Biological Journal of the Linnean Society (1988), *35:* 95–125. With 5 figures

Variation in mutualisms: the spatio-temporal mosaic of a pollinator assemblage

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Received 5 January 1988, accepted for publication 15 March 1988

Variation in time (annual and seasonal) and space (between- and within-population) is examined for the pollinator assemblage of *Lavandula latifolia* (Labiatae), an insect-pollinated, summer-flowering, evergreen shrub of Mediterranean woodlands in southeastern Spain. *Lavandula latifolia* is pollinated there by nearly 85 species of comparatively long-tongued Hymenoptera, Diptera and Lepidoptera.

The diversity, composition and abundance of pollinators varied markedly between years. Lepidopteran taxa prevailed numerically in one year, hymenopterans in four years, and both groups had similar abundance in the remaining year. The vast majority of pollinators exhibited significant annual differences in average abundance. Only 35.7% of taxa were recorded in all of the six study years. The pollinator assemblage had marked seasonal dynamics. Important changes in species richness, abundance and composition took place over the flowering season of *L. latifolia* (nearly 3 months). Only 21.7% of insect taxa occurred throughout the flowering season. *Lavandula latifolia* populations at different distances from water courses differed broadly in the abundance and composition of pollinators. Hymenopterans dominated numerically at the water-distant sites, whereas lepidopterans prevailed in populations growing in the vicinity of streams. Only 40.7% of taxa were recorded at all of the four study populations. Within the same plant population, horizontal distances of the order of 25 m resulted in significant changes in pollinator composition.

Variations at the four scales considered combine to produce, from the viewpoint of *L. latifolia*, a spatio-temporal mosaic of pollinators. As these differ broadly in frequency of pollen transfer, size of pollen loads deposited, and between-flower flight distance patterns, spatio-temporal variation will predictably result in inconsistent or contradictory selective pressures on the plant, thus hindering specialization in relation to particular pollinators.

KEY WORDS:—Annual variation – coevolution – environmental heterogeneity – Labiatae – mutualism – pollination – pollinator abundance – seasonality – specialization.

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0024–4066/88/100095+31 $03.00/0

INTRODUCTION

Theoretical models have often illustrated the influence of environmental heterogeneity on character evolution (for reviews see Christiansen & Feldman, 1975; Hedrick, Ginevan & Ewing, 1976; Felsenstein, 1976). Although environmental heterogeneity may be perceived in a variety of ways and scales, underlying all these is the notion of a mosaic of contradictory selective regimes over one species' range, resulting in an interaction between the disruptive effect of contradictory local selection regimes and the unifying effect of gene flow (Spieth, 1979). In this context, a reasonable degree of predictability in mutual selective pressures has been proposed as one prerequisite for coevolution to occur in plant–animal mutualisms (Horvitz & Schemske, 1984; Howe, 1984; Herrera, 1985, 1986). All else being equal, the more spatio-temporally predictable are the nature and strength of the selective pressures exerted by mutualists on one species, the more likely will be an evolutionary modification in response to these pressures (the first step towards coevolution; Janzen, 1980). Assessing the magnitude of spatio-temporal variation in mutualisms is thus critical to understanding their evolution. In spite of this, few studies have directly examined patterns of variation in mutualisms (see, for example, Pudlo, Beattie & Culver, 1980; Mesler & Lu, 1983; Barton, 1986; Heithaus, 1986; and Horvitz & Schemske, 1986, for plant–ant systems; Herrera, 1988, for plant–bird seed dispersal systems; Aker, 1982; Feinsinger, Wolfe & Swarm, 1982, for plant–pollinator systems).

In the case of a plant species that interacts mutualistically with animals for pollination or seed dispersal, one of the most obvious potential causes of unpredictability in selective pressures (on the plant) is variation in time or space of the assemblage of animal mutualists with which it interacts. If animal species differ in their effects on the fitness of the plant, then spatio-temporal variation in the composition of the assemblage will most likely result in variation in selective pressures on the plant (i.e. a mosaic of selection regimes). A two-step procedure may thus be envisaged to assess the magnitude and potential implications for a plant of variation in a mutualism. The first step would consist of determining the extent and nature of differences between mutualists in their effects on the fitness of the plant (the 'quality' component of the interaction, as defined in Herrera, 1987b). If significant differences are found between mutualists, then the second step would involve the analysis of the variation in time and space of the assemblage of mutualists (variation in the 'quantity' component; Herrera, 1987b). This paper presents such a second step in the analysis of variation in a plant–pollinator system. I describe here the variation in time (annual and seasonal) and space (between- and within-population) in the pollinator assemblage of *Lavandula latifolia* (Labiatae), an insect-pollinated shrub, in south-eastern Spain. One previous study examined the variation between pollinators in the 'quality' component (the first step above), and found important interspecific differences in frequency of pollen deposition on the stigma, size of pollen loads deposited, and between-flower flight distance patterns (Herrera, 1987b). *Lavandula latifolia* has a diverse pollinator assemblage, made up of nearly 85 species (see below), and aspects of pollinating quality have been evaluated for nearly half of these (Herrera, 1987a, b).

Earlier studies have often documented variation between populations (e.g.

Willson & Bertin, 1979; Hannan, 1981; Udovic, 1981; Lindsey, 1984; Spears, 1987) and between years (e.g. Beattie, Breedlove & Ehrlich, 1973; Waser, 1979; Kwak, 1980; Calder *et al.*, 1983; Boyle & Philogène, 1983) in the size and composition of pollinator assemblages. Seasonal (Teräs, 1976; Aker, 1982; Montalvo & Ackerman, 1986) and within-population (Beattie, 1971) variation have been evaluated less frequently. To my knowledge, no previous study has examined simultaneously spatial and temporal variation in a pollinator assemblage for which detailed data existed on the differential pollinating quality of many of its component species.

Lavandula latifolia is a low evergreen shrub (up to 35 cm high) producing long-stalked (up to 1.25 cm high) inflorescences in early summer. It is a common species in the undergrowth of mixed woodlands on limestone-derived soils at low to middle elevations in the eastern and south-eastern Iberian Peninsula. The flowers are hermaphroditic, protandrous, have pale-blue, narrow tubular corollas (tube length 7–8 mm), and are produced over a short (3–6 cm) terminal portion of the stalks. The species is self-compatible, but spontaneous autogamy occurs very infrequently and seed set in the absence of pollinators is negligible. Aspects of its reproductive biology, with particular reference to pollination, have been studied by Herrera (1987a, b) (see Devesa, Arroyo & Herrera, 1985; Muñoz & Devesa, 1987; for studies on the floral biology of other southern Spanish *Lavandula* species).

STUDY AREA AND GENERAL METHODS

The study was conducted in the Sierra de Cazorla (Jaén province, south-eastern Spain) between 1982 and 1987. Most data were collected at a *L. latifolia* population growing around the intersection of Arroyo Aguaderillos and the track joining Roblehondo and Hoyos de Muñoz (1160 m elevation, 'Aguaderillos-1' hereafter) (see J. Herrera, 1984, for a description of the vegetation of the area). Analyses of annual, seasonal and within-population variation in pollinators were performed on the data obtained from this population.

Three further *L. latifolia* populations were selected for study of pollinator variation between localities. One of these ('Aguaderillos-2') was only 300 m away from Aguaderillos-1. The other two sites were 3.5 km to the east (1300 m elevation, 'Cuevas Bermejas'), and 4.5 km to the south-west (1140 m elevation, 'Las Navillas') of Aguaderillos-1. At all sites, *L. latifolia* plants occurred in open *Pinus nigra–Quercus rotundifolia* mixed woodlands, and were growing on shallow soils originating from limestone. These populations were chosen after a survey of all *L. latifolia* populations occurring within a radius of 5 km around Aguaderillos-1, and were selected because the size distribution, plant density and flowering phenology of *L. latifolia* plants were similar to those of the Aguaderillos-1 main study population.

Pollinator variation was examined at four different levels, namely annual, seasonal, between- and within-population. Simultaneously studying pollinator populations at these four levels (a full factorial sampling design) would have required a vast amount of field work (6 study years × 4 populations × 3-month long flowering seasons × several subpopulations at each site). For this reason, I selected an incomplete sampling design. Methodological details specific to each of the four levels of variation examined (including dates, sites and sample sizes) are presented below under the appropriate headings. Only general methods are described in this section.

The composition and abundance of the pollinator assemblage were assessed by conducting counts of floral visitors along permanent 80-m long transects crossing the plant populations. One transect was laid out at each site. I walked slowly along the transect, recording the identity of every insect seen visiting *L. latifolia* flowers within 5 m to either side of the transect. Each of these individual censuses (i.e. walking the transect once) is called here a 'count', and is the sampling unit used in all the statistical analyses below. Only insect taxa actually or potentially performing pollination have been included in the analyses. The decision to assign a particular floral visitor to the pollinator category was based in many instances (nearly 40 species) on actual evidence derived from an earlier study of pollen deposition on stigmas (Herrera, 1987b). In the remaining cases it was based on inference, derived from extensive observations on foraging patterns and behaviour at flowers (Herrera, unpublished), and similarity with species for which actual data existed. Nearly 85 insect species, belonging to the Hymenoptera, Diptera and Lepidoptera, are included in the analyses.

Specimens of all insect taxa recorded visiting *L. latifolia* flowers were collected at the start of the study (1982) for taxonomic determination or corroboration, and thereafter whenever a species was recorded at flowers for the first time. Voucher specimens are in the author's collection, deposited in the Estación Biológica de Doñana, and in the home institutions of taxonomists mentioned in the Acknowledgements section. Particular care was taken in the counts to record floral visitors at the species level. This was not always possible, however, as very similar congeneric species could not be reliably separated in the field (e.g. species in the genera *Ceratina*, *Volucella*, *Gonepteryx* and *Hyponephele*), and I tried to keep collections to a minimum in order to avoid disturbances to the insects frequenting the flowers which would interfere with other studies (preliminary mark–recapture data revealed considerable local constancy for the individuals of some pollinator species). In these instances, results are presented at the level of genus or of small groups of congeneric species.

ANNUAL VARIATION

Methods

Annual variation in the pollinator assemblage of *Lavandula latifolia* was examined over a 6-year period (1982–1987) in Aguaderillos-1, the main study site. Due to the long duration of the flowering season of *L. latifolia* (nearly 3 months), it was impractical to conduct counts of floral visitors throughout the whole flowering periods of all study years. For this reason, a 17-day long 'standard' census period was chosen (1–17 August), and counts were performed annually on these dates. This period was chosen because it usually encompassed the peak of flowering of the local *L. latifolia* population, and because of my subjective impression at the start of the study that the greatest abundance and diversity of pollinators occurred in that period. Variation between years was examined using these 1–17 August counts ($N = 320$, all years combined). To obtain comparable data, counts were evenly distributed each year from sunrise

Table 1. Annual variation in the abundance of the three major groups of floral visitors (all species combined). Entries represent mean numbers of individuals (±1 s.d.) per count in the period 1–17 August (first row), and proportion (%) with respect to the total of individuals for that year (second row). *N* = number of counts

	1982 (*N* = 45)	1983 (*N* = 21)	1984 (*N* = 59)	1985 (*N* = 59)	1986 (*N* = 55)	1987 (*N* = 81)	*F* value†
Hymenopterans	24.8±9.9 65.6	13.1±4.9 51.8	18.9±7.1 36.1	23.1±10.6 48.5	14.0±6.2 50.7	21.2±14.7 57.8	10.9****
Dipterans	3.2±2.9 8.5	3.4±3.3 13.4	3.0±2.9 5.7	5.1±4.8 10.7	2.5±2.6 9.1	4.8±4.0 13.1	5.5***
Lepidopterans	9.8±7.9 25.9	8.8±10.4 34.8	30.5±27.8 58.2	19.4±14.3 40.8	11.1±9.3 40.2	10.7±9.0 29.1	18.0****
Total	37.8±13.7	25.3±14.3	52.4±30.9	47.6±20.8	27.6±13.2	36.7±15.2	14.7****

†Brown–Forsythe *F* test without assumption for equal variances: *** $P < 0.001$; **** $P < 0.0001$.

to sunset, to avoid the likely biases derived from the marked daily variation in pollinator assemblage composition and abundance (Herrera, unpublished). Each year, count dates were spaced as evenly as possible between the start and the end of the standard census period.

Results

The total abundance of insect visitors to *L. latifolia* flowers fluctuated significantly between years (Table 1). Yearly averages for the period 1–17 August ranged between 25.3 individuals/count (1983) and 52.4 individuals/count (1984), a two-fold variation over the 6-year study period. Each of the three major insect groups exhibited significant annual variation in abundance (Table 1): hymenopterans (range of yearly averages = 13.1–24.8 individuals/count); dipterans (2.5–5.1 individuals/count); lepidopterans (8.8–30.5 individuals/count). The three groups had similar levels of relative variation between years ($F = 2.61$, df = 2, 15, $P = 0.11$; Levene's test for relative variation—Van Valen, 1978).

None of the three possible pairwise correlations between the yearly averages of the three major groups was significant ($P > 0.25$), revealing that their local abundances varied asynchronously over the study years. The proportions contributed by each group to the total of floral visitors changed markedly between years. The pollinator assemblage was dominated numerically by hymenopterans in four years (1982, 1983, 1986, 1987) and by lepidopterans in one year (1984), while the two groups contributed roughly similar proportions in one year (1985).

A total of 70 field-recognizable insect taxa were recorded visiting *L. latifolia* flowers during the 1–17 August counts of years 1982–1986 (Table 2). On

TABLE 2. Average abundance of floral visitors to *Lavandula latifolia* flowers in the period 1–17 August during the six study years. Numbers of counts per year are shown in Table 1. —, indicates that the species was not recorded in the counts for that year. For 'constant' taxa (those occurring in all study years), the significance of annual differences in average abundance is shown†

	Individuals/ten counts					
	1982	1983	1984	1985	1986	1987
Hymenoptera						
1 *Bembix zonata* (Sphecidae)****	3.3	0.5	5.8	11.4	2.9	5.1
2 *Ammophila* sp. (aff. *sabulosa*) (Sphecidae)	—	—	—	0.3	0.4	0.7
3 Sphecidae gen. sp.	0.2	—	—	—	—	0.2
4 Scoliidae gen. sp.	—	—	—	—	0.2	—
5 *Katamenes arbustorum* (Eumenidae)	—	—	0.3	0.2	0.2	—
6 *Halictus* sp. (aff. *scabiosae*) (Halictidae)	—	—	0.2	1.9	0.4	—
7 *Anthidium cingulatum* (Megachilidae)	—	—	1.0	2.4	—	0.1
8 *Anthidium florentinum* (Megachilidae)****	42.0	13.3	31.1	70.5	19.6	17.0
9 *Anthidiellum breviusculum* (Megachilidae)***	10.2	11.9	31.7	16.6	26.5	15.4
10 *Megachile pilidens* (Megachilidae)	—	—	0.3	0.2	0.2	0.5
11 *Megachile* sp.****	0.4	1.4	3.7	5.6	0.9	1.2
12 *Anthophora crassipes* (Anthophoridae)	—	—	0.2	2.2	1.1	0.6
13 *Anthophora ochroleuca* (Anthophoridae)**	6.2	1.4	2.4	4.7	3.8	6.4
14 *Anthophora quadrifasciata* (Anthophoridae)***	1.6	1.0	2.9	1.7	0.2	0.2
15 *Anthophora albigena* (Anthophoridae)****	1.8	1.0	4.6	5.6	0.4	2.7
16 *Melecta* sp. (Anthophoridae)	—	—	0.2	—	—	0.3
17 *Ceratina cyanea* + *mocsaryi* (Anthophoridae)	—	—	3.7	5.9	5.1	11.1

TABLE 2. Continued

	Individuals/ten counts					
	1982	1983	1984	1985	1986	1987
18 *Xylocopa cantabrita* (Anthophoridae)	—	—	—	1.0	0.2	—
19 *Xylocopa violacea* (Anthophoridae)	3.6	1.4	4.1	13.6	1.1	2.7
20 *Apis mellifera* (Apidae)****	110.2	78.6	78.3	77.8	72.9	140.7
21 *Bombus terrestris* (Apidae)****	59.6	21.0	18.1	5.8	3.8	5.8
22 *Bombus pascuorum* (Apidae)	8.2	—	0.3	2.9	0.4	0.2
Diptera						
23 *Systoechus* nov. sp. (?) (Bombyliidae)$^{\text{n.s.}}$	0.4	3.8	2.4	2.5	0.9	1.6
24 Bombyliidae gen. sp.	1.1	0.5	—	0.2	—	0.1
25 *Conops* sp. (Conopidae)	—	—	—	0.2	0.6	0.3
26 *Merodon geniculatus* (Syrphidae)	—	—	—	2.7	0.7	0.7
27 *Eristalis tenax* (Syrphidae)	—	—	3.4	1.4	1.5	3.6
28 *Volucella* spp.‡ (Syrphidae)***	28.4	16.7	13.9	22.7	14.0	29.1
29 *Sphaerophoria scripta* (Syrphidae)***	0.7	0.5	6.1	0.3	0.6	0.6
30 *Chrysotoxum intermedium* (Syrphidae)	—	—	1.2	0.7	0.9	1.0
31 *Scaeva pyrastri* (Syrphidae)	—	—	—	—	0.4	—
32 *Xanthogramma marginale* (Syrphidae)	—	—	—	0.3	—	0.3
33 *Pangonius* sp. (Tabanidae)	—	—	0.7	—	0.2	—
34 Calliphoridae gen. sp. ****	0.9	1.9	2.5	12.4	2.6	4.8
35 Tachinidae gen. sp.	—	10.5	—	7.3	2.4	5.9
Lepidoptera						
36 *Macroglossum stellatarum* (Sphingidae)****	19.1	4.8	37.3	21.7	7.1	1.4
37 *Tyta luctuosa* (Noctuidae)	—	—	0.5	0.3	—	—
38 *Zygaena* sp. (Zygaenidae)	—	—	0.3	—	—	—
39 *Papilio machaon* (Papilionidae)	—	—	0.2	—	—	—
40 *Iphiclides podalirius* (Papilionidae)	0.2	—	0.5	0.3	0.7	0.1
41 *Colias crocea* (Pieridae)	0.9	—	4.1	3.7	3.8	0.5
42 *Pieris rapae* (Pieridae)	—	—	0.7	0.3	0.2	—
43 *Pontia daplidice* (Pieridae)	0.4	—	—	—	—	—
44 *Gonepteryx rhamni + cleopatra* (Pieridae)**	0.2	1.0	3.9	2.2	0.9	1.4
45 *Pandoriana pandora* (Nymphalidae)****	0.4	1.4	3.1	4.9	9.8	17.3
46 *Argynnis paphia* (Nymphalidae****	18.2	9.5	20.2	34.9	8.9	22.5
47 *Fabriciana adippe* (Nymphalidae)**	13.8	16.2	21.4	22.9	14.4	10.5
48 *Issoria lathonia* (Nymphalidae)	—	1.0	1.2	0.5	0.9	1.0
49 *Brenthis hecate + daphne* (Nymphalidae)	—	—	0.2	0.2	0.2	—
50 *Melanargia galathea* (Satyridae)****	2.7	17.1	120.0	30.2	23.4	14.4
51 *Hipparchia alcyone* (Satyridae)	—	—	—	—	0.7	0.9
52 *Satyrus actaea* (Satyridae)	—	—	—	0.9	—	—
53 *Hyponephele lupina + lycaon* (Satyridae)*	1.1	0.5	0.2	2.0	2.6	1.7
54 *Pyronia bathseba* (Satyridae)	0.4	1.0	5.6	0.2	1.6	—
55 *Pyronia tithonus + cecilia* (Satyridae)	1.6	—	1.0	1.0	1.1	2.0
56 *Coenonympha dorus* (Satyridae)	—	—	0.3	1.0	1.1	—
57 *Lasiommata maera* (Satyridae)	0.2	—	0.2	0.7	—	0.1
58 *Lasiommata megera* (Satyridae)	—	—	0.9	1.4	1.1	0.6
59 *Laeosopis roboris* (Lycaenidae)	—	—	0.3	0.5	—	—
60 *Strymonidia spini* (Lycaenidae)	—	—	1.2	—	—	—
61 *Lycaena phlaeas* (Lycaenidae)	—	1.0	0.2	2.7	0.2	2.7
62 *Lampides boeticus* (Lycaenidae)	0.4	—	0.7	0.5	0.2	—
63 *Syntarucus pirithous* (Lycaenidae)	—	—	0.2	—	0.7	—
64 *Plebicula escheri* (Lycaenidae)**	1.1	1.4	5.8	5.1	3.5	4.4
65 *Lysandra albicans/hispana* (Lycaenidae)$^{\text{n.s.}}$	7.3	8.6	11.0	8.0	5.3	8.0
66 *Hesperia comma* (Hesperiidae)**	11.8	8.1	7.8	10.2	5.3	4.1
67 *Ochlodes venatus* (Hesperiidae)	—	—	0.5	—	—	—
68 *Spialia sertorius* (Hesperiidae)	1.8	—	2.7	3.4	0.6	0.9
69 *Thymelicus acteon* (Hesperiidae)****	15.8	16.2	51.4	33.2	15.5	10.9
70 *Muschampia proto* (Hesperiidae)	—	—	1.4	1.2	1.3	1.9

†Brown–Forsythe *F* test: $^{\text{n.s.}}$ non-significant; *$P < 0.05$; ** $P < 0.01$; ***$P < 0.001$; ****$P < 0.0001$.

‡Includes *V. elegans*, *V. zonaria* and *V. inanis*.

average, 48 taxa were recorded yearly per 17-day period, and the observed range was from 30 (1983) to 58 (1985) taxa, a two-fold variation. There were therefore important differences between years in pollinator diversity.

The number of years in which a particular pollinator occurred may be used as a measure of its predictability as a member of the pollinator assemblage. Hymenopteran, dipteran and lepidopteran taxa did not differ significantly in this measure ($H = 1.17$, $df = 2$, $P = 0.56$; Kruskal–Wallis analysis of variance). Combining all visitors into a single sample, only 25 taxa (35.7%) were recorded in all of the six years ('constant' taxa hereafter), while eight (11.4%), 11 (15.7%), nine (12.9%), nine (12.9%) and eight (11.4%) taxa occurred only in five, four, three, two and one years, respectively ('irregular' taxa hereafter). The full spectrum of predictabilities thus occurred in the species sample, and only about one-third of the 70-taxa pollinator assemblage occurred predictably year after year at the study locality.

In all years, the vast majority of pollinators averaged less than 1 individual/count (Table 2). The ten most abundant taxa (17.2–33.3% of those annually present) accounted for 87.1% (1982), 83.4% (1983), 80.8% (1984), 72.3% (1985), 76.4% (1986) and 78.7% (1987) of the total number of individuals for all taxa combined. The identity of species in this numerically dominant group, however, changed between years. In general the proportional contribution of most individual species to total abundance varied considerably from year to year, as a result of marked annual fluctuations in their absolute abundances (Table 2). For each year, taxa were ranked in decreasing order of abundance, and scored accordingly. Considering only the 25 constant taxa, most species exhibited broad ranges of variation in rank order of abundance (Fig. 1). As examples, *Melanargia galathea* (Satyridae) ranked 16th in abundance in 1982, 3rd in 1983, 1st in 1984, 5th in 1985, 3rd in 1986, and 7th in 1987; *Pandoriana pandora* (Nymphalidae) ranked 27th in 1982, 18th in 1983, 24th in 1984, 21st in 1985, 8th in 1986, and 4th in 1987; *Bombus terrestris* was 2nd in 1982 and 1983, 9th in 1984, 17th in 1987, 16th in 1986, and 14th in 1987. The single exception to this general pattern of broad variation in relative importance was *Apis mellifera* (Apidae), which ranked first in every year except 1984 (2nd only to *M. galathea*) (Fig. 1). For 24 out of 26 constant taxa, annual differences in average abundance were statistically significant (Table 2).

Although the number of study years is too small to perform a detailed analysis, distinct annual trends in the local abundance (at *L. latifolia* flowers) of several pollinator species are apparent in Table 2. One species increased steadily from 1982 through 1987 (*P. pandora*, from 0.4 to 17.3 individuals/10 counts), another exhibited a steady decline (*B. terrestris*, from 59.6 to 5.8 individuals/10 counts), and two species increased to a peak in 1984 and declined thereafter (*M. galathea*, *Thymelicus acteon*). At their respective peak years, each of these species ranked among the four locally most abundant pollinators (Table 2, Fig. 1). The peaks of *M. galathea* and *T. acteon* in 1984 were largely responsible for the numerical dominance of lepidopterans that year.

Discussion

A broad variety of causes are probably responsible for annual variations in pollinator abundance. In a few instances (e.g. *Bombus* spp., *Pandoriana pandora*), steadily decreasing or increasing trends probably represent population processes

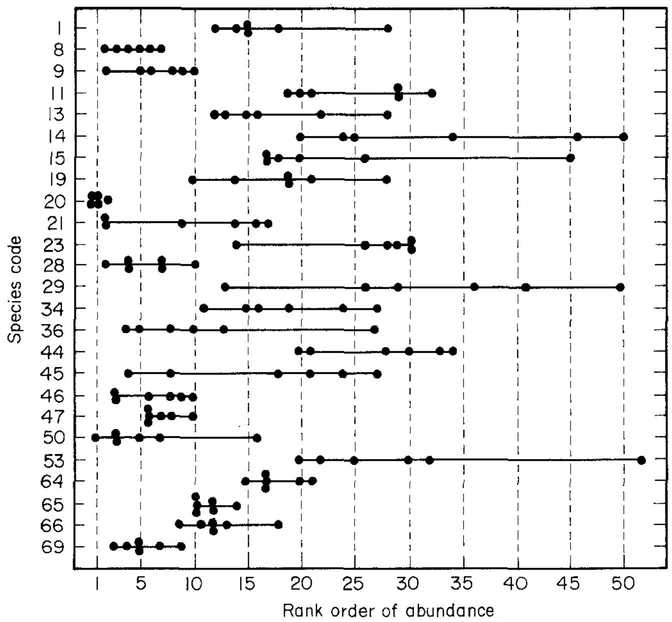

Figure 1. Annual variation in rank order of abundance of insect taxa visiting *Lavandula latifolia* flowers (Aguaderillos-1 site, 1982–1987). Shown are the rank scores in each of the six study years (●) for each floral visitor (rows, identified by their numbers in Table 2). Horizontal lines connect extreme scores for a given species. Only taxa occurring in all study years ('constant' taxa, $N = 25$) have been represented, but yearly ranks were obtained considering the whole set of species present that year.

at medium or long term on a regional scale (Herrera, unpublished observations). Population cycles elsewhere or differences in migratory timing may explain the variation in the abundance of some species with migratory habits (e.g. *Macroglossum stellatarum*, *Sphaerophoria scripta*). For some others, local or regional population cycles may account for observed abundance variation (e.g. *M. galathea*, *T. acteon*). In at least one case, variation in abundance was due to annual changes in feeding behaviour. *Hipparchia alcyone* was abundant at Aguaderillos-1 every study year, yet it was observed visiting *L. latifolia* flowers only in 1986 and 1987. Unusual altitudinal displacements of species ordinarily occurring at higher elevations in the region (*Ochlodes venatus* in 1984; *Satyrus actaea* in 1985), or delayed phenologies of species with flight periods usually not overlapping with the *L. latifolia* flowering season (*Strymonidia spini* in 1984), also accounted for some of the observed annual variation. Regardless of the causes, however, variations in the abundance of individual taxa combine to produce marked annual changes in the abundance and composition of the *L. latifolia* pollinator assemblage. Only about one-third of recorded taxa were present in all years, and even these constant species occurred at broadly variable absolute and relative abundances. With the single exception of *A. mellifera*, which was the most abundant species in five out of six years, the proportional contribution of all species changed markedly between years. Considering the major taxonomic groups, lepidopterans prevailed in one year, hymenopterans in four years, and both groups had roughly similar abundances in the remaining year.

At the study population, the maximum longevity recorded for *L. latifolia* shrubs was 32 years, although most plants were usually senescent and produced few, if any, flowers after age 25. The first reproduction generally took place at ages of 5–10 years (Herrera, unpublished data for Aguaderillos-2 site). These observations indicate that *L. latifolia* reproductive lifetime spans a period of nearly 15 years, hence the 6-year period over which I performed pollinator counts represents a significant portion (40%) of the reproductive life of an average *L. latifolia* individual plant. In other words, annual variation observed in the characteristics of the pollinator assemblage represents a fairly accurate description of the actual changes in identity and abundance of pollinators that an individual of *L. latifolia* faces in the course of its reproductive lifetime. From the viewpoint of *L. latifolia* plants, therefore, the composition, diversity and abundance of the local pollinator assemblage were markedly unpredictable, and fairly inconsistent between consecutive flowering seasons.

SEASONAL VARIATION

Methods

Seasonal variation in the composition and abundance of the *L. latifolia* pollinator assemblage was studied in 1984 at the Aguaderillos-1 study site. A total of 246 counts of floral visitors were conducted from 22 July to 17 October. This period encompassed nearly 95% of the flowering period of the local *L. latifolia* population that year (Herrera, unpublished). Counts were performed on 35 different dates (every 2.5 days on average), distributed as evenly as possible over the study season. Likewise, counts were evenly distributed from sunrise to sunset (to avoid biases resulting from daily rhythms, as noted earlier).

For the purpose of the analyses, counts were grouped into six half-month periods (15–31 July, 1–15 August, 16–31 August, 1–15 September, 16–30 September, 1–17 October). Seasonal variation was studied by examination of average values for these half-month periods.

Results

The total abundance of *L. latifolia* floral visitors changed significantly through the 1984 flowering season (Table 3), declining steadily from a peak in July (75.6 individuals/count) to a minimum in October (9.3 individuals/count) (an eight-fold variation). Each of the three major insect groups exhibited significant seasonal variation in abundance (Table 3). Hymenopterans increased to a peak in the first half of August (19.3 individuals/count), decreasing afterwards to a minimum in October (3.5 individuals/count). Dipteran abundance first increased from July to a distinct peak in early September (9.0 individuals/count), and then declined to a minimum in October. Lepidopterans decreased steadily in abundance from July through October. The abundances of the three major pollinator groups thus exhibited contrasting seasonal trends (none of the pairwise correlations between their respective half-month averages is significant; $P > 0.25$). Half-month averages for the three groups exhibited similar levels of relative variation along the flowering period ($F = 1.42$, df = 2, 15, $P = 0.27$; Levene's test for relative variation).

The proportional contribution of the three major taxonomic groups to the pollinator assemblage varied broadly over the flowering season (Table 3).

TABLE 3. Seasonal variation in the abundance of the three major groups of floral visitors (all species combined) during the 1984 *L. latifolia* flowering season. Entries represent mean number of individuals (±1 S.D.) per count in each period (first row), and proportion (%) with respect to the total of individuals for each period (second row). N = number of counts

	15–31 July (N = 38)	1–15 Aug. (N = 44)	16–31 Aug. (N = 50)	1–15 Sept. (N = 26)	16–30 Sept. (N = 48)	1–17 Oct. (N = 40)	F value†
Hymenopterans	6.8±6.4	19.3±7.7	16.1±6.6	16.0±6.4	10.3±6.0	3.5±4.1	38.8****
	8.9	34.4	46.7	45.2	46.9	38.0	
Dipterans	1.7±2.1	2.6±2.9	6.5±5.2	9.0±8.8	3.2±3.5	1.3±1.4	14.0****
	2.3	4.6	18.9	25.6	14.6	14.0	
Lepidopterans	67.1±56.8	34.3±29.9	11.9±12.0	10.3±9.4	8.5±9.1	4.5±4.9	30.5****
	88.8	61.0	34.4	29.2	38.5	48.0	
Total	75.6±60.4	56.2±33.5	34.4±15.0	35.4±16.0	22.1±15.9	9.3±8.8	24.4****

†Brown-Forsythe F test without assumption for equal variances: **** $P < 0.0001$.

TABLE 4. Seasonal variation in the composition of the *Lavandula latifolia* pollinator assemblage in 1984. Numbers of counts per period are shown in Table 3. —, indicates that the species was not recorded in the counts for that period. For 'constant' taxa (those occurring in all study periods), the significance of seasonal differences in average abundance is shown†

	Individuals/ten counts					
	15–31 July	1–15 Aug.	16–31 Aug.	1–15 Sept.	16–30 Sept.	1–17 Oct.
Hymenoptera						
1 *Bembix zonata* (Sphecidae)	2.1	5.0	2.8	2.3	3.3	—
2 *Ammophila* sp. (aff. *sabulosa*) (Sphecidae)	—	—	0.6	1.5	—	—
3 Scoliidae gen. sp.	—	—	—	0.4	—	—
4 *Katamenes arbustorum* (Eumenidae)	—	0.2	0.2	1.5	—	—
5 *Halictus* sp. (aff. *scabiosae*) (Halictidae)	—	0.2	0.2	—	1.0	
6 *Anthidium cingulatum* (Megachilidae)	—	0.7	0.6	1.1	3.8	0.8
7 *Anthidium florentinum* (Megachilidae)	1.6	31.8	19.6	8.5	—	—
8 *Anthidiellum breviusculum* (Megachilidae)	41.8	32.3	15.2	10.8	5.0	—
9 *Megachile pilidens* (Megachilidae)	—	0.5	—	—	3.3	0.3
10 *Megachile* sp.***	0.5	3.9	2.2	4.6	8.5	0.3
11 *Anthophora crassipes* (Anthophoridae)	0.3	0.2	0.2	0.8	—	6.3
12 *Anthophora ochroleuca* (Anthophoridae)****	0.3	1.6	5.8	6.2	2.5	0.3
13 *Anthophora quadrifasciata* (Anthophoridae)	—	3.2	2.6	1.1	3.1	9.5
14 *Anthophora albigena* (Anthophoridae)****	0.5	5.2	3.0	0.4	2.5	0.8
15 *Melecta* sp. (Anthophoridae)	—	0.2	0.2	—	0.6	0.3
16 *Ceratina cyanea*+*mocsaryi* (Anthophoridae)	15.0	3.9	3.0	2.7	0.6	
17 *Xylocopa cantabrita* (Anthophoridae)	—	—	0.4	1.5	0.2	
18 *Xylocopa violacea* (Anthophoridae)	—	4.3	2.2	0.4	0.8	—
19 *Apis mellifera* (Apidae)****	3.7	79.8	92.4	109.2	52.5	11.3
20 *Bombus terrestris* (Apidae)****	1.8	20.0	8.4	6.2	14.6	2.5
21 *Bombus pascuorum* (Apidae)	—	0.5	1.0	0.8	0.8	3.3
Diptera						
22 *Systoechus* nov. sp. (?) (Bombyliidae)	9.5	2.9	0.4	—	—	—
23 Bombyliidae gen. sp.	—	—	—	—	0.2	—
24 *Eristalis tenax* (Syrphidae)****	0.3	2.9	9.8	12.7	8.5	2.0
25 *Volucella* spp.‡ (Syrphidae)	—	9.1	42.2	50.0	6.3	—
26 *Chrysotoxum intermedium* (Syrphidae)	—	0.7	1.6	1.5	0.8	
27 *Scaeva pyrastri* (Syrphidae)	—	—	—	—	1.7	0.8
28 Other Syrphidae§**	3.4	6.1	3.4	2.3	6.3	10.0
29 *Pangonius* sp. (Tabanidae)	3.4	0.9	—	—	—	—
30 Calliphoridae gen. sp.****	0.3	2.9	6.4	15.8	5.8	0.3
31 Tachinidae gen. sp.	—		1.4	8.1	2.7	—
Lepidoptera						
32 *Macroglossum stellatarum* (Sphingidae)****	1.3	40.5	18.6	18.1	10.2	5.5
33 *Tyta luctuosa* (Noctuidae)	0.3	0.5	0.2	—	—	—
34 *Euplagia quadripunctaria* (Arctiidae)	—	—	—	—	0.6	—
35 *Agdistis* sp. (Pterophoridae)	6.8	—	—	—	—	—
36 *Zygaena faustina* (Zygaenidae)	—	—	—	—	4.8	0.3
37 *Zygaena* sp. (Zygaenidae)	0.3	0.5	—		—	—
38 *Papilio machaon* (Papilionidae)	—	0.2	—	—	0.2	—
39 *Iphiclides podalirius* (Papilionidae)	—	0.5	0.2	—	—	—
40 *Colias crocea* (Pieridae)**	0.3	3.4	4.0	5.4	8.1	5.3
41 *Pieris rapae* (Pieridae)	—	0.9	0.2	0.4	1.0	2.3
42 *Pieris brassicae* (Pieridae)	0.3	—		—	—	—
43 *Pontia daplidice* (Pieridae)	0.3	—	—	—	2.9	4.5
44 *Gonepteryx rhamni*+*cleopatra* (Pieridae)	1.0	5.0	0.2	—	0.2	0.8
45 *Pandoriana pandora* (Nymphalidae)****	0.3	0.9	7.8	11.9	10.0	0.5
46 *Argynnis paphia* (Nymphalidae)	0.3	16.1	26.4	26.1	5.8	—
47 *Fabriciana adippe* (Nymphalidae)	7.1	21.6	10.4	5.0	2.1	—
48 *Issoria lathonia* (Nymphalidae)	—	0.9	0.8	0.4	0.6	1.5
49 *Brenthis hecate*+*daphne* (Nymphalidae)	—	0.2	—	—	—	—

TABLE 4. Continued

	Individuals/ten counts					
	15–31 July	1–15 Aug.	16–31 Aug.	1–15 Sept.	16–30 Sept.	1–17 Oct.
50 *Melanargia galathea* (Satyridae)	374.5	150.9	13.6	3.8	—	—
51 *Hipparchia alcyone* (Satyridae)	—	—	0.6	1.5	4.8	—
52 *Hyponephele lupina + lycaon* (Satyridae)	—	—	0.2	0.4	—	—
53 *Pyronia bathseba* (Satyridae)	57.9	6.6	0.8	—	—	—
54 *Pyronia tithonus + cecilia* (Satyridae)	0.5	1.1	1.0	0.4	0.6	—
55 *Coenonympha dorus* (Satyridae)	—	—	0.4	1.1	0.8	—
56 *Lasiommata maera* (Satyridae)	0.3	0.2	0.4	—	0.6	0.3
57 *Lasiommata megera* (Satyridae)****	0.5	0.9	0.2	1.5	9.4	20.5
58 *Laeosopis roboris* (Lycaenidae)	7.4	0.5	—	—	—	—
59 *Strymonidia spini* (Lycaenidae)	1.8	1.6	—	—	—	—
60 *Lycaena phlaeas* (Lycaenidae)	—	—	0.2	0.8	2.5	1.3
61 *Lampides boeticus* (Lycaenidae)*	0.8	0.7	1.0	0.4	3.1	1.3
62 *Syntarucus pirithous* (Lycaenidae)	1.0	0.2	0.2	—	—	—
63 *Plebicula escheri* (Lycaenidae)****	29.2	7.3	2.2	1.9	2.9	0.3
64 *Lysandra albicans/hispana* (Lycaenidae)**	4.2	10.2	8.4	11.5	7.5	0.5
65 *Hesperia comma* (Hesperiidae)	2.6	9.6	2.4	3.8	2.3	—
66 *Ochlodes venatus* (Hesperiidae)		0.7	—	—	—	—
67 *Spialia sertorius* (Hesperiidae)	4.5	2.5	1.6	2.7	2.9	—
68 *Thymelicus acteon* (Hesperiidae)	167.9	57.5	16.0	5.0	0.4	—
69 *Muschampia proto* (Hesperiidae)	—	1.4	0.6	0.8	0.4	—

†Brown–Forsythe *F* test: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$.

‡Includes *V. zonaria*, *V. elegans* and *V. inanis*.

§Includes *Sphaerophoria scripta*, *Episyrphus balteatus* and *Metasyrphus corollae*.

Lepidopterans dominated numerically in July, early August, and October, while hymenopterans prevailed in late August and throughout September. Dipterans contributed an important proportion (25.6%) of total individuals in early September.

A total of 69 insect taxa were recorded at *L. latifolia* flowers during the 1984 flowering season (Table 4). On average, only 45 taxa occurred per half-month period. The pollinator assemblage was most diverse in August (53–54 taxa per half-month period), and least diverse in October (29 taxa). There was considerable seasonal species turnover. Consecutive half-month periods shared, on average, only 69% of the combined species list (range = 56–81%). Only 15 taxa (21.7%) were present over the whole flowering season ('constant' taxa), while 17 (24.6%), eight (11.6%), 12 (17.4%), ten (14.5%) and seven (10.1%) taxa occurred only in five, four, three, two and one half-month periods, respectively ('irregular' taxa). Hymenopteran, dipteran and lepidopteran taxa did not differ significantly with regard to the number of periods in which they occurred ($H = 1.98$, df = 2, $P = 0.36$; Kruskal–Wallis analysis of variance). The relative numerical importance of constant taxa combined fluctuated broadly over the flowering season, ranging from 6.3% of total individuals in July to 69.2% in late September (average = 47.2%).

The proportional contributions of individual taxa to the pollinator assemblage exhibited broad seasonal variation. Considering constant taxa alone, the rank order of abundance (computed for the whole set of pollinators present in each half-month period) varied markedly between half-month periods

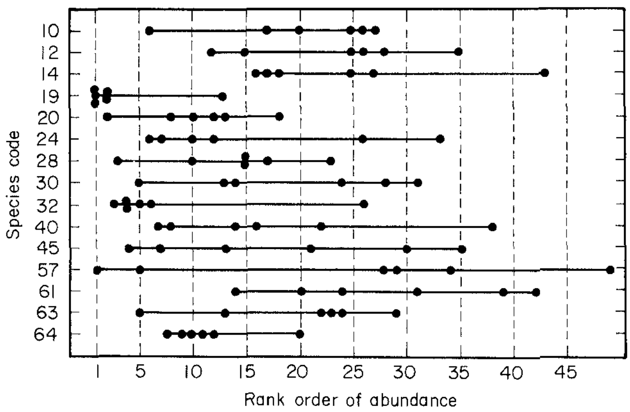

Figure 2. Seasonal variation in rank order of abundance of insect taxa visiting *Lavandula latifolia* flowers (Aguaderillos-1, 1984). Shown are the rank scores in each half-month period (●) for each floral visitor (rows, identified by their numbers in Table 4). Horizontal lines connect extreme scores for a given species. Only taxa occurring in all half-month periods ('constant' taxa, $N = 15$) have been represented, but ranks were obtained considering the whole set of species present in each period.

(Fig. 2). Extreme cases of seasonal variability are exemplified by *Apis mellifera* (range of ranks, 1st to 13th) on the one hand, and by *Lasiommata megera* (range, 1st to 49th) on the other. Seasonal variation in average abundance was statistically significant for all constant taxa (Table 4).

Discussion

In 1984, the pollinator assemblage of *L. latifolia* exhibited marked seasonal dynamics, with important changes in species richness, abundance and composition taking place over the flowering season. Occasional observations at the study site between 1982–1987 indicated that analogous changes occurred consistently every year. Marked seasonality in the pollinator assemblage thus seems to be a normal feature in the flowering ecology of *L. latifolia*.

For most species, seasonal variation in abundance apparently reflected their local or regional phenologies (flight periods). This applies to most bees and flies, and to all univoltine resident butterflies (e.g. *M. galathea*, *Pyronia bathseba*, *T. acteon*). In the case of some bivoltine or multivoltine butterflies, local population changes over the flowering season probably reflected not only the phenology of local or regional populations, but also irregular influxes of dispersing individuals (e.g. Papilionidae, Pieridae). Long-range migratory phenomena may partly account for abundance changes in the Sphingid moth (*M. stellatarum*) and some Syrphid flies. The category of 'Other Syrphidae' in Table 4 included three different species because I was sometimes unable to differentiate them in the field at a distance. This group exhibited a bimodal abundance pattern, with peaks in early August (largely accounted for by *S. scripta*) and late September–October (almost exclusively accounted for by *Episyrphus balteatus* and *Metasyrphus corollae*). The later peak was most likely due to a migratory influx of the two species involved (Svensson & Janzon, 1984; Gilbert, 1986). In contrast, the bimodal abundance patterns exhibited by *Anthophora quadrifasciata* and *A. albigena* are explained by differential phenologies of the sexes at *L. latifolia* flowers (females accounted for the early peak, males for the late peak). Some of the observed seasonal changes did not reflect variations in local abundance, but rather shifts in foraging behaviour of pollinators. The sharp increase of *Argynnis paphia* and *Fabriciana adippe* from late July to early August reflected the shift of these species to forage on *L. latifolia* flowers as the apparently preferred flowers of the locally coexisting *Rubus ulmifolius* (Rosaceae) became unavailable.

At the population level, *L. latifolia* flowering lasted for nearly 3 months in 1984. Although individual plants had slightly shorter periods (range = 2.25–2.75 months; Herrera, unpublished), the flowering season of individual shrubs invariably encompassed several half-month periods. Individual plants thus faced in the course of a single flowering episode a succession of pollinator species, with important changes in abundance and relative proportions.

VARIATION BETWEEN POPULATIONS

Methods

Differences between *L. latifolia* populations in their pollinator assemblages were studied at four sites (described earlier). At two localities (Aguaderillos-1 and Cuevas Bermejas), *L. latifolia* plants were growing within 50 m of the margins of narrow permanent water courses (Arroyo Agüerillos and Fuente de Cuevas Bermejas, respectively). At the other two populations, the nearest permanent waters were 500 m (Aguaderillos-2) and 1.5 km (Las Navillas) away. The substrate and other general characteristics of the habitats were otherwise similar at the four sites.

Pollinator counts were conducted at the four populations during 1–15 August 1987. The duration of the census period was selected so as to minimize the influence of seasonal variation in pollinator composition, yet provide the opportunity of obtaining sufficient sample sizes. As it was impractical to count pollinators from sunrise to sunset at the four populations, a standard daily census period was chosen for the purpose of comparisons, extending from 11.00 to 15.00 hours (Peninsular Summer Time, GMT +2). This period encompassed the daily peak in pollinator abundance and diversity (Herrera, unpublished observations for Aguaderillos-1). Counts were conducted on four different dates in each population, except in Aguaderillos-1 (three dates), where unusually cloudy and cool weather on one sampling date made it inadvisable to conduct the counts. For each site and date, counts were evenly spaced over the daily census period.

Results

The overall abundance and composition of pollinators varied markedly between populations (Fig. 3). Observed differences were statistically significant for total, hymenopteran, dipteran and lepidopteran abundance ($P < 0.0001$ in every case, Brown–Forsythe F-test). Total abundance was consistently greater at the two near-water populations (46.4–68.8 individuals/count on average) than at the two water-distant populations (11.8–18.9 individuals/count). The same pattern held for major pollinator groups considered separately (Fig. 3). There were also some significant differences between populations belonging to

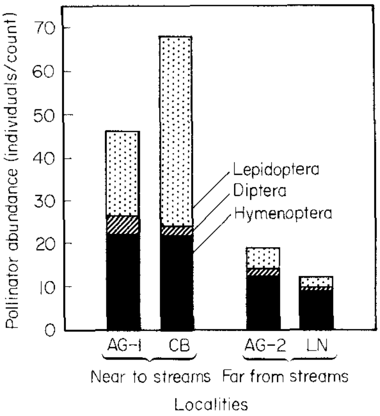

Figure 3. Variation between populations in the overall composition of the *Lavandula latifolia* pollinator assemblage (1987). Localities are coded as follows (number of counts in parentheses): AG-1, Aguaderillos-1 (25); CB, Cuevas Bermejas (32); AG-2, Aguaderillos-2 (36); LN, Las Navillas (36).

the same group. In the near-water group, the two populations differed in total, dipteran and lepidopteran, but not hymenopteran, abundance. In the water-distant group, populations differed in hymenopteran and total, but not dipteran and lepidopteran, abundance ($\alpha = 0.05$, Student–Newman–Keuls multiple-comparisons tests performed on the four-population set).

The proportional contribution of the three major groups to the pollinator assemblage changed markedly between populations (Fig. 3). Hymenopterans dominated numerically at the two water-distant sites (66.3 and 75.5% of all individuals). In contrast, lepidopterans prevailed at one of the near-water sites (Cuevas Bermejas, 64.8% of individuals), and their importance was comparable to that of hymenopterans at the other site (Aguaderillos-1, 42.3 *vs.* 48.0%). Dipterans accounted for less than 10% of individuals in all populations, and no distinct pattern of proportional abundance between sites was discernible. The pattern of differential relative abundance of hymenopterans and lepidopterans across sites reflected differential responses to the near-water *vs.* water-distant environmental gradient. Although both groups exhibited a decline in abundance from near-water to water-distant sites, the reduction was proportionally most important for lepidopterans (Fig. 3).

A total of 59 taxa were recorded at *L. latifolia* flowers in the four localities (Table 5). The pollinator assemblage was slightly more diverse at the two near-water sites (44–48 taxa) than at the two water-distant ones (38–39 taxa). Only 24 taxa (40.7% of total) occurred at all of the four sites ('constant' taxa), while 14 (23.7%), ten (16.9%) and 11 (18.6%) taxa occurred at three, two and one site, respectively ('irregular' taxa). Hymenopteran, dipteran and lepidopteran taxa did not differ significantly with regard to the number of sites in which they occurred ($H = 2.10$, $P = 0.34$, Kruskal–Wallis analysis of variance). For 21 out of 24 constant taxa, differences between sites in average abundance were statistically significant (Table 5).

The identity of the most abundant pollinators differed between sites (Table 5). The three numerically most important species were *A. mellifera*, *A. paphia* and *M. galathea* in Aguaderillos-1 (accounting altogether for 37.1% of all individuals); *Hesperia comma*, *Anthidiellum breviusculum* and *F. adippe* in Cuevas Bermejas (38.9% of individuals); *Anthidium florentinum*, *A. breviusculum* and *A. mellifera* in Aguaderillos-2 (46.5% of individuals); and *A. mellifera*, *A. florentinum* and *P. pandora* in Las Navillas (60.3% of individuals). In general, the relative numerical importance of individual taxa varied broadly between localities, as revealed by the broad ranges of abundance ranks exhibited by most constant taxa (Fig. 4). *Anthidiellum breviusculum*, with the narrowest range (1st–4th), was the species whose relative abundance changed the least between populations, being predictably abundant at all sites. At the opposite extreme, *M. galathea* (2nd–34th), *Megachile pilidens* (12th–43rd) and *Anthophora ochroleuca* (6th–39th), were the species changing most markedly in relative abundance between localities.

Discussion

The identity of the pollinators interacting with an individual *L. latifolia* plant depends to a considerable extent on the physical characteristics of the environment where the plant grows. Populations at different distances from water differed broadly in the abundance and composition of their pollinator assemblages. The contrasts between populations in the same category of distance from water, although significant, were comparatively minor. Differences between populations took place over short distances, as exemplified by Aguaderillos-1 and Aguaderillos-2. These two populations were only 300 m apart, yet had contrasting pollinator assemblages (Table 5, Fig. 3).

Lavandula latifolia is one of the few woody species in its habitat that flower in

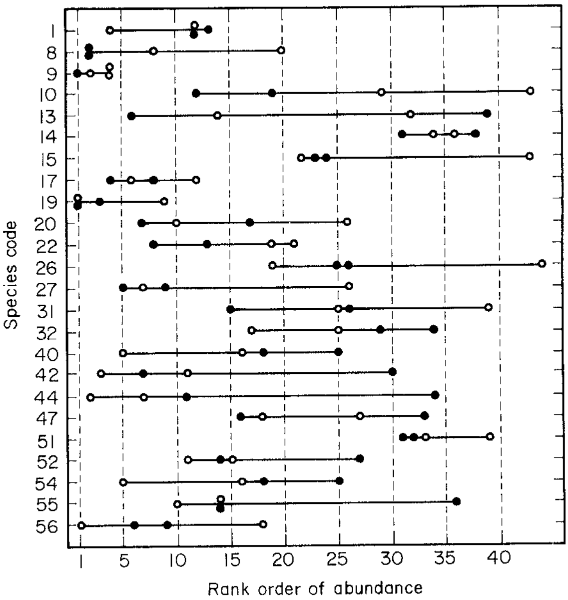

Figure 4. Variation between populations in rank order of abundance of insect taxa visiting *Lavandula latifolia* flowers (1987). Shown are the rank scores in each of the four study sites (○, ●) for each floral visitor (rows, identified by their numbers in Table 5). Horizontal lines connect extreme scores for a given species. Only taxa occurring in all localities ('constant' taxa, $N = 24$) have been represented, but ranks were obtained considering the whole set of species present at each site. ●, Water-distant sites; ○, near-water sites.

TABLE 5. Variation between populations in the composition of the *Lavandula latifolia* pollinator assemblage (1987). Entries represent mean number of individuals per ten counts. Numbers of counts per locality are shown in Fig. 3. —, indicates that the species was not recorded in the counts for that locality. For 'constant' taxa (those occurring in all study sites), the significance of observed differences in average abundance is shown†

	Near streams		Far from water	
	Aguaderillos-1	Cuevas Bermejas	Aguaderillos-2	Las Navillas
Hymenoptera				
1 *Bembix zonata* (Sphecidae)****	11.2	43.4	4.2	1.4
2 *Ammophila* sp. (aff. *sabulosa*) (Sphecidae)	0.4	—	—	1.1
3 Sphecidae gen. sp.	—	—	—	0.3
4 Scoliidae gen. sp.	—	0.6	1.1	—
5 *Halictus* sp. (aff. *scabiosae*) (Halictidae)	—	1.2	0.8	—
6 *Colletes* sp. (Colletidae)	—	0.6	0.6	0.8
7 *Anthidium cingulatum* (Megachilidae)	0.4	—	—	0.8
8 *Anthidium florentinum* (Megachilidae)****	24.0	6.9	26.1	14.8
9 *Anthidiellum breviusculum* (Megachilidae)****	34.4	70.0	45.0	6.1
10 *Megachile pilidens* (Megachilidae)*	0.4	1.9	4.7	0.8
11 *Megachile* sp.	2.0	13.4	2.8	—
12 *Anthophora crassipes* (Anthophoridae)	0.4	0.3	—	0.8
13 *Anthophora ochroleuca* (Anthophoridae)***	6.0	1.6	0.3	5.3
14 *Anthophora quadrifasciata* (Anthophoridae) n.s.	1.2	0.9	0.6	0.3
15 *Anthophora albigena* (Anthophoridae)*	3.6	0.3	0.8	0.8
16 *Melecta* sp. (Anthophoridae)	0.8	5.3	1.1	—
17 *Ceratina cyanea*+*mocsaryi* (Anthophoridae)****	28.4	19.4	15.8	2.5
18 *Xylocopa violacea* (Anthophoridae)	7.2	—	1.1	0.6
19 *Apis mellifera* (Apidae)****	99.6	25.3	16.7	46.4
20 *Bombus terrestris* (Apidae)****	2.4	24.7	2.5	4.2
21 *Bombus pascuorum* (Apidae)	—	4.4	0.6	1.4
Diptera				
22 *Systoechus* nov. sp. (?) (Bombyliidae)****	3.6	10.6	5.8	1.4
23 Bombyliidae gen. sp.	0.4	—	—	0.3
24 *Conops* sp. (Conopidae)	0.4	—	—	—
25 *Merodon geniculatus* (Syrphidae)	1.2	0.3	—	—
26 *Eristalis tenax* (Syrphidae)**	4.0	0.3	0.8	0.6

27 *Volucella* spp. (Syrphidae)‡****	25.2	4.1	5.3	5.6
28 *Sphaerophoria scripta* (Syrphidae)	0.8	—	—	—
29 *Chrysotoxum intermedium* (Syrphidae)	1.2	—	0.3	—
30 *Xanthogramma marginale* (Syrphidae)	0.4	—	—	—
31 Calliphoridae gen. sp.$^{\text{n.s.}}$	2.4	0.6	0.8	1.1
32 Tachinidae gen. sp.**	5.2	4.1	0.3	0.6
Lepidoptera				
33 *Macroglossum stellatarum* (Sphingidae)	2.0	—	—	0.3
34 *Agdistis* sp. (Pterophoridae)	—	—	0.6	—
35 *Iphiclides podalirius* (Papilionidae)	0.4	—	—	—
36 *Colias crocea* (Pieridae)	1.6	1.6	—	0.8
37 *Pieris rapae* (Pieridae)	—	1.6	—	—
38 *Pontia daplidice* (Pieridae)	—	1.9	—	—
39 *Gonopteryx rhamni + cleopatra* (Pieridae)	4.0	1.9	—	0.8
40 *Pandoriana pandora* (Nymphalidae)****	30.4	0.6	12.5	9.7
41 *Argynnis paphia* (Nymphalidae)	34.8	16.2	5.0	—
42 *Fabriciana adippe* (Nymphalidae)****	16.8	64.4	7.2	0.3
43 *Issoria lathonia* (Nymphalidae)	1.6	5.9	0.3	
44 *Melanargia galathea* (Satyridae)****	37.6	27.5	5.0	0.3
45 *Hipparchia alcyone* (Satyridae)	1.2	—	0.3	1.7
46 *Satyrus actaea* (Satyridae)	—	32.2	—	—
47 *Hyponephele lupina + lycaon* (Satyridae)****	2.4	12.5	2.5	0.3
48 *Pyronia tithonus + cecilia* (Satyridae)	3.2	4.4	0.3	—
49 *Coenonympha dorus* (Satyridae)	—	—	—	0.3
50 *Lasiommata maera* (Satyridae)	0.4	1.6	—	—
51 *Lasiommata megera* (Satyridae)$^{\text{n.s.}}$	0.8	1.6	0.3	0.3
52 *Lycaena phlaeas* (Lycaenidae)****	5.6	20.9	3.9	0.6
53 *Lampides boeticus* (Lycaenidae)	—	—	0.8	—
54 *Plebicula escheri* (Lycaenidae)****	5.6	42.8	2.2	0.6
55 *Lysandra albicans/hispana* (Lycaenidae)****	17.6	16.6	0.3	1.1
56 *Hesperia comma* (Hesperiidae)****	4.8	132.8	7.5	1.7
57 *Spialia sertorius* (Hesperiidae)	1.6	17.5	—	—
58 *Thymelicus acteon* (Hesperiidae)	21.2	25.6	1.7	—
59 *Muschampia proto* (Hesperiidae)	2.8	15.6	—	0.8

†Brown–Forsythe *F* test: $^{\text{n.s.}}$ non-significant; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; ****$P < 0.0001$.
‡Includes *V. zonaria*, *V. elegans* and *V. inanis*.

summer (Bonet, Rita & Sebastià, 1985; Herrera, unpublished). The dry and hot conditions prevailing during this period are a characteristic feature of the Mediterranean climate, and several studies have demonstrated a marked summer reduction in insect abundance, diversity and activity in a variety of southern Spanish woodlands and scrublands (Herrera, 1980; Fernández Haeger & Jordano Barbudo, 1982; Jordano, 1984; Baz Ramos, 1986). During the summer months, insect activity and abundance are greatest in the vicinity of the few water courses available, probably as a consequence of improved microclimate compared to the arid surroundings. Patchiness in the summer distribution of insects in Mediterranean habitats has been shown to be particularly pronounced for the very drought-sensitive diurnal lepidopterans (Viejo & Pino, 1983; Galiano, Sterling & Viejo, 1985; Viejo, Fernández-Galiano & Sterling, 1985). The results reported above agree with these general patterns. The abundance and diversity of insect pollinators decreased significantly from the *L. latifolia* populations growing near streams to those in arid places, and the reduction was most marked for lepidopterans. As a consequence, not only were pollinators less abundant in arid-site populations, but also the proportional importance of lepidopterans was much reduced compared to sites near streams.

WITHIN-POPULATION VARIATION

Methods

Within-population variation in the composition of the pollinator assemblage was examined in the Aguaderillos-1 site. The 80-m transect used for the counts was divided there into three adjacent segments of similar length ('sectors' A, B and C hereafter), and separate record was kept of floral visitors observed in each sector.

Sectors differed slightly in the size (height, basal area) and density of *L. latifolia* plants (size increased, and density decreased, from A through B to C), and in aspect and substrate inclination. Sector A was on a south-facing slope, sector B was on flat terrain, and sector C was on a north-facing slope. These differences resulted in differential insolation during daytime. Sector A had at least 50% of its length in full insolation 7.5 hours a day; sector B, 9 hours a day; and sector C only 6 hours a day (observations in the period 15–20 August). The three sectors were otherwise similar in their proximity to the water course.

With few exceptions, I walked the three sectors in succession, thus obtaining three sector counts on each census occasion. Slight differences between sectors in sample sizes (see Table 6) are explained by incomplete sampling of the three-sector set on a few days at the start of the study. Data for Aguaderillos-1 used in the preceding sections were the result of combining into single samples the three sector counts on each census occasion (after excluding the incomplete samples mentioned above). Counts for all years (1982–1987), months and times of day combined ($N = 1540$ counts for the three sectors combined), totalling 19 266 individual insects, form the basis for the analyses presented in this section.

Results

There was no significant heterogeneity between sectors in total abundance of pollinators (Table 6). Among major groups, hymenopterans and dipterans did

TABLE 6. Within-population variation in the abundance of the three major groups of floral visitors (all species combined) at the Aguaderillos-1 site (all years and months combined). Entries represent mean number of individuals (±1 S.D.) per count in each sector (first row), and proportion (%) with respect to the total of individuals for each sector (second row). N = number of counts

	Sector A (N = 526)	Sector B (N = 507)	Sector C (N = 507)	F value†
Hymenopterans	6.0±4.4	4.8±3.6	5.5±5.0	10.7****
	48.0	39.1	43.3	
Dipterans	0.8±1.3	1.0±1.6	2.1±2.5	65.7****
	6.7	8.2	16.3	
Lepidopterans	5.7±7.3	6.5±13.2	5.1±6.6	$2.7^{\text{n.s.}}$
	45.3	52.7	40.4	
Total	12.6±9.4	12.3±14.1	12.7±8.2	$0.2^{\text{n.s.}}$

†Brown–Forsythe F test without assumption for equal variances: **** $P < 0.0001$; $^{\text{n.s.}}$ non-significant.

exhibit significant differences between sectors in average abundance, while lepidopterans did not. The proportions contributed by the three groups varied between sectors. Hymenopterans and lepidopterans contributed roughly similar proportions in sectors A and B, while lepidopterans dominated numerically in sector B. The proportional significance of dipterans was greatest at sector C.

The complete list of pollinators recorded at the Aguaderillos-1 site, all years and months combined, comprised 74 taxa. Of these, 62 (83.7%) occurred on the three sectors ('constant' taxa), while seven (9.5%) and five (6.8%) occurred on two and one sectors, respectively ('irregular' taxa). Hymenopteran, dipteran and lepidopteran taxa did not differ significantly with regard to the number of sectors on which they occurred ($H = 1.4$, df $= 2$, $P = 0.49$; Kruskal–Wallis test). Taxa that did not occur on the three sectors were characterized by their low abundances, and contributed altogether less than 0.5% of total individuals in every sector.

Considering constant taxa alone, significant heterogeneity between sectors in average abundance occurred in 38 taxa ($P < 0.05$ or better, F-tests), while no significant differences existed in the remaining 24 taxa ($P > 0.05$). The three major groups of pollinators did not differ with regard to the proportion of taxa exhibiting significant differences in average abundance between sectors ($G = 1.70$, df $= 2$, $P = 0.43$). For most species, differences in abundance between sectors were of small magnitude (even though statistically significant), and detailed presentation of mean abundances by species and sectors is omitted. There were, however, a few exceptions to this general pattern, as some species exhibited appreciable variation in abundance between sectors. Prominent among these were (range of mean abundance per sector in parentheses) *A. mellifera* (19.6–33.6 individuals/10 counts), *Ceratina* spp. (0.8–2.7), *M. galathea* (12.0–26.4), *Eristalis tenax* (0.3–2.4) and *Volucella* spp. (3.9–12.2).

The relative contribution of individual taxa to the total number of individuals remained virtually constant between sectors. The three pairwise rank correlations between sectors for the average abundances of insect taxa were highly significant (Spearman $r_s = 0.876$–0.892, $N = 74$, $P < 10^{-10}$), demonstrating considerable consistency between sectors in the abundance rank of individual pollinators.

Discussion

The pollinator assemblage of *L. latifolia* experienced significant variation on a very small spatial scale. The observed variation is mainly related to changes in pollinator abundance, as differences between sectors in species composition are negligible and affect only rare species infrequently recorded in the counts. Significant variation in abundance between sectors was detected for 38 taxa and two of the three major groups of pollinators (hymenopterans and dipterans).

The centres of contiguous sectors are only about 25 m apart, well within the range of normal foraging flights exhibited at the study locality by all floral visitors (Herrera, 1987a, and unpublished observations). Differences observed between sectors should thus be attributed to the existence of microhabitat selection by pollinators (Beattie, 1971). These may be related to slight differences between sectors in features of the flower supply (e.g. flower density), plant characteristics (e.g. plant size, nectar secretion rates), microclimatic aspects (insolation, ambient humidity) or, most likely, a complex combination of these factors. Different causes are also likely to apply to different pollinators. Regardless of these proximate causes, however, the ultimate consequence of the observed patterns is that individual *L. latifolia* shrubs in the same population, and only 25 m apart, face in the course of their lifetimes pollinator assemblages differing in composition. This applies not only to differences in abundance of individual pollinator taxa, but also to variation in the relative significance of major groups. Plants in sector A have a hymenopteran-dominated pollinator assemblage, whereas plants in the contiguous sector B have a lepidopteran-dominated one.

SPATIO-TEMPORAL PREDICTABILITY

In this section, spatio-temporal patterns of variation in the *L. latifolia* pollinator assemblage are examined by combining information from the four scales of variation considered. The following questions are addressed: (1) How do we compare the relative predictabilities of individual pollinator taxa at the four scales of variation considered (annual, seasonal, between- and within-population)? (2) Do major groups of pollinators differ with regard to their degree of spatio-temporal variability? (3) To what extent are the four levels of variation considered here independent of each other?

Only the 52 pollinator taxa with data simultaneously available in the analyses of annual, seasonal, between- and within-population variation, are considered in this section (19 hymenopterans, eight dipterans, and 25 lepidopterans). For each of the four scales of variation considered, the coefficient of variation (CV = 100 × mean/standard deviation) of average abundances was obtained for each individual pollinator. At each scale of variation, CVs were computed over average abundances in the respective categories (years, half-month periods, populations, sectors). As used here, CV values provide an inverse measure of predictability in the abundance of individual taxa at each of the scales of variation considered.

Frequency distributions of CVs for the four scales of variation are shown in Fig. 5. There is significant heterogeneity between spatio-temporal scales in this

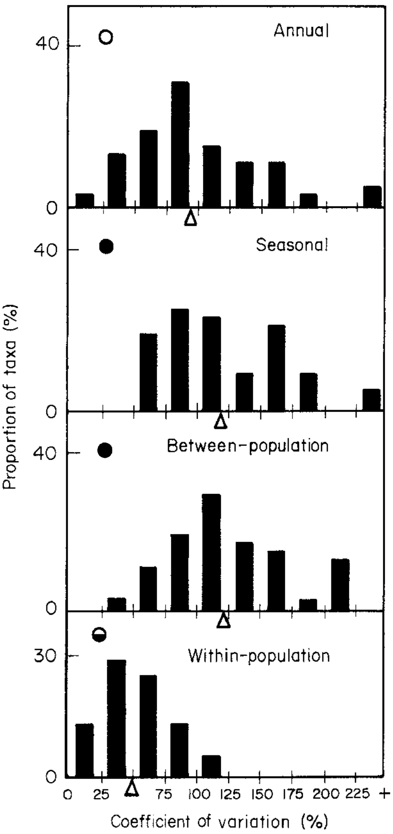

Figure 5. Frequency distributions of the coefficients of variation of pollinator abundance at the four scales of spatio-temporal variation considered. △, Mean of the distribution. Distributions sharing the geometric symbol at the top left corner of the graph do not differ significantly in their means ($P > 0.05$, Student–Newman–Keuls test). $N = 52$ taxa in all distributions.

statistic ($F = 33.2$, df = 3, 182, $P < 10^{-10}$; Brown–Forsythe F-test). On average, intraspecific variability in abundance increases from the within-population (average CV = 51.8%) through the annual (average CV = 98.3%) to the seasonal (average CV = 120.3%) and the population (average CV = 123.5%) scales. No significant difference in CVs exists between the seasonal and population variation scales (Fig. 5). These results indicate that the abundance of individual pollinators is most predictable within a *L. latifolia* population (as would be expected), intermediate at the between-year level, and least predictable seasonally and between populations. With the exception of the within-population scale, the absolute values of the CVs are indicative of important levels of intraspecific unpredictability at every scale considered.

Hymenopteran, dipteran and lepidopteran taxa did not differ significantly in CV values for annual ($H = 1.84$, df = 2, $P = 0.40$; Kruskal–Wallis analysis of variance), seasonal ($H = 0.79$, $P = 0.67$) and within-population ($H = 0.037$, $P = 0.98$) variation. The difference was marginally significant for between-population variation ($H = 5.73$, $P = 0.06$). In this case, lepidopterans were significantly more variable between populations than hymenopteran and dipteran taxa combined ($H = 5.67$, df = 1, $P = 0.017$).

TABLE 7. Correlation matrix (Pearson product-moment) for the coefficients of variation (CVs) of the abundance of individual pollinator taxa ($N = 52$) at the four scales of variation examined

	Scale of variation			
	Temporal		Population	
	Annual (CVANN)	Seasonal (CVSEA)	Between (CVPOP)	Within (CVSEC)
CVANN	1.000			
CVSEA	0.409**	1.000		
CVPOP	0.293*	−0.136$^{\text{n.s.}}$	1.000	
CVSEC	0.444***	0.250$^{\text{n.s.}}$	0.375**	1.000

†$^{\text{n.s.}}$, non-significant; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

Correlation coefficients between the CVs of abundance at the four variation scales are shown in Table 7. Four out of six correlations are significant and positive, and two are non-significant. Annual and seasonal CVs are positively correlated, as are between- and within-population ones. The two non-significant correlations are between CVs for spatial and temporal dimensions (Table 7), but there are two significant coefficients in this group (annual CVs with both between- and within-population CVs). A significant trend therefore exists for species that are variable on one scale to be also variable on others, and vice versa. This trend, however, is relatively weak, as abundance variability in space is not consistently related to variability in time, and the proportions of variance accounted for by the correlations (squared r) are small in all cases (range = 0.086–0.197 for the significant coefficients).

GENERAL DISCUSSION

Pollinator variation

In the study region, the size and composition of the pollinator assemblage of *L. latifolia* vary markedly in time and space. This variation occurs on all scales considered, and involves both major insect groups and individual species. Although no previous study has simultaneously examined variation in pollinators at the four levels considered here (but see Aker, 1982), considerable evidence exists for a variety of habitats and plant species demonstrating pollinator variation in time or space. Variation between populations has almost invariably been found whenever a plant species has been studied at several sites, in both temperate and tropical habitats (Miller, 1978; Willson, Bertin & Price, 1979; Willson & Bertin, 1979; Cruden & Hermann-Parker, 1979; Dorr, 1981; Hannan, 1981; Hippa, Koponen & Osmonen, 1981; Udovic, 1981; Bertin, 1982; Wille, Orozco & Raabe, 1983; Pellmyr, 1984; Lindsey, 1984; Spears, 1987). Similarly, variation between years seems also to be the rule whenever a study encompassed more than a single season (Beattie, Breedlove & Ehrlich, 1973; Teräs, 1976; Waser, 1979; Kwak, 1980; Aker, 1982; Boyle & Philogène, 1983; Calder *et al.*, 1983; Spears, 1987). Seasonal variation in pollinator assemblages has also been documented frequently (Teräs, 1976; Aker, 1982; Motten, 1982;

Montalvo & Ackerman, 1986). Small-scale, within-population variation may be inferred from Beattie's (1971) study on the influence of microclimate on local pollinator activity. In the case of insect-pollinated plants, these findings are not unexpected, as spatio-temporal variation in pollinators is the logical consequence of well-known, widespread phenomena such as annual variation in insect population sizes (Wolda, 1978; Dempster & Pollard, 1981; Connell & Sousa, 1983; Pollard, 1984; Wallner, 1987), seasonal cycles (Poursin & Plateaux-Quenu, 1982; Ackerman, 1983a; Scott & Epstein, 1987), habitat selection (Erhardt, 1985; Viejo & Templado, 1986), and microclimatic preferences related to physiological tolerance (Taylor, 1963; Rawlins, 1980; Bailey, Lerer & Mills, 1982; Chappell, 1982; Gilbert, 1985; Boyle-Makowski & Philogène, 1985). All these processes, acting in concert, will generally tend to produce an irregular distribution of insect species in time and space, as shown here for *L. latifolia.* Variation in the assemblage of pollinators with which one plant species interacts thus seems to be the rule, rather than the exception, in nature. In the case of *L. latifolia* there is but a weak relationship between the predictability of a pollinator on a given scale of variation and its predictability on the remaining scales considered. This suggests that the spatio-temporal mosaic of pollinators 'perceived' by this species in the study region is irregularly, rather erratically structured, and thus has a strong stochastic component.

Implications of variation

For variation in a pollinator assemblage to result in a spatio-temporal mosaic of selection regimes on the plant, it is necessary that pollinators differ as to the fitness consequences (to the plant) of their activity at flowers (e.g. pollinating effectiveness, frequency of cross pollination). These aspects have received less attention in the literature than variations in abundance, but all studies that have directly examined them have invariably found differences between pollinators in the consequences of their interactions with individual plant species. Reported interspecific differences relate to frequency of pollen deposition on the stigma, number of pollen grains left when delivery occurs, and 'quality' of transferred pollen from the viewpoint of the maternal plant (Motten, Campbell, Alexander & Miller, 1981; Arnold, 1982; Motten, 1983, 1986; Schemske & Horvitz, 1984; Montalvo & Ackerman, 1986; Herrera, 1987b). By affecting the number and genetic constitution of the resulting seeds, these factors may potentially influence the plant's fitness (Winsor, Davis & Stephenson, 1987; Herrera, 1987b; and references therein).

In *L. latifolia*, pollinators differ in frequency of pollen transfer, number of pollen grains deposited on the stigma, selection of floral sexual stage (flowers are markedly protandrous), and patterns of flight distance between flowers (Herrera, 1987a,b). Hand-pollination experiments demonstrated that these variations may translate into differential fitness of *L. latifolia* plants through their effects on number of fruit and seed produced, and also, possibly, eventual success of resulting offspring. Considering major insect groups, hymenopteran species delivered more pollen grains and more often than lepidopteran and dipteran taxa. Lepidopteran species tended to fly longer distances between consecutive flowers than hymenopteran and dipteran taxa. Bees pollinate flowers frequently and with large pollen loads, but generally promote geitonogamy; butterflies pollinate flowers less often and with smaller loads, but then most often with cross pollen; and flies pollinate flowers infrequently, with small pollen loads, and generally promote geitonogamy. There were, however, conspicuous exceptions to this prevailing pattern at the level of individual species, since broad interspecific variation in pollinating characteristics existed within each major group (Herrera, 1987a,b). This indicates that individual species generally are not 'interchangeable' from the viewpoint of the plant, and that spatio-temporal variation in detailed aspects of species composition documented in this paper will most likely have some pollination consequences to plants. For this reason, examining the potential implications to plants of spatio-temporal variation in pollinators at the level of major groups is admittedly a simplification.

Variations reported in this paper in the overall composition of the *L. latifolia* pollinator assemblage will most likely result in spatio-temporal variations in the consequences of pollination as 'perceived' by the mother plant. Proportionally more outcrossing, reduced pollen load size (and hence presumably pollen tube interactions), and lower frequency of pollen transfer to stigmas, are to be expected in those years when butterflies dominated the assemblage, during the first half of the flowering season, and in populations growing near streams. In contrast, geitonogamy, frequent pollen transfer, and increased pollen load size (and pollen tube interactions), should characterize years with bee dominance, the second half of the flowering period, and populations growing in more xeric places. Without further studies on the ecology of *L. latifolia* in the area, it is not possible at present to suggest the precise nature of the selective implications to the plant of the components of the breeding system affected by pollinator variation. Nevertheless, it seems safe to infer that their *variation* will most likely result in shifting selection regimes (in time and space), regardless of the actual sign and magnitude of the fitness consequences inherent to each breeding system attribute.

At the level of local populations, temporal (both annual and seasonal) and within-population variation in pollinators will most likely result in inconsistent selective regimes. The fitness consequences to plants of their interaction with the set of pollinators are expected to vary between years, in the course of a single flowering episode, and between individuals separated by a few dozen metres. This inconsistency will greatly reduce the possibilities of adaptation of *L. latifolia* to particular pollinators. Similarly, variation between populations will produce a spatial mosaic of selective regimes which, if sufficient gene flow occurs between populations, will hinder adaptations to particular pollinators (Spieth, 1979). Regular movements between riparian and adjacent xeric habitats which could enhance gene flow have been reported for some butterflies in mediterranean habitats of central Spain (Galiano *et al.*, 1985; Viejo *et al.*, 1985). Furthermore, differences in pollinators exist between populations only a few hundred metres apart (Aguaderillos-1 and Aguaderillos-2), a distance well within the range of usual foraging movements of most pollinators.

Specialization in relation to pollinators

The flowers of *L. latifolia* are tubular, zygomorphic, with the nectar deeply concealed at the base of the narrow corolla tube (7–8 mm long). These morphological and structural features should presumably limit the diversity of floral visitors. Contrary to this expectation, however, the pollinator assemblage of *L. latifolia* is taxonomically very diverse, with 40–50 species visiting and pollinating flowers at any given time and place. This broad spectrum of pollinators is only comparable to those reported for plant species with open, actinomorphic flowers of the 'dish- to bowl-shaped' morphological type (Faegri & van der Pijl, 1979), whose floral rewards are readily accessible to a variety of visitors (e.g. Hippa *et al.*, 1981; Boyle & Philogène, 1983; Pellmyr, 1984). In contrast to these other diverse pollinator assemblages, however, that of *L. latifolia* is made up of relatively efficient, 'specialized' (at least on the basis of mouthparts' length and differentiation) pollinators, hence floral morphology seems to have effectively limited the variety of pollinators. Medium to large butterflies with long proboscides, and long-tongued Megachilid, Anthophorid and Apid bees dominate the assemblage. Even among flies, relatively long-tongued Syrphidae (*Eristalis*, *Volucella*) dominate numerically. *Lavandula latifolia* thus has a taxonomically diverse, but morphologically limited pollinator assemblage.

The "most effective pollinator principle" (Stebbins, 1970) holds that selection should favour traits that attract and maintain only those visitors that provide the best pollination service (both in frequency and effectiveness). Nevertheless, unpredictability in pollinator composition (and concomitant inconsistency in selective regimes) of the kind reported here will preclude specialization (Feinsinger, 1983). The variety of *L. latifolia* pollinators is consistent with these notions. It may thus be hypothesized that *L. latifolia* has as diverse a pollinator assemblage because further 'pruning' of the assemblage has been hindered by the inconsistencies in selective regimes resulting from spatio-temporal variation in pollinators, and because the vast majority of component species fall within a relatively narrow range of high pollinating 'quality' (Herrera, 1987b). Two ecological factors probably have also contributed to the observed diversity of pollinators, through being ultimately responsible for the local levels of species richness. (1) By flowering at a time of year when no other plant does in its habitat, *L. latifolia* becomes an almost obligate target for virtually every insect seeking pollen or nectar. Other summer-fruiting Labiatae, occurring at different elevations in the region and differing markedly in floral morphology from *L. latifolia*, have also broad pollinator assemblages which have many species in common with that of *L. latifolia* (e.g. *Satureja cuneifolia*, *Teucrium polium*; Herrera, unpublished). (2) This study was conducted in an area of Mediterranean montane woodlands which is unique for the high degree of integrity of its ecosystems, high biological diversity, and virtually undisturbed vegetation over thousands of hectares. Insect diversity has not experienced there the well-known devastating effects of man-made perturbations of natural habitats (Johansen, 1977; Janzen, 1987).

CONCLUDING REMARKS

Predictability (or consistency) of selective pressures involving mutualistically interacting organisms seems to be a prerequisite for reciprocal evolutionary changes to occur (Howe, 1984; Herrera, 1985, 1986). Nevertheless, spatio-temporal mosaics, frequently examined by theoreticians and model builders in the fields of genetics and evolutionary ecology, have often been ignored by field researchers interested in mutualisms (with the exceptions noted earlier). Variations occurring in nature have been either disregarded as unimportant or, most often, obscured by pooling relatively insufficient samples into aggregated categories; by combining data from several species, years, seasons or populations, into single figures; and by usually presenting the data as summaries of average values. These procedures, albeit formally correct and often imposed upon researchers by editorial policies, have had the rather undesirable consequences of artificially making the diverse, often inconsistent spatio-temporal mosaics actually faced by species in nature coalesce into unrealistic summaries, and consequently conveying the illusory impression that mutualistic interactions are much less stochastic than they surely are. Stochasticity in mutualisms has been demonstrated whenever specific attention has been paid to spatio-temporal variation (e.g. Pudlo *et al.*, 1980; Barton, 1986; Horvitz & Schemske, 1986). This applies even to as classical an example of coevolved mutualism as the orchid-euglossine bee interaction for pollination in tropical forests (Janzen, De Vries, Higgins & Kimsey, 1982; Ackerman, 1983b). The results of the present study are no exception. A strong spatio-temporal patterning exists in the size and composition of the mutualistic assemblage interacting with *L. latifolia* for pollination. The erratic nature of much of this variation will predictably result in an inconstant spatio-temporal mosaic of selective regimes, and may actually hinder the specialization of the plant in relation to particular pollinators, thus constraining the potential for mutualism-related evolutionary changes.

ACKNOWLEDGEMENTS

Insect identifications were generously provided by María A. Marcos (Universidad de Salamanca; Syrphidae), Marcos Báez (Universidad de La Laguna; Bombyliidae), Enrique Asensio (I.N.I.A. Valladolid; Megachilidae, Anthophoridae), Leopoldo Castro (Teruel; Eumenidae, Apidae), and José L. Yela (Madrid; Noctuidae, Pterophoridae). Manolo Carrión and my wife, Dori, provided companionship and helped with many aspects of the field work. The Instituto para la Conservación de la Naturaleza (1982–1984) and the Agencia de Medio Ambiente (1985–1987) authorized my work in the Sierra de Cazorla and provided invaluable housing facilities.

REFERENCES

ACKERMAN, J. D., 1983a. Diversity and seasonality of male euglossine bees (Hymenoptera: Apidae) in central Panamá. *Ecology, 64:* 274–283.

ACKERMAN, J. D., 1983b. Specificity and mutual dependency of the orchid–euglossine bee interaction. *Biological Journal of the Linnean Society, 20:* 301–314.

AKER, C. L., 1982. Spatial and temporal dispersion patterns of pollinators and their relationship to the flowering strategy of *Yucca whipplei* (Agavaceae). *Oecologia (Berlin), 54:* 243–252.

ARNOLD, R. M., 1982. Pollination, predation and seed set in *Linaria vulgaris* (Scrophulariaceae). *American Midland Naturalist, 107:* 360–369.

BAILEY, W. G., LERER, H. & MILLS, P. F., 1982. Humidity and the pollination activity of *Megachile rotundata. Environmental Entomology, 11:* 1063–1066.

BARTON, A. M., 1986. Spatial variation in the effects of ants on an extrafloral nectary plant. *Ecology, 67:* 495–504.

BAZ RAMOS, A., 1986. Sobre la estacionalidad de las comunidades de mariposas (Lepidoptera) de la zona centro de la Península Ibérica. *Boletín de la Asociación Española de Entomología, 10:* 139–157.

BEATTIE, A. J., 1971. Itinerant pollinators in a forest. *Madroño, 21:* 120–124.

BEATTIE, A. J., BREEDLOVE, D. E. & EHRLICH, P. R., 1973. The ecology of the pollinators and predators of *Frasera speciosa*. *Ecology, 54:* 81–91.

BERTIN, R. I., 1982. Floral biology, hummingbird pollination and fruit production of trumpet creeper (*Campsis radicans*, Bignoniaceae). *American Journal of Botany, 69:* 122–134.

BONET, A., RITA, J. & SEBASTIÀ, M. T., 1985. *La flora mellífera de la circumscripció de Barcelona.* Barcelona: Servei d'Agricultura i Ramaderia, Diputació de Barcelona.

BOYLE, R. M. D. & PHILOGÈNE, B. J. R., 1983. The native pollinators of an apple orchard: variations and significance. *Journal of Horticultural Science, 58:* 355–363.

BOYLE-MAKOWSKI, R. M. D. & PHILOGÈNE, B. J. R. 1985. Pollinator activity and abiotic factors in an apple orchard. *Canadian Entomologist, 117:* 1509–1521.

CALDER, W. A., WASER, N. M., HIEBERT, S. M., INOUYE, D. W. & MILLER, S., 1983. Site-fidelity, longevity, and population dynamics of Broad-tailed hummingbirds: a ten year study. *Oecologia (Berlin), 56:* 359–364.

CHAPPELL, M. A., 1982. Temperature regulation of carpenter bees (*Xylocopa californica*) foraging in the Colorado desert of southern California. *Physiological Zoology, 55:* 267–280.

CHRISTIANSEN, F. B. & FELDMAN, M. W., 1975. Subdivided populations: a review of the one- and two-locus deterministic theory. *Theoretical Population Biology, 7:* 13–38.

CONNELL, J. H. & SOUSA, W. P., 1983. On the evidence needed to judge ecological stability or persistence. *American Naturalist, 121:* 789–824.

CRUDEN, R. W. & HERMANN-PARKER, S. M., 1979. Butterfly pollination of *Caesalpinia pulcherrima*, with observations on a psychophilous syndrome. *Journal of Ecology, 67:* 155–168.

DEMPSTER, J. P. & POLLARD, E., 1981. Fluctuations in resource availability and insect populations. *Oecologia (Berlin), 50:* 412–416.

DEVESA, J. A., ARROYO, J. & HERRERA, J., 1985. Contribución al conocimiento de la biología floral del género *Lavandula* L. *Anales del Jardín Botánico de Madrid, 42:* 165–186.

DORR, L. J., 1981. The pollination ecology of *Zenobia* (Ericaceae). *American Journal of Botany, 68:* 1325–1332.

ERHARDT, A., 1985. Diurnal Lepidoptera: sensitive indicators of cultivated and abandoned grassland. *Journal of Applied Ecology, 22:* 849–861.

FAEGRI, K. & VAN DER PIJL, L., 1979. *The Principles of Pollination Ecology.* 3rd Edition. Oxford: Pergamon Press.

FEINSINGER, P., 1983. Coevolution and pollination. In D. J. Futuyma & M. Slatkin (Eds), *Coevolution:* 282–310. Sunderland: Sinauer Associates.

FEINSINGER, P., WOLFE, J. A. & SWARM, L. A., 1982. Island ecology: reduced hummingbird diversity and the pollination biology of plants, Trinidad and Tobago, West Indies. *Ecology, 63:* 494–506.

FELSENSTEIN, J., 1976. The theoretical population genetics of variable selection and migration. *Annual Review of Genetics, 10:* 253–280.

FERNÁNDEZ HAEGER, J. & JORDANO BARBUDO, D., 1982. Fenología de una comunidad mediterránea de mariposas diurnas. *Biologie-Ecologie Méditerranéenne, 9:* 19–28.

GALIANO, E. F., STERLING, A. & VIEJO, J. L., 1985. The role of riparian forests in the conservation of butterflies in a Mediterranean area. *Environmental Conservation, 12:* 361–362.

GILBERT, F. S., 1985. Diurnal activity patterns in hoverflies (Diptera, Syrphidae). *Ecological Entomology, 10:* 385–392.

GILBERT, F. S., 1986. *Hoverflies.* Cambridge: Cambridge University Press.

HANNAN, G. L., 1981. Flower color polymorphism and pollination biology of *Platystemon californicus* Benth. (Papaveraceae). *American Journal of Botany, 68:* 233–243.

HEDRICK, P. W., GINEVAN, M. E. & EWING, E. P., 1976. Genetic polymorphism in heterogeneous environments. *Annual Review of Ecology and Systematics, 7:* 1–32.

HEITHAUS, E. R., 1986. Seed dispersal mutualism and the population density of *Asarum canadense*, an ant-dispersed plant. In A. Estrada & T. H. Fleming (Eds), *Frugivores and Seed Dispersal:* 199–210. Dordrecht: Dr. W. Junk Publishers.

HERRERA, C. M., 1980. Composición y estructura de dos comunidades mediterráneas de passeriformes. *Doñana Acta Vertebrata, 7 (Suppl.):* 1–340.

HERRERA, C. M., 1985. Determinants of plant–animal coevolution: the case of mutualistic dispersal of seeds by vertebrates. *Oikos, 44:* 132–141.

HERRERA, C. M., 1986. Vertebrate-dispersed plants: why they don't behave the way they should. In A. Estrada & T. H. Fleming (Eds), *Frugivores and Seed Dispersal:* 5–18. Dordrecht: Dr. W. Junk Publishers.

HERRERA, C. M., 1987a. Componentes del flujo génico en *Lavandula latifolia* Medicus: polinización y dispersión de semillas. *Anales del Jardín Botánico de Madrid, 44:* 49–61.

HERRERA, C. M., 1987b. Components of pollinator 'quality': comparative analysis of a diverse insect assemblage. *Oikos, 50:* 79–90.

HERRERA, C. M., in press. Avian frugivory and seed dispersal in Mediterranean habitats: regional variation in plant–animal interaction. *Proceedings of the 19th International Ornithological Congress, Ottawa, Canada.*

HERRERA, J., 1984. Vegetación del Valle del Guadahornillos (Sierra de Cazorla, Jaén). *Studia Oecologica, 5:* 77–96.

HIPPA, H., KOPONEN, S. & OSMONEN, O., 1981. Flower visitors to the cloudberry (*Rubus chamaemorus* L.) in northern Fennoscandia. *Reports of the Kevo Subarctic Research Station, 17:* 44–54.

HORVITZ, C. C. & SCHEMSKE, D. W., 1984. Effects of ants and an ant-tended herbivore on seed production of a Neotropical herb. *Ecology, 65:* 1369–1378.

HORVITZ, C. C. & SCHEMSKE, D. W., 1986. Seed dispersal of a Neotropical myrmecochore: variation in removal rates and dispersal distances. *Biotropica, 18:* 319–323.

HOWE, H. F., 1984. Constraints on the evolution of mutualisms. *American Naturalist, 123:* 764–777.

JANZEN, D. H., 1980. When is it coevolution? *Evolution, 34:* 611–612.

JANZEN, D. H., 1987. Insect diversity of a Costa Rican dry forest: why keep it, and how? *Biological Journal of the Linnean Society, 30:* 343–356.

JANZEN, D. H., DE VRIES, P. J., HIGGINS, M. L. & KIMSEY, L. S., 1982. Seasonal and site variation in Costa Rican euglossine bees at chemical baits in lowland deciduous and evergreen forests. *Ecology, 63:* 66–74.

JOHANSEN, C. A., 1977. Pesticides and pollinators. *Annual Review of Entomology, 22:* 177–192.

JORDANO, P., 1984. *Relaciones entre plantas y aves frugívoras en el matorral mediterráneo del área de Doñana.* Unpublished Dissertation, University of Sevilla, Sevilla, Spain.

KWAK, M. M., 1980. The pollination value of honeybees to the bumblebee plant *Rhinanthus. Acta Botanica Neerlandica, 29:* 597–603.

LINDSEY, A. H., 1984. Reproductive biology of Apiaceae. I. Floral visitors to *Thaspium* and *Zizia* and their importance in pollination. *American Journal of Botany, 71:* 375–387.

MESLER, M. R. & LU, K. L., 1983. Seed dispersal of *Trillium ovatum* (Liliaceae) in second-growth redwood forests. *American Journal of Botany, 70:* 1460–1467.

MILLER, R. B., 1978. The pollination ecology of *Aquilegia elegantula* and *A. caerulea* (Ranunculaceae) in Colorado. *American Journal of Botany, 65:* 406–414.

MONTALVO, A. M. & ACKERMAN, J. D., 1986. Relative pollinator effectiveness and evolution of floral traits in *Spathiphyllum friedrichsthalii* (Araceae). *American Journal of Botany, 73:* 1665–1676.

MOTTEN, A. F., 1982. Autogamy and competition for pollinators in *Hepatica americana* (Ranunculaceae). *American Journal of Botany, 69:* 1296–1305.

MOTTEN, A. F., 1983. Reproduction of *Erythronium umbilicatum* (Liliaceae): pollination success and pollinator effectiveness. *Oecologia (Berlin), 59:* 351–359.

MOTTEN, A. F., 1986. Pollination ecology of the spring wildflower community of a temperate deciduous forest. *Ecological Monographs, 56:* 21–42.

MOTTEN, A. F., CAMPBELL, D. R., ALEXANDER, D. E. & MILLER, H. L., 1981. Pollination effectiveness of specialist and generalist visitors to a North Carolina population of *Claytonia virginica. Ecology 62:* 1278–1287.

MUÑOZ, A. & DEVESA, J. A., 1987. Contribución al conocimiento de la biología floral del género *Lavandula* L. II. *Lavandula stoechas* L., subsp. *stoechas. Anales del Jardín Botánico de Madrid, 44:* 63–78.

PELLMYR, O., 1984. The pollination ecology of *Actaea spicata* (Ranunculaceae). *Nordic Journal of Botany, 4:* 443–456.

POLLARD, E., 1984. Fluctuations in the abundance of butterflies, 1976–82. *Ecological Entomology, 9:* 179–188.

POURSIN, J. M. & PLATEAUX-QUENU, C., 1982. Niches écologiques de quelques Halictinae. I. Comparaison des cycles annuels. *Apidologie, 13:* 215–226.

PUDLO, R. J., BEATTIE, A. J. & CULVER, D. C., 1980. Population consequences of changes in an ant-seed mutualism in *Sanguinaria canadensis. Oecologia (Berlin), 46:* 32–37.

RAWLINS, J. E., 1980. Thermoregulation by the black swallowtail butterfly, *Papilio polyxenes* (Lepidoptera: Papilionidae). *Ecology, 61:* 345–357.

SCHEMSKE, D. W. & HORVITZ, C. C., 1984. Variation among floral visitors in pollination ability: a precondition for mutualism specialization. *Science, 225:* 519–521.

SCOTT, J. A. & EPSTEIN, M. E., 1987. Factors affecting phenology in a temperate insect community. *American Midland Naturalist, 117:* 103–118.

SPEARS, E. E., 1987. Island and mainland pollination ecology of *Centrosema virginianum* and *Opuntia stricta. Journal of Ecology, 75:* 351–362.

SPIETH, P. T., 1979. Environmental heterogeneity: a problem of contradictory selection pressures, gene flow, and local polymorphism. *American Naturalist, 113:* 247–260.

STEBBINS, G. L., 1970. Adaptive radiation of reproductive characteristics in angiosperms, I: pollination mechanisms. *Annual Review of Ecology and Systematics, 1:* 307–326.

SVENSSON, B. G. & JANZON, L., 1984. Why does the hoverfly *Metasyrphus corollae* migrate? *Ecological Entomology, 9:* 329–335.

TAYLOR, L. R., 1963. Analysis of the effect of temperature on insects in flight. *Journal of Animal Ecology, 32:* 99–117.

TERÄS, I., 1976. Bumblebees, *Bombus* Latr. (Hymenoptera, Apidae), on red clover in South Savo, Finland. *Annales Agriculturae Fenniae, 15:* 116–127.

UDOVIC, D., 1981. Determinants of fruit set in *Yucca whipplei*: reproductive expenditure vs. pollinator availability. *Oecologia (Berlin), 48:* 389–399.

VAN VALEN, L., 1978. The statistics of variation. *Evolutionary Theory, 4:* 33–43.

VIEJO, J. L. & PINO, A., 1983. Acerca de los efectos de la sequía sobre las poblaciones de lepidópteros ropalóceros en el centro de la Península Ibérica. *SHILAP, Revista de Lepidopterología, 11:* 295–300.

VIEJO, J. L., FERNÁNDEZ-GALIANO, E. & STERLING, A., 1985. Influencia de los sotos sobre los ropalóceros (Lep.) de la cuenca del Río Guadarrama. *Boletim da Sociedade Portuguesa de Entomologia, 3:* 403–412.

VIEJO, J. L. & TEMPLADO, J., 1986. Los piéridos, satíridos y ninfálidos (Lep.) de la región de Madrid en relación con las formaciones vegetales. *Graellsia, 42:* 237–265.

WALLNER, W. E., 1987. Factors affecting insect population dynamics: differences between outbreak and non-outbreak species. *Annual Review of Entomology, 32:* 317–340.

WASER, N. M., 1979. Pollinator availability as a determinant of flowering time in Ocotillo (*Fouquieria splendens*). *Oecologia (Berlin), 39:* 107–121.

WILLE, A., OROZCO, E. & RAABE, C., 1983. Polinización del chayote *Sechium edule* (Jacq.) Swartz en Costa Rica. *Revista de Biología Tropical, 31:* 145–154.

WILLSON, M. F. & BERTIN, R. I., 1979. Flower-visitors, nectar production, and inflorescence size of *Asclepias syriaca. Canadian Journal of Botany, 57:* 1380–1388.

WILLSON, M. F., BERTIN, R. I. & PRICE, P. W., 1979. Nectar production and flower visitors of *Asclepias verticillata. American Midland Naturalist, 102:* 23–35.

WINSOR, J. A., DAVIS, L. E. & STEPHENSON, A. G., 1987. The relationship between pollen load and fruit maturation and the effect of pollen load on offspring vigor in *Cucurbita pepo. American Naturalist, 129:* 643–656.

WOLDA, H., 1978. Fluctuations in abundance of tropical insects. *American Naturalist, 112:* 1017–1045.