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Patterns of insect flower visitation in *Lavandula buchii* Webb (Lamiaceae), an endemic shrub of Tenerife (Canary Islands)

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The foraging ecology of insect visitors of the endemic lavender *Lavandula buchii* (Lamiaceae) was studied in a relict population of the plant in north-west Tenerife (Canary Islands). Timed observations were used to describe this pollination system in terms of the structure of the visitor assemblage, foraging patterns and efficiencies of the main insect species. The visitor pool was dominated by anthophorid solitary bees. Furthermore, it was characterized by a high level of endemicity and a small number of species compared with continental relatives of *Lavandula*. The main visitors, two anthophorids and a bombyliid fly, clearly differed in their foraging behaviour, i.e. visitation frequency, visit duration, rate of flower probing, and in anatomical traits (body size and proboscis length). In these terms, the bees were by far more efficient foragers than the fly. These results are discussed in the context of insect–flower interactions in insular pollination systems.

Keywords: *Amegilla*, *Anastoechus*, Canary Islands, Diptera, flowers, foraging ecology, Hymenoptera, *Lavandula buchii*, visitation rates.

Introduction

The Canary Islands, a Macaronesian archipelago, support a extraordinary high level of endemicity in flowering plants (about 600 species, 48% of the total species pool) (Hansen and Sunding, 1993). Furthermore, *ca* 2100 insect species (42% of the total insect fauna) belong to three major groups of pollinators, namely dipterans, lepidopterans and hymenopterans, and also show a large proportion of endemics (Becerra *et al.*, 1992). This high diversity of plants and potential pollinators suggests the existence of a large number of pollination mutualisms on these islands. For example, there are about 370 taxa of hymenopterans (within the suborder Aculeata), that have been circumstantially reported visiting a wide variety of phanerogam families in the Canarian flora (La Roche, 1992; Hohmann *et al.*, 1993). Previously, the scarce literature on pollination ecology in this archipelago has traditionally focused on bird–flower relationships (Yeo, 1972; Vogel *et al.*, 1984; Olesen

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1985, 1988; Westerkamp, 1990). There are at least 12 plant species of nine genera that display ornithophilous traits in the Canaries (Vogel *et al.*, 1984; Olesen, 1985; Kraemer and Schmitt, 1997). Nevertheless, a vast majority of zoophilous, endemic flowering plants in this archipelago are chiefly entomophilous. Despite this, the importance of insects as visitors and pollinators for most of the endemic plant species, many of which are rare or threatened in relict Canarian ecosystems, remains largely unexplored (see, however, Kraemer and Schmitt, 1997).

In this study I examine the interaction between *Lavandula buchii* Webb, an endemic shrub of the xerophytic lowlands of Tenerife (Canary Islands), and its insect visitors. I focused on the visitation patterns and the among-species differences in foraging habits and efficiencies. The goal was to assess visitor efficiency in terms of visit frequency (an indirect measure of visitor abundance), mean visit duration and mean rate of flower probing. These measures constitute the quantity component of a given plant–pollinator system (Herrera, 1989), and along with the quality component (see C. M. Herrera, 1987a), they influence the strength of such a mutualism (Howe, 1984) and the overall pollination efficiency (Fishbein and Venable, 1996).

Study site and species

Field work was conducted at an arid lowland site located in the Teno Massive (Barranco de Las Cuevas, 27° 37′–29° 25′ N, 13°20 ′–29° 25′ W, 150 m a.s.l.), in the north-west of Tenerife (Canary Islands). The climate is typical of dry Canarian coastal habitats (*Euphorbia*-dominated scrublands). Annual average temperatures and rainfall are about 21°C and 203.9 mm, respectively. Maximum rainfall occurs mainly between November and January, May to September being the driest period (< 3 mm). The site is a rocky ravine bed covered by shrubs of *Euphorbia* spp. (Euphorbiaceae), *Rubia fruticosa* and *Plocama pendula* (Rubiaceae), *Periploca laevigata* (Asclepiadaceae), *Lavandula buchii*, and the introduced *Opuntia dillenii* (Cactaceae).

In Macaronesia, the genus *Lavandula* (Lamiaceae) comprises nine species of insect-pollinated shrubs, of which three are endemic to the Canary Islands, and one (*L. buchii*) is endemic to Tenerife (Hansen and Sunding, 1993). *Lavandula* species are also present in Mediterranean habitats of southern Spain. On the continent, their pollination biology and evolutionary ecology have been thoroughly investigated (see C. M. Herrera, 1987a, 1987b, 1989, 1990, 1995, for *L. latifolia* Med.; J. Herrera, 1987, 1997, for *L. stoechas* L.). These studies provide the opportunity to compare the pollination systems associated with continental and insular *Lavandula* representatives.

Lavandula buchii Webb shows a disjunct distribution in Tenerife, with small, localized populations isolated in the extreme massives of Teno (NW) and Anaga (NE), 80 km apart (León and Wildpret, 1986; Santos and Romero, 1996). The shrubs are up to 1 m tall, and inflorescences are terminal, ramified spikes bearing one to eight violet flowers (mean and standard deviation = 3.79 SD 1.61, $n = 85$ inflorescences, 10 plants). The mean length of the tubular calyx is 7.33 SD 0.79 mm (range = 4.64–9.01, $n = 114$ flowers, 10 plants). The upper and lower lips of the corolla have two and three lobes, respectively. Flowering occurs from early spring to mid-summer and seeds are produced in summer (Santos and Romero, 1996). Flowers are eaten by lizards (*Gallotia galloti*) and seeds are predated by the canary (*Serinus canarius*). *L. buchii* hybridizes with another Canarian-endemic lavender, *L. canariensis*, and is included in a red data book as an endangered plant species for the Canaries (Santos and Romero, 1996). Additional information about natural history, taxonomic status and identification of insect visitors can be found in Becerra *et al.* (1992) and Hohmann *et al.* (1993).

Methods

Insect visitation patterns were studied in 10 shrubs of *L. buchii* during a week in August 1995. At the same hour each day, I counted the number of fresh flowers (open and closed) on each shrub to estimate the size of the flower display. I did not count dessicated, apparently unattractive corollas. I also recorded separately the number of open flowers per day to check for possible variations in effective flower availability throughout the study, in relation to the performance of insect visits. For each plant, I measured the distance to all the neighbouring shrubs within a 5 m-radius circle. I estimated the size of the neighbouring flower display by counting all inflorescences on each individual shrub within the circular plot. Neighbouring flower display was then expressed as number of inflorescences per 78.5 m^2 (see the Appendix). Flower number was strongly correlated to inflorescence number on each plant (Spearman rank correlation, $r_s = 0.95$, $p < 0.001$, $n = 36$ plants), so I estimated the flower number in conspecific shrubs by extrapolating the mean number of flowers per inflorescence. These data were taken in order to relate them to visitation descriptors described below.

To characterize visitation patterns, I recorded flying-insect visits at the 10 study plants using 5-min census intervals as the sample unit (see Herrera, 1995 for a similar methodology). Thus, total observation time was 8.33 h, with 10 intervals performed per plant (i.e. 100 census units). Observations were made each day between 12:00 and 14:30 h (local time) in good weather conditions (absence of strong wind). Within this time interval, sunlight was homogeneously distributed over the ravine bed, making the irradiance regime practically identical for each observed plant. Thus, biases in visitation rate measurements due to differential light intensities were minimized (Herrera, 1995). Census intervals were distributed randomly among plants and census days in order to avoid possible biases of order of plant censusing. For each plant and census interval, I recorded the number of insect visits (visit frequency), and measured with a stop-watch the duration of the visit for each species to the nearest second. When more than one visitor was contacted simultaneously, I followed a focal individual until the end of its visit to obtain the duration, then turning to a different specimen, until the completion of the time interval. In each timed visit, I also counted the number of flowers probed by an insect to determinate the rate of flower probing (flowers probed per minute). Body size and length of the mouthparts were measured for the main visitor species with a digital caliper. Proboscis length (including promentum + glossa) was measured stretching the organ with soft forceps over a slide.

Specific requisites of parametric tests (i.e. normality and homocedasticity) were not achieved for some plant and insect variables in the original data set, even after data transformation. This was probably due to small sample sizes of study plants and visit descriptors of one of the insect species, and to the 'count' character of data for some plant and visitor variables (Fowler and Cohen, 1992). Thus, non-parametric statistics were applied following Siegel (1970), and tests are appropriately indicated in the text.

Results

The insect visitors

Insect visitors recorded at *L. buchii* plants over the study period are shown in table 1. About 81% of the total visits were performed by two congeneric solitary bees (Hymenoptera, Anthophoridae): *Amegilla quadrifasciata* (Villers), distributed throughout the Palaearctic (including central Asia), Ethiopian and Macaronesian regions, and *A. canifrons* (Smith), endemic to the Canaries. However, more than 50% of the total visits were realized by *A. quadrifasciata* alone. As a group, anthophorids (including the small contribution made by another anthophorid solitary bee, *Thyreus histrionicus* Illiger) accounted for 81.5% of the total number of visits. Some visitors to *L. buchii* were casual, not being recorded during formal observation intervals. The bee *Lassioglossum arctifrons* (Saunders) (Hymenoptera: Halictidae), was observed incidentally at non-monitored *Lavandula* plants. The bumblebee *Bombus terrestris canariensis* Pérez (Hymenoptera: Apidae, endemic subspecies) was detected several times at the study site but it was not observed visiting *Lavandula* flowers. One species of ant (Hymenoptera, Formicidae) of the genus *Camponotus* was observed frequently on the plants. However, it was not included in the analysis of visitation patterns because recording of visit data and ant numbers on the plant at a time was not feasible with the same census methods used for flying insects. *Camponotus* interacted aggressively with practically all the visitor species approaching a flower.

The Canarian-endemic fly *Anastoechus latifrons* (Macquart) (Diptera, Bombyliidae) was the third most frequent visitor. A number of unidentified dipterans (mainly Calliphoridae, but also some Syrphidae) visited the plants, although they contributed comparatively little when considered individually, or when compared to *A. latifrons*. Lepidopterans (1.62% of the total in table 1) paid only occasional visits to *L. buchii*. Hereafter, this study will focus on the two *Amegilla* species and the fly *A. latifrons*, to compare patterns of plant visitation and flower use for the most important insect visitors.

Visit and foraging patterns

Main taxa visited the plants with very different frequencies (number of visits per 5 min; Kruskal–Wallis one-way ANOVA, KW = 65.2013; 2 df; $p < 0.001$; figure 1).

Table 1. Insect species recorded at *Lavandula buchii.* Total number of visits per taxon (*n*) and the relative contribution (%) of each group for the whole observation period (8.33 h distributed among 7 days) are shown.

Species	Order	*n* (%)
Amegilla quadrifasciata	Hy	291 (52.81)
Amegilla canifrons	Hy	156 (28.31)
Diptera undet.	Di	60 (10.89)†
Anastoechus latifrons	Di	32 (5.81)
Hyles euphorbiae	Le	4 (0.72)
Ropalocera undet.	Le	3 (0.54)
Thyreus histrionicus	Hy	2 (0.36)
Pieris rapae	Le	1 (0.18)
Pontia daplidice	Le	1 (0.18)
Spilostethus pandurus	He	1 (0.18)

Hy, Hymenoptera; Di, Diptera; Le, Lepidoptera; He, Hemiptera.
†Includes several species of Calliphoridae and Syrphidae.

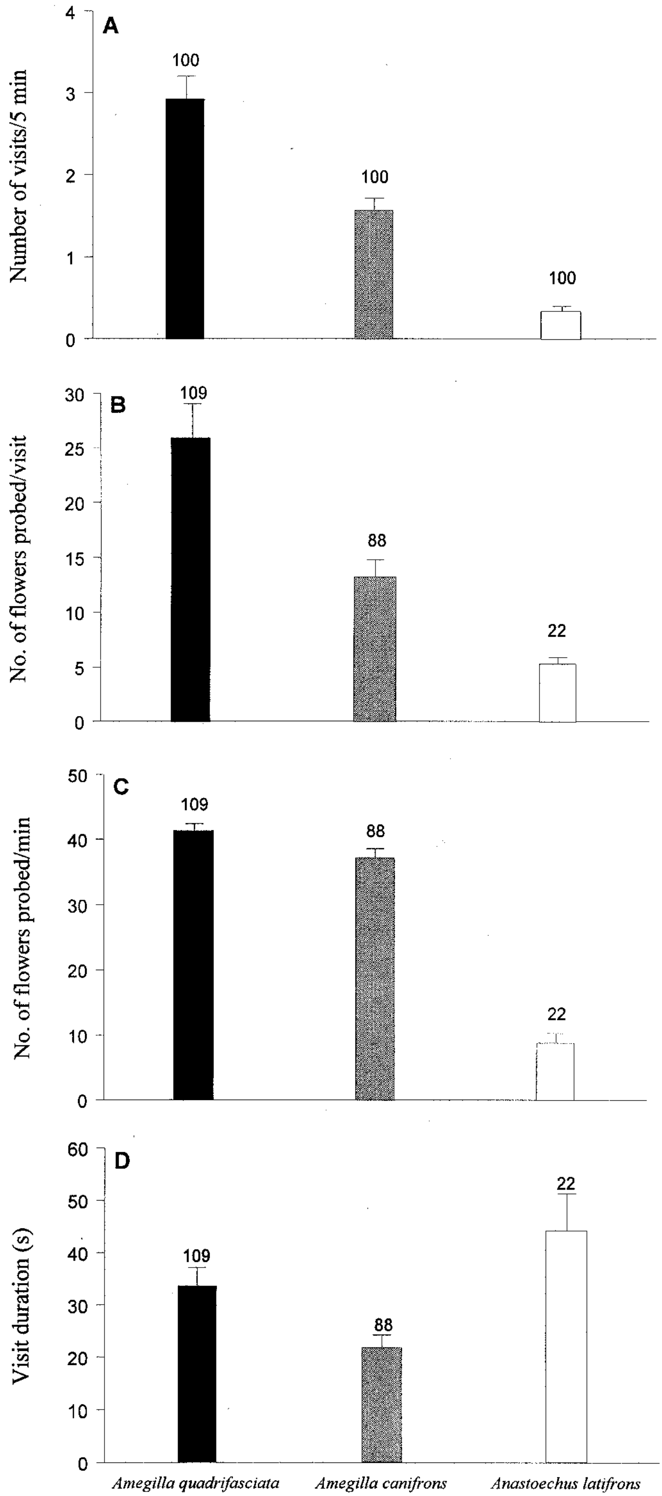
The two anthophorid bees exhibited the higher visitation rates (range of visits per 5 min: *A. quadrifasciata*: 0–12; *A. canifrons*: 0–8), as compared to the fly *A. latifrons* (0–4 visits per 5 min) (figure 1). Visitation rate for the three species pooled was moderately related to the daily variation in flower display (number of open flowers/plant/day) (Spearman correlation coeficient, $r_s = 0.695$; $p < 0.01$; $n = 10$ plants) (figure 2). These display sizes oscillated between 1 and 396 open flowers/day. The study period encompassed a peak in the flowering of *Lavandula*, and all the studied shrubs reached this maximum synchronously. Flower display size was clearly correlated with visitation frequency of the two bees (*A. quadrifasciata*: $r_s = 0.82$; $p < 0.05$; *A. canifrons*: $r_s = 0.92$; $p < 0.001$; $n = 10$ plants) but not with fly visitation frequency. I found no relationship between visitation frequency of either species and corolla length, size of the neighbouring flower display, or distance among conspecific shrubs.

Bee and fly species showed contrasting foraging behaviours in their feeding bouts at the plants. The two anthophorids probed flowers while hovering, partially introducing the hairy head in the corolla tube and rapidly passing from one flower to another. The fly alighted on the corolla lips and spent significantly more time per flower than the hymenopterans. Between two consecutive feeding bouts, the fly landed on the ground beneath the plant for a few seconds, then flew up to a new flower. Both *Amegilla* species were similar in their visit duration (*A. quadrifasciata*: 33.39 s, *A. canifrons*: 21.73 s; Mann–Whitney's $U = 4476.0$; $p = 0.080$), but differed when compared to *Anastoechus*, which spent much longer periods (mean = 43.85 s) on the foraging plants (*A. latifrons* vs *A. quadrifasciata*: $U = 805.5$; $p < 0.05$; *A. latifrons* vs *A. canifrons*: $U = 442.0$; $p < 0.001$; figure 1). Visit duration was moderately related to flower number in *A. quadrifasciata* $r_s = 0.68$; $p < 0.05$) and strongly related in *A. canifrons* ($r_s = 0.92$; $p < 0.05$), but not in *A. latifrons*.

The three species differed substantially in the number of flowers probed per visit (KW = 15.1052; 2 df; $p < 0.001$) and per time unit (KW = 58.7078; 2 df; $p < 0.001$) (figure 1). *A. quadrifasciata* was faster than *A. canifrons* and *A. latifrons*, and differences were even more pronounced between the two anthophorids (pooled) and the fly. Number of flowers probed and time spent visiting a plant were strongly correlated in both *A. quadrifasciata* ($r_s = 0.9697$; $p < 0.0001$) and *A. canifrons* ($r_s = 0.9322$; $p < 0.0001$), but only modestly correlated in *A. latifrons* ($r_s = 0.6041$; $p < 0.01$), indicating that this last species was the least efficient in flower visitation. The Palaearctic hawkmoth *Hyles euphorbiae* (Boisduval) probed flowers rapidly before leaving (mean and standard deviation = 33.1 SD 2.6 flowers; $n = 3$ visits), whereas pierid butterflies probed flowers at a much lower rate.

Discussion

Contrasting with continental populations of related *Lavandula* species, the oceanic island system reported here had strikingly fewer potential pollinators associated with *L. buchii*. The relative contribution of each pollinator species and their respective foraging habits also differed (see C. M. Herrera, 1987a, 1989, 1995, and J. Herrera, 1988, for comparison). However, the general taxonomic structure of the entire visitor pool is very similar for both continental and insular plant relatives (see e.g. C. M. Herrera, 1987a, 1989; J. Herrera, 1988). *Lavandula latifolia* in southern Spain has a high number of associated pollinators, including about 80 bee, fly and butterfly species having moderate to low abundances (Herrera, 1989). As can be expected from biogeographical constraints, the Canary Islands support a relatively poorer hymenopteran fauna compared with the continent (Olesen, 1985; Hohmann,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C
No. of flowers probed/min
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Visit duration (s)
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Amegilla quadrifasciata
Amegilla canifrons
Anastoechus latifrons

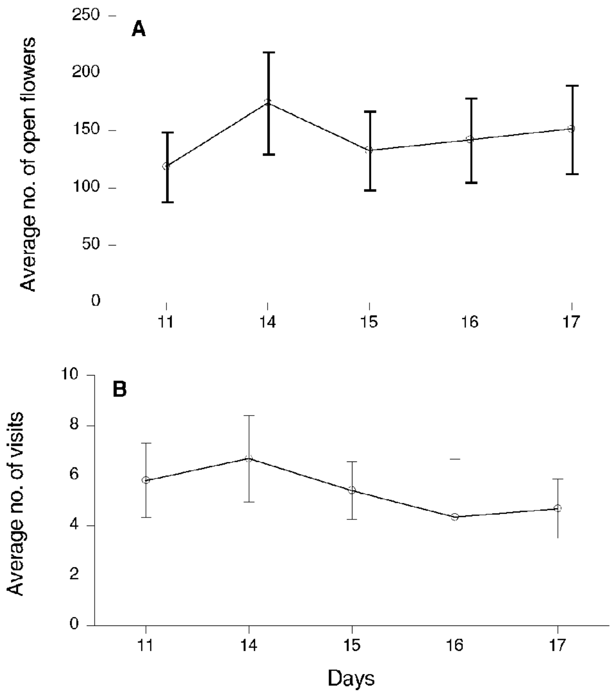

FIG. 2. Daily variation in the size of flower display (A) and temporal distribution of insect visits (B) in *Lavandula buchii*. Shown are means ± 1 SE. Mean values of number of open flowers and visitation frequency were averaged for 10 plants. Visitation rates were pooled for the three insect species reported in Results.

1993; Kraemer and Schmitt, 1997), although the level of endemism is high. Thus, whereas 75% of the visits to *L. latifolia* in southern Spain were performed by as many as 13 species of hymenopterans (mainly Apidae) (Herrera, 1995), only two anthophorids performed more than 80% of the visits to *L. buchii* in this study. Dipterans (particularly bombyliids) were infrequent visitors both in this study and in that of Herrera (1995). Butterflies were much more important foragers in terms of species number and visit frequency for *L. latifolia* than for *L. buchii*. This small spectrum of flower visitors seems to be generalized to other Canarian endemic plants (Olesen, 1985). For instance, *Echium wildpretii* (Boraginaceae), an endemic of the Tenerife summit scrub, received visits from only six insect species (Kraemer and Schmitt, 1997).

Some earlier workers have shown great variation between pollinators in flower foraging rates (e.g. Augspurger, 1980; Schmitt, 1983; Schemske and Horvitz, 1984; Willmer *et al.*, 1994; Fishbein and Venable, 1996). This study reveals large differences in foraging behaviours and feeding apparati between the main visitor groups, that may influence these foraging rates. In fact, two distinct strategies are used by the

FIG. 1. Variation in visitation patterns among the main insect species at *Lavandula buchii* plants (bars are means + 1 SE). Figures above bars are sample sizes (total number of census intervals in A, and total number of insect recordings for which the visit descriptors were obtained in B–D).

fly and the solitary bees at *Lavandula* flowers. *Amegilla* bees fly faster and have a longer proboscis, probing on average four times more flowers per visit and five times more flowers per time unit than the fly *Anastoechus*, which has a shorter proboscis and a poor flying ability (see table 2 for biometric data). The narrow corolla of *L. buchii* (and related species) would favour visitation by specialized, long-tongued pollinators that could reach the nectar easier than short-tongued ones (Goldblatt *et al.*, 1995). I did not find, however, a relation between corolla length and mean visitation frequency, visit duration or flower-probing rate. The mean length of the proboscis for *Anastoechus* lies within the range of corolla lengths for *L. buchii* (see table 2 and the Appendix), although it is clearly shorter than the proboscis of both *Amegilla* bees. Thus, in terms of suitability of the proboscis as a nectar-feeding organ, *Amegilla* would reach the nectar in deeper or nectar-depleted corollas more easily than *Anastoechus*. Handling time of flowers by the visitor is a component of visit duration that decreases as proboscis length increases (Herrera, 1989). Similar several-fold differences between visitation rates of bombyliid flies (*Systoechus* sp.) and some anthophorids (including *A. quadrifasciata*) visiting *Lavandula* in continental areas have been previously shown (Herrera, 1989). The larger number of flowers used per visit and time unit by *Amegilla* bees make these species more efficient foragers than the bombyliid flies. Nectar-feeding bombyliids and bees may respond differentially to similar patterns of floral display, because they have different visual and olfactory capabilities, different body size, locomotory performances and proboscis length (see Grimaldi, 1988; Goldblatt *et al.*, 1995).

Flower-probing rates were very high for the two bee species in this study, compared to those of other hymenopterans. In the neotropics, the eusocial bee *Melipona interrupta* visited *Hybanthus* (Violaceae) flowers with a mean rate of 6.2 flowers/min (Augspurger, 1980). The anthophorids *Ceratina laeta* and *Paratetrapedia calcarata*, respectively, probed 2.2 and 1.8 flowers/min (Augspurger, 1980). *Bombus* and *Apis* species showed respective mean rates of 4.8 and 4.1 flowers/min at *Rubus* (Rosaceae) in a temperate site (Willmer *et al.*, 1994). Rates for *Amegilla* at *Lavandula* species in insular and continental populations are well above all these figures (see figure 1 for *L. buchii* and Herrera, 1989 for *L. latifolia*). In southern Spain, *A. quadrifasciata* paid visits to *L. latifolia* with a mean rate of 29.6 flowers/min. Similarly high were the performances shown by *Anthophora alluaudi* and *Apis mellifera* in Tenerife which, respectively, probed 29 and 15 flowers/min in *Echium wildpretii* (Kraemer and Schmitt, 1997). Differences in distribution and density of flowers within a plant could partially explain this variation in rates of flower use, because flying distances between two consecutive flowers, and hence flying time, tends to

Table 2. Biometric data for the three main visitors recorded at *Lavandula buchii*. Body size (expressed as length of the thorax, in mm) and length of the proboscis (promentum + glossa, in mm). On the first line are means (SD); on the second, the range.

	Amegilla quadrifasciata ($n=5$)	*Amegilla canifrons* ($n=6$)	*Anastoechus latifrons* ($n=4$)
Thorax length	4.06 (0.10)	4.28 (0.13)	3.50 (0.21)
	(3.91–4.15)	(4.06–4.40)	(3.34–3.80)
Proboscis length	9.16 (0.61)	10.19 (0.43)	5.65 (0.65)
	(8. 38–10.09)	(9.38–10.61)	(5.02–6.53)

increase with the degree of flower dispersion (Augspurger, 1980; Schmitt, 1983). Interspecific variation in flower visitation rate may also be due to the different investment of time flying between consecutive flowers and/or differences in flower handling time (Herrera, 1989).

Visitation frequency by *Amegilla* species in this study was positively related to the size of the floral display, suggesting selection of those plants showing a larger display. Frequently, pollinator taxa differ in their foraging responses to plant attributes and its variation (Eckhart, 1992; Herrera, 1995; Inoue *et al.*, 1995). Pollinator efficiency in flower visitation may depend upon intrinsic traits of the foraging plants, the environment of individual plants and the characteristics of the pollinator itself (Inouye, 1980; Herrera, 1993; Ohara and Higashi, 1994; Willmer *et al.*, 1994). It is commonly accepted that pollinators preferentially visit plants providing many flowers on large inflorescences, characters that are often associated with greater rewards of nectar and/or pollen. Microenvironments with greater densities of flowering individuals are similarly favoured (Schmitt, 1983; Feisinger *et al.*, 1986). A high flower density also promotes higher visitation rates and increases the number of flowers probed per time unit. Furthermore, from the plant's perspective, those individuals bearing more flowers are able to retain the pollinator for a longer period, and this could benefit the plant in terms of pollination success (if it is self-compatible, as is the case of other *Lavandula* species, J. Herrera, personal communication; Ohara and Higashi, 1994).

As a concluding remark, the low pollinator richness of this island system, and the dominance shown by a few insect species could be attributed to their local abundance and distribution. One of the main visitors (the endemic *A. canifrons*) seems to have an almost disjunct distribution in the island (Hohmann *et al.*, 1993), roughly co-ocurrent in space with the present distribution of *L. buchii*, in the isolated mountainous massives of Teno and Anaga (Santos and Romero, 1996). Geologically, these two areas are the oldest parts of Tenerife (5 and 3.5 million years, respectively), and were initially islands isolated by the sea until the emergence of the central part of the island (the Teide-Cañadas complex) (Carracedo, 1979). Further research should pay attention to the associations of endemic plant–insect taxa at an island scale, focusing on the degree of mutual dependence of both partners of the plant–pollinator interaction (taking into account other potential pollinators, such as ants). One of the questions to be addressed is whether pollination systems in the Canaries are specialized, as compared with continental systems (see Waser *et al.*, 1996). To achieve this, a first step is to measure pollination effectiveness for the whole visitor pool. Present mesoclimatic and orographic diversity, along with recent geological history, may be important factors for the isolation of both plant and insect populations, thus allowing the evolution of a high diversity of pollination mutualisms on these islands.

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Appendix

Summary statistics of the plant and neighbourhood traits from 10 *Lavandula* shrubs. Corolla length measurements were taken from 114 flowers ($n = 10$ plants). Neighbour density is expressed as number of flowering shrubs/78.5 m^2; neighbouring flower display is the number of flowers in that area.

	Mean (SD)	Range
Height (m)	0.93 (0.30)	54.50–165.0
Cover (m^2)	0.92 (0.93)	0.25–2.59
No. flowers/plant	118.6 (95.5)	1–279
No. inflorescences/plant	50.2 (37.5)	1–105
Corolla length (mm)	7.33 (0.79)	4.64–9.01
Neighbour density	3.7 (2.06)	1–7
Neighbour distance	3.06 (1.08)	1.97–5
Neighbouring flower display	510.04 (333.33)	70.7–1051.3

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