Thermal biology and foraging responses of insect pollinators to the forest floor irradiance mosaic

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This paper examines the responses of the insect pollinators of the summer-flowering, understorey shrub, *Lavandula latifolia* (Labiatae) to the irradiance mosaic of the forest floor in a southeastern Spanish locality, and assesses the relationship between these responses and interspecific variation in thermal biology. Pollinators differed significantly in the mean irradiance at capture points (MICP), and a large percentage of species (59%) preferentially selected plants in either shaded or sunlit conditions. Taxonomic affiliation (at the order level) and body size explained 78% of interspecific variance in MICP. Dipterans tended to be restricted to situations of relatively low irradiance, whereas hymenopterans foraged over the entire irradiance gradient. MICP was inversely related to body size. Pollinators differed significantly in mean thoracic temperature (T_{th}), thoracic temperature excess ($T_{exc} = T_{th} - T_a$ [air temperature]), and slope of the T_{th}/T_a regression (which may be taken as a rough index of thermoregulatory ability). Hymenopterans had higher T_{th} and T_{exc}, and smaller T_{th}/T_a slopes, than dipterans. After accounting for this taxonomic effect, T_{th} and T_{exc}, but not T_{th}/T_a slope, increased with body size. MICP depended significantly on T_{exc} and, to a lesser degree, on T_{th}, and species characterised by high T_{exc} tended to select low-irradiance conditions. The relationship between MICP and body size was thus mediated by the correlations between the latter variable and thermal biology parameters. In the hot Mediterranean summer, as in other thermally stressing environments, thermal constraints of the kind reported in this study may generate within- and between-habitat variation in the composition and size structure of pollinator assemblages, which may be consequential for plant reproduction.

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During daytime, forest understorey plants are immersed in a spatio-temporal mosaic of sunlit and shaded patches whose geometrical characteristics depend in complex ways on season, time of day, and the size and arrangement of overlying tree crowns (Gay et al. 1971, Reifsnyder et al. 1971). Site-dependent variation in the irradiance regime experienced by understorey plants generates individual variation in growth, photosynthesis, herbivory, pollination and seed dispersal (Thompson and Willson 1978, Maiorana 1981, Moore and Willson 1982, Louda et al. 1987, Chazdon 1988, Piper 1989, Niesenbaum 1994, Herrera 1995a). The causes

and magnitude of these and other (e.g., Manasse and Howe 1983, Denslow 1987, Sowig 1989, Sargent 1990, Laverty 1992) site-dependent effects are important from an evolutionary ecological perspective, since differences between individual plants in fitness-related parameters (e.g., growth, reproduction) may have evolutionary implications only if they depend more on intrinsic (*how* plants are) than on extrinsic (*where* they are) attributes. An earlier study on the insect-pollinated, understorey shrub *Lavandula latifolia* Med. (Labiatae) in southeastern Spain showed that variation among plants in pollinator composition depended on plant location on the

forest floor and its associated irradiance regime, but was unrelated to such intrinsic characteristics as floral morphology, floral display size, and nectar standing crop (Herrera 1995a). In that study, site-dependent effects and individual plant variation in pollinator taxonomic composition were ultimately due to the contrasting responses of pollinator taxa to the spatio-temporal irradiance mosaic, and it was suggested that these differential responses were related to variation in thermal biology.

The objective of the present paper is to examine in greater detail the responses of *Lavandula latifolia* pollinators to the irradiance mosaic of the forest floor, and to assess the relationships between these responses and interspecific variation in thermal biology. *L. latifolia* is pollinated by a diverse array of insects comprising nearly 80 bee, fly and butterfly species (Herrera 1988). The earlier study mentioned above (Herrera 1995a) considered only the foraging responses of ten of these species. By examining a broader subset of pollinators, the present paper attempts to extend the previous results, obtain a more realistic assessment of the frequency of occurrence of foraging responses to the irradiance mosaic, and identify possible taxonomic correlates. Furthermore, the thermal biology of the different pollinators is studied here by examining patterns of variation of thoracic temperature in relation to ambient temperature. Specifically, the questions addressed are: (1) What is the frequency of occurrence of irradiance-biased foraging in a relatively large, taxonomically diverse sample of pollinator taxa?, and (2) Are there some predictable relationships between irradiance-biased foraging, thermal biology, body size, and taxonomic affiliation?

Methods

Study area

This study was conducted during July–August 1990 in the Reserva de Navahondona-Guadahornillos, Parque Natural de Cazorla-Segura-Las Villas (Jaén province, southeastern Spain; see Valle et al. 1989 for descriptions of flora and vegetation), at a *Lavandula 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 earlier studies (Herrera 1988, 1991, where further details may be found). Climate is of a Mediterranean type, with warm-to-hot, dry summers. At the nearest meteorological station (Vadillo-Castril, 4.5 km away, similar elevation), averages of maximum and minimum mean monthly temperature for July were 31.9°C and 10.9°C, respectively, and for August 31.4°C and 11.3°C ($N = 18$ yr).

Data collection

At the study site, *L. latifolia* plants occupy the understorey of open *Quercus rotundifolia* Lam. – *Pinus nigra* Arnold mixed forest and, during daytime, they occur in a changing mosaic of insolated and shaded patches (Herrera 1995a). Random sampling of foraging pollinators, along with a detailed characterisation of the sunlight regime, were conducted at the study site. To characterise the mosaic of irradiance levels available to pollinators in the forest understorey over daytime, 60 permanent recording stations were set, regularly spaced at 2-m intervals along a transect that crossed the *L. latifolia* study population. Solar irradiance (on the horizontal plane) was measured periodically from dawn to dusk at all stations during several consecutive days using a Li-Cor LI-200SZ Pyranometer Sensor (calibrated spectral range 400–1100 nM) connected to a LI-1000 data logger (Li-Cor Inc., Lincoln, NE). Irradiance measurements were also taken continuously from dawn to dusk on a single date in the centre of a large forest clearing nearby. These data will be used for comparison with the irradiance regime in the forest understorey. Almost all days in the study period were characterised by windless, cloudless weather, and all irradiance measurements and pollinator captures (see below) were conducted under these conditions.

Insect pollinators were netted systematically from dawn to dusk while they were visiting *L. latifolia* flowers. Within 5 s of capture, the thoracic temperature of insects was measured to the nearest 0.1°C using a fast-response (time constant 0.025 s) 0.33 mm-diameter needle microprobe (Type MT-29/1; Physitemp Instruments, Clifton, NJ). Readings were obtained by inserting the probe 1 mm into the insect's thorax while the insect was restrained in the net. Air temperature (measured using a fast-response 0.5 mm-diameter Type T thermocouple connected to a digital thermometer) and solar irradiance on the horizontal plane were also measured at all capture points within 1 min of netting. Comparisons of irradiance at the capture points of insect species with the combined sample of measurements at the permanent sampling points were used to elucidate patterns of microhabitat selection by pollinators.

The species set

At the study locality, butterflies account, on average, for 51% of species and 38% of individuals of *L. latifolia* pollinators (Herrera 1988), and they are responsible for nearly 18% of total pollinator visits to plants (C. M. Herrera unpubl.). All species involved apparently have the same thermoregulatory method (behavioural regulation based on sun-basking; Heinrich 1993) and uniformly tend to select sunlit patches for foraging (C. M.

Table 1. Body size and irradiance at capture points of *Lavandula latifolia* pollinators considered in this study. Body length averages are based on measurements taken on insects from the study site ($N = 4$–9 individuals per species). χ^2 and P values refer to comparisons with mean irradiance at the permanent recording stations (performed using Kruskal-Wallis ANOVA's). Significant departures are shown in bold type. N = sample size.

Species[1]	Mean body length (mm)	Irradiance at capture points			
		N	Mean $\pm$ SD (W/m^2)	χ^2	P
Hymenoptera					
Anthidium breviusculum Pér. (ME)	6.2	51	842 ± 160	65.0	**<0.001**
Anthidium florentinum Fabr. (ME)	12.6	62	524 ± 345	9.1	**0.003**
Anthophora albigena Lep. (AN)	9.4	27	588 ± 361	8.6	**0.003**
Anthophora crassipes Lep. (AN)	11.2	33	155 ± 155	5.1	**0.024**
Anthophora ochroleuca Pér. (AN)	14.0	21	230 ± 286	1.2	0.28
Anthophora quadrifasciata Vill. (AN)	13.0	14	340 ± 345	0.5	0.47
Apis mellifera L. (AP)	11.8	203	401 ± 415	0.9	0.35
Bembix zonata Klug. (SP)	18.4	33	519 ± 374	4.4	**0.035**
Bombus pascuorum Scop. (AP)	13.1	36	170 ± 267	10.7	**0.001**
Bombus terrestris L. (AP)	15.3	115	301 ± 356	4.5	**0.034**
Ceratina cyanea Kirb. + *mocsaryi* Fri. (AN)	6.9	43	884 ± 166	65.9	**<0.001**
Magachile pilidens Alfk. (ME)	8.8	10	625 ± 350	3.0	0.08
Xylocopa violacea L. (AN)	22.5	15	601 ± 372	5.6	**0.018**
Diptera					
Eristalis tenax L. (SY)	13.8	148	323 ± 332	0.01	0.92
Milesia crabroniformis Fabr. (SY)	21.7	33	320 ± 288	0.05	0.81
Nowickia ferox Panz. (TA)	14.6	78	207 ± 222	1.2	0.08
Rhynchomya felina Fabr. (CA)	12.3	100	231 ± 265	11.5	**0.001**
Rhynchomya zernyana Vill. (CA)	10.0	18	338 ± 277	0.03	0.86
Sphaerophoria scripta L. (SY)	9.7	32	336 ± 311	0.4	0.55
Volucella elegans Loew. (SY)	18.0	70	209 ± 226	9.6	**0.002**
Volucella inanis L. (SY)	16.1	21	129 ± 160	8.8	**0.003**
Volucella zonaria Poda (SY)	18.4	11	78 ± 55	5.3	**0.021**

[1] Family codes (in parentheses following species names) are as follows: AN, Anthophoridae; AP, Apidae; CA, Calliphoridae; ME, Megachilidae; SP, Sphecidae; SY, Syrphidae; TA, Tachinidae.

Herrera unpubl.). To enhance the possibilities of detecting interspecific differences in microhabitat selection and thermal biology, and due to time limitations, I did not sample butterflies for this study, but rather focused on hymenopterans and dipterans.

Data for 13 hymenopteran and 9 dipteran taxa, encompassing a broad range of body size and taxonomic affiliation, are considered in this study (see Table 1 for a list of species). Bees of the families Anthophoridae ($N = 6$ species), Apidae ($N = 3$) and Megachilidae ($N = 3$) predominate among the hymenopterans, while species of Syrphidae ($N = 6$) predominate among the dipterans. Mean body length (measured on dry specimens from the study locality) will be used here to assess insect body size. Live body mass would have been a more appropriate magnitude, but these data were not available for all species. In a subset of 13 species with mean live body mass (range $= 82$–688 mg) and mean body length (range $= 11.2$–22.5 mm) data simultaneously available, the two magnitudes were closely correlated ($r = 0.780$, $P = 0.0017$), thus providing justification for using body length, rather than body mass, as a descriptor of body size.

On the basis of information from previous investigations (Herrera 1987a), all the insect species included in this study are considered effective pollinators of *L. latifolia*.

Data analysis

Unless otherwise indicated, all analyses were performed with the SAS statistical package (SAS Institute 1990). Comparisons of means were conducted using Kruskal-Wallis nonparametric analysis of variance (procedure NPAR1WAY). Analyses of covariance and generalised linear models used procedure GLM with Type III sum of squares. In these cases, normality of data was assessed prior to the analyses.

Results

Irradiance patterns

Frequency distributions of dawn-to-dusk irradiance measurements differed markedly between the forest understorey and the nearby forest clearing (Fig. 1). In comparison with the clearing, the irradiance regime in the forest study site was characterised by a distinct

bimodality, with predominance of low-irradiance (<200 W/m²) conditions and a relative scarcity of high-irradiance, fully isolated conditions (>900 W/m²).

No significant difference existed between mean irradiance (± 1 SD; this notation will be used subsequently unless otherwise stated) at the permanent recording stations along the understorey transect (384 ± 374 W/m², $N = 1620$) and at the pollinator capture points at the same site (367 ± 363 W/m², $N = 1174$, all species combined) ($\chi^2 = 0.014$, df = 1, $P = 0.91$). This indicates that sampling of foraging pollinators was not biased in any serious way with regard to the irradiance values of capture points.

Microhabitat selection

Mean irradiance at capture points (MICP hereafter) differed significantly among pollinator taxa ($\chi^2 = 239.5$, df = 21, $P < 0.0001$). MICP ranged from <130 W/m² for two syrphid flies (*Volucella inanis* and *V. zonaria*) which foraged almost exclusively on shaded plants, to >800 W/m² for the two smallest-sized bees (*Anthidium breviusculum* and *Ceratina* spp.), which were captured only under full insolation and intense irradiance (Table 1). Average MICP of hymenopteran taxa (475 ± 236 W/m², $N = 13$) significantly exceeded that of dipterans (241 ± 95 W/m², $N = 9$) ($\chi^2 = 5.62$, df = 1, $P = 0.018$).

Interspecific variation in MICP reflects differential patterns of microhabitat selection. MICP departs significantly from mean irradiance at permanent recording stations for 13 out of 22 taxa (Table 1). Among hymenopterans, these irradiance-selective taxa tended to forage under both lower-than-average ("shade-seeking"; one *Anthophora* and the two *Bombus* species) and higher-than-average ("sun-seeking"; one sphecid wasp, two megachilid and three anthophorid bees) irradiance conditions. Among dipterans, in contrast, all instances of significant differences between irradiance at capture points and at recording stations involved shade-seeking taxa (three syrphid and one calliphorid species; Table 1). MICP of all dipteran taxa fell below the mean irradiance recorded at permanent sampling stations (Table 1).

Thermal biology

Pollinator taxa differed significantly in mean thoracic temperature (T_{th}) ($\chi^2 = 814.9$, df = 21, $P < 0.0001$). Species means ranged from 27.2°C in the syrphid fly *Sphaerophoria scripta* to 43.4°C in the large carpenter bee *Xylocopa violacea* (Table 2). T_{th} means of hymenopteran taxa were significantly higher than those of dipterans ($\chi^2 = 14.3$, df = 1, $P = 0.0002$), and there was almost no overlap between the ranges of the two groups (27.2–34.4°C for dipterans, 33.6–43.4°C for hymenopterans; Table 2).

Interspecific variation in mean T_{th} mainly reflected differences in thoracic temperature excess ($T_{exc} = T_{th} - T_a$ [=air temperature at the capture point]) (Figs 2–4; Table 2). T_{exc} means of hymenopteran taxa (Range = 5.3–17.3°C) significantly exceeded those of dipteran ones (Range = 4.9–9.8°C) ($\chi^2 = 8.05$, df = 1, $P = 0.0045$). Except for the smallest-sized bees (*Anthidium breviusculum*, *Ceratina* spp.), all hymenopterans had mean $T_{exc} > 10$°C, and several species had mean $T_{exc} > 15$°C (Table 2).

I regressed T_{th} against T_a separately for each pollinator taxon, and examined the range of variation in the T_{th}/T_a relationship occurring in the pollinator assemblage (Figs 2–4). The slope of regressions represents the amount of variation in T_{th} that is expected in response to a variation of 1°C in T_a. A zero slope would indicate complete independence of insect T_{th} with respect to T_a (equivalent to perfect temperature regulation), while a slope of unity would reflect that T_{th} changes perfectly with T_a. For comparative purposes, regression slopes may thus be used as rough indexes of thermoregulatory ability (e.g., Morgan and Heinrich 1987; potential limitations of this approach are considered in the Discussion). All T_{th}/T_a regressions have slopes significantly different from zero (Table 2). A nested ANCOVA was used to examine the significance of variation among orders (hymenopterans and dipterans) and among taxa (nested within orders) in regression slopes. There was significant heterogeneity of slopes both among orders ($F_{1,1130} = 31.1$, $P < 0.0001$)
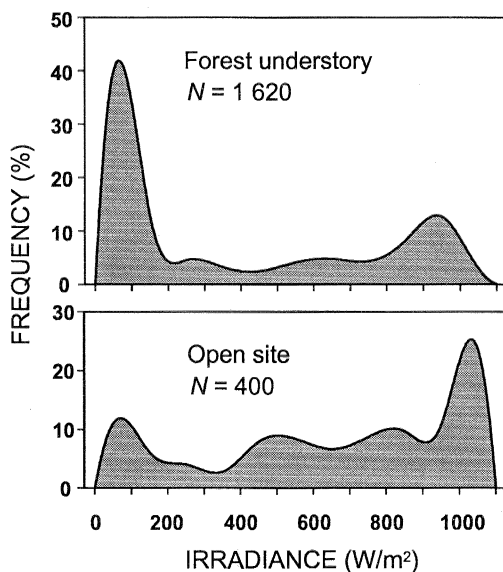

Fig. 1. Frequency distributions of dawn-to-dusk irradiance measurements at two nearby sites differing in vegetation structure. Measurements in the forest understorey site (where this study was conducted) were taken on several consecutive days at 60 permanent recording stations along a transect, while those at the open site (in the centre of a large forest clearing nearby) were taken at one point on a single date. N = number of measurements.

Table 2. Thoracic temperature (T_{th}), thoracic temperature excess ($T_{exc} = T_{th} - T_a$ [air temperature]), and the relationship between T_{th} and T_a, in the set of *Lavandula latifolia* pollinators considered in this study. Regressions of T_{th} vs T_a were fitted using the least squares method. Sample sizes as in Table 1.

Species	T_{th} (°C)		T_{exc} (°C)		Regression T_{th} vs T_a		
	Range	Mean ± SD	Range	Mean ± SD	F	P	Slope[1]
Hymenoptera							
Anthidium breviusculum	29.4–39.8	34.2 ± 3.0	1.7–16.2	6.9 ± 2.4	45.3	<0.001	0.669*
Anthidium florentinum	34.2–44.1	38.5 ± 2.4	6.7–17.5	12.4 ± 2.2	108.5	<0.001	0.542*
Anthophora albigena	35.7–41.7	39.3 ± 1.7	8.9–18.9	12.7 ± 2.6	14.1	0.0009	0.311*
Anthophora crassipes	32.6–41.6	38.5 ± 1.7	9.7–18.6	14.3 ± 2.2	34.6	<0.001	0.409*
Anthophora ochroleuca	33.1–43.9	39.7 ± 2.5	11.0–19.0	16.1 ± 2.0	24.7	<0.001	0.626*
Anthophora quadrifasciata	40.1–43.5	41.8 ± 1.1	11.0–19.2	15.6 ± 2.3	19.8	0.0008	0.282*
Apis mellifera	31.8–45.5	39.8 ± 3.0	6.8–21.4	15.6 ± 2.9	485.3	<0.001	0.512*
Bembix zonata	38.1–46.4	42.8 ± 2.0	9.8–19.3	15.5 ± 2.2	25.5	<0.001	0.449*
Bombus pascuorum	36.2–41.8	39.5 ± 1.3	9.6–19.7	15.8 ± 2.2	33.4	<0.001	0.303*
Bombus terrestris	34.3–44.5	39.8 ± 2.3	7.8–24.1	16.0 ± 3.0	54.9	<0.001	0.354*
Ceratina cyanea/mocsaryi	28.2–40.2	33.6 ± 2.8	0.8–11.2	5.3 ± 2.9	18.3	0.0001	0.491*
Megachile pilidens	31.5–42.0	37.8 ± 2.9	9.4–13.4	11.8 ± 1.4	28.9	0.0007	1.025
Xylocopa violacea	38.2–45.6	43.4 ± 1.8	12.3–21.7	17.3 ± 2.6	5.6	0.033	0.309*
Diptera							
Eristalis tenax	23.1–39.8	33.1 ± 3.4	3.8–16.1	8.9 ± 2.4	220.7	<0.001	0.725*
Milesia crabroniformis	25.5–37.3	33.3 ± 2.7	4.6–12.8	9.0 ± 2.1	24.0	<0.001	0.788
Nowickia ferox	27.1–39.7	34.4 ± 2.8	4.0–13.3	8.2 ± 2.1	89.5	<0.001	0.712*
Rhynchomya felina	25.6–36.9	31.3 ± 2.5	4.6–13.6	8.3 ± 1.9	95.2	<0.001	0.767*
Rhynchomya zernyana	24.8–34.0	28.6 ± 2.7	2.7–10.6	7.0 ± 2.0	20.3	0.0004	1.679
Sphaerophoria scripta	20.3–35.9	27.2 ± 4.1	0.6–9.2	5.0 ± 2.1	90.4	<0.001	1.053
Volucella elegans	28.6–38.4	33.0 ± 1.9	5.6–15.0	9.8 ± 1.9	26.3	<0.001	0.465*
Volucella inanis	24.6–34.2	29.6 ± 2.9	4.0–11.1	7.5 ± 2.2	15.6	0.0009	0.913
Volucella zonaria	27.6–35.1	31.7 ± 2.1	5.0–10.2	7.9 ± 1.6	9.8	0.012	0.687*

[1] Slope estimates marked with asterisks differ significantly from unity ($P < 0.05$).

and among taxa within orders ($F_{20,1130} = 2.8$, $P < 0.0001$). Hymenopterans were characterised by smaller regression slopes (Range = 0.282–1.025, Mean = 0.483 ± 0.026) than dipterans (Range = 0.465–1.679, Mean = 0.865 ± 0.345) (Table 2), which denotes a greater independence of T_{th} from T_a in the former group.

The effect of interspecific differences in body size on variation in the three thermal biology parameters considered here (T_{th}, T_{exc}, T_{th}/T_a regression slope) was tested using linear models with body length, its square (to account for potential nonlinearities), and insect order as independent variables. The three models were statistically significant (Table 3). After accounting for the effect of higher-level taxonomic affiliation, T_{th} and T_{exc}, but not the T_{th}/T_a regression slope, were significantly, positively related to body size (Fig. 5). Body size and insect order explained nearly 90% of interspecific variation in T_{th} and T_{exc}, and the relationship with the latter two variables was significantly nonlinear (Table 3). Within insect orders, both T_{th} and T_{exc} increased monotonically with body size, and large-sized taxa tended to have proportionally lower T_{th} and T_{exc} than small-sized ones (Fig. 5).

Correlates of microhabitat selection

To test the hypothesis that differential microhabitat choice by pollinators (with regard to irradiance) is

explained by differences in their thermal biology, MICP was entered as the dependent variable in a linear model that included mean T_{th}, mean T_{exc} and the slope of the T_{th}/T_a regression of individual species as independent variables. Insect order was also added as a covariate to account for the effects of taxonomic affiliation. Using MICP as the dependent variable is justified by the results reported above, showing that interspecific variation in this magnitude actually reflects habitat choice by pollinators (i.e., non-random usage of the irradiance gradient available).

With the exception of T_{th}/T_a slope (whose effect is only marginally significant), all the variables included have significant effects on MICP (Table 4), which demonstrates an association between thermal biology and microhabitat selection. After accounting for the influence of taxonomic affiliation on MICP, the latter is positively related to T_{th}, and negatively to T_{exc}. Fit of the data to the model was highly significant ($F_{4,17} = 16.80$, $P < 0.001$) and it explained most interspecific variation in MICP ($R^2 = 0.798$). Variation in T_{exc} was most influential, as it explained 37.7% of interspecific variance in MICP when the other effects were statistically accounted for. Insect order explained 28.3% of variance, and T_{th} only 9.6%.

As would be expected from the dependence of T_{th} and T_{exc} on body size, MICP is also size-dependent. MICP and body size are inversely correlated across species ($r_s = -0.483$, $N = 22$, $P = 0.023$), and the relationship
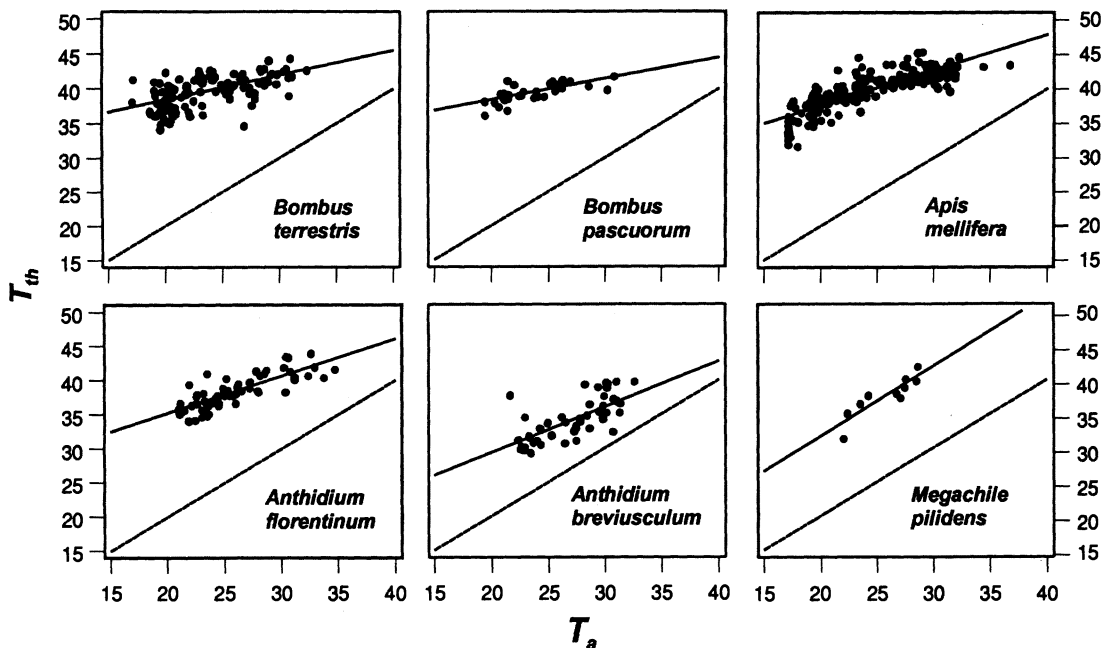
Fig. 2. Relationship between thoracic temperature (T_{th}) and air temperature (T_a) in bees of the families Apidae (top row) and Megachilidae (bottom row). Solid lines are least squares-fitted regressions, and broken lines represent $T_{th} = T_a$. See Tables 1 and 2 for sample sizes and regression parameters.

departs significantly from linearity (Fig. 5). With increasing body length, MICP decreases over the range 6–16 mm and subsequently increases. Nonlinearity is caused by the high MICP values of the three largest insects in the sample (*Xylocopa violacea*, Anthophoridae; *Bembix zonata*, Sphecidae; *Milesia crabroniformis*, Syrphidae). Interspecific variation in MICP is satisfactorily explained by a linear model that includes body length, its square, and insect order as independent variables ($F_{3,18} = 21.5$, $P < 0.001$, $R^2 = 0.781$).

Discussion

Microhabitat selection and thermal biology

Compared with an open habitat, the forest understorey study site was characterised by a bimodal distribution of irradiance levels, with contrasting sunlit and shaded conditions. The pollinators of *L. latifolia* considered in this study foraged differentially over that irradiance gradient. Dipterans tended to prefer situations of relatively low irradiance, whereas hymenopterans foraged over the whole gradient, and a large proportion of species (59%) selected situations of either higher or lower than average irradiance. An earlier study at the same site (Herrera 1995a) revealed evidence of irradiance-biased foraging for two bee species (*Anthidium breviusculum* and *Ceratina*), whereas no bias was found for four species (*Anthidium florentinum*, *Anthophora ochroleuca*, *Apis mellifera*, *Bombus terrestris*). Two of

the latter, however, were found in the present study to be significantly irradiance-selective. This contrasting result may be due to the larger sample sizes used here. Additional instances of significant microhabitat selection may have remained undetected due to insufficient sample size. Nevertheless, the proportion of irradiance-responsive taxa found here probably represents a good estimate of their actual frequency of occurrence in the pollinator assemblage, as the probability of detecting significant microhabitat selection for a given species did not depend significantly on its sample size ($\chi^2 = 0.471$, df = 1, $P = 0.49$; logistic regression).

All pollinators considered in this study visit *L. latifolia* flowers for nectar (some bees also visit for pollen), hence non-random foraging over the irradiance gradient might be related to predictable between-plant differences in nectar availability due to differential irradiance regime. This possibility, however, must be ruled out. At the study site, nectar standing crop (mean volume per flower) of *L. latifolia* plants was unrelated to their mean dawn-to-dusk irradiance ($r_s = -0.179$, $N = 15$ plants, $P = 0.52$; computed from data in Herrera 1995a; Appendix). Several lines of evidence indicate that differential use of the irradiance gradient by pollinators in this study reflects differences in thermoregulatory behaviour and limitations imposed by thermal biology.

There are many documented examples of insects actively seeking sun or shade to change body temperature, and short-term selection of sunny or shaded substrates is probably the most common mechanism for control of body temperature in insects (May 1979,
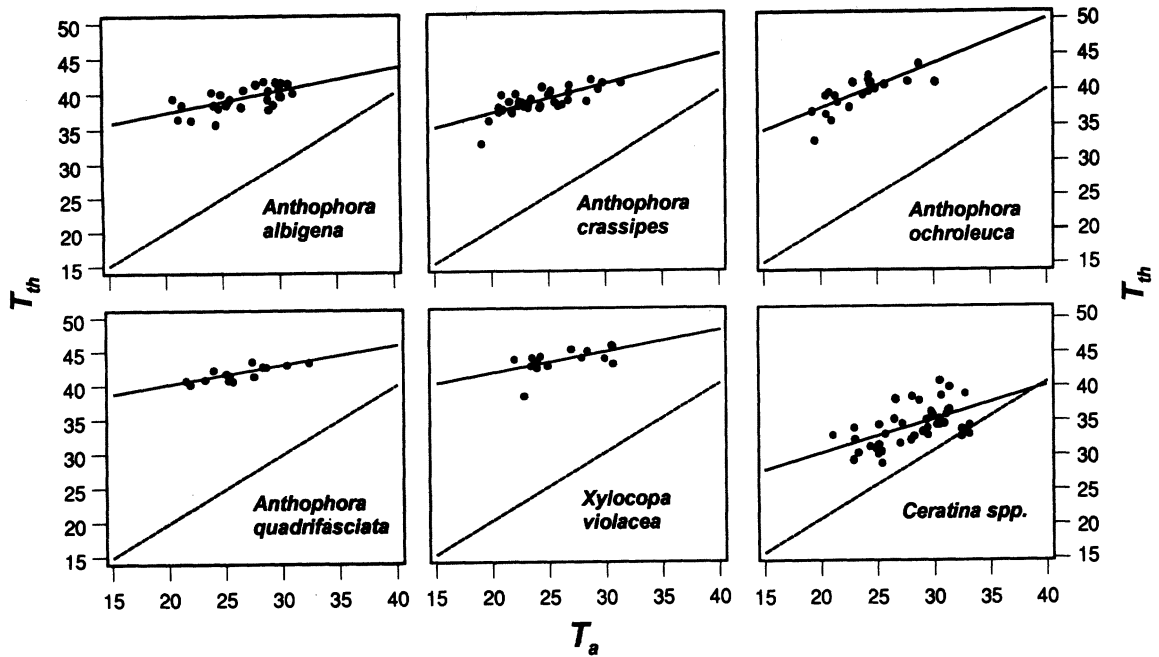
Fig. 3. Relationship between thoracic temperature (T_{th}) and air temperature (T_a) in bees of the family Anthophoridae. Solid lines are least squares-fitted regressions, and broken lines represent $T_{th} = T_a$. See Tables 1 and 2 for sample sizes and regression parameters.

Heinrich 1993). Furthermore, theoretical models predict that, in environments where solar irradiation is available, behavioural mechanisms (including microhabitat selection) are the most effective means of adjusting body temperature in ectotherms (Stevenson 1985). If the instances of microhabitat selection found in this study were a consequence, at least in part, of thermoregulatory behaviour, then irradiance-selective taxa should exhibit greater independence of T_{th} with respect to T_a than non-selective ones. This is supported by my results. On average, T_{th}/T_a regression slopes were significantly smaller for irradiance-selective (0.513 ± 0.194, $N = 13$) than for non-selective (0.822 ± 0.399, $N = 9$) taxa ($\chi^2 = 4.42$, df = 1, $P = 0.035$), suggesting that selectivity in microhabitat effectively resulted in improved thermoregulation. T_{th}/T_a regression slope has been customarily interpreted in terms of thermoregulatory ability (e.g., May 1976, May and Casey 1983, Baird 1986, Heinrich and Buchmann 1986, Morgan and Heinrich 1987, Stone and Willmer 1989a, Stone 1993), yet there are indications that the method may sometimes be inappropriate or lead to biased estimates (Stone and Willmer 1989b, Hertz et al. 1993). No data are available to evaluate the potential biases inherent to my estimates of T_{th}/T_a slopes, but these, if any, are not expected to be very influential on the results. Interspecific differences in T_{th}/T_a slopes found here, particularly the contrast between hymenopterans and dipterans, are consistent with predictions of differential thermoregulatory ability based on detailed field and laboratory studies of the same (e.g., *Apis mellifera*,

Bombus pascuorum, *B. terrestris*, *Bembix zonata*) or congeneric (*Anthophora, Megachile, Xylocopa, Nowickia, Eristalis*) species (Stone and Willmer 1989b, Heinrich 1993, Stone 1993, Ghazoul and Willmer 1994, and references therein).

As in other hot environments, heat stress most likely constrains insect activity in the Mediterranean summer and, all else being equal, the ability to withstand the heat load imposed by prolonged exposure to high irradiance will be directly proportional to the ability to forage at high thoracic temperatures (Chappell 1982, 1984, Cooper et al. 1985, Heinrich 1993, Polcyn 1994). Results of the present study are consistent with this interpretation, as a positive relationship exists between T_{th} and MICP when the effects of taxonomic affiliation, T_{exc} and T_{th}/T_a slope are statistically accounted for. Dipteran taxa (largely Syrphidae), which in this study were uniformly characterised by relatively low T_{th} (see also Heinrich and Pantle 1975, Willmer 1982, Gilbert 1984, Morgan and Heinrich 1987, for similar results), avoided high-irradiance conditions. Hymenopterans, in contrast, with intrinsically higher T_{th} (see also Stone and Willmer 1989b, Heinrich 1993, and references therein), tended to forage under conditions of greater insolation. In an assemblage of tropical robber flies (Asilidae), Shelly (1984) also found that shade-seeking taxa had lower T_{th} than sun-seeking ones.

After controlling for taxonomic differences and for the effects of T_{th} and T_{th}/T_a slope, MICP was negatively related to T_{exc}. This latter variable explained most variance in MICP, and was thus the most impor-
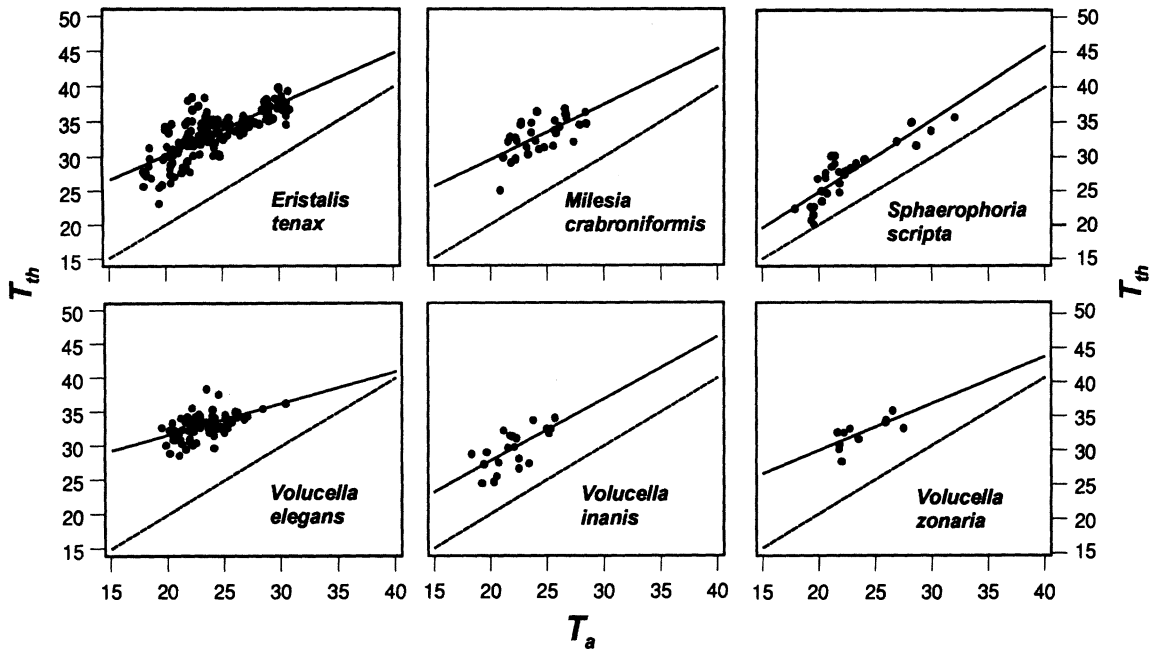
Fig. 4. Relationship between thoracic temperature (T_{th}) and air temperature (T_a) in flies of the family Syrphidae. Solid lines are least squares-fitted regressions, and broken lines represent $T_{th} = T_a$. See Tables 1 and 2 for sample sizes and regression parameters.

tant predictor of interspecific differences in microhabitat selection. Among bees, taxa with the smallest T_{exc} (e.g., small-sized, presumably ectothermic bees like *Anthidium breviusculum* and *Ceratina*) foraged only under high-irradiance conditions, while those with large T_{exc} (e.g., medium- to large-sized endotherms like *Bombus* and *Anthophora*) selected conditions of low irradiance. Within orders, T_{exc} increased steadily with body size, as has often been reported from comparative studies in both inter (Digby 1955, Stone and Willmer 1989b) and intraspecific (Stone 1993) contexts. This relationship must be attributed, among other factors, to the increase in warm-up rates and decrease in cooling rates that take place with increasing body size (Digby 1955, May 1976, Stone and Willmer 1989b).

For most species in the sample, MICP declines steadily with increasing body size and, with the exceptions noted below, MICP of a given pollinator may be reliably predicted from its body size alone. The negative relationship between MICP and body size may be explained by the positive effect of the latter on T_{exc}, and the negative effect of T_{exc} on MICP. The relationship between T_{exc} and body size departs, however, from linearity, and T_{exc} tends to increase more slowly as body size increases. This may help to explain why the relationship between MICP and body size is not linear, and the largest-sized insects in my sample (*Xylocopa*, *Bembix*, *Milesia*) foraged under higher irradiance conditions than would be predicted from a monotonically decreasing, linear relationship between MICP and body size. At least in *Xylocopa* and *Bembix*, the proportional

decline in T_{exc} is not due to behavioural avoidance of high irradiance, as they precisely select insolated conditions for foraging (this preference seems a characteristic of *Bembix* species; Schöne and Tengö 1992, Ghazoul and Willmer 1994). In *Xylocopa*, its proportionally low T_{exc} (relative to body size) is probably due to enhanced efficiency of physiologically based cooling mechanisms (Chappel 1982, Baird 1986, Heinrich and Buchmann 1986).

Potential implications of observed patterns

The main finding of this investigation is that interspecific differences in thermal biology generate predictable patterns of irradiance-biased microhabitat selection in the set of hymenopteran and dipteran pollinators of *L. latifolia* considered in this study. The inclusion of predominantly sun-seeking butterfly species in the species sample would presumably have enhanced these results still further. Body length and insect order, the two closest correlates of thermal biology, explained as much as 78% of interspecific variance in MICP in the species sample studied. A corollary following from this finding is that *L. latifolia* plants growing at different locations in the forest understorey and subject to different average irradiance regimes are expected to be exposed to pollinator assemblages differing in size structure and taxonomic composition, and previous results support this prediction (Herrera 1995a). On average, flowers on extensively insolated plants are expected to receive pro-

Table 3. Summary of linear models testing for the effects of body size (length) and insect order (Hymenoptera or Diptera) on thoracic temperature (T_{th}), thoracic temperature excess (T_{exc}) and slope of the T_{th}/T_a regression. $N = 22$ taxa.

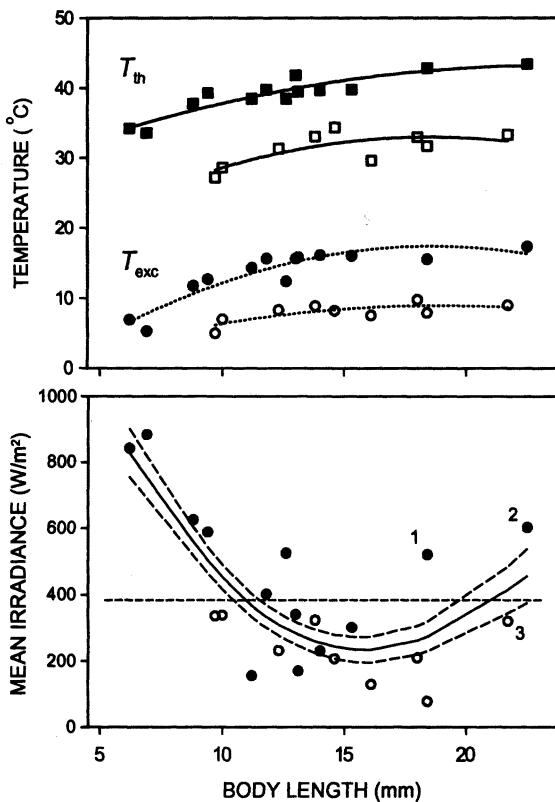| Effect	Dependent variable					
	T_{th}		T_{exc}		T_{th}/T_a slope	
	Regression parameter	P	Regression parameter	P	Regression parameter	P
Length	1.57	0.002	2.48	<0.001	−0.09	0.21
(Length)^2	−0.04	0.020	−0.07	0.0001	0.002	0.40
Insect order	–	<0.001	–	<0.001	–	0.0004
Significance of model						
F	67.05		49.83		6.84	
P	<0.001		<0.001		0.003	
R^2	0.918		0.893		0.533	

Fig. 5. Relationships between mean body length, thoracic temperature (T_{th}), thoracic temperature excess (T_{exc}), and mean irradiance at capture points, in the set of insect pollinators studied (filled symbols, hymenopterans; open symbols, dipterans). Upper graph: Variation of T_{th} (squares, solid lines) and T_{exc} (circles, dotted lines) with body length. Lines are least squares-fitted quadratic regressions (see Table 3 for analytical results). Lower graph: Regression line (continuous line) was fitted using a nonparametric, generalised cross-validation method (Schluter 1988). Dashed lines indicate ±1 SE of predicted values from 10 000 bootstrap regression replicates. Mean irradiance at permanent recording stations is shown also for reference (horizontal dashed line). The three data points corresponding to the largest-sized pollinators in the sample and responsible for the nonlinearity of the relationship, are individually identified: 1, *Bembix zonata* (Sphecidae); 2, *Xylocopa violacea* (Anthophoridae); 3, *Milesia crabroniformis* (Syrphidae).

Table 4. Summary of the results of a linear model testing simultaneously for the effect on mean irradiance at capture points of mean thoracic temperature (T_{th}), mean thoracic temperature excess (T_{exc}), slope of the regression of T_{th} against air temperature (T_a), and insect order (Hymenoptera or Diptera).

Effect	Regression parameter	F	P
T_{th}	69.44	11.52	0.003
T_{exc}	−93.81	31.25	<0.001
T_{th}/T_a slope	209.05	3.52	0.078
Insect order	–	10.08	0.006

portionally more visits of small-sized bees, while flowers on extensively shaded plants will be more extensively visited by dipterans and large bees.

Irradiance-biased foraging of pollinators found in this study (see also Beattie 1971) may have implications beyond the within-habitat spatial scale, as the same thermal constraints that operate within the forest understorey may also give rise to seasonal and between-habitat differences in the size structure and composition of pollinator assemblages. A testable prediction is that, during the hot Mediterranean summer, dipteran and/or large pollinators would be overrepresented in wooded habitats that provide "thermal refuges" (in the form of shaded understorey patches), whereas small pollinators would be overrepresented in open habitats that are subject to uniformly high-irradiance conditions. Similarly, small bees would be predicted to prevail during summer in open, extensively insolated habitats. As predicted, mean body size of bees decreases seasonally to a minimum during summer in Mediterranean scrublands of Israel, and almost all summer-active species are small-sized (Shmida and Dukas 1990). This pattern was interpreted in terms of size-related thermal constraints, and results of this study support that interpretation.

The pollinators of *L. latifolia* differ in flower visitation rate, proportion of visits resulting in pollen delivery to the stigma, amount of pollen deposited and removed per floral visit, and flight distance between

consecutive flower visits, and some of these differences are predictably related to body size and taxonomic affiliation (Herrera 1987a, b, 1989, unpubl.). On average, bee taxa deposit more pollen, and more frequently, on the stigma of visited flowers, and fly shorter distances between consecutive flower visits, than dipterans. Within orders, there is also a trend for larger insects to deliver more pollen and more frequently than smaller ones. Analogous differences between pollinator taxa in aspects of pollinating effectiveness have been reported from numerous plant species, and these differences often are also associated with variation in body size and taxonomic affiliation (e.g., Motten et al. 1981, Schemske and Horvitz 1984, Herrera 1987a, Wolfe and Barrett 1989, Eckhart 1992, Harder and Barrett 1993). Within- and between-habitat variations in pollinator composition generated by thermal limitations should thus not be dismissed a priori as inconsequential for plant reproduction, and further studies should be undertaken to assess the magnitude and predictability of their consequences. The abiotic determinants of plant–pollinator interactions in thermally unfavourable habitats is a relatively neglected field of study that certainly deserves more attention than it has received so far (Herrera 1995b).

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