

Components of pollinator “quality”: comparative analysis of a diverse insect assemblage

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A total of 34 floral visitors of *Lavandula latifolia* (Labiatae) at a southern Spanish locality were examined from the perspective of their “quality” as pollinators. I considered frequency of pollen transfer, number of pollen grains deposited on the stigma, selection of floral sexual stage (flowers are markedly protandrous), and patterns of flight distance between flowers. Hymenoptera deposited more pollen and more often than Lepidoptera or Diptera. The latter two groups did not differ in this respect. Interspecific variation in frequency of pollen delivery depended on differences in proportional visitation to female-stage (receptive) flowers as well as total pollen delivery to these flowers. Lepidoptera tended to fly longer distances between consecutive flowers than Hymenoptera. Hand-pollination experiments demonstrate that variation among floral visitors in reproductive services rendered may translate into differential fitness of *L. latifolia* plants. Nevertheless, the potential for plant specialization on specific insects is constrained by counterbalancing variation in components of pollination quality.

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1. Introduction

1.1. General

From the perspective of its evolutionary implications, the “intensity” of an ecological interaction between two species is proportional to its frequency of occurrence multiplied by the magnitude of its fitness consequences when it occurs. These two factors roughly correspond to “quantity” and “quality” components, respectively (Herrera and Jordano 1981, Waser and Price 1983, Schemske 1983). This is particularly relevant in the context of certain plant-animal interactions (plant-pollinator, plant-disperser) that have been often analyzed from a coevolutionary perspective (Wheelwright and Orians 1982, Howe 1984, Herrera 1985, and references therein). For coevolution to occur between a plant and some of the animal species with which it interacts for pollination or seed dispersal, it is necessary (although not sufficient) that species in the array differ in the strength of their respective interactions with the plant.

In plant-pollinator systems, differences between pol-

len vectors with regard to the “quantity” component have been evaluated frequently. Pollinator censuses coupled with observations on flower visitation rates, have produced substantial information on differential frequencies of interaction between given pollinator and plant species. The “quality” component, i.e., differences in pollinator effectiveness, has received less attention, even though it is generally acknowledged as an important precondition for mutualism specialization (Schemske and Horvitz 1984 present a review up to that date). In this paper, I examine from this perspective a major fraction of the diverse insect assemblage visiting the flowers of *Lavandula latifolia* (Labiatae) in a southern Spanish locality. Data for 34 flower visitors, including wasp, bee, fly, moth and butterfly species, are presented (Fig. 1). The study is restricted to components of pollinator quality on a per caput basis, disregarding interspecific differences in abundance, flower visitation rates, and variation of these among seasons and years. These latter aspects, all related to the “quantity” component, will be considered in a separate paper. I analyze

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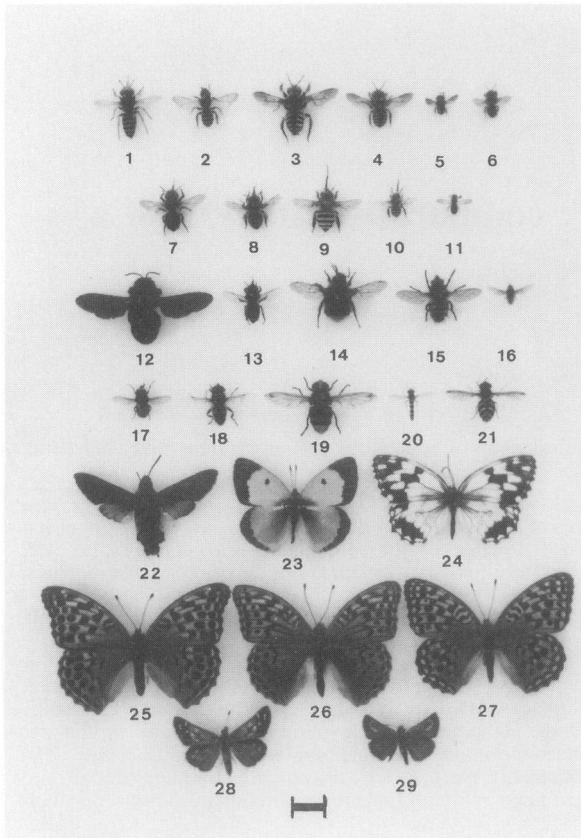


Fig. 1. Insect visitors to *Lavandula latifolia* flowers considered in this study, illustrating the taxonomical and morphological diversity represented (see Tab. 2 for a complete list of species and further details). 1, *Bembix zonata*; 2, *Halictus* sp. (aff. *scabiosae*); 3, *Anthidium florentinum* male; 4, *A. florentinum* female; 5, *Anthidiellum brevisculum*; 6, *Megachile pilidensis*; 7, *Megachile* sp. (aff. *lagopoda*); 8, *Anthophora crassipes*; 9, *A. ochroleuca*; 10, *A. albigena*; 11, *Ceratina* sp.; 12, *Xylocopa violacea*; 13, *Apis mellifera*; 14, *Bombus lucorum*; 15, Tachinidae gen. sp.; 16, *Systoechus* sp.; 17, Calliphoridae gen. sp.; 18, *Eristalis tenax*; 19, *Volucella zonaria*; 20, *Sphaerophoria scripta*; 21, *Chrysotoxum intermedium*; 22, *Macroglossum stelarum*; 23, *Colias crocea*; 24, *Melanargia galathea*; 25, *Argynnis paphia*; 26, *Pandoriana pandora*; 27, *Fabriciana adippe*; 28, *Hesperia comma*; 29, *Thymelicus acteon*. Scale bar is 1 cm long.

here interspecific differences in frequency of pollen transfer, size of pollen loads delivered on stigmas, selection of floral sexual stage by insect foragers, and patterns of flight distance between flowers.

1.2. Components of pollinator "quality"

Holding the product abundance \times activity at flowers constant, one pollinator may be "better" than another for one or several of the following reasons:

1) It delivers pollen more often to the stigma of visited flowers (Motten et al. 1981, Motten 1983, 1986, Schemske and Horvitz 1984). In the case of a dichogamous hermaphroditic plant like *L. latifolia*, this may be

accomplished through greater frequency of pollination when it visits female-stage (receptive) flowers, and/or greater proportional visitation to female-stage flowers.

2) When pollen delivery occurs, a greater number of pollen grains are left on the stigma (Arnold 1982a, Bertin 1982, Motten 1983). Increased number of pollen grains will have a direct influence on the maximum number of ovules potentially fertilized (Snow 1982, McDade 1983, McDade and Davidar 1984, Shore and Barrett 1984), but may also have an indirect effect via improved pollen germination and/or pollen tube growth (Jennings and Topham 1971, Schemske and Fenster 1983, Mulcahy et al. 1983, Cruzan 1986).

3) The pollen it delivers is consistently "better" from the viewpoint of the maternal plant, as in the obvious case of predominantly non-self pollen loads in a self-incompatible species. More generally, however, pollinator foraging behaviour may influence the quality of the pollen delivered to stigmas through its effects on average distance from the mother plant to the pollen source, and the number of pollen donors represented in the load (Price and Waser 1979, Waser and Price 1983, Bookman 1984, Schemske and Pautler 1984, Vander Kloet and Tosh 1984). These factors may not only influence seed set, but also seed size, germination, and seedling success (Price and Waser 1979, Waser and Price 1983, Schemske and Pautler 1984, Vander Kloet and Tosh 1984).

In addition to analyzing interspecific variation in each of these components of pollinator quality, this paper also examines covariation of quality components across species and higher categories of pollinators. Covariation of these factors may either constrain or enhance the possibilities of plant specialization on particular pollinators. The reduced number of visitors considered in earlier studies has precluded any analysis of the patterns of covariation of quality components across taxa.

2. Methods

Most of the data used here were obtained in the summers of 1985 and 1986 at a *Lavandula latifolia* population growing around the intersection of Arroyo Aguaderillos and the track joining Roblehondo and Hoyos de Muñoz in the Sierra de Cazorla, Jaén province, south-eastern Spain. Each year, 1 \times 1 \times 1 m insect enclosures (made of wooden frames and 0.75 mm mesh size plastic netting) were placed on each of five plants in early July, just before the start of flowering for the population, and held in place throughout the flowering season (July–October). Enclosures precluded access of all floral visitors, as demonstrated by frequent checks over the entire flowering seasons. Every few days from mid-July through mid-August, one of the enclosures was removed and the enclosed plant watched at close range. Any insect coming to flowers was allowed to visit 1–2 individual flowers, and then chased away. The flowers visited were immediately removed and placed in small

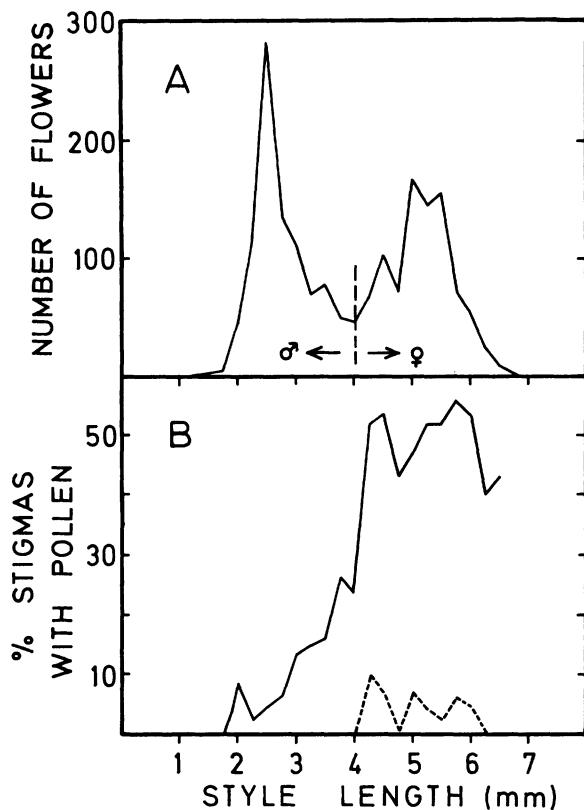


Fig. 2. A. Frequency distribution of style length in the sample of flowers studied ($N=1799$; control and insect-visited flowers combined). Styles <4.0 mm correspond to male-stage, those >4 mm to female-stage receptive flowers (see text). B. Variation in the probability of pollen deposition with style length. Flowers were grouped into 0.25 mm classes of style length, and the proportion of stigmas with pollen computed for each class. Continuous line insect-visited, broken line control flowers.

glass vials. Separate vials were used for different pollinator species or, in the case of *Anthidium florentinum*, for different sexes. At the end of every observation session (usually 3–4 h), a sample of unvisited flowers was taken as a control, and the enclosure replaced on the plant. Total number of flowers collected per session (visited and unvisited) was always small relative to the total number of flowers open on the plant at the time. Within 2–4 h of the end of observations, collected flowers were dissected individually, the style removed and measured (to the nearest 0.25 mm), and the number of pollen grains on the stigma counted under a dissecting microscope. The contrasting stigma (blue) and pollen (yellow) colors made counts reliable without staining or fixation. A total of 1374 insect-visited and 425 control flowers were examined, collected over 69 observation hours. Only *L. latifolia* pollen was recorded on the stigmas examined.

Data were not obtained on the translation of pollen delivery into seed output. The methods needed for

flower collection in the field, so that pollen loads could be scored, made this impractical.

In 1985 and 1986 hand-pollination was done to determine differential effectiveness of pollen coming from sources at various distances from the mother plant. In mid-August, virgin flowers inside the enclosures were hand-pollinated using pollen from five different sources: the same plant (selfing), the two nearest neighbours (usually 2–3 m away), and plants growing at 250 m, 3.0 km (Arroyo de los Ubios) and 3.5 km (Cuevas Bermejas). Control flowers (no pollination) were also marked at that time. Mature fruits were collected in early October and the number and individual mass of seeds determined (to the nearest 0.1 mg).

Detailed observations on the foraging behaviour of pollinators were conducted in the summers of 1982–1984. Only data related to distances moved between consecutive flower visits are used here.

3. Results

3.1. Floral biology

Lavandula latifolia is a low evergreen shrub (up to 3 cm high) producing long-stalked (up to 1.25 m high) inflorescences in early summer. Flowers are hermaphroditic, protandrous, have pale-blue tubular corollas (tube length 7–8 mm), and are produced over a short (3–6 cm) terminal portion of the stalks according to a dichasium-like arrangement (Devesa et al. 1985). During the first 1–2 d after flowers open, the anthers liberate pollen, while the stigma remains hidden within the tube and is not receptive. Nectar secretion is negligible in this period. The transition from male to female stage is abrupt, with rapid elongation of the style, modification of stigma shape, and initiation of moderate stigmatic secretion and substantial nectar production at the corolla base. Usually by this time no pollen remains in the anthers.

The rapid transition from male to female stages produces clear differentiation of most open flowers in the population into either functionally male or female (Fig. 2A). Styles under 4.0 mm length correspond to male, and those above that length to female. Changes in floral morphology are paralleled by modification of stigma receptivity. The peroxide test was used to detect stigmatic surface activity (and thus presumably receptivity; Arnold 1982b). It yielded positive results in 96.3% of flowers with styles >4.5 mm long ($N=27$), 41.7% with styles 3.5–4.5 mm long ($N=12$), and none with styles <3.5 mm long ($N=26$) ($P < 0.0001$, Exact Test of Wells and King 1980). Flower visitors most often transfer pollen to receptive stigmas of female-stage flowers, and only infrequently to unreceptive stigmas of male-stage ones (Fig. 2B). For both insect-visited and unvisited (control) flowers, a sharp increase in the probability of pollen de-

Tab. 1. Summary of hand pollination results with *Lavandula latifolia*. Means are shown \pm 1 SD (sample sizes in parentheses). Figures in the same column sharing a superscript do not differ statistically ($P > 0.05$; G-test for frequencies, Student-Newman-Keuls test for means).

Pollen source	% Flowers setting seed	Seeds set ¹ /fruit	Average seed mass (mg)
Control ²	3.7 ^a (460)	1.1 \pm 0.3 ^a (17)	1.5 \pm 0.4 ^a (19)
Selfed	11.2 ^b (412)	1.5 \pm 0.5 ^b (46)	1.4 \pm 0.4 ^{a,b} (70)
Crossed: ³			
2–3 m	17.5 ^c (406)	1.6 \pm 0.5 ^b (71)	1.4 \pm 0.4 ^{a,b} (110)
250 m	18.3 ^c (350)	1.5 \pm 0.6 ^b (64)	1.3 \pm 0.4 ^b (98)
3000 m	19.6 ^c (367)	1.7 \pm 0.7 ^b (72)	1.5 \pm 0.4 ^a (118)
3500 m	18.3 ^c (361)	1.6 \pm 0.7 ^b (66)	1.3 \pm 0.4 ^b (106)

¹ Computed for flowers actually setting seed (zeros excluded). Maximum potential seeds/flower is 4.

² Unpollinated.

³ Pollen from plants at various distances (see Methods).

position occurs beyond 4.0 mm, the start of the female phase. No pollen was ever observed on unvisited flowers with styles < 4.25 mm ($N=233$), while it was present on 10.0% of stigmas of insect-visited flowers in this category ($N=698$, all visitors combined). In contrast, 5.7% (control, $N=192$) and 52.2% (visited, $N=676$) of longer styles had some pollen on the stigma.

Results of hand pollinations of virgin flowers within exclosures are summarized in Tab. 1. *L. latifolia* flowers are self-compatible, but a pollen vector is required to effect pollination (see also Fig. 2B). Unpollinated flowers have negligible fruit set (3.7%). This figure does not differ from the 2.6% of virgin flowers within exclosures ($N=425$) which showed pollen on the stigma without insect visit ($G=0.89$, $P=0.12$). Fruit set of cross-pollinated flowers significantly exceeded that of selfed flowers (pollen from other flowers on the same plant). Among cross-pollen treatments, distance to the pollen source did not significantly influence fruit set. Among flowers setting fruit, mean number of seeds produced by selfed and crossed flowers were similar, and greater than that produced by unpollinated (control) ones. Although there were some statistically significant differences between treatments in mean seed mass, the absolute magnitude of the variation was small. In short, cross-pollen (regardless of distance to source) increased the percent of flowers setting fruit relative to self-pollen, but did not significantly modify either the mass of individual seeds produced or the number of seeds per fruit.

3.2. Pollinator effectiveness

The proportion of visited flowers receiving some pollen on the stigma ("pollinator effectiveness", PE hereafter) is shown in Tab. 2 for the 34 floral visitors considered. Comparisons with control (unvisited) flowers were statistically significant for 27 (79.4%) of these visitors, thus indicating that they were effective pollen vectors of *L. latifolia*. The activity at flowers of the remaining 7 visitors (3 flies and 4 butterflies) did not significantly increase the percentage of stigmas with pollen above the level of unvisited flowers. All Hymenoptera were effective pollinators.

PE ranges for significant bee and wasp (12.7–69.6%), fly (11.4–24.3%), and butterfly and moth (11.3–40.0%) pollinators denote broad variation both between and within these three major categories. Among bees, female *Anthidium florentinum* (69.6%), *Bombus lucorum* (66.7%) and *Megachile* sp. (aff. *lagopoda*) (65.2%), had the highest PE values, roughly corresponding to an average of 2 successful pollen transfers every 3 visits. Among Lepidoptera, the highest PE's were exhibited by *Pandoriana pandora* (40.0%), *Macroglossum stellatarum* (33.3%), "other Satyridae" (31.6%) and *Fabriciana adippe* (30.7%), thus an average of 1 successful pollen transfer every 3 visits. Among flies, the highest PE's were shown by *Eristalis tenax* (24.3%) and *Volucella* spp. (18.6%), hence an average of 1 pollen transfer every 4–5 visits. There was significant heterogeneity among groups in PE ($H=17.44$, $df=2$, $P=0.0002$, Kruskal-Wallis analysis of variance). This is due to the significantly larger values for bees and wasps compared with the other two groups combined ($H=17.21$, $df=1$, $P<0.001$). Flies and Lepidoptera did not differ significantly ($H=0.40$, $df=1$, $P=0.52$). Despite the significance of the difference between Hymenoptera and Diptera-Lepidoptera combined, there is considerable overlap within the lowest section of the PE range (Tab. 2). The most reliable pollinators (as assessed with PE), therefore, were invariably bees, but the least reliable ones belonged to either group. The large nymphalids, *P. pandora*, *Argynnis paphia* and *F. adippe*, for instance, had PE values exceeding those of the smallest megachilid bees (*Anthidiellum*), and some flies had values comparable to those of the smallest megachilid and anthophorid (*Ceratina*) bees (Tab. 2).

A few taxonomic patterns in PE are apparent within major groups. Among butterflies, Pieridae and Lycaenidae were not significant pollinators, the three Nymphalidae were the most significant pollen vectors, and the Satyridae and Hesperidae were intermediate. Among flies, three out of four significant pollinators were in the Syrphidae. Family-level patterns were not apparent among bees, where PE ranges for the major families (Megachilidae, Anthophoridae) were roughly similar.

Tab. 2. Frequency of pollen deposition on stigmas of virgin *Lavandula latifolia* flowers after single insect visits (= “pollinator effectiveness”), selection of sexual stages by pollinators, and pollination rate of receptive flowers.

	Pollinator effectiveness		Components of effectiveness			
	Percent pollinated (N)	Diff. ¹ with control	Sexual stage selection			% Females pollinated
			Percent females visited	Diff. ¹ with control	Sex stage favored	
Hymenoptera:						
<i>Bembix zonata</i> (Sphecidae)	40.0(10)	14.9***	40.0	0.1 ^{n.s.}		75.0
<i>Halictus</i> sp. (aff. <i>scabiosae</i>) (Halictidae)	54.5(11)	26.4****	72.7	3.3(*)	(F)	62.5
<i>Anthidium florentinum</i> (Megachilidae)						
Males	50.0(34)	61.6****	55.9	1.5 ^{n.s.}		84.2
Females	69.6(56)	150.1****	53.6	1.4 ^{n.s.}		93.3
<i>Anthidiellum brevisculum</i> (Megachilidae)	12.7(63)	10.5**	20.6	14.6***	M	61.5
<i>Megachile pilidens</i> (Megachilidae)	45.2(31)	49.0****	54.8	1.1 ^{n.s.}		76.5
<i>Megachile</i> sp. (aff. <i>lagopoda</i>) (Megachilidae)	65.2(46)	117.0****	63.0	5.3*	F	93.1
<i>Anthophora crassipes</i> (Anthophoridae)	41.2(17)	25.4****	41.2	0.1 ^{n.s.}		100.
<i>Anthophora ochroleuca</i> (Anthophoridae)	39.3(28)	36.4****	46.4	0.02 ^{n.s.}		69.2
<i>Anthophora albigena</i> (Anthophoridae)	54.9(51)	97.5****	66.7	8.5**	F	76.5
Other <i>Anthophora</i> ² (Anthophoridae)	23.8(21)	12.8****	52.4	0.4 ^{n.s.}		36.4
<i>Ceratina</i> spp. ³ (Anthophoridae)	18.3(82)	25.0****	63.4	9.2**	F	23.1
<i>Xylocopa violacea</i> (Anthophoridae)	50.0(30)	55.6****	53.3	0.8 ^{n.s.}		75.0
<i>Apis mellifera</i> (Apidae)	44.6(148)	146.7****	48.6	0.5 ^{n.s.}		75.0
<i>Bombus lucorum</i> (Apidae)	66.7(12)	38.9****	50.0	0.1 ^{n.s.}		100.
Diptera:						
<i>Systoechus</i> nov. sp. (?) (Bombyliidae)	0.0(13)	0.7 ^{n.s.}	15.4	5.1*	M	0.0
Tachinidae gen. sp.	7.7(13)	0.9 ^{n.s.}	30.8	1.1 ^{n.s.}		0.0
Calliphoridae gen. sp.	16.3(49)	13.8***	67.3	8.8**	F	24.2
<i>Eristalis tenax</i> (Syrphidae)	24.3(37)	21.6****	62.2	4.0*	F	39.1
<i>Volucella</i> spp. ⁴ (Syrphidae)	18.6(59)	20.1****	57.6	3.3(*)	(F)	32.4
<i>Sphaerophoria scripta</i> (Syrphidae)	11.4(35)	5.2*	48.6	0.2 ^{n.s.}		23.5
<i>Chrysotoxum intermedium</i> (Syrphidae)	6.9(29)	1.4 ^{n.s.}	55.2	1.1 ^{n.s.}		12.5
Lepidoptera:						
<i>Macroglossum stellatarum</i> (Sphingidae)	33.3(42)	39.4****	40.5	0.3 ^{n.s.}		64.7
<i>Colias crocea</i> (Pieridae)	0.0(11)	0.6 ^{n.s.}	18.2	3.5(*)	(M)	0.0
Other Pieridae ⁵	11.8(17)	2.9 ^{n.s.}	41.2	0.1 ^{n.s.}		28.6
<i>Melanargia galathea</i> (Satyridae)	12.2(41)	6.8**	46.3	0.02 ^{n.s.}		21.1
Other Satyridae ⁶	31.6(19)	18.5****	52.6	0.4 ^{n.s.}		40.0
<i>Argynnis paphia</i> (Nymphalidae)	23.8(42)	23.1****	40.5	0.3 ^{n.s.}		29.4
<i>Pandoriana pandora</i> (Nymphalidae)	40.0(15)	21.7****	60.0	1.3 ^{n.s.}		55.6
<i>Fabriciana adippe</i> (Nymphalidae)	30.7(127)	76.7****	40.2	1.0 ^{n.s.}		56.9
Lycaenidae ⁷	5.9(17)	0.5 ^{n.s.}	35.3	0.7 ^{n.s.}		16.7
<i>Hesperia comma</i> (Hesperiidae)	11.3(62)	8.2**	38.7	0.9 ^{n.s.}		25.0
<i>Thymelicus acteon</i> (Hesperiidae)	17.4(92)	24.9****	51.1	1.1 ^{n.s.}		27.7
Other Hesperiidae ⁸	0.0(14)	0.7 ^{n.s.}	50.0	0.1 ^{n.s.}		0.0

¹ G-statistic and significance level; n.s., not significant; (*), 0.05<P<0.07; *, P<0.05; **, P<0.01; ***, P<0.001; ****, P<0.0001. F, female-, M, male-stage favored.

² Mostly *Anthophora quadrifasciata*.

³ Includes *C. cyanea* and *C. mocsaryi*.

⁴ Includes *V. elegans*, *V. zonaria* and *V. inanis*.

⁵ Includes *Gonepteryx* spp., *Pontia daplidice* and *Pieris rapae*.

⁶ Includes *Lasiommata megera*, *Pyronia* spp. and *Hyponephele* sp.

⁷ Includes *Lysandra albicans*, *Plebicula escheri* and *Syntharucus pyrithous*.

⁸ Includes *Spialia sertorius* and *Pyrgus* sp.

3.3. Components of pollinator effectiveness

Overall effectiveness at pollen transfer depends on the frequency of visitation to female-stage receptive flowers, and the frequency of pollen deposition when receptive flowers are visited.

Flowers were assigned to either male or female stages

on the basis of style length (Fig. 2A). Control (unvisited) flowers were 45.2% in female-, and 54.8% in male-stage, proportions not differing significantly from 1:1 ($G=1.98$, $P=0.16$). The proportional representation of sexual stages in the samples of insect-visited flowers is shown in Tab. 2 for all floral visitors. Seven species visited sexual stages in proportions departing signifi-

Tab. 3. Statistics for pollen loads deposited on *Lavandula latifolia* stigmas after single insect visits, and distances moved by floral visitors between consecutive flower visits. For pollen loads, only data for stigmas receiving some pollen, and pollinators with frequency of pollination significantly departing from control (Tab. 2), are considered. Species with insufficient sample sizes for distance analyses (N<30) are omitted. N = sample size, CV = coefficient of variation, SD = standard deviation, SE = standard error.

	Size of pollen loads (Number of grains)				Flight distance				
	N	Mean	Range	CV	N	Mean ± SD (cm)	% of flights		Kurtosis (g ₂ ± SE)
							<10 cm	>160 cm	
Hymenoptera:									
<i>Bembix zonata</i>	4	10.5	1-23	92.5	177	37±102	28.8	2.3	61.1±0.4
<i>Halictus</i> sp. (aff. <i>scabiosae</i>)	6	37.7	5-130	124.2					
<i>Anthidium florentinum</i>									
Males	17	17.6	3-56	85.2	144	61±98	27.1	11.8	5.1±0.4
Females	39	17.2	1-85	98.8	325	23±40	52.0	2.5	23.0±0.3
<i>Anthidiellum brevisculum</i>	8	10.4	3-22	77.3	124	43±105	37.1	3.2	66.5±0.4
<i>Megachile pilidens</i>	14	21.1	1-125	157.4	69	25±24	28.9	0	4.9±0.6
<i>Megachile</i> sp. (aff. <i>lagopoda</i>)	30	34.4	2-91	78.5					
<i>Anthophora crassipes</i>	7	27.1	2-95	124.1	41	23±31	46.3	2.4	13.3±0.7
<i>Anthophora ochroleuca</i>	11	26.5	2-72	103.2	209	17±34	59.8	0.5	131.7±0.3
<i>Anthophora albigena</i>	28	16.9	2-85	112.9					
Other <i>Anthophora</i>	5	17.8	3-45	98.7					
<i>Ceratina</i> spp.	15	8.3	1-26	84.5	30	49±85	33.3	10.0	3.9±0.8
<i>Xylocopa violacea</i>	15	18.1	2-56	106.4	264	65±163	28.4	10.2	84.2±0.3
<i>Apis mellifera</i>	66	27.4	1-130	102.4	301	21±34	46.5	1.0	54.4±0.3
<i>Bombus lucorum</i>	8	26.4	3-55	89.0	485	23±45	50.1	1.6	51.6±0.2
Diptera:									
<i>Systoechus</i> nov. sp. (?)					41	18±16	48.8	0.	0.7±0.7
Calliphoridae gen sp.	8	4.0	1-15	126.0					
<i>Eristalis tenax</i>	9	15.9	1-65	138.2	105	32±57	38.1	3.8	14.6±0.5
<i>Volucella</i> spp.	11	11.4	1-38	120.4	214	72±110	19.1	13.1	12.4±0.3
<i>Sphaerophoria scripta</i>	4	12.3	1-37	139.1					
Lepidoptera:									
<i>Macroglossum stellatarum</i>	14	7.4	1-26	90.6	575	28±55	46.6	2.1	46.9±0.2
<i>Colias crocea</i>					190	74±148	20.0	7.9	21.4±0.4
<i>Melanargia galathea</i>	5	7.0	1-17	94.7	97	110±216	15.4	15.5	20.9±0.5
Other Satyridae	6	6.0	1-19	112.5					
<i>Argynnis paphia</i>	10	2.3	1-7	79.6	120	168±242	15.0	28.3	-0.7±0.4
<i>Pandoriana pandora</i>	6	11.0	1-20	84.1	143	159±329	7.0	21.0	22.6±0.4
<i>Fabriciana adippe</i>	39	8.2	1-42	123.6	134	95±204	14.9	12.0	10.2±0.4
<i>Hesperia comma</i>	7	14.0	1-41	99.6	105	88±122	19.1	18.1	0.9±0.5
<i>Thymelicus acteon</i>	16	9.7	1-35	95.9	81	44±88	35.8	4.9	17.3±0.5
Other Hesperidae					58	92±163	10.3	13.8	18.6±0.6

cantly from those observed among control flowers, and another 3 species had marginally significant differences with respect to controls (these are also included here among "sex-selective" visitors). No significant bias with regard to sexual stage was observed for the remaining 24 visitors. Seven species (4 bees, 3 flies) tended to select preferentially flowers in female stage, while 3 (1 bee, 1 fly, 1 butterfly) showed the opposite preference. *Ceratina* spp. (63.4% female flowers) and Calliphoridae gen. sp. (67.3%) in the first group, and *Anthidiellum brevisculum* (20.6%) in the second, represent the most extreme cases. Sex-selective visitors tend to be more frequent among Hymenoptera and Diptera than among Lepidoptera (G=3.81, df=1, P=0.05; the first two groups combined compared with Lepidoptera).

Interspecific differences in frequency of pollination of female-stage flowers (Tab. 2) in general parallel those reported earlier for PE, and are not discussed further here.

The relative importance of the proportion of visits to female flowers (%FV) and the proportion of these which are pollinated (%FP) in explaining interspecific variation in overall pollinator effectiveness (PE) was examined by multiple regression (PE the dependent variable, %FV and %FP the independent ones). The regression is highly significant (F=141.6, df=2,31, P<<0.001), and the two independent variables contribute significantly (F=185.9 and 15.1 for %FP and %FV, respectively). The percent increases in R² contributed by each variable differ widely: 85.3% for %FP, 4.8%

Tab. 4. Spearman rank correlation coefficients between variables influencing pollinator quality. PE = pollinator effectiveness; APL = average number of pollen grains deposited on the stigma; AFD = average flight distance (see text for further details). N = sample size; n.s., nonsignificant ($P>0.10$); *, $P<0.05$; **, $P<0.01$; ***, $P<0.001$.

	Variables correlated	Rank correlation	N
All species	PE - APL	0.767***	34
	PE - AFD	-0.383*	23
	APL - AFD	-0.534**	23
Hymenoptera	PE - APL	0.364 ^{n.s.}	15
	PE - AFD	-0.023 ^{n.s.}	11
	APL - AFD	-0.670*	11
Lepidoptera	PE - APL	0.593*	12
	PE - AFD	0.218 ^{n.s.}	9
	APL - AFD	-0.050 ^{n.s.}	9

for %FV. These results indicate that, although both factors significantly influence PE, variation in intrinsic pollinating ability (%FP) was far more important than foraging behaviour differences (%FV) in explaining variation in pollinator effectiveness. However, some exceptions to this prevailing pattern must be noted. The three species significantly selecting male-stage flowers either were not significant pollinators (*Systoechus*, *Colias crocea*; PE not different from control flowers, Tab. 2), or had a low PE value (*A. brevisculum*). The latter species had a %FP value (61.5%) comparable to that of other bees, suggesting an intrinsic ability to pollinate female flowers when it visits them. In this species at least (and also presumably the other two), low effectiveness must be attributed to its flower selection pattern, and not to inability to deposit pollen on receptive flowers.

3.4. Size of pollen loads

In this section, only data for insect-visited flowers actually receiving some pollen, and significant floral visitors (Tab. 2), are considered. The number of pollen grains deposited on the stigma in a single visit ("pollen load" hereafter) was very variable for all floral visitors, as shown by ranges and coefficients of variation (CV) (Tab. 3). CV's are roughly of the same magnitude for all visitors (mostly in the range 80–110%), suggestive of similar levels of intraspecific variability in pollen load size (when pollen deposition actually takes place).

Average pollen loads (APL) fell in the range 8.3–37.7 grains for Hymenoptera, 4.0–15.9 grains for Diptera, and 2.3–14.0 grains for Lepidoptera (Tab. 3). Among bees, *Halictus* sp. (aff. *scabiosae*), *Megachile* sp. (aff. *lagopoda*) and *Apis mellifera* produced, on average, the largest pollen loads. *Hesperia comma* and *P. pandora*

among butterflies, and the three Syrphid flies among Diptera, were the visitors delivering most pollen in these two groups. There was significant heterogeneity among groups in APL ($H=13.71$, $df=2$, $P=0.0011$, Kruskal-Wallis analysis of variance), due to the significant difference between Hymenoptera and the other two groups combined ($H=13.04$, $df=1$, $P=0.0003$). Diptera and Lepidoptera did not differ in APL values ($H=1.41$, $df=1$, $P=0.23$).

3.5. Flight distances

Distances moved by floral visitors between consecutive flower visits (measured on a straight line) are analyzed in this section. Sufficiently large samples are available for 23 visitors (Tab. 3).

Average flight distances (AFD) ranged between 17 and 65 cm (Hymenoptera), 18 and 72 cm (Diptera), and 28 and 168 cm (Lepidoptera). There was significant heterogeneity between groups in AFD ($H=10.77$, $df=2$, $P=0.005$; Kruskal-Wallis analysis of variance). As a group, Lepidoptera tended to fly longer distances between consecutive flower visits than bees and wasps ($H=9.94$, $df=1$, $P=0.002$). The nymphalids *A. paphia* and *P. pandora* had the largest AFD's observed (168 cm and 159 cm, respectively). There is little overlap between the AFD ranges of these two groups, except for *M. stellatarum* (Sphingidae) and *Thymelicus acteon* (Hesperiidae), which have values falling in the range observed for Hymenoptera. Differences between groups in AFD are paralleled by differences in the proportion of flights at "short" (<10 cm) and "long" (>160 cm) distances. These two cutoff points have been chosen to separate reliably flights between flowers of the same and different individual plants, respectively (in the conditions of the study site). Among Hymenoptera, the proportion of short flights was significantly larger, and of long flights significantly smaller, than among Lepidoptera ($H=7.69$, $df=1$, $P=0.006$). There is, however, some overlap between the two groups. The moth, *M. stellatarum*, and the skipper, *Th. acteon*, showed values in the range of bees while, in turn, the bees *Xylocopa violacea* and *A. florentinum* (males) had values in the range of butterflies.

With the exceptions of *Systoechus* (Bombyliidae) and *A. paphia* (Nymphalidae), all frequency distributions of flight distances are significantly leptokurtic ($g_2>0$). Leptokurtosis is particularly strong among some Hymenoptera (Tab. 3), with five species having $g_2>50$. Among Lepidoptera, *M. stellatarum* shows the greatest leptokurtosis ($g_2=46.9$), while the remaining species have $g_2<25$. The two groups, however, do not differ significantly in g_2 values ($H=2.67$, $df=1$, $P=0.10$).

3.6. Covariation between quality components

Rank correlations were computed between the major components of pollinator quality considered here (over-

all effectiveness, PE; pollen load size, APL; flight distance, AFD) (Tab. 4). For all visitors combined, the three correlations are statistically significant. PE and APL are each negatively correlated with AFD, and positively between them. Across species, therefore, there is complementarity between the average distance a pollinator moves between consecutive flower visits, on the one hand, and its pollinating effectiveness and size of pollen load delivered, on the other. In other words, pollinators may score high on either PE-APL or AFD, but not on both quality components.

This result mainly reflects the contrasting characteristics of the two major groups represented in the sample, namely Hymenoptera (short flights, large pollen loads, high effectiveness) and Lepidoptera (long flights, small loads, medium to low effectiveness) (Tabs 2 and 3). When correlations are run separately for each group (Tab. 4), a different picture emerges. Within Hymenoptera, effectiveness (PE) is not significantly related to either the size of pollen load (APL) or flight distance (AFD), while load and distance are inversely correlated. The only predictable relation is thus that those bees flying farther between flowers deliver smaller pollen loads than those flying over shorter distances, and vice versa. Within Lepidoptera, in contrast, the only significant correlation is between effectiveness and load size. Butterflies that deposit the largest loads are also those most effective at pollination. No significant relation exists between either of these variables and flight distance in this group.

In conclusion, predictable additive or complementary covariation of quality components mainly takes place at the level of higher taxonomic groups (Hymenoptera, Lepidoptera). Within each of these, covariation across species is much less predictable and consistent (complementary in Hymenoptera, additive in Lepidoptera).

4. Discussion

4.1. Floral biology

Lavandula latifolia is self-compatible, but spontaneous autogamy occurs very infrequently and seed set in absence of pollinators is negligible. The marked protandry of flowers, with virtually non-overlapping male and female stages, along with the changes in intrafloral morphology during anthesis, explain the low rate of spontaneous self-pollination. Blossoms are not synchronous within one inflorescence (asynchronous dichogamy; Lloyd and Webb 1986). The pollen and stigma stages of different flowers are not in phase with each other, and geitonogamous self-pollination can readily take place.

Percent fruit set of selfed flowers was lower than that of crossed flowers, and the two groups did not differ in number of seeds set per fruit. *L. latifolia* plants did not seem to discriminate among cross pollen on the basis of

distance to source plants. Percent fruit set and number of seeds set/fruit were similar for flowers pollinated with pollen from plants growing at a broad range of distances (2–3500 m). This contrasts with previous findings (e.g., Price and Waser 1979, Waser and Price 1983, Levin 1984) of differential reproductive success related to outcrossing distance. In *L. latifolia*, therefore, the reproductive output (number of seeds produced) potentially obtainable by an individual through allogamy exceeds that obtainable through geitonogamy, but increasing distance to pollen source beyond the nearest neighbour did not significantly improve reproduction.

No significant differences in average seed mass were found between fruits produced from selfed and crossed flowers, and between the different outcrossing distances. This would tend to rule out possible effects of pollen source on probability of seedling establishment mediated by its well-known relationship with seed size (e.g., Salisbury 1942, Kaufmann and McFadden 1960, Dunlap and Barnett 1983, Dolan 1984, Marshall 1986). Nevertheless, the influence of paternity on realized reproductive output cannot be ruled out completely, as previous studies have often shown greater survival of seedlings from crossed vs. inbred or selfed progeny (Price and Waser 1979, Garnock-Jones and Molloy 1982, Schoen 1983, Waser and Price 1983, Cram 1984, Waller 1984, Mitchell-Olds and Waller 1985). If this relation also holds for *L. latifolia*, differential survival of seedlings differing in paternity would enhance the differences in reproductive output between allogamous and geitonogamous pollination noted above.

4.2. Frequency of pollen deposition

There are broad differences in the frequency with which animal visitors deposited pollen on the stigma of visited flowers. As a group, Hymenoptera deposit pollen more often than Lepidoptera and Diptera, while the latter two groups did not differ. Broad interspecific variation existed within each group, and some exceptions to the general pattern were apparent. Large nymphalid butterflies, for example, pollinated flowers more often than small bees, and some flies were superior to some Hymenoptera. This suggests a cautionary methodological note. Species within single orders, families or genera may differ widely in frequency of pollination (Tab. 2). Pooling data of individual species into broader categories (order, family) may make statistical sense, but almost certainly will underestimate the actual range of pollinator effectivenesses faced by the plant. This effect is particularly relevant in the context of the evolutionary implications to the plant of differential pollinator effectiveness.

Some studies have indirectly evaluated pollinator effectiveness by counting pollen grains on the body of floral visitors. These have often found that bee species carry more pollen grains than butterfly and fly species (Ehrenfeld 1979, O'Brien 1980, Hipa et al. 1981b,

Boyle and Philogène 1983, Lindsey 1984, Wolin et al. 1984; but see Grace and Nelson 1981, Sugden 1986). My results are consistent with these findings and indicate that some butterflies may be important pollinating agents (at least with regard to frequency of pollen delivery on stigmas). This is contrary to some earlier generalizations (Wiklund et al. 1979, Jennersten 1984) based on counts of pollen grains on insects' bodies (see also Levin and Berube 1972, Courtney et al. 1982, Murphy 1984).

Interspecific variation in frequency of pollination (PE) depends significantly on differences in proportional visitation to female-stage (receptive) flowers and frequency of pollination of these flowers. Choice of floral stages, however, explains little variation in PE, even though 10 visitors visited sexual stages in proportions departing from those found in the plant population. Differences in PE thus are best explained by differential intrinsic pollinating ability when insects visit receptive female flowers. Correlates of this ability could only be properly investigated within broad, but taxonomically, behaviourally and morphologically homogeneous, species groups. Bees in the genus *Anthophora* were the only group in my sample approaching these requirements. The four species studied are similar in behaviour at flowers, and differ moderately in body size (average body length: *A. albigena*, 9.8 mm; *A. crasipes*, 12.0 mm; *A. quadrifasciata*, 13.1 mm; *A. ochroleuca*, 14.4 mm), yet differed markedly in percent female flowers pollinated (36.4–100%; Tab. 2). The corollary is that, if relative pollinating effectivenesses of closely related species are generally as unpredictable as found here, "subjective scores" (e.g., Ehrenfeld 1979, Sugden 1986) are probably of little use in evaluating actual pollinator effectiveness.

Discrimination by pollinators between conspecific flowers on the basis of sex has been reported for monoecious and dioecious species (Tepedino 1981, Hippa et al. 1981a, Kay 1982, Kay et al. 1984). In these instances, preferences for one or other sex vary temporally and between species, and no explanation seems to apply generally to all situations. For a dichogamous, protandrous species, Bell et al. (1984) found that several insect visitors consistently preferred the most nectariferous male stage. In the case of *L. latifolia* pollinators, sex-related variation in floral reward (pollen in male-stage, nectar in female-stage) does not explain all the cases of sex-biased floral visitation. Three visitors significantly selected male-stage flowers, among these two exclusive nectar feeders (*Systoechus*, *C. crocea*). This is difficult to reconcile with the observation that *L. latifolia* flowers secrete little nectar during this phase, and other factors are probably involved in the foraging behaviour of these species. In contrast, the strong floral selection exhibited by *Anthidiellum* (Megachilidae), which includes 80% of male-stage flowers in its foraging sequence, is readily related to almost exclusive pollen-gathering behaviour. Seven species significantly selected female-stage flow-

ers. Here again, the type of food sought by the insects in the flower does not explain the sex-related floral preferences. Female-stage flowers only exceptionally contain some pollen, yet two almost exclusive pollen feeders (*Ceratina*, Calliphoridae gen. sp.) selected this stage instead of the male-stage. The preference of *Volucella* spp. and *E. tenax* (Syrphidae) for female-stage flowers does agree with their predominantly nectarivorous habit.

4.3. Number of pollen grains deposited

Some studies have shown that the number of pollen grains deposited on the stigma (pollen load, as used here) must exceed a minimum threshold for fruit set to occur. Reported values for this threshold, expressed as the ratio of pollen load size to number of ovules, are approximately 1:1 (Silander and Primack 1978, McDade 1983, Waser and Fugate 1986), 1:2.5 (Bertin 1982) and 1:12 (Snow 1982). These figures indicate that fruit set may occur even at minimal pollination intensities (see also Mulcahy et al. 1983, McDade and Davidar 1984), and that the minimum number of pollen grains required is generally equal or less than the total number of ovules in the ovary. I have no data on the pollination intensity threshold, if any, of *L. latifolia*. The above figures, however, may tentatively be used to predict a minimum of 1–4 pollen grains for fruit set (*L. latifolia* flowers have 4 ovules). All significant pollinators considered in this study, including those delivering the smallest average pollen loads (Tab. 3), are thus potentially able to promote fruit set after single visits to flower (if other factors are not limiting fruit production).

Number of seeds set per fruit usually increases steadily with increasing pollen load size in species with many ovules per flower (Silander and Primack 1978, Snow 1982, Schemske and Fenster 1983, Shore and Barret 1984, Kohn and Waser 1985). Nevertheless, this relationship becomes much weaker, if significant at all, in flowers with few ovules (Mulcahy et al. 1983, McDade and Davidar 1984). In *L. latifolia*, number of seeds set per fruit apparently does not depend on the number of pollen grains reaching the stigma. Hand-pollinated flowers receiving pollen in excess of the number of ovules set only 37% of the maximum possible seed number (4/fruit) (Tab. 1). In this respect, therefore, pollinators of *L. latifolia* delivering greater average pollen loads (bees) would not be expected to increase seed production significantly (through increases in seeds per fruit) relative to those depositing smaller loads (flies, butterflies).

4.4. Flight distance

There is significant heterogeneity between major insect groups in the average distance flown between consecutive flower visits, with butterflies flying farther than bees (only three fly species had sufficient data, thus

comparisons did not include this group). In spite of these overall differences, however, there exists within-group variation, and overlap between groups, in average flight distance. There is also considerable within-group heterogeneity in the degree of leptokurtosis of flight distance frequency distributions. Earlier studies analyzing flight patterns at the species level have also documented sex- and species-related differences between and within taxonomically defined groups (Waddington 1979, Waser 1982, Böcher and Phillipp 1985, Ginsberg 1985).

Pollinator flight distances have been often used to evaluate pollen flow distances (Levin and Kerster 1968, 1974, Schmitt 1980, Waddington 1981). This method tends to underestimate actual pollen flow (Schaal 1980, Levin 1981), mainly due to pollen carry-over effects (pollen from any one flower is not always completely deposited on the next one in sequence; Thomson and Plowright 1980, Price and Waser 1982, Thomson 1986). Nevertheless, for comparative purposes it seems safe to infer differential outcrossing distances on the basis of differential pollinator flight distance patterns (Levin 1981, Waser 1982, Handel 1983, Webb and Bawa 1983, Brown and Clegg 1984). On the basis of average flight distances, therefore, pollinations of *L. latifolia* flowers effected by Lepidoptera are expected to involve cross pollen much more often than in pollinations effected by Hymenoptera, which will most often imply geitonogamy. It must be emphasized, however, that this represents a statistically prevailing trend, and that it does not always hold when individual species of these pollinator groups are considered.

4.5. Covariation of quality components and plant specialization

The variation observed between floral visitors in the components of pollinator quality examined may translate into differential fitness of *L. latifolia* plants, through their effects on number of fruit and seed produced, and also, possibly, eventual success of resulting offspring. All else being equal, an individual plant pollinated exclusively by pollinators frequently transferring cross pollen would gain a reproductive advantage over conspecifics pollinated exclusively by pollinators infrequently delivering pollen and/or generally inducing geitonogamy. The potential therefore exists for plant specialization on pollinators. This potential, however, is modified by covariation of quality components across species. Differences in aspects of "quantity" (i.e., total numbers of each insect species visiting flowers) will also modify the potential for specialization, as outlined in the Introduction. The following discussion tentatively assumes the null hypothesis that quality and quantity factors are statistically unrelated in my insect species sample.

If all possible pairwise correlations between quality components were positive (i.e., additive covariation),

this correlational structure would reflect a single underlying gradient of pollinator quality. Floral visitors could thus be ranked along this axis. In other words, each species of pollinator could be scored for quality on a single linear measurement scale. In these circumstances, the evolutionary pathway for plant specialization on pollinators would be defined by the single quality gradient, with a distinct potential direction towards its positive extreme. On the other hand, if some pairwise correlations between quality components are negative (i.e., complementary variation), at least two mutually exclusive gradients of pollinator quality exist. In this case, two potential pathways are open to plants for specialization, defined by the two gradients. This is the case for *L. latifolia* at my study site. For all pollinators combined, there is inverse variation of average flight distance, on one side, and pollinator effectiveness and size of pollen load, on the other (the latter two magnitudes are directly related). Frequent deposition of large loads and long distance to the pollen source thus tend to be mutually exclusive features in the *L. latifolia* pollinator assemblage. This pattern mainly results from the contrasting characteristics of the two major groups represented in the sample (Hymenoptera and Lepidoptera). Bees pollinate flowers frequently, but generally promote geitonogamy; butterflies pollinate flowers less often, but then most often with cross pollen. Specialization on either group would have its advantages and thus is theoretically possible, but there are strong commitments associated with each option. A shift towards exclusive bee pollination would presumably imply increased inbreeding depression, while a trend towards exclusive butterfly pollination would result in reduced proportion of flowers pollinated. Evolutionarily choosing one or other pathway would require that the correlations of plant fitness with number of seeds produced and genetic constitution of offspring be markedly unequal.

Covariation of quality components across bee and butterfly taxa considered separately follows different trends and is much weaker than for all species combined (Tab. 4). Little additive or complementary variation of quality components exists, and no clear interspecific gradient in pollinator quality may be identified, within each of these pollinator groups. On the basis of pollinator quality alone, therefore, the potential pathways for plant specialization on pollinators are ill-defined beyond the two predictable gradients generated by the major groups discussed above. In short, a distinct potential exists for *L. latifolia* evolving specialization for "bee" or "butterfly" pollination, but much less so for specialization on particular species of either group.

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