, MC, EC, AA), *A. 4-fasciata* Vill. (LP, EC), *Anthophora acervorum* L. (LS), *A. dispar* Lepelletier (RO, LS), *Anthophora* sp. (SG), *Epeolus fallax* Mor. (CV), *Eucera hispaliensis* Per. (LS), *Ceratina cucurbitina* Rossi (LS, CS, RU, TM, MC, DG, CV), *C. cyanea* K. (HP, AA, DG, EC), *C. mocsaryi* Fr. (DG, EC, RO), *Nomada mutabilis* Mor. (RO), *Tetralonia berlandi* Dusmet (LS, RO), *Xylocopa cantabrita* Lep. (RO, RU, CL, LP, EC, CV, DG), *X. violacea* L. (LP); APIDAE (1287): *Apis mellifera* L. (UP, RO, LS, HC, SG, PA, CS, CL, OQ, CG, HH, RU, CV, UM), *Bombus lucorum* L. (LS, RU); COLLETIDAE (33): *Colletes acutus* Per. (AV, CS, OQ),

C. caspicus subsp. *dusmeti* Nosk. (HP, DG, CV, AA), *C. fodiens* subsp. *hispanicus* Nosk. (HP), *C. succintus* L. (CV, UM, DG), *Colletes* sp. (SA, SG); HALICTIDAE (715): *Lasioglossum aegyptiellum* Stdr. (DG), *L. albocinctum* Luc. (LS, RU, HP, DG), *L. callizonium* Per. (DG), *L. immunitum* Vach. (HC, CL, CS, AV, HH, TM, DG, EC), *L. littorals* Blut. (CL, RO, AV, AA, DG, SA, CV), *L. pallens* BR. (OA), *L. prasinum* Sm. (HC, AV, CL, OQ, RU, HH, AA, DG, SA, CV), *L. punctatissimum* Schck. (CL, HP, AA, TM, DG, EC, CV), *L. villosulum* K. (SA), *Lasioglossum* sp. (RO, UM, OQ, AA, DG, SG), *Halictus 4-cinctus* F. (LS, CS, TM, HP, HH, DG), *H. fulvipes* Kl. (DG), *H. gemmeus* Dours. (DG), *H. scabiosae* Rossi (DG), *H. seladonia-smaragdulus* Vach. (AA), *Sphecodes hirtellus* B1. (OQ), *S. pellucidus* Sm. (CS); MEGACHILIDAE (53): *Anthidiellum strigatum* Pz. (TM, DG), *Stelis signata* Latr. (AV, DG), *Megachile marina* K. (RU, LP, EC), *M. leachella* Curtiss (MC), *M. pilaeus* Alfken (MC, DG, EC), *Heriades crenulatus* Nyl. (DG), *Osmia* sp. (DG); MELITTIDAE (16): *Dasygaster cingulata* Erich. (AV, RU, TM, DG), *D. iberica* War. (CL).

Hymenoptera

Non-apoidea: EUMENIDAE (41): *Eumenes dubius* Saussure (DG), *Odynerus* sp. (DG), NI (AA, DG, CV); FORMICIDAE: *Camponotus lateralis* (Oliv.) (CS, CH), *C. sicheli* Mayr. (RL, OQ), *Cataglyphis viatica* Fabr. (AA), *Crematogaster auberti* Emery (AV), *Lasius niger* (L.) (CH, CL, HP, AV, SA, RU, AA), *Tapinoma erraticum* (Latr.) (CH), *Tapinoma* sp. (AV); POMPILIDAE (4): NI (TM, HP, OQ); SCOLIIDAE (13): *Ells cilliosa* Fabr. (TM, HP, DG); SPHECIDAE (93): *Ammophila heydeni* Dahlbom (DG), *Bembix flavescens* Handlirsch (DG), *B. olivacea* Fabr. (DG), *Cerceris arenaria* L. (SA, CV), *C. rybiensis* L. (OQ, TM), *Diodontus insidiosus* Spooner (CS), *Gorytes* sp. (DG), *Lindenus luteiventris* A. Moravitz (CL, HP), *Mellinus arrensis* L. (CV), *Philanthus triangulum* Fabr. (OQ), *Philanthus aff. renustus* Rossi (TM), *Podalonia tydei senilis* Dahlbom (RO), *Pryonix kirbii* Vander Linden (DG); TIPHIIDAE (37): *Meria tripunctata* Rossi (TM, HP, DG), *Meria* sp. (OQ, TM, DG), *Tiphia morio* Fabr. (CL, OQ); OTHER FAMILIES (43).

Lepidoptera

LYCAENIDAE (751): *Aricia cramera* Eschscholtz (DG, CV), *Laeosopis roboris* Esper (RU), *Lampides baeticus* L. (DG), *Lycaena phlaeas* L. (RO), *Plebejus argus* L. (RU, TM, HP), *Polyommatus icarus* Rottemburg (LS, DG), *Smylaricus pirithous* L. (DG, EC, AA, CV, SA); HESPERIDAE (2): *Gegenes* sp. (DG, EC); PIERIDAE (15): *Colias croceus* Fourc. (DG), *Gonepteryx cleopatra* L. (CL), *Pieris brassicae* L. (DG), *P. rapae* L. (DG, RU), *Pontia daplidice* L. (DG); SATYRIDAE (2): *Pyronia cecilia* Vallantin (DG); SPHINGIDAE (24): *Macroglossum stellatarum* L. (DG, LP); MOTHS (222) including: ARCTIIDAE: *Edema complana* L. (DG); GEOMETRIDAE: *Rhodometra sacaria* L. (DG), NI (DG); NOCTUIDAE: *Hoplodrina ambigua* Schiff. (DG), *Agrotis puta* Hb. (DG), *Mythimna vitellina* Hb. (DG), *Metachrostis dardouinii* B. (DG), *M. relox* Hb. (DG), *Heliothis armigera* Hb. (DG), *H. nubigera* H. S. (DG), *H. peltigera* Schiff. (DG), *Cerocala scapulosa* Hb. (DG), *Discestra sodae* Rbr. (DG), *Pechipogo plumigeralis* Hb. (DG), *Autographa gamma* L. (DG), *Spodoptera exigua* Hb. (DG); PHYCITIDAE: *Acrobasis porphyrella* Dup. (DG), *Pempeliella plufnbella* Schiff. (DG), *Psorosa brephiella* Stgr. (DG), *P. genistella* Dup. (DG); PYRAUSTIDAE: *Erergestis politalis* Schiff. (DG), *Mecyna* sp. (DG), *Palpita unionalis* Hb. (DG), *Udaea martialis* Gn. (DG); OTHER FAMILIES (43).

Introduction

Study area and methods

Pollinator censuses

Data analysis

Results

Plants

Insects

Seasonality

Pollination relationships

Discussion

Acknowledgments

References

Appendix. Insect visitors recorded...

Table 1. Floral features...

Table 2. Abundance of the major insect...

Table 3. Physical features of pollinators...

Table 4. Number of scrub species...

Figure 1. Number of insects...

Figure 2. Distribution of insects...