

Daily patterns of pollinator activity, differential pollinating effectiveness, and floral resource availability, in a summer-flowering Mediterranean shrub

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This study examined the daily activity patterns of the pollinators of *Lavandula latifolia* (Labiatae), a summer-flowering, insect-pollinated evergreen shrub of Mediterranean woodlands. The question is addressed, What is the degree of matching between the daily floral cycle of *L. latifolia* and the daily profile of pollinating potential of its pollinator assemblage? *L. latifolia* open flowers and produce nectar uninterruptedly over daytime, and both flower production and nectar secretion rates are highest early in the morning and late in the afternoon. Pollen availability in the flower population, as estimated by the proportion of pollen-bearing, male-phase flowers, reaches a maximum in late afternoon, while nectar and sugar availability peak around the middle of the day. There was considerable variation both among major groups (hymenopterans, dipterans, lepidopterans), and among species within groups, in the timing of foraging at flowers. As a consequence of this, and of interspecific differences in pollen transfer effectiveness and average flight distance between consecutively visited flowers, the daytime period is not homogeneous with regard to the potential pollinating effectiveness of the pollinators active at a given time. There is not, however, a good correlation between the daily cycles of floral resource production and availability, on one hand, and of components of pollinating effectiveness, on the other. It is suggested that both the plant's and the pollinators' daily cycles largely represent independent responses to diel rhythmicity of the physical environment, and that matches and mismatches found here between daily patterns of floral resources and aspects of pollinating effectiveness are epiphenomena lacking particular adaptive significance to the plant.

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Introduction

Floral morphology largely determines pollinator composition among insect-pollinated plants (Baker and Hurd 1968, Proctor and Yeo 1973, Faegri and van der Pijl 1978). Non-structural traits, however, may also influence pollinator composition. By opening flowers or making floral rewards available to pollinators at different times of the daily cycle, plants might be able to 'select out' a subset of pollinators from the broad taxonomic array potentially available.

Foraging activity of insect floral visitors depends on a

combination of extrinsic and intrinsic factors. Extrinsic factors include abiotic parameters, such as ambient temperature, wind velocity and solar radiation, and biotic ones, as predation and competitive interactions at flowers (Beattie 1971, Hubbell and Johnson 1978, Lundberg 1980, Brown et al. 1981, Brantjes 1982, Gill et al. 1982, Lerer et al. 1982, Louda 1982, Kevan and Baker 1983, Boyle-Makowski and Philogène 1985, Gilbert 1985, Stone et al. 1988). Intrinsic factors range from taxonomic affiliation (e.g., diurnal butterflies vs nocturnal moths) to physiological attributes like thermoregulatory ability (Heinrich 1979a,b, Chappell 1982, Pivnick and

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McNeil 1987). The species-specific environmental tolerances set by these intrinsic factors, in relation to the daily course of extrinsic ones, determine definite 'daily activity windows' for different pollinators (Schlising 1970, Willmer 1983, 1986, Boyle-Makowski and Philogène 1985, Gilbert 1985). Interspecific differences in timing of activity windows lead to a succession of pollinators ordinarily visiting the flowers of a given plant species in the course of a day (Real 1981, Willmer and Corbet 1981, Eguiarte et al. 1987, Stone et al. 1988). By timing anthesis and/or presentation of floral rewards so as to match activity peaks of its most efficient pollinators (sensu Stebbins 1970, i.e., those providing the best pollination service in frequency and effectiveness), plants might thus theoretically enhance reproductive output (via increased pollen export and seed production).

Daily patterns of floral resource production, particularly nectar, have been investigated in detail for many species, and these patterns have been often examined in relation to daily variation in pollinator activity (Corbet 1978, Corbet et al. 1979, Willson et al. 1979, Cruden et al. 1983, Frankie and Haber 1983, Pleasants 1983, Zimmerman 1988, Thomson et al. 1989). Comparatively few studies, however, have examined the three-way relationship between the rhythm of floral resource presentation, the activity rhythm of pollinators, and the differential pollinating effectiveness of these latter, and even in these instances some of the three components were not assessed on a quantitative basis (Willson et al. 1979, Ottosen 1986, Dafni et al. 1987, Davis 1987, Ramsey 1988, Thomson et al. 1989). This renders difficult a proper examination of the hypothesis that timing of anthesis and/or presentation of floral rewards may evolve to match the activity peaks of the most efficient pollinators.

I examine in this paper the daily activity patterns of the pollinators of *Lavandula latifolia* (Labiatae). *L. latifolia* is an insect-pollinated, evergreen shrub, and one of the few plants that flower in the hot-dry summer characteristic of southern Spanish Mediterranean woodlands. This species has a diverse pollinator assemblage comprising nearly 80 bee, fly, and butterfly species (Herrera 1988), and pollinators differ broadly in several components of pollinating effectiveness (Herrera 1987a,b, 1989). The daily activity patterns of different pollinators are described here, and this information is then combined with data on their differential pollinating effectiveness, to determine the daily profile of pollinating potential for the assemblage of insect visitors. This profile may then be compared with the plant's floral daily cycle (opening and withering of flowers, and nectar and pollen availability). Specifically, I address the question, What is the degree of matching between the daily floral cycle of *L. latifolia* and the daily profile of pollinating potential of its pollinator assemblage?

Study area and methods

This study was conducted in the Reserva de Navahondona-Guadahornillos, Sierra de Cazorla (Jaén province, southeastern Spain) between 1982 and 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). A description of the vegetation of the area may be found in Herrera (1984). In that population, the flowering season of *L. latifolia* encompasses the period July–October, with the number of open flowers reaching a maximum in August. For the purpose of this study, only data for this latter month, the six study years combined, have been considered. Seasonal and annual variation in pollinator composition and abundance have been described in detail elsewhere (Herrera 1988). Climate at the study locality is of a Mediterranean type. In the period 1982–1987, averages ($N = 6$) of maximum and minimum mean monthly temperatures for August were, respectively, 31.8°C (range 29.3–33.3°C) and 10.6°C (range 9.5–12.8°C).

An 80-m long transect was laid out crossing the *L. latifolia* population. I slowly walked the transect at different times of day, from around 1 h before local sunrise to around 1 h after local sunset (roughly 0500–1900 hours GMT; throughout this paper, all times are reported as GMT), recording all insects seen foraging actively in the flowers of *L. latifolia* within 5 m to either side of the transect (night observations at the start of the study did not provide evidence of nocturnal insect visitation). The results of walking the transect once represent a 'count', and this is the sampling unit used here in the analyses of pollinator abundance (see also Herrera 1988 for further considerations on pollinator count methods). A total of 355 counts are examined here, grouped at hourly intervals for the analyses.

Information on relevant aspects of *L. latifolia* floral biology was gathered from 1982 to 1986 at the same population as part of other studies on the reproductive biology of this species. I present here a summary of data related to the variation during daytime in nectar sugar concentration, production and availability, as well as the proportion of flowers in the various phases of anthesis. Nectar availability and concentration were determined by sampling flowers at different times of day from plants falling within the area covered in pollinator counts. Nectar volume was measured with calibrated micropipettes, and concentration with a hand refractometer. The volume of nectar present in individual flowers was always too small for determining sugar concentration on a per flower basis. For this reason, concentration measurements were taken on pooled nectar samples from a number of flowers. The daily pattern of nectar secretion was investigated by bagging inflorescences on plants falling within the area surveyed for pollinator counts (5–8 plants on each occasion). Fine

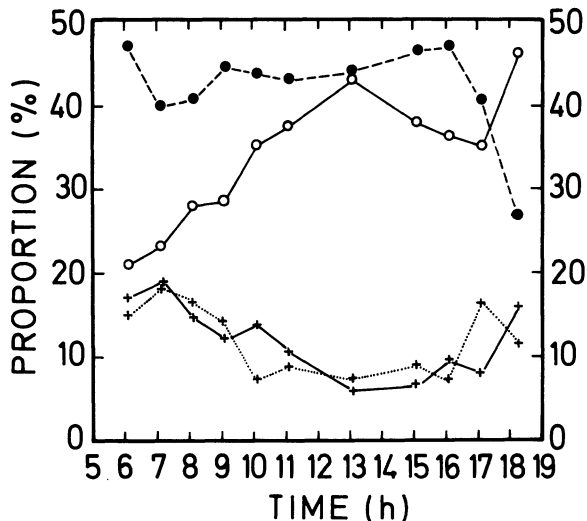


Fig. 1. Daily variation in the proportion of *Lavandula latifolia* flowers at the various stages of anthesis. Dots, flowers rewarding to pollinators (open dots: nectarless, pollen-bearing male-phase flowers; filled dots, pollenless, nectar-producing female-phase flowers); crosses, unrewarding flowers (dotted line, opening flowers; continuous line, withering flowers). N = 150 flowers for each time period.

nylon mesh bags were placed at dusk, and nectar volume and sugar concentration were determined from bagged flowers sampled periodically during the following day. As nectar extraction required destruction of the flower, I could not determine the daily pattern of nectar accumulation within the bags by repeated sampling of the same flowers; instead, I compared average values for different flowers sampled at different times.

L. latifolia flowers are markedly protandrous, and male- and female-phase flowers provided different rewards to pollinators. The proportion of flowers in the different stages of anthesis was determined for the study population at different times of day. Four consecutive stages were recognized, characterized by differences in the nature and amount of resources presented to pollinators. In opening flowers (corolla still unfolding), neither nectar nor pollen are generally produced (this phase generally last for < 1 d). Male-phase flowers (fully extended corolla, dehisced anthers), lasting for 1–2 d, have moderate amounts of pollen, but extremely little or no nectar. Mean nectar volume (± 1 SD) in male-phase flowers exposed to pollinators was $0.008 \pm 0.017 \mu\text{l}$ (N = 19). During the ensuing female phase, lasting for 2–5 d, only vestigial amounts of pollen may be found, but nectar secretion reaches a maximum. Mean nectar volume was $0.076 \pm 0.079 \mu\text{l}$ (N = 27) for female-phase flowers exposed to pollinators. Finally, withering flowers (corolla slightly discolored, darkening stigma), lasting for about 1 d, provide, at best, a negligible amount of nectar (see Herrera 1987a for further details on the floral biology of *L. latifolia*). Flowers at these four stages were visited by insects.

Components of pollinator effectiveness have been studied by Herrera (1987a,b, 1989), and pertinent methodological details may be found there. Data on average number of pollen grains deposited on the stigma per floral visit (computed as the proportion of floral visits that result in effective pollen deposition in the stigma times the average number of pollen grains delivered when deposition occurs) were taken from Herrera (1987a: Tables 2 and 3). Information on average flight distance between consecutive flower visits and on flower visitation rates was taken from Herrera (1987b: Table 1) and Herrera (1989: Table 1), respectively. These data are used here to evaluate daily changes in average potential pollinating effectiveness of the *L. latifolia* pollinator assemblage.

To quantify interspecific differences in body size, body masses of pollinators were obtained from dry specimens collected at the study site.

Results

Floral resources

Both pollen (all bees, some flies) and nectar (all bees and butterflies, and some flies) were sought by insect foragers in *L. latifolia* flowers. Opening and withering flowers, predictably offering little or no reward to pollinators, were present at all times of day (Fig. 1). Averaged over daytime, the two groups combined ('unrewarding' flowers) represented 22.0% of total flowers, and were proportionally most abundant early in the morning (0600–0700 hours) and late in the afternoon (1700–1800 hours). The mean proportions of opening (10.9%) and withering (11.1%) flowers in the population did not differ significantly from each other at any time of day (paired samples $t = 0.16$, N = 12, $P = 0.87$). The two magnitudes tended to vary in unison over the day. Their correlation across time was barely significant ($r = 0.583$, N = 11, $0.05 < P < 0.10$), but it became significant after lagging the time series for withering flowers one period behind the series for opening ones ($r = 0.792$, N = 10, $P < 0.01$). These results indicate that, during the study period, the population of open flowers tended to remain in equilibrium, with changes in the number of withering flowers closely matching, within about 1–1.5 h, variations in the numbers of opening ones.

Rewarding flowers (pollen- plus nectar-bearing) were proportionally most abundant around midday (1100–1300 hours) (Fig. 1). The proportion of pollen-bearing, nectarless male-phase flowers increased in the course of the day, rising from a minimum around sunrise to two maxima, occurring shortly after midday (1300 hours) and around sunset (1800 hours). The proportion of pollenless, nectar-producing female-phase flowers remained fairly constant throughout the day, with a sharp decline from 1600 hours onwards. For most of the day, nectar-producing flowers predominated among reward-

Table 1. Daily pattern of nectar abundance in 'rewarding' (male- plus female-phase) *Lavandula latifolia* flowers. N = number of flowers sampled. Two different estimates of mean nectar volume per flower are presented: A, computed over all the flowers sampled; B, computed over the flowers having non-zero nectar content only.

Daytime period (hours GMT)	Open to visitors				Visitors excluded			
	N	% with nectar	Mean volume (μ l)		N	% with nectar	Mean volume (μ l)	
			A	B			A	B
0500–0700	275	53.8	0.07	0.13	98	82.7	0.17	0.20
0700–0900	188	51.6	0.07	0.14	362	75.4	0.25	0.33
0900–1100	189	50.3	0.08	0.16	195	79.0	0.29	0.37
1100–1300	102	51.0	0.11	0.21	98	73.5	0.21	0.29
1300–1500	105	36.2	0.05	0.14	81	75.3	0.32	0.43
1500–1700	200	47.5	0.06	0.13	164	61.6	0.32	0.52
1700–1900	100	37.0	0.06	0.16	147	58.5	0.40	0.69

ing flowers, while pollen-bearing ones represented an important fraction of these only in the afternoon.

The proportion of rewarding flowers containing some nectar tended to decline through the day in both bagged and exposed flowers (Table 1). As only female- and male-phase flowers were used for nectar measurements (no opening or withering flowers were examined), the decline in the proportion of nectar-containing flowers in this subsample of the flower population is consistent with the increase in the proportion of nectarless, male-phase flowers in the course of the day noted above.

The average volume of nectar in flowers exposed to pollinators varied little over the day, reaching a weak maximum around midday (Table 1). In bagged flowers, average nectar volume increased almost continuously (although at a variable rate) over the day, from 0.17 μ l in the period 0500–0700 hours up to 0.40 μ l in the period 1700–1900 hours, with the exception of the period 1100–1300 hours, when a decrease in average volume takes place (Table 1). This could be attributed to a combination of reduced secretion with increased sugar concentration due to increased evaporation (see below). Nectar production rate was highest early in the morning and late in the afternoon, and lowest around midday.

Nectar sugar concentration (measured as mass of sugar per mass of solution) varied significantly during daytime (Table 2). The most dilute nectars were found in the early morning and late afternoon, and the most concentrated ones from 0900 through 1700 hours (see Table 2 for statistical significance of differences in nectar concentration between periods). The absolute maximum (67.5% sucrose-equivalents) was recorded in the period 0900–1200 hours, when average concentration also reached the daily maximum (60.8%).

The amount of sugar present in individual flowers exposed to pollinators was estimated by combining information on nectar volume and concentration (nectar density was computed using the expression in Prýs-Jones and Corbet 1987: 74). Peak sugar availability occurred around midday (1100–1300 hours; 0.06 mg/flower and 0.12 mg/flower, for all and nectar-containing

only flowers, respectively), when volume and concentration simultaneously reach their daily maxima.

Insect activity: major groups

The three major groups of insects visiting the flowers of *L. latifolia* (Hymenoptera, Diptera and Lepidoptera; all species recorded, combined by group) differed markedly in their daily patterns of abundance (Fig. 2). Hymenopterans (largely bees) were active at flowers of *L. latifolia* over the whole 0500–1900 hours daytime period. Their abundance, all species combined, remained fairly high throughout the day, with three peaks occurring in early morning, midday, and late afternoon. Butterfly foraging at *L. latifolia* flowers started at about 0700 hours, and finished around 1700 hours. The abundance of this group increased steadily throughout the morning up to a distinct peak at 1100 hours, then declining in the afternoon. Flies generally started foraging at flowers at about 0600 hours, and there was still some activity at 1900 hours. They exhibited a bimodal activity pattern, with a major peak at 0700 hours, a minimum around midday, and a secondary peak at 1700 hours. Between 0500 and 0700 hours, therefore, *L. latifolia* flowers were visited almost exclusively by Hymenoptera. Between 0700 and 1000 hours the importance of Hymenoptera, Diptera and Lepidoptera was roughly

Table 2. Sugar concentration (mass/mass basis; % sucrose equivalents) of nectar of *Lavandula latifolia* at different times of day. There is significant heterogeneity between periods ($F = 9.93$, $P < 0.0001$). Means sharing a supercript are not significantly different ($P > 0.05$, Student-Newman-Keuls test). N = number of measurements (each involving a pooled nectar sample from a variable number of flowers, see Methods).

Daytime period (hours GMT)	N	Mean \pm SD (%)	Range(%)
0500–0900	9	44.9 \pm 9.5 ^a	30.0–59.0
0900–1200	8	60.8 \pm 6.5 ^b	53.0–67.5
1200–1500	8	53.8 \pm 5.8 ^b	46.0–61.5
1500–1700	13	54.6 \pm 5.1 ^b	47.5–62.5
1700–1900	4	39.3 \pm 7.0 ^a	34.0–49.4

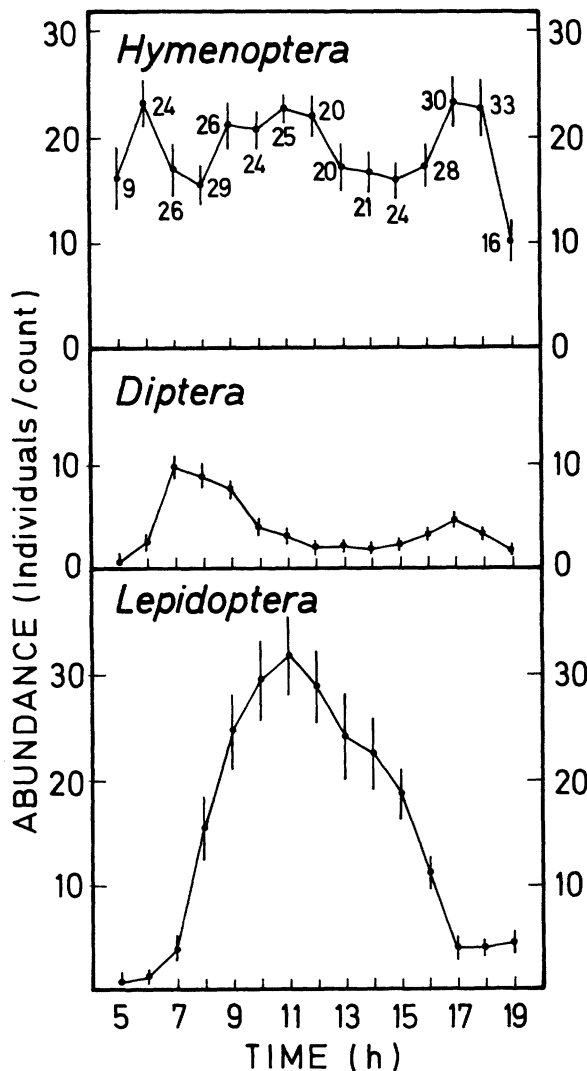


Fig. 2. Daily variation in the mean abundance of the three major groups of insects, all species combined, foraging at the flowers of *Lavandula latifolia* (August 1982–1987, all years combined). Vertical bars extend ± 1 SE around the mean. Figures beside the curve for hymenopterans indicate the number of counts conducted per one-hour period (the N's for the respective means), and these values hold also for dipterans and lepidopterans.

similar, and the Lepidoptera were numerically dominant in the period 1000–1300 hours. In the afternoon, patterns of relative group dominance largely mirrored those occurring in the morning.

Insect activity: individual species

Curves describing the daily variation in abundance of major insect groups (Fig. 2) reflect both temporal changes in the activity of individual component species, and differences in their absolute abundances. Furthermore, there is broad interspecific variation in aspects of

pollinating effectiveness (Herrera 1987a,b). Activity patterns of individual species are thus examined in detail in this section. A complete list of insect taxa ($N = 70$) visiting *L. latifolia* flowers in the study period (August, 1982–1987) may be found in Herrera (1988: Table 2). In this section, only 34 taxa (11 bees, 6 flies and 17 butterflies) will be considered. Depending on year, this set of taxa accounted altogether for 88.3–96.8% of total individuals recorded at flowers (mean = 92.7%). For each species, average abundance values (individuals/count) were obtained for each one-hour period, and expressed as percentages of the mean abundance value at its daily peak of activity (= period with maximum abundance). In this way, interspecific comparisons of daily activity rhythms are unaffected by differences in absolute abundances.

Bee species belong to three families, and their activity curves are depicted separately in Fig. 3. The three species of Apidae (*Apis mellifera*, *Bombus terrestris* and *B.*

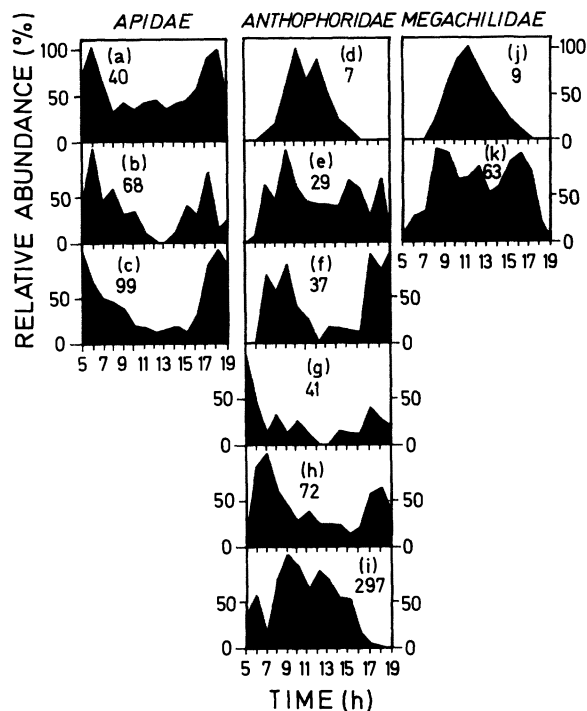


Fig. 3. Daily variation in the abundance of 11 bee taxa at the flowers of *Lavandula latifolia*. For individual taxa, mean abundance at a given hourly period is expressed as a percentage of its mean abundance at the daily peak (in parentheses following species names, expressed as individuals/count). The three columns of graphs correspond to the three families represented in the species sample. Within each of these, average body dry mass (in mg; shown under the graph identification letter) increases from top to bottom. Apidae: (a), *Apis mellifera* (17.75 ind/count); (b), *Bombus pascuorum* (0.54); (c), *Bombus terrestris* (3.49). Anthophoridae: (d), *Ceratina cyanea* + *mocsaryi* (1.83); (e), *Anthophora albigena* (0.62); (f), *Anthophora quadrifasciata* (0.30); (g), *Anthophora crassipes* (0.33); (h), *Anthophora ochroleuca* (1.08); (i), *Xylocopa violacea* (0.96). Megachilidae: (j), *Anthidiellum brevisculum* (6.00); (k), *Anthidium florentinum* (5.25).

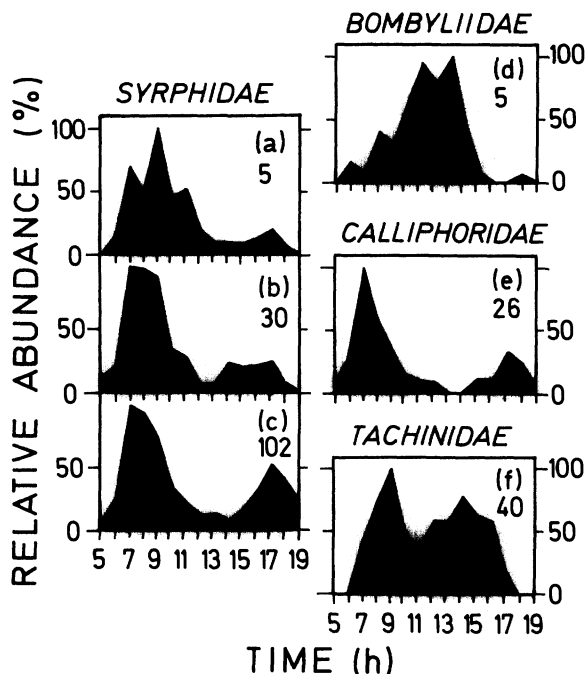


Fig. 4. Daily variation in the abundance of 6 fly taxa at the flowers of *Lavandula latifolia*. For individual taxa, mean abundance at a given hourly period is expressed as a percentage of its mean abundance at the daily peak (in parentheses following species names, expressed as individuals/count). Average body dry mass (in mg) is shown under the graph identification letter. Syrphidae: (a), *Sphaerophoria scripta* (0.54 ind/count); (b), *Eristalis tenax* (0.85); (c), *Volucella inanis* + *zonaria* + *elegans* (6.00). Bombyliidae: (d), *Systoechus* sp. (0.50). Calliphoridae: (e), *Rhynchomya felina* + *zerynana* (1.92). Tachinidae: (f), *Nowickia strobelsi* (0.85).

pascuorum) are similar in exhibiting distinctly bimodal activity patterns, with peaks in early morning and late afternoon and a marked decrease (particularly for bumblebees) around midday (Fig. 3a-c). Activity curves for the Anthophoridae reveal some intra-familial variation. The smallest species (*Ceratina cyanea* + *mocsaryi*; Fig. 3d) tend to display a unimodal activity pattern, with maximum abundance occurring around midday. In contrast, medium- to large-sized *Anthophora* species (Fig. 3e-h) have bimodal activity patterns, with peaks in early-mid morning and mid-late afternoon, and a minimum (least marked in the smallest *A. albigena*, Fig. 3e) around midday. In contrast, *Xylocopa violacea*, the largest bee in the sample, has sustained activity for most of the day, excepting early morning and late afternoon, without any discernible decline around midday (Fig. 3i). Finally, the two species of Megachilidae, differing widely in body size, have contrasting rhythms of activity at flowers. The small *Anthidiellum brevisculum* displays a unimodal pattern with a peak around midday (Fig. 3j), while the medium-sized *Anthidium florentinum* (Fig. 3k) has a bimodal pattern, with peaks at mid-morning and mid-afternoon and a weak decline around midday.

Four dipteran families are represented in the sample. The three taxa of syrphid flies (Fig. 4a-c) exhibit activity peaks around mid-morning, and a secondary peak in late afternoon, with little activity at flowers for the remainder of the day. *Systoechus* sp. (Bombyliidae), a small-bodied species, has a unimodal activity pattern centered around midday (Fig. 4d). *Rhynchomya felina* + *zerynana* (Calliphoridae; this is 'Calliphoridae gen. sp.' in Herrera 1988) has a pattern similar to that described above for syrphids (bimodal with unequal peaks; Fig. 4e), and *Nowickia strobelsi* (Tachinidae; this species is 'Tachinidae gen. sp.' in Herrera 1988) has a bimodal pattern with roughly similar peaks at mid-morning and mid-afternoon (Fig. 4f).

Five butterfly families are represented in the sample. Among the Hesperidae, activity patterns vary from unimodal with peaks around midday for the smallest species (*Thymelicus acteon*, *Spialia sertorius*; Fig. 5a-b) to bimodal with a marked minimum at midday in *Hesperia comma*, the largest species (Fig. 5d). The Nymphalidae (Fig. 5e-h) tend to exhibit sustained activity for most of the day, with peaks around midday (*Argynnis paphia* displays a weak bimodality, with a minimum in early afternoon). Lycaenidae and Pieridae all have unimodal activity patterns with peaks at midday (*Lysandra albicans/hispana*, *Plebicula escheri*, *Colias crocea*, *Gonepteryx* spp.; Fig. 5j-m) or mid-morning (*Lycaena phlaeas*; Fig. 5i). Finally, the Satyridae exhibit considerable interspecific variation in activity patterns (Fig. 5n-q), ranging from unimodal to bimodal patterns with peaks at different times of day.

Variation in components of pollinating effectiveness

An index of pollen transfer effectiveness (IPE) was obtained for each of the 29 taxa with sufficient data. It was computed by multiplying the average number of flowers visited min^{-1} by the average number of pollen grains deposited on the stigma in single floral visits (see Methods for data sources). This is a species-specific index, independent of pollinator population size (IPE and average abundance are uncorrelated in the species sample examined here; $r_s = -0.010$, $N = 29$, $P = 0.96$). For each species, the period(s) of the day when activity was $\geq 75\%$ of its daily maximum was determined, and its IPE value plotted against daytime using as horizontal coordinate(s) the hour(s) included in the period of high ($\geq 75\%$) relative activity. The 75% threshold was (arbitrarily) chosen to separate high- versus low-activity periods in the daily cycle. This method has the advantage of eliminating the biases that would result if only a single activity peak (equivalent to a 100% threshold) were used for each species, and it produces a 'daily profile' of the pollen-transfer effectiveness of the assemblage of insects visiting *L. latifolia* flowers, regardless of differential abundance of species.

The daily turnover in the composition of the pollinator assemblage results in a distinct cycle of average IPE

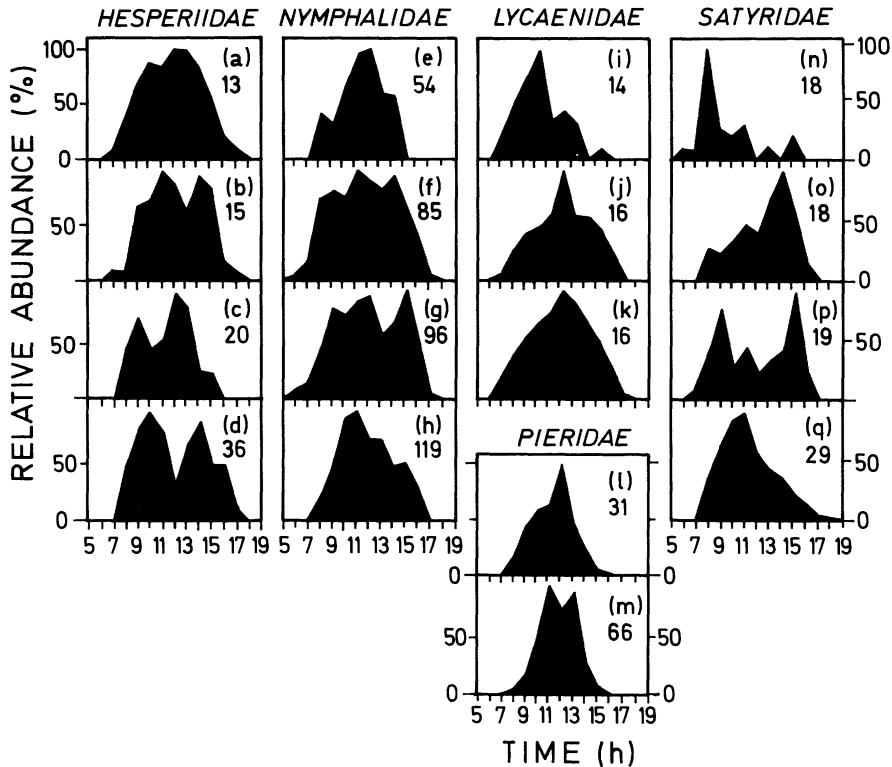


Fig. 5. Daily variation in the abundance of 17 butterfly taxa at the flowers of *Lavandula latifolia*. For individual taxa, mean abundance at a given hourly period is expressed as a percentage of its mean abundance at the daily peak (in parentheses following species names, expressed as individuals/count). Graphs are arranged into blocks corresponding to different families. Within each block, average body dry mass (in mg, shown under the graph identification letter) increases from top to bottom. HesperIIDae: (a), *Thymelicus acteon* (5.30 ind/count); (b), *Spialia sertorius* (0.40); (c), *Muschampia proto* (0.35); (d), *Hesperia comma* (1.63). Nymphalidae: (e), *Issoria lathonia* (0.25); (f), *Fabriciana adippe* (3.12); (g), *Argynnis paphia* (4.42); (h), *Pandoriana pandora* (2.16). Lycaenidae: (i), *Lycaena phlaeas* (0.46); (j), *Lysandra albicans/hispana* (2.55); (k), *Plebicula escheri* (0.95). Pieridae: (l), *Colias crocea* (1.05); (m), *Gonepteryx cleopatra + rhamnii* (0.64). Satyridae: (n), *Lasiommata megera* (0.38); (o), *Hyponphele lycaon + lupina* (0.48); (p), *Pyronia tithonus* (0.42); (q), *Melanargia galathea* (10.12).

values (Fig. 6A). Pollinators with activity peaks in early morning and late afternoon are characterized by high pollen-transfer effectivenesses, while those with activity peaks in the intervening period (roughly 0700–1400 hours) have predominantly low IPE values.

A further variable relevant to pollination effectiveness is the average distance flown by pollinators between consecutive flower visits, as variations in this magnitude will presumably result in changes in the relative proportions of xenogamous and geitonogamous pollinations (Herrera 1987a). The daily cycle in average flight distance of pollinators was examined using the same method as above (i.e., plotting average flight distance for individual species against the daytime period (s) on which the activity for the species is $\geq 75\%$ of the daily peak; Fig. 6B). Daily variation of this variable is complementary to that displayed by IPE. Pollinators with activity peaks in early morning and late afternoon are characterized by short inter-flower flights, while pollinators with peaks in the intervening period fly longer distances between consecutive flower visits.

Discussion

Determinants of activity rhythms

Previous investigations on insect pollinators have provided evidence that the interaction between thermal balance and diel rhythmicity is responsible for many of the patterns of insect activity seen in nature. Insect body size strongly influences thermal balance, and temporal patterns at flowers are often better explained from size, reflectance and the hygrothermal characteristics of the environment than from the amount and characteristics of the floral rewards available (Hippa et al. 1981, Willmer and Unwin 1981, Willmer 1983, Gilbert 1985, Stone et al. 1988). Results of the present study are not an exception to this pattern.

Among bees, interspecific differences in activity patterns are readily related to variation in body size. Smaller insects, having lower temperatures excesses (difference between body and ambient temperatures) and higher cooling rates, are expected to be most active at greater radiation levels, such as those occurring in the middle of the day (Willmer and Unwin 1981). The

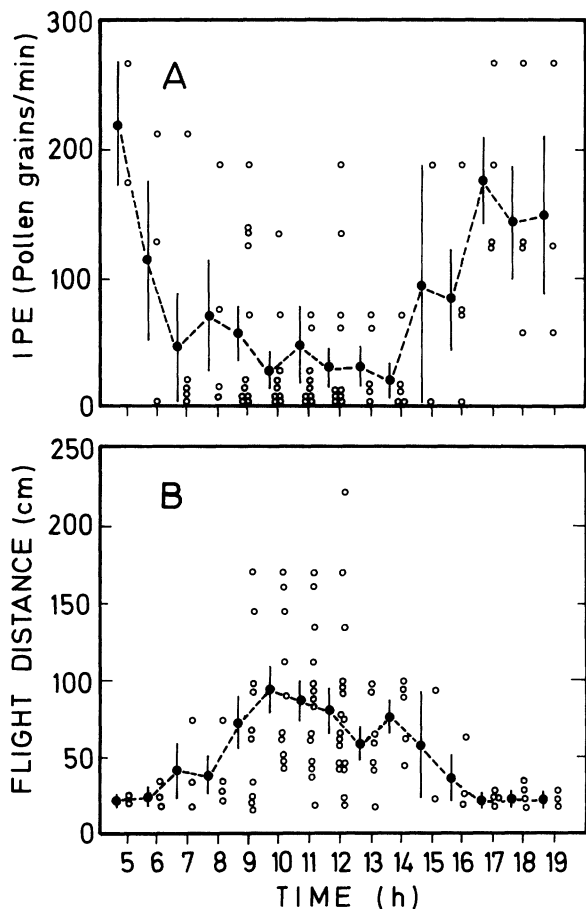


Fig. 6. Daily variation of two components of pollinating effectiveness in the *Lavandula latifolia* pollinator assemblage. A, an index of pollen transfer effectiveness (IPE), expressed as average number of pollen grains transferred per min to stigmas by individual insects. B, mean distance flown by individual insect visitors between consecutive flower visits. IPE and mean fly distance were obtained for individual taxa, and plotted against time for those hourly periods(s) when the activity of the respective species was $\geq 75\%$ of its daily maximum (open dots). Average values for each one-hour period are shown as filled dots (vertical bars extend over ± 1 SE).

smallest bees in the sample examined here (*Ceratina mocsaryi* + *cyanea* and *Anthidiellum brevisculum*; 7 mg and 9 mg dry mass, respectively) have unimodal activity patterns with distinct peaks at midday. Large insects attain and maintain high temperature excesses fairly easily, and may readily reach a temperature conducive to activity even under conditions of low solar radiation (Willmer and Unwin 1981). At high radiation levels, however, such as those occurring at the middle of summer days at my study site ($> 1100 \text{ Wm}^{-2}$; L. López-Soria, pers. comm.), they will risk overheating, particularly in the case of endothermic taxa like *Bombus*, *Apis* and *Anthophora* (Heinrich 1979a,b, Stone et al. 1988). The risk of overheating is probably still greater for hovering species, as is the case with the species of *Anthophora* considered in this study (see also Stone et

al. 1988), which beat their wings uninterrupted while foraging. The activity patterns of medium- to large-sized bees found here are consistent with these expectations (with the exception of *Xylocopa violacea* discussed below). *Bombus*, *Apis* and *Anthophora* species were most active early in the morning and late in the afternoon, at times when rewarding (male- plus female-phase) flowers were proportionally scarcest in the population, and when these contained comparatively little nectar. They exhibited reduced foraging activity under the heavily insolated conditions of the middle of the day, even though nectar was then at its daily peak of availability. In addition to radiation, a further factor that could determine the decreased activity of these bees at the middle of the day is increased nectar concentration. For some bees of arid habitats, water from nectar is the most vital factor, overriding energy rewards (Willmer 1986, Olesen 1988). The very concentrated nectar of *L. latifolia* in the middle of the day may fail to provide the minimum water requirements for some species in the dry Mediterranean summer. *Apis mellifera* is able to forage at ambient temperatures of up to 46°C , but thermoregulation at high temperature depends on evaporative cooling following nectar regurgitation (Heinrich 1979b, 1980a,b), and water limitation may constrain this thermoregulatory behavior.

Xylocopa violacea is a conspicuous exception to a body size-based explanation of bee activity patterns. It is the largest bee in the sample (297 mg dry mass), yet it is most active around the middle of the day, under conditions of high insolation. The high reflectance of this nearly hairless, shining-black bee may reduce radiative gain (Willmer and Unwin 1981). Other species in the genus *Xylocopa* are able to forage without thermal stress until air temperature exceeds $41\text{--}42^\circ\text{C}$ (Chappell 1982). It thus appears that the departure of *X. violacea* from a rule based on consideration of body size alone is due to tolerance of high ambient temperatures being a characteristic of this genus of large endothermic bees well adapted to hot-dry environments (Watmough 1974, Gerling et al. 1989). Cooling is apparently not achieved by evaporative water loss (Nicolson and Louw 1982, Gerling et al. 1989), hence potential water limitations posed by concentrated nectar probably does not affect the thermoregulatory ability of these bees (in fact, concentrated nectar seems essential for the male flights of some *Xylocopa* species; Wittmann and Scholz 1989).

The set of dipteran taxa considered here feed on pollen (*Sphaerophoria scripta*), pollen and nectar (*Eristalis tenax*, *Volucella* spp., *Rhynchomya* spp.), and nectar (*Systoechus* sp., *Nowickia strobili*) of *L. latifolia* flowers. The activity patterns of these three groups do not match the daily rhythms of availability of their respective resources. For syrphid flies, Gilbert (1985) found that large species became active at lower temperatures (earlier in the day) than small ones. The three syrphid taxa considered here start activity at the same time, regardless of broad differences in body size, but

midday cessation of activity tends to occur earlier as body size increases. The same general pattern found here, namely a bimodal activity curve with unequal peaks occurring at mid-morning and mid-afternoon, has been found for flies from several families in previous studies involving different plant species and contrasting daily rhythms of floral resource availability (Corbet et al. 1979, Willmer 1983, Gilbert 1985, Ottosen 1986). Willmer (1983) found reduced activity of flies above radiation values of 600 Wm^{-2} , presumably as a consequence of overheating. As noted above, maximum radiation levels at midday at my study site were $> 1100 \text{ Wm}^{-2}$, hence avoidance of overheating probably is responsible for the bimodal activity of flies. The relation between body size and timing of midday cessation of activity found here for syrphid flies supports this interpretation.

Activity patterns of butterflies were interspecifically less variable than those of bees or flies. Most interspecific variation is explainable in terms of familial affiliation, as activity patterns tend to be fairly constant within families (with the exception of the Satyridae), regardless of variations in body size. With minor exceptions, most species display activity peaks around midday, and little, if any, foraging activity early in the morning and late in the afternoon. Overheating may occur at high ambient temperatures (Clench 1966, Kingsolver and Watt 1983), and this might lead to reduced foraging activity in the middle of the day under conditions of high solar radiation. Among butterflies visiting *L. latifolia* flowers, however, only *H. comma* (Hesperiidae) and *P. tithonus* (Satyridae) exhibited a sharp decline in activity in the middle of the day.

Optimal nectar concentration for butterflies seems to fall around 40%, and nectars above this concentration become increasingly unprofitable (Pivnick and McNeil 1985, May 1985). The high concentration reached by the nectar of *L. latifolia* during the period of maximum butterfly activity is well above the optimum, thus ruling out the possibility of butterflies timing their foraging activity in relation to profitability of floral resources. Among these butterflies, thermoregulation is exclusively behavioral, and solar radiation is the exclusive source of heat gain for warm-up (Rawlins 1980, Polcyn and Chappell 1986, Tsuji et al. 1986, Pivnick and McNeil 1987). This explains the absence of butterfly activity found here during the cooler periods of the day (see also Heinrich 1986a,b, Stone et al. 1988), even though the concentration of the nectar of *L. latifolia* then lies around the optimal value of 40%.

Biotic interactions, particularly interference competition at flowers, may influence the foraging activity of pollinators (Primack and Howe 1975, Hubbell and Johnson 1978, Brown et al. 1981, Gill et al. 1982). The relatively restricted activity period of butterflies relative to bees could thus perhaps be interpreted as a behavioral adaptation to reduce interference from bees, rather than (or in addition to) as a response to the

thermal environment as suggested above. This study does not provide information that may be used to test this possibility, but data on aggressive displacements at *L. latifolia* flowers gathered at the study population do not support it. In August 1982–1983, a total of 83 “supplanting encounters” (an insect actively foraging at a flower was displaced and supplanted by an arriving visitor) involving bees and/or butterflies were recorded in the period 0800–1600 hours, when the two groups overlapped most extensively in flower use (Fig. 1). In 56.6% of these encounters, both the supplanter and the displaced insect was a butterfly, and in 15.7% of instances the two participants were bees. Inter-group encounters represented only 27.7% of total (in these, bees were supplanted in 20.5%, and butterflies in 7.2% of instances) (C. M. Herrera, unpubl.). These preliminary data point to a prevalence of intra- over inter-group interference, hence disturbances experienced by butterflies while foraging probably are not much reduced as a consequence of decreasing temporal overlap with bees.

Pollinating effectiveness and floral resources

From the viewpoint of *L. latifolia* plants, the daily cycle is not homogeneous with regard to the potential pollinating effectiveness of insect visitors active at a given time.

Early morning and late afternoon are the periods potentially providing most opportunities of pollen transfer to stigmas because of the higher IPE values of insect taxa active at these times. These periods are also characterized by predictably short average flight distances of pollinators between flowers. Opportunities for pollen transfer decline around the middle of the day but, in turn, pollinators active in that period fly predictably longer distances between consecutive floral visits. The proportion of pollen-bearing flowers in the population was highest in late afternoon, and lowest in early morning (Fig. 1). Furthermore, most field determinations of magnitudes entering into the computations of IPE (Herrera 1987a) were conducted over a relatively short daytime period (0800–1200 hours). All these considerations suggest that daily variation in IPE actually reflects variation in intrinsic pollen transfer ability of pollinators, and is not an artifact of daily variation in the proportional abundance of pollen-bearing flowers in the population.

The daily pattern of variation in the two components of pollinating effectiveness is largely generated by differences between bees and butterflies in pollen-transfer effectiveness and inter-flower movement patterns, coupled with differential activity patterns (on average, bees tend to deposit more pollen and more often, but to fly shorter distances between flowers, than butterflies; Herrera 1987a). Likely consequences for the plant will be more numerous, predominantly geitonogamous pollinations taking place in early morning and late afternoon, and comparatively few, but more xenogamous,

pollinations around the middle of the day (i.e., pollen transfers are quantitatively high, but qualitatively less good, early and late in the day). Number of pollen-transfer events is decisive in determining seed production, as spontaneous autogamy is negligible in *L. latifolia*, but the proportion of xenogamous pollinations also influences fruit set, as xenogamy results in greater fruit production (on a per-flower basis) than geitonogamy (Herrera 1987a), and it may also result in improved germination and seedling success. There is thus asynchronous daily variation of two features of the pollinator assemblage enhancing reproductive success, as a consequence of the shifting numerical dominance of bees and butterflies in the pollinator assemblage. This situation leads to a dilemma if plants were to 'evolutionarily choose' an optimal time for presenting floral rewards so as to match the activity period of the most efficient pollinators (see Herrera 1987a for further discussion on the constraints imposed on *L. latifolia* by the bee-butterfly dilemma).

L. latifolia plants open flowers and produce nectar uninterruptedly over daytime, with maximum secretion rates occurring early in the morning and late in the afternoon. The pattern of resource presentation thus closely matches the daily course of pollen-transfer effectiveness as measured by IPE, but not the pattern of expected proportional occurrence of xenogamy. Pollen availability, as estimated by the proportion of pollen-bearing male-phase flowers, reaches a maximum in late afternoon, while nectar and sugar availability peak around the middle of the day. Nectar availability thus matches the daily pattern of expected frequency of xenogamous pollinations but not IPE variation, while pollen availability incompletely matches the pattern of IPE. It is difficult to interpret as adaptive (on the part of the plant) this complex combination of matches and mismatches without resorting to a set of similarly complex ad hoc explanations. Furthermore, no data are available on the comparative value (in terms of contribution to fitness) for individual *L. latifolia* plants of seeds produced by geitonogamy and xenogamy. A parsimonious, non-evolutionary explanation may, however, be put forward. As discussed above, daily activity rhythms of pollinators seem essentially the consequence of the behavioral adjustment of individual species to the thermal environment, and the asynchronous daily variation of the two components of pollinating effectiveness is an incidental byproduct of these adjustments. *L. latifolia* plants are also themselves subject to environmental abiotic stress and, as in other Mediterranean plants in summer, a daily rhythm in water stress is to be expected, with extremely low water potential values occurring around midday (Tenhunen et al. 1980, 1982). It is not unexpected to find that production of nectar and new flowers decline at the most water-stressed period of the day, an observation made long ago by Bonnier (1879) with respect to nectar for southern European and northern African plants. Peak nectar and

sugar availability at midday would simply be the consequence of increasing evaporation and declining foraging activity of very active, large bees as the morning proceeds. Under this explanation, both matches and mismatches found here between daily patterns of floral resources and aspects of pollinating effectiveness would be seen as epiphenomena lacking particular adaptive significance to the plant.

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