Oecologia (1989) 80:241–248

Oecologia

Pollinator abundance, morphology, and flower visitation rate: analysis of the "quantity" component in a plant-pollinator system

Carlos M. Herrera
Estación Biológica de Doñana, Apartado 1056, E-41080 Sevilla, Spain

Summary. Abundance and flower visitation rate of the pollinators of *Lavandula latifolia* (Labiatae), an insect-pollinated shrub, were studied over a 6-year period. The objective was to elucidate interspecific patterns in the "quantity" component of the plant-pollinator interaction. A total of 54 insect taxa are considered in the analyses, including hymenopterans, dipterans and lepidopterans. Most pollinators were comparatively scarce, with a few taxa acounting collectively for the majority of individuals. Pollinators differed broadly in flower visitation rate (0.2–30 flowers/min). Most of this variation was explained by differences in flower handling time (HT). Regardless of proboscis length, hymenopterans had intrinsically shorter handling times than lepidopterans. Within each group, HT decreased exponentially with increasing proboscis length. Abundance and visitation rate were uncorrelated across pollinator taxa. The total number of visits that each pollinator contributed to the plant (NFV) was estimated as the product of abundance × visitation rate. NFV values spanned four orders of magnitude. A small, taxonomically diverse group of species (1 moth, 1 butterfly, 4 bees) accounted for most visits and thus could effectively exert some selection on floral features. Nevertheless, the morphological diversity represented in this group of dominant pollinators probably constrains plant specialization, as they will most likely select for different floral features or in opposing directions on the same traits.

Key words: Foraging behavior – *Lavandula latifolia* – Mutualism – Pollinator abundance – Specialization

In an evolutionary context, the intensity of an interaction between two species is proportional to its frequency of occurrence multiplied by the magnitude of its fitness consequences when it occurs. Recognition of these two factors, which may be termed respectively the "quantity" and "quality" components of the interaction, is particularly relevant to understanding the evolution of plant-pollinator and plant-disperser mutualistic systems (Herrera and Jordano 1981; Motten et al. 1981; Waser and Price 1983; Schemske 1983; Schemske and Horvitz 1984; Herrera 1987a). In these mutualisms, the interaction between plants and animals may generate mutual selective pressures and reciprocal adaptation (Thompson 1982; Wheelwright and Orians 1982; Feinsinger 1983; Schemske 1983; Howe 1984; Herrera 1985).

A method of exploring the evolutionary potential inherent in a given plant-mutualist system is dissecting it into the quality and quantity components outlined above, and then examining their variation between mutualists (Herrera 1987a; 1988). For a plant to evolve adaptations to some of the animal species with which it interacts mutualistically, it is necessary that mutualists differ in the strength of their respective interactions with the plant (Thompson 1982; Schemske and Horvitz 1984). This may stem from differences in quality *or* quantity of interactions, and both components should be examined to evaluate the evolutionary potential for a plant of its interaction with an array of mutualists. In plant-pollinator systems, differences in pollinator quality depend on variation in frequency of pollen deposition on stigmas, number of pollen grains delivered when deposition occurs, and suitability of the pollen from the viewpoint of the mother plant (Arnold 1982; Motten 1983; 1986; Wolin et al. 1984; Winsor et al. 1987; Herrera 1987a; Richards 1987; Snow and Roubik 1987; Waser et al. 1987). Interspecific differences in the quantity component, on the other hand, depend on variation in pollinator abundance and flower visitation rates.

I examine in this paper interspecific patterns in the quantity component for the diverse insect pollinator assemblage of *Lavandula latifolia* (Labiatae) in a southern Spanish locality. The aspects related to pollinator quality were examined by Herrera (1987a). That study documented important differences between pollinators in all factors influencing quality, as well as a distinct covariation structure (across higher taxa) between quality factors. My purpose in this paper is to provide analogous information for the quantity-related aspects. In addition to analyzing interspecific patterns in pollinator abundance and flower visitation rates, covariation of these factors across taxa and morphological correlates of visitation rate are also examined.

Lavandula latifolia is a low evergreen shrub (up to 35 cm high) producing long-stalked (up to 1.25 m high) inflorescences. The flowering period lasts for nearly two months, from mid-July to late September. It is a common species in the undergrowth of mixed woodlands on limestone-derived soils at low to middle elevations in the eastern and southeastern Iberian Peninsula. 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 absence of pollinators is negligible.

Aspects of its reproductive biology have been studied by Herrera (1987a, b) (see Devesa et al. 1985; Muñoz and Devesa 1987; for studies on the floral biology of other southern Spanish *Lavandula* species). The composition of the pollinator assemblage of *L. latifolia* and its variation in time and space have been described by Herrera (1988).

Study area and methods

The study was conducted in the Sierra de Cazorla (Jaén province, southeastern Spain) from 1982 to 1987. Data were collected at a *L. latifolia* population growing around the intersection of Arroyo Aguaderillos and the track joining Roblehondo and Hoyos de Muñoz, at 1160 m elevation (this is the "Aguaderillos-1" site of Herrera 1988, and the same study population of Herrera 1987a, b). Plants grow there in a mixed woodland dominated by *Pinus nigra* and *Quercus rotundifolia*. A description of the vegetation of the area may be found in J. Herrera (1984).

The composition and abundance of pollinators were assessed by conducting counts of floral visitors along a permanent 80 m long transect crossing the study population. 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. Specimens of all insect taxa recorded were collected at the start of the study (1982) for taxonomic determination or corroboration, and thereafter whenever a species was recorded for the first time. Every year, pollinator counts were performed during the period 1–17 August. This period usually encompassed the flowering peak of the local *L. latifolia* population. Counts were evenly distributed from sunrise to sunset, and count dates were spaced as evenly as possible between the start and the end of the census period. A total of 320 pollinator counts were conducted over the 6-year study period (range = 21–81 counts/year). An average abundance figure, in terms of individuals recorded per count, was obtained for every pollinator and study year (Herrera 1988: Table 2). For the purpose of this paper, each pollinator has been characterized by the mean of these average yearly abundances, computed over the 6-year period. A total of 54 insect taxa, totalling 12615 individuals in the counts, form the basis for the analyses presented here. All species recorded in at least three of the six study years are included. The taxa considered here are legitimate pollinators of *L. latifolia* (Herrera 1987a; 1988).

Observations were carried out on the foraging behavior of pollinators to determine their flower visitation rates. Individual insects were followed continuously at close range for as long as possible up to a maximum of 3 min while they were actively foraging at *L. latifolia* flowers. For each observation sequence, total time spent in flowers (TF; from landing or contact with mouthparts to departure) and total observation time (TT; which included time in flowers plus time in flight between consecutive flowers) were accumulated in separate stopwatches. The total number of flowers visited over the entire observation period (NF) was also recorded for each sequence. A total of 1289 foraging sequences, corresponding to 1312 min of continuous observation for 52 different pollinator taxa, are included in the analyses below. TF, TT and NF figures obtained in individual sequences have been totalled by species. From the resulting figures, the following magnitudes have been computed for each pollinator: (1) Visitation rate, the average number of flowers visited per time unit (NF/TT); (2) Average time spent on each visited flower, or "handling time", computed as TF/NF; and (3) Average time spent in flight between consecutive flower visits, of "flight time", computed as (TT-TF)/NF.

Length of mouthparts was measured for as many lepidopteran and hymenopteran taxa as possible. For the former group, proboscis length was measured from live specimens in the field. Using fine forceps, the proboscis was gently uncoiled on a ruler, and its length measured. In the case of bees, the dimension considered was the distance between the tip of the stretched glossa (using fine forceps to gently stretch it) and the basal extreme of the prementum. I used this measure intead of glossa length alone, as recommended by Harder (1982) for bumble bees, because it seemed to describe better the functional proboscis length for Megachilidae and Anthophoridae, the families contributing most species to my sample. For the single sphecid wasp considered (*Bembix zonata*), I used the length of the modified labrum as a measure of proboscis size. Measurements were taken on freshly killed (using ethyl acetate) specimens in the case of small- and medium-sized bees, and on anaesthesized individuals in the case of the largest species.

Results

Pollinator abundance

The vast majority of pollinators of *L. latifolia* had moderate to low abundances (Table 1), and the frequency distribution of species abundances is strongly skewed to the right (Fig. 1A). Average abundance was less than 0.25 individuals/count for 33 taxa (61% of total), and 91% of the species considered here averaged <2 individuals/count. The honeybee (*Apis mellifera*) was the most abundant pollinator, accounting alone for 24.8% of all individuals. The frequency distribution of average abundances (Fig. 1A) does not depart significantly from a lognormal (Chi-square = 2.00, df = 6, $P = 0.92$).

Flower visitation rates

Most pollinator species exhibited moderate to low flower visitation rates (Table 1). The frequency distribution of this magnitude is markedly skewed to the right (Fig. 1B), and does not depart significantly from a lognormal (Chi-square = 2.76, df = 4, $P = 0.60$). The highest values were exhibited by *Anthophora quadrifasciata* (Anthophoridae; 29.6 flowers/min), *Macroglossum stellatarum* (Sphingidae; 23.6 flowers/min), *Bombus pascuorum* (Apidae; 21.4 flowers/min) and *Anthophora ochroleuca* (Anthophoridae; 20.3 flowers/min).

Interspecific differences in flower visitation rates may be due to differences in time spent flying between consecutive flower visits ("flight time", FT) and/or differences in time spent on each visited flower ("handling time", HT) (Table 1). A multiple regression, using flight time and handling time as independent variables and visitation rate as the dependent one (all variables log-transformed), was run to evaluate the relative significance of HT and FT in accounting for variation in visitation rate. Both handling and flight time entered the regression significantly ($P < 0.0001$), but their importance as predictors of visitation rates was

Table 1. Abundance, foraging behavior, and length of proboscis of the pollinators of *Lavandula latifolia* at a southern Spanish locality. Abundance data represent average values for the period 1982–1987 (see text). "Flight time" is the average time spent in flight between consecutive flower visits; "handling time" is the average time spent in each visited flower. Sample sizes (number of insects measured) for proboscis length averages are given in parentheses

	Mean abundance ±1 SD (individuals/count)	Foraging behavior statistics				Average proboscis length (mm)
		Total observation time (min)	Visitation rate (flowers/min)	Handling time (s)	Flight time (s)	
HYMENOPTERA:						
Bembix zonata (Sphecidae)	0.48±0.37	18.8	14.4	2.8	1.4	6.8 (2)
Ammophila sp. (aff. *sabulosa*) (Sphecidae)	0.02±0.03	7.7	7.7	6.3	1.5	–
Halictus sp. (aff. *scabiosae*) (Halictidae)	0.04±0.07	–	–	–	–	–
Anthidium cingulatum (Megachilidae)	0.06±0.09	20.0	9.5	2.5	3.8	–
Anthidium florentinum (Megachilidae)	3.23±2.14	51.9	12.2	1.9	3.0	6.7 (14)
Anthidiellum breviusculum (Megachilidae)	1.87±0.85	21.1	6.7	4.4	4.6	4.0 (5)
Megachile pilidens (Megachilidae)	0.02±0.01	9.2	8.0	4.6	2.8	–
Megachile (*ligniseca*?) (Megachilidae)	0.22±0.20	8.1	14.9	2.3	1.7	7.2 (4)
Anthophora crassipes (Anthophoridae)	0.07±0.09	12.1	15.5	1.5	2.4	11.3 (2)
Anthophora ochroleuca (Anthophoridae)	0.42±0.20	22.7	20.3	1.2	1.8	12.6 (9)
Anthophora quadrifasciata (Anthophoridae)	0.14±0.10	19.2	29.6	0.8	1.2	11.1 (5)
Anthophora albigena (Anthophoridae)	0.27±0.20	18.2	14.6	1.3	2.8	8.2 (5)
Melecta sp. (Anthophoridae)	0.01±0.01	–	–	–	–	–
Ceratina cyanea+*mocsaryi* (Anthophoridae)	0.43±0.41	7.9	5.7	5.5	5.1	3.6 (3)
Xylocopa cantabrita (Anthophoridae)	0.02±0.04	3.8	15.3	2.0	2.0	–
Xylocopa violacea (Anthophoridae)	0.44±0.46	32.4	14.8	2.4	1.7	9.8 (4)
Apis mellifera (Apidae)	9.31±2.69	85.6	10.5	3.6	2.1	5.1 (10)
Bombus terrestris (Apidae)	1.90±2.11	56.6	15.2	2.5	1.5	7.7 (13)
Bombus pascuorum (Apidae)	0.20±0.32	9.4	21.4	1.3	1.5	9.0 (14)
DIPTERA:						
Systoechus sp. (Bombyliidae)	0.20±0.12	4.5	8.2	4.2	3.1	–
Eristalis tenax (Syrphidae)	0.16±0.15	72.0	4.0	12.9	2.1	–
Scaeva pyrastri (Syrphidae)	0.01±0.01	4.4	4.3	7.9	6.0	–
Sphaerophoria scripta (Syrphidae)	0.15+0.22	27.8	2.7	14.3	7.9	–
Chrysotoxum intermedium (Syrphidae)	0.06±0.05	16.8	3.4	15.1	2.6	–
Volucella spp. (Syrphidae)[a]	2.08±0.69	85.0	2.8	18.8	2.3	–
Nowickia strobeli (Tachinidae)	0.43±0.42	18.4	3.6	15.3	1.5	–
Calliphoridae gen. sp.	0.42±0.42	51.2	0.8	77.7	1.1	–
LEPIDOPTERA:						
Macroglossum stellatarum (Sphingidae)	1.52±1.35	30.4	23.6	1.5	1.0	26.4 (19)
Papilio machaon (Papilionidae)	0.01±0.00	9.4	6.8	3.3	5.5	17.3 (2)
Iphiclides podalirius (Papilionidae)	0.03±0.02	11.0	6.9	5.8	2.9	14.4 (7)
Colias crocea (Pieridae)	0.22±0.19	50.8	5.4	8.4	2.8	13.6 (17)
Pontia daplidice (Pieridae)	0.01±0.01	22.4	7.0	6.1	2.4	–
Gonepteryx cleopatra (Pieridae)	0.16±0.13	11.5	9.7	3.6	2.5	20.0 (12)
Pieris rapae (Pieridae)	0.02±0.02	12.0	5.2	7.9	3.5	–
Pandoriana pandora (Nymphalidae)	0.62±0.63	58.3	6.1	7.0	2.9	18.8 (12)
Argynnis paphia (Nymphalidae)	1.90±0.95	84.4	3.8	12.2	3.6	14.6 (23)
Fabriciana adippe (Nymphalidae)	1.65±0.47	61.4	5.2	9.0	2.7	15.8 (23)
Issoria lathonia (Nymphalidae)	0.08±0.04	5.7	3.3	15.5	2.5	11.5 (7)
Brenthis daphne (Nymphalidae)	0.01±0.01	10.2	3.4	14.7	2.7	12.8 (8)
Melanargia galathea (Satyridae)	3.46±4.28	38.4	1.8	29.0	3.5	12.0 (24)
Hipparchia alcyone (Satyridae)	0.03±0.04	12.2	0.9	64.9	1.6	13.0 (1)
Pyronia bathseba (Satyridae)	0.15±0.21	13.5	1.5	36.9	3.6	9.0 (16)
Pyronia cecilia (Satyridae)	0.11±0.06	1.8	1.1	39.0	15.0	7.2 (8)
Coenonympha dorus (Satyridae)	0.04±0.05	12.6	0.2	248.0	4.0	6.5 (5)
Lasiommata maera (Satyridae)	0.02±0.02	2.7	5.6	7.6	3.2	13.0 (1)
Lasiommata megera (Satyridae)	0.07±0.05	9.5	3.4	14.2	3.6	–
Lycaena phlaeas (Lycaenidae)	0.11±0.12	28.5	0.9	62.3	3.5	7.4 (3)
Lampides boeticus (Lycaenidae)	0.03±0.02	19.1	1.0	56.8	3.5	6.6 (2)
Plebicula escheri (Lycaenidae)	0.36±0.19	13.4	0.7	72.6	7.8	7.9 (9)
Lysandra albicans/hispana (Lycaenidae)	0.80±0.18	49.7	1.3	34.6	10.6	9.9 (17)
Hesperia comma (Hesperiidae)	0.79±0.28	24.8	4.4	11.6	2.0	17.3 (21)
Spialia sertorius (Hesperiidae)	0.16±0.13	19.0	3.2	17.0	2.0	9.7 (8)
Thymelicus acteon (Hesperiidae)	2.38±1.55	14.0	6.8	7.1	1.7	14.7 (19)
Muschampia proto (Hesperiidae)	0.09±0.07	0.8	7.5	4.0	4.0	–

[a] Includes *V. inanis*, *V. zonaria* and *V. elegans*

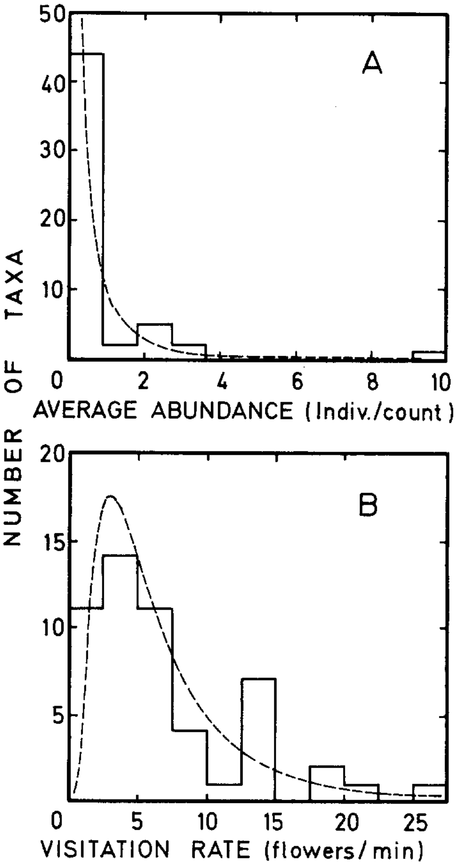

Fig. 1. **A, B** Frequency distributions of average abundance (**A**) and flower visitation rate (**B**) for the pollinators of *Lavandula latifolia*. Shown are also the lognormal curves fitted to the data (none of the two distributions departs significantly from a lognormal)

very unequal. Handling time produced an increase in R^2 of 0.979, while flight time was responsible for a change in R^2 of only 0.007. Interspecific variation in flower visitation rates is thus almost entirely accounted for by differences in flower handling time.

There is significant heterogeneity among the three major groups of pollinators in flower visitation rates ($F = 17.10$, df = 2,49, $P < 0.0001$; log-transformed data). On average, hymenopteran taxa visited significantly more flowers per time unit (mean ± SD = 13.9 ± 6.0 flowers/min) than either dipteran (3.7 ± 2.1 flowers/min) or lepidopteran (4.7 ± 4.6 flowers/min) taxa. These differences are almost entirely due to intergroup differences in handling time. The latter magnitude differs significantly between pollinator groups ($F = 20.71$, df = 2,49, $P < 0.0001$; log-transformed data), while flight time does only marginally ($F = 2.87$, df = 2,49, $P = 0.07$; log-transformed data). Mean handling time (± 1 SD) for hymenopteran taxa was 2.8 ± 1.6 s, while it was 20.8 ± 23.4 s for dipterans and 29.7 ± 48.4 s for lepidopterans. Dipteran and lepidopteran taxa did not differ in this regard ($F = 0.001$, df = 1,49, $P = 0.99$).

There is a negative linear relation between log (handling time) and proboscis length (Fig. 2) for both lepidopterans and hymenopterans (no morphological data were collected for dipterans). Regressions are highly significant for both groups ($F = 34.62$, df = 1,11, for hymenopterans; $F = 66.93$, df = 1,21 for lepidopterans; $P < 0.0001$ in both cases). The slopes of the regressions for hymenopterans and lepidopterans do not differ significantly ($F = 0.45$, df = 1,32, $P = 0.51$; analysis of covariance), indicating that an unit increase in proboscis length produces similar proportional decreases of log (handling time) in the two groups. In order to equal a hymenopteran taxa in handling time, a lepidopteran one must have a proboscis about 15 mm longer (Fig. 2). This is exemplified by the sphingid moth, *Macroglossum stellatarum*. This species, with the longest proboscis of all lepidopterans considered here (26.4 mm) had a handling time similar to that exhibited by hymenopterans with proboscides 11–12 mm long (*Anthophora* spp.) (Table 1).

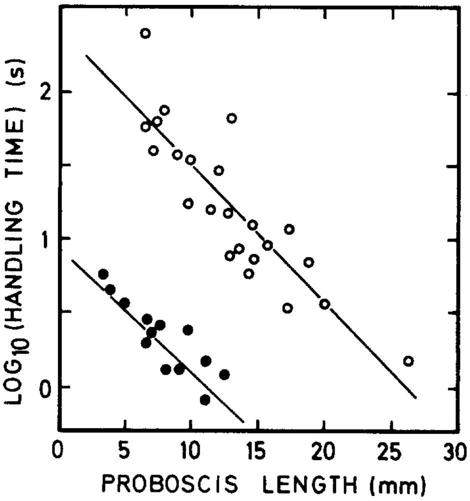

Fig. 2. Variation of flower handling time (note logarithmic transformation) with proboscis length for hymenopteran (filled dots) and lepidopteran (open dots) taxa. Shown are also the regression lines for each group ($Y = 0.922 – 0.076\ X$ for hymenopterans; $Y = 2.428 - 0.093\ X$ for lepidopterans; $P < 0.0001$ in both cases)

The "quantity" component

Abundance and flower visitation rate, the two factors determining the quantity component in the interaction between *L. latifolia* and its pollinators, vary independently of each other across taxa ($r = 0.076$ and $r = 0.143$ for original and log-transformed data, respectively; $N = 52$, $P > 0.30$). Correlations between abundance and visitation rate run separately for the three major pollinator groups are likewise nonsignificant ($P > 0.20$). Most pollinators have both low flower visitation rate and low abundance (Fig. 3; lower left area of the graph). A few taxa have low to moderate abundances and high visitation rates, and a single species exhibits high abundance and moderate visitation rate. No species has both high visitation rate and high abundance.

The total number of *L. latifolia* flowers visited by the population of one pollinator (e.g., on a daily basis) should be proportional to the product of its abundance by its visitation rate (NFV, expressed as flowers/min). This magnitude estimates the "quantity" of interactions of *L. latifolia* with each pollinator. The plane defined by abundance and flower visitation rate (Fig. 3) may thus be divided into areas differing in NFV values. Curves separating these areas are drawn in Fig. 3, corresponding to total visits of 10 and 100 flowers/min. Forty-six species out of 52 fall in the area of minimal NFV (< 10 flowers), and the remaining 6 species fall in the area of intermediate NFV (10 < NFV < 100). These latter species account collectively for 72.1% of total NFV, while the remaining 46 species (88.5% of the taxa)

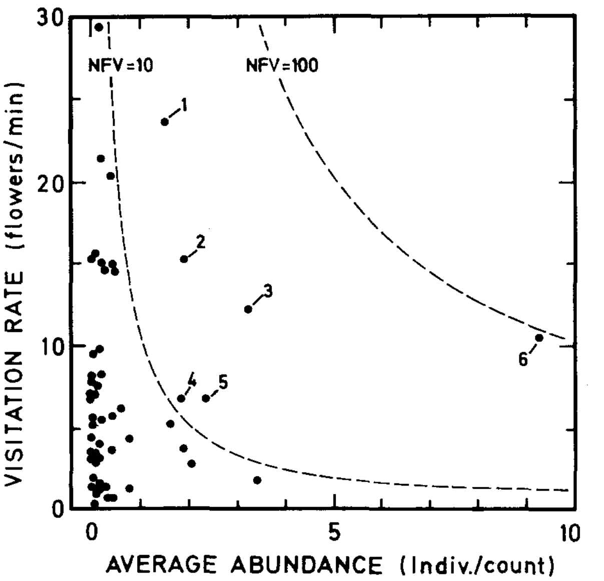

Fig. 3. Distribution of pollinators over the plane defined by average abundance and flower visitation rate. The curves divide the plane into zones of "low", "moderate" and "high" quantity of interactions with the plant (NFV = the product of abundance by visitation rate, see text). The six species with the highest NFV values are coded as follows: *1, Macroglossum stellatarum* (Sphingidae); *2, Bombus terrestris* (Apidae); *3, Anthidium florentinum* (Megachilidae); *4, Anthidiellum breviusculum* (Megachilidae); *5, Thymelicus acteon* (Hesperiidae); *6, Apis mellifera* (Apidae)

contribute only 27.9% of floral visits. Among the dominant species, one achieves this status mostly because of its high abundance (*Apis mellifera*), one because its high flower visitation rate (*Macroglossum stellatarum*), and four because they combine moderate abundances with moderate visitation rates (*Anthidiellum breviusculum, Bombus terrestris, Anthidium florentinum* and *Thymelicus acteon*).

Discussion

Pollinator abundance

Most pollinators of *L. latifolia* are comparatively rare, a few taxa accounting for the vast majority of individuals recorded foraging at flowers. *Apis mellifera* was the most abundant pollinator, representing 25% of all individuals. Foragers of this species recorded at my study site almost certainly belong to wild colonies, as the nearest beehives are more than 8 km away on a straight line. Although honeybees have been reported to forage up to 10 km from their nests, most foraging apparently takes place within a radius of 5 km from the colony (Visscher and Seeley 1982; Seeley 1985).

The frequency distribution of abundances of *L. latifolia* pollinators does not depart significantly from a lognormal. Similar species abundance patterns are discernible in previous studies involving diverse pollinator assemblages. I tested for lognormality the species abundance distributions of the pollinators of several temperate plants, considering studies reporting samples of at least 250 individual insects and 30 taxa (Table 2). The distribution of species abundances does not depart significantly from lognormality in any of the 9 assemblages examined (Table 2). The lognormal distribution, to which the species-abundance pattern of pollinators apparently conform for a variety of plants having diverse pollinator assemblages, is a long-known statistical model for the abundance of species in natural and man-made collections of individuals (Preston 1948; Williams 1964; Kempton and Taylor 1974). If plants often face a lognormal pattern of pollinator abundances, as Table 2 suggests, then the abundance component of plant-pollinator interactive systems may sometimes be ruled by the same statistical determinants that presumably generate lognormal species-abundance distributions in a broad variety of ecological and sampling contexts.

Table 2. Sample characteristics and summary of goodness-of-fit tests, for several insect pollinator assemblages of temperate latitudes. The frequency distributions of individual pollinator abundances were tested for lognormality

Plant species	Sample characteristics		Departure from lognormal	
	Number of taxa	Number of individuals	Chi-square	*P*
Actaea spicata[a]	38	2135	4.23	0.24
Actaea pachypoda[b]	31	271	2.90	0.23
Aquilegia caerulea[c]	37	725	0.92	0.34
Epipactis palustris[d]	102	364	1.46	0.48
Hedysarum boreale[e]	37	361	0.003	0.96
Heracleum sphondylium[f]	60	396	0.04	0.84
Heracleum montegazzianum[f]	48	264	0.52	0.47
Lavandula latifolia[g]	52	12615	2.00	0.92

References: [a] Pellmyr (1984); [b] Pellmyr (1985); [c] Miller (1978); [d] Nilsson (1978b); [e] Tepedino and Stackhouse (1987); [f] Grace and Nelson (1981); [g] present study

Flower visitation rates

Previous investigations have often shown variation between pollinators in flower foraging rates (e.g., Hopper 1980; Ranta 1983; Schmitt 1983; Böcher and Phillipp 1985; Sugden 1986). Considerable variation exists also between the pollinators of *L. latifolia* in visitation rate, which ranges between 0.2–29.6 flowers/min, a 100-fold difference. This variation is almost entirely accounted for by differences in flower handling time. Although most female bees and some Syrphid flies also gather some pollen, nectar is the main reward sought by pollinators in *L. latifolia* flowers, thus interspecific variation in flower handling time should be mainly related to differential efficiency in nectar extraction. The nectar of *L. latifolia* is relatively concentrated, and individual flowers contain very small volumes. Average nectar concentration is 52.1% (sucrose equivalents by weight; range 30–68%), and mean daily production is 0.33 µL/flower. Individual flowers exposed to pollinators have, on average, only 0.07 µL of nectar available (Herrera, unpubl.). The nectar is deeply concealed at the base of the relatively narrow, 7–8 mm long tubular corolla.

Regardless of proboscis length, hymenopterans have inherently shorter handling times than lepidopterans, and log (handling time) decreases linearly with increasing proboscis length within each group. Decreasing handling time with increasing proboscis length has been often reported in studies of bumble bee foraging behavior (Inouye 1980; Ranta and Lundberg 1980; Harder 1983; Ranta 1983), but I am not aware of any study reporting a similar relation for lepidopterans. Intrinsic differences between hymenopterans and lepidopterans are presumably the consequence of their different nectar extraction techniques. While bees drink nectar by lapping with their hairy glossae (Harder 1982), lepidopterans do it by active suction (Kingsolver and Daniel 1979). Confronted with the nectar environment of *L. latifolia* flowers (minute amounts per flower of a fairly concentrated nectar), lapping proboscides are able to extract nectar at a much faster rate than sucking ones of similar length (Fig. 2).

The negative linear relationship between log (handling time) and proboscis length in hymenopterans suggests that nectar extraction rate, and thus presumably the lapping capacity of the glossa, increase disproportionately with increased proboscis length. If body mass has some direct influence on the nectar extraction process (e.g., via power output of tongue muscles and lapping rate), then the relationship existing between body mass and proboscis length (Herrera unpubl.; see also Harder 1985) could help to explain the exponential relationship between handling time and proboscis length. Results reported by Harder (1983; 1986) for bumble bees support this hypothesis. This author found that morphologically dissimilar bees drank nectar at different rates because glossa length affected lapping rate and volume ingested per lap, and body mass affected lapping rate.

The mechanics and energetics of nectar feeding by butterflies has been examined recently (Kingsolver and Daniel 1979; May 1985; Pivnick and McNeil 1985). According to one of these models (Pivnick and McNeil 1985: Eq. 11), nectar intake rate would be directly related to the power output of the insect's cibarial pump (P) and the internal radius of the food canal within the proboscis (r), and negatively to proboscis length. Holding all other factors contant, nectar intake rate should thus be inversely related to proboscis length. Results of this study do not agree with this prediction, as long-tongued butterflies have shorter handling times, and by inference higher nectar intake rates, than short-tongued ones. This is probably because P and r vary among species. Data and equations presented by Kingsolver and Daniel (1979), May (1985), and Pivnick and McNeil (1985), suggest positive correlations between P and r, and body mass. Proboscis length and body length (an indirect estimate of body mass) are linearly related in a sample of the species studied here ($r = 0.791$, $N = 17$, $P = 0.002$; Herrera unpubl.), and in the species set examined by Schemske (1976: Tables 1 and 2; $r = 0.802$, $N = 36$, $P < 0.0001$). The negative exponential relationship found here between handling time and proboscis length may thus actually reflect a relationship between body mass and nectar extraction rate, implying that long-tongued butterflies are faster in extracting nectar than short-tongued ones not because they are long-tongued, but because their larger body size.

The regressions relating log (handling time) with proboscis length have similar slopes for hymenopterans and lepidopterans, suggesting that both groups have the same scaling factor in the allometric relation between proboscis and handling time. This is a striking result in view of the contrasting morphology and feeding methods of the two groups, and no satisfactory hypothesis may be advanced at present to explain it.

For some time, butterflies were thought to prefer nectar concentrations in the range of 20–25% sucrose, with nectars above this range becoming increasingly unprofitable (Watt et al. 1974; Kingsolver and Daniel 1979; Pyke and Waser 1981). Recent studies have shown, however, that butterflies actually are able to feed intensively on nectars having 30–65% sucrose (Pivnick and McNeil 1985; May 1988), and that the optimum nectar concentration is approximately 40% (Pivnick and McNeil 1985; May 1985). The present study (see also Herrera 1988) further shows that a broad variety of lepidopterans are able to feed on concentrated nectar.

Potential for plant specialization

There are important differences between pollinators in the total number of visits contributed to *L. latifolia* flowers (NFV = abundance × visitation rate). NFV values for extreme species span four orders of magnitude, from 0.01 visits/min in *Coenonympha dorus* to 98.2 visits/min in *Apis mellifera*. From the viewpoint of *L. latifolia* plants, most of their interactions with pollinators take place with individuals of a small number of species. Similar patterns occur in other pollinator assemblages where the total number of floral visits has been estimated for the different pollinators (Schemske 1976; Motten 1983; Campbell 1985; Montalvo and Ackerman 1986). In the case of *L. latifolia*, skewness in the distribution of NFV values is due to the fact that the frequency distributions of species abundance and flower visitation rates (the two factors determining NFV) are both skewed to the right (in fact, neither departs from a lognormal), and that the two magnitudes are uncorrelated across species. The product of two uncorrelated variables, each approaching a lognormal, is bound to have also a distribution approaching a lognormal.

Comparing the results of the present study with those of Herrera (1987a), no predictable relationship is apparent between the quantity and quality components among the pollinators of *L. latifolia*. A similar conclusion emerges from other investigations (Spears 1983; Schemske and Horvitz 1984; Snow and Roubik 1987; Richards 1987). The broad range in quantity of interactions faced by the plants in their relation with pollinators may then translate into contrasting contributions of the different pollinators to the plant's fitness, via variation in the number of pollen transfers effected by each. Plants could respond to these unequal interaction intensities by evolving floral characteristics enhancing the number of interactions with those pollinators contributing most to its fitness. This reasoning is based on the "most effective pollinator principle" (Stebbins 1970), which implies that selection should favor traits that attract only those visitors that provide the best pollination service (see also Waser 1983; Schemske and Horvitz 1984; Montalvo and Ackerman 1986; Herrera 1987a; and references therein). A distinct potential for specialization thus exists in the interaction between *L. latifolia* and its pollinators, in the direction of increasing the number of interactions with the reduced set of pollinators having the highest NFV values. Nevertheless, abundance and visitation rate covary randomly among the pollinators of *L. latifolia*, and the highest NFV values observed (those potentially setting the direction for specialization) arise from a variety of combinations. No pollinator is both abundant and an efficient forager. The most efficient foragers are scarce, and the most abundant pollinators have only modest flower visitation rates. Furthermore, the few species contributing most visits to flowers are taxonomically (four bees, one moth, one butterfly) and morphologically (body size, proboscis length) diverse, and will most likely select for different floral features or in opposing directions on the same traits. The contrasting floral characteristics of plants adapted to bee, butterfly and moth pollination (Proctor and Yeo 1973; Faegri and van der Pijl 1979) give us an idea of the opposing selective pressures potentially exerted on *L. latifolia* by its dominant pollinators. This fact most likely sets a consistent limit on the possibilities of this plant of evolving adaptations to particular pollinators.

Acknowledgements. Insect determinations were generously provided by S. Andersen (Tachinidae), E. Asensio (Megachilidae, Anthophoridae), M. Báez (Bombyliidae), L. Castro (Apidae), and M.A. Marcos (Syrphidae). Thanks are also due to Dori for her assistance in all the phases of the field work, and to Carlitos for his skillful help in netting pollinators for proboscis measurements. The Agencia de Medio Ambiente provided invaluable logistical support in the Sierra de Cazorla.

References

Arnold RM (1982) Pollination, predation and seed set in *Linaria vulgaris* (Scrophulariaceae). Am Midl Nat 107:360–369

Beattie AJ, Breedlove DE, Ehrlich PR (1973) The ecology of the pollinators and predators of *Frasera speciosa*. Ecology 54:81–91

Böcher J, Phillipp M (1985) Aspects of the reproductive biology of *Mimulus repens* (Scrophulariaceae) at Lake Ellesmere, Canterbury, New Zealand. N Z J Bot 23:141–149

Campbell DR (1985) Pollinator sharing and seed set of *Stellaria pubera:* competition for pollination. Ecology 66:544–553

Devesa JA, Arroyo J, Herrera J (1985) Contribución al conocimiento de la biología floral del género *Lavandula*. Anal Jard Bot Madrid 42:165–186

Faegri K, van der Pijl L (1979) The Principles of Pollination Ecology. 3rd ed. Pergamon Press, Oxford

Feinsinger P (1983) Coevolution and pollination. In: Futuyma DJ, Slatkin M (eds), Coevolution, Sinauer, Sunderland, MA, pp 282–310

Grace J, Nelson M (1981) Insects and their pollen loads at a hybrid *Heracleum* site. New Phytol 87:413–423

Harder LD (1982) Measurement and estimation of functional proboscis length in bumblebees (Hymenoptera: Apidae). Can J Zool 60:1073–1079

Harder LD (1983) Flower handling efficiency of bumble bees: morphological aspects of probing time. Oecologia 57:274–280

Harder LD (1985) Morphology as a predictor of flower choice by bumble bees. Ecology 66:198–210

Harder LD (1986) Effects of nectar concentration and flower depth on flower handling efficiency of bumble bees. Oecologia 69:309–315

Herrera CM (1985) Determinants of plant-animal coevolution: the case of mutualistic dispersal of seeds by vertebrates. Oikos 44:132–141

Herrera CM (1987a) Components of pollinator "quality": comparative analysis of a diverse insect assemblage. Oikos 50:79–90

Herrera CM (1987b) Componentes del flujo génico en *Lavandula latifolia* Medicus: polinización y dispersión de semillas. Anal Jard Bot Madrid 44:49–61

Herrera CM (1988) Variation in mutualisms: the spatio-temporal mosaic of a pollinator assemblage. Biol J Linn Soc 35:95–125

Herrera CM, Jordano P (1981) *Prunus mahaleb* and birds: the high-efficiency seed dispersal system of a temperate fruiting tree. Ecol Monogr 51:203–218

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

Hopper SD (1980) Pollination of the rain-forest tree *Syzygium tierneyanum* (Myrtaceae) at Kuranda, Northern Queensland. Aust J Bot 28:223–237

Howe HF (1984) Constraints on the evolution of mutualisms. Am Nat 123:764–777

Inouye DW (1980) The effect of proboscis and corolla tube lengths on patterns and rates of flower visitation by bumblebees. Oecologia 45:197–201

Kempton RA, Taylor LR (1974) Log-series and log-normal parameters as diversity discriminants for the Lepidoptera. J Anim Ecol 43:381–399

Kingsolver JG, Daniel TL (1979) On the mechanics and energetics of nectar feeding in butterflies. J Theor Biol 76:167–179

May PG (1985) Nectar uptake rates and optimal nectar concentrations of two butterfly species. Oecologia 66:381–386

May PG (1988) Determinants of foraging profitability in two nectarivorous butterflies. Ecol Entomol 13:171–184

Miller RB (1978) The pollination ecology of *Aquilegia elegantula* and *A. caerulea* (Ranunculaceae) in Colorado. Am J Bot 65:406–414

Montalvo AM, Ackerman JD (1986) Relative pollinator effectiveness and evolution of floral traits in *Spatiphyllum friedrichsthalii* (Araceae). Am J Bot 73:1665–1676

Motten AF (1983) Reproduction of *Erythronium umbilicatum* (Liliaceae): pollination success and pollinator effectiveness. Oecologia 59:351–359

Motten AF (1986) Pollination ecology of the spring wildflower community of a temperate deciduous forest. Ecol Monogr 56:21–42

Motten AF, Campbell DR, Alexander DE, Miller HL (1981) Pollination effectiveness of specialist and generalist visitors to a North Carolina population of *Claytonia virginica*. Ecology 62:1278–1287

Muñoz A, Devesa JA (1987) Contribución al conocimiento de la biología floral del género *Lavandula* L. II. *Lavandula stoechas* L., subsp. *stoechas*. Anal Jard Bot Madrid 44:63–78

Nilsson LA (1978) Pollination ecology of *Epipactis palustris* (Orchidaceae). Bot Notiser 131:355–368

Pellmyr O (1984) The pollination ecology of *Actaea spicata* (Ranunculaceae). Nord J Bot 4:443–456

Pellmyr O (1985) The pollination biology of *Actaea pachypoda* and *A. rubra* (including *A. erythrocarpa*) in northern Michigan and Finland. Bull Torrey Bot Club 112:265–273

Pivnick KA, McNeil JN (1985) Effects of nectar concentration on butterfly feeding: measured feeding rates for *Thymelicus lineola* (Lepidoptera: Hesperiidae) and a general feeding model for adult Lepidoptera. Oecologia 66:226–237

Preston FW (1948) The commonness, and rarity, of species. Ecology 29:254–283

Proctor M, Yeo P (1973) The pollination of flowers. Collins, London

Pyke GH, Waser NM (1981) The production of dilute nectars by hummingbird and honeyeater flowers. Biotropica 13:260–270

Ranta E (1983) Foraging differences in bumblebees. Ann Ent Fenn 49:17–22

Ranta E, Lundberg H (1980) Resource partitioning in bumblebees: the significance of differences in proboscis length. Oikos 35:298–302

Richards KW (1987) Diversity, density, efficiency, and effectiveness of pollinators of cicer milkvetch, *Astragalus cicer* L. Can J Zool 65:2168–2176

Schemske DW (1976) Pollinator specificity in *Lantana camara* and *L. trifolia* (Verbenaceae). Biotropica 8:260–264

Schemske DW (1983) Limits to specialization and coevolution in plant-animal mutualisms. In: Nitecki MH (ed) Coevolution, Univ Chicago Press, Chicago, pp 67–109

Schemske DW, Horvitz CC (1984) Variation among floral visitors in pollination ability: a precondition for mutualism specialization. Science 225:519–521

Schmitt J (1983) Flowering plant density and pollinator visitation in *Senecio*. Oecologia 60:97–102

Seeley TD (1985) Honeybee Ecology. Princeton University Press, Princeton, NJ

Snow AA, Roubik DW (1987) Pollen deposition and removal by bees visiting two tree species in Panamá. Biotropica 19:57–63

Spears EE (1983) A direct measure of pollinator effectiveness. Oecologia 57:196–199

Stebbins GL (1970) Adaptive radiation of reproductive characteristics in angiosperms, I: pollination mechanisms. Ann Rev Ecol Syst 1:307–326

Sugden EA (1986) Anthecology and pollinator efficacy of *Styrax officinale* subsp. *redivivum* (Styracaceae). Am J Bot 73:919–930

Tepedino VJ, Stackhouse M (1987) Bee visitors of sweetvetch, *Hedysarum boreale boreale* (Leguminosae), and their pollen-collecting activities. Great Basin Nat 47:314–318

Thompson JN (1982) Interaction and Coevolution. Wiley, New York

Visscher PK, Seeley TD (1982) Foraging strategy of honeybee colonies in a temperate deciduous forest. Ecology 63:1790–1801

Waser NM (1983) The adaptive nature of floral traits: ideas and evidence. In: Real L (ed) Pollination biology, Academic Press, London, pp 241–285

Waser NM, Price MV (1983) Optimal and actual outcrossing in plants, and the nature of plant-pollinator interaction. In: Jones CE, Little RJ (eds) Handbook of Experimental Pollination Biology, Van Nostrand Reinhold, NY, pp 341–359

Waser NM, Price MV, Montalvo AM, Gray RN (1987) Female mate choice in a perennial herbaceous wildflower, *Delphinium nelsonii*. Evol Trends Plants 1:29–33

Watt WB, Hoch PC, Mills SG (1974) Nectar resource use by *Colias* butterflies. Chemical and visual aspects. Oecologia 14:353–374

Wheelwright NT, Orians GH (1982) Seed dispersal by animals: contrasts with pollen dispersal, problems of terminology, and constraints on coevolution. Am Nat 119:402–413

Williams CB (1964) Patterns in the Balance of Nature. Academic Press, London

Winsor JA, Davis LE, Stephenson AG (1987) The relationship between pollen load and fruit maturation and the effect of pollen load on offspring vigor in *Cucurbita pepo*. Am Nat 129:643–656

Wolin CL, Galen C, Watkins L (1984) The breeding system and aspects of pollination effectiveness in *Oenothera speciosa* (Onagraceae). Southwest Nat 29:15–20

Received September 23, 1988