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Pollination of *Euphorbia dendroides* by lizards and insects: Spatio-temporal variation in patterns of flower visitation

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Abstract The patterns of flower visitation by lizards (*Podarcis lilfordi*, Lacertidae) and insects (mainly flies, bees and wasps) on the shrub *Euphorbia dendroides*, were studied in the island of Cabrera (Balearic Islands) during the flowering seasons of 1995 and 1996. Lizards act as true pollinators of the plant, moving large quantities of pollen within and among shrubs. To our knowledge, this is the first time that pollination by lizards has been empirically demonstrated. Variation in the quantitative component of pollination (frequency of visits \times flower visitation rate) by the two groups of pollinators (lizards and insects) is documented at both spatial (within a plant population) and temporal scales (throughout the flowering season and between seasons). Variation in lizard density on a small spatial scale (within *c.* 200 m), presumably due to differences in vegetation cover, strongly affected their frequency of flower visitation. Insects were rather scarce, mainly because the plant flowers at a time (mid-March) when temperatures are still low. At the site where lizards were abundant, their frequency of flower visits was more than 3 times that of insects, they stayed on the shrubs about 3 times longer and visited about 8 times more cyathia per minute than did insects. Fruit and seed set were greater at this site, and this is attributed to the different frequency of flower visits by lizards, as shrubs are similar in size and produce similar amounts of cyathia in the two sites compared. Both, lizards and insects went more frequently to plants with large flower crops. However, flower crop was not associated with seed viability. We found no evidence for pollinator-mediated selection on plant traits related to fitness.

Key words Lizard pollination · Insect pollination · *Euphorbia dendroides* · *Podarcis lilfordi* · Balearic Islands

Introduction

The contribution of a pollinator to plant fitness, so-called pollinator effectiveness, depends on (1) the number of flowers it pollinates (quantitative component of pollination) and (2) its efficiency as a pollinator (qualitative component). While the former is related to the frequency of pollinator visits and to flower visitation rate, the latter is a function of the pollen delivered to stigmas, the foraging patterns and the selection of floral sexual stage by the pollinator. Both aspects have been examined in different pollination systems (see for instance Cruden 1972; Herrera 1989; Eckhart 1992; Gómez and Zamora 1992; Vaughton 1992, for studies on the quantitative component; and Motten 1983; Schemske and Horvitz 1984; Herrera 1987; Ramsey 1988; Waser and Price 1990; Eckhart 1992, for studies on the qualitative component). Temporal and/or spatial variation in the pollinator assemblage of a plant species obviously translates into variation in both components. Temporal variation has often been documented, within a flowering season or across seasons (Herrera 1988, 1995; Wolfe and Barrett 1988; Schemske and Horvitz 1989; Horvitz and Schemske 1990; Ashman and Stanton 1991; Eckhart 1992; Vaughton 1992; Cane and Paine 1993). Spatial variation has also been repeatedly reported, although few studies have examined differences in taxonomic composition on a local scale (but see Sih and Baltus 1987; Herrera 1988, 1995; Schemske and Horvitz 1989; Horvitz and Schemske 1990; Eckhart 1992; Jennersten and Nilson 1993; Conner and Neumeier 1995). Different taxonomic compositions can exert different selective pressures on the plant, creating a mosaic of selective regimes (Herrera 1988; Thompson 1994). It seems evident, thus, that to understand the evolution of a plant-

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pollinator system we need to assess the variation, at either scale, in the assemblage of pollinators of the plant.

The present study examines the quantitative composition of a plant-pollinator system, evaluating local spatial variation (within a plant population) and temporal variation (throughout the flowering season and between seasons). The plant is *Euphorbia dendroides* L., a Mediterranean shrub commonly found in the Balearic Islands. The flowers of this shrub are visited by different species of insects and by *Podarcis lilfordi*, a lizard endemic to the Balearic Islands.

Lizards have been suggested to act as pollinators in at least two island ecosystems: Madeira (Elvers 1977, 1978) and New Zealand (Whitaker 1987), although empirical evidence that these reptiles actually perform pollination is non-existent so far. Therefore, the main objectives of this study were: (1) to show that *P. lilfordi* acts as a pollinator; (2) to compare the patterns of flower visitation between lizards and insects and their effect on reproductive success; (3) to document the spatio-temporal variation in visitation patterns by the different pollinators, and (4) to know whether pollinators are likely to exert selection on plant characters related to fitness. The breeding system of the plant was also examined through hand-pollination experiments to evaluate how important are such pollinators for plant reproduction.

Materials and methods

Study area

Field work took place in Cabrera island (c. 1130 ha) and encompassed the flowering and fruiting peaks of *Euphorbia dendroides* (March 21–May 4 1995, and March 19–May 7 1996). The vegetation of Cabrera is mediterranean scrubland dominated by *Pistacia lentiscus*, *Olea europaea*, *Phillyrea* spp., *Juniperus phoenicea*, *J. oxycedrus*, *Rosmarinus officinalis*, and *E. dendroides*. A detailed description of the vegetation and climate of Cabrera can be found in Alcover et al. (1993).

We studied a population of *E. dendroides* in the area of S'Espalmador. Preliminary observations suggested that the number of lizards differed between two sites, separated by c. 200 m, within this population. We decided, therefore, to divide it into two "subpopulations", sites A and B hereafter, which represent the extremes of the plant distribution in this area. Site A is located about 20 m above sea level whereas site B is at sea level. Plant species composition and density of *E. dendroides* shrubs do not differ between the two sites, but vegetation cover is greater at site A.

Study organisms

Euphorbia dendroides (Euphorbiaceae) is a deciduous shrub (up to 2 m tall, but usually shorter on Cabrera), single-stemmed, that grows in the thermophilous scrubland of the western and central Mediterranean region. The flowering peak is usually in mid-March and lasts 2–3 weeks (Traveset 1995a). Each adult plant produces hundreds to thousands of inflorescences (cyathia) grouped in clusters of one to five – rarely six – cyathia. Each cyathium (c. 5 mm in diameter) consists of one female flower, with a three-lobed ovary, and several – up to six – male flowers, surrounded by four or five round yellow or orange-coloured glands. These glands produce copious and highly concentrated nectar (70–90% sucrose, measured with a Bellingham hand-refractometer modified for small

volumes) during 6–15 days ($n = 122$ cyathia from 6 plants); the standing nectar crop was found to be $0.1 \mu\text{l}/\text{cyathium}$ ($n = 10$ cyathia), and the volume accumulated over 24 h was 1.15 ± 0.21 (SD) $\mu\text{l}/\text{cyathium}$ ($n = 10$). During the flowering period, a second blossom of cyathia may emerge at each side of the older cyathia. Soon after anthesis the three-lobed stigma becomes receptive while the style juts out vertically from the cyathium, which facilitates pollen deposition. Several days later, the style – which has by then elongated several millimeters – bends towards one side while the stigma stops being receptive and the stamens (also in an erect position which makes pollen removal easier) start dehiscing. The species is self-compatible, but there is no autogamy (see Results). There is much asynchrony in flower development within a plant, so a large fraction of the matings are probably geitonogamous.

Podarcis lilfordi (Günther 1984) (Sauria, Lacertidae) is a small lizard (81 mm maximum snout to vent length), very abundant in some of the islands surrounding Mallorca and Menorca. Recent studies (Pérez-Mellado and Corti 1993; Sáez and Traveset 1995) have reported large proportions of plant material in the lizard's diet and have shown that it acts as a legitimate seed disperser (Traveset 1995b).

Different species of insects, mainly flies, bees and wasps (see results) are potential pollinators of *E. dendroides* in Cabrera. Small ants of the species *Plagiolepis pygmaea* are also found feeding upon nectar but they probably act as nectar thieves.

Breeding system of the plant

Hand-pollination experiments in five plants of S'Espalmador were carried out to determine to what degree the plant relies on pollinators for its reproduction, and how they can affect the production of viable seeds. On March 19 1996, white cloth bags were placed around cyathia still in the bud stage. About a week later, when stigmas were receptive, two groups of 9–25 flowers were pollinated, using a thin brush, with either cross-pollen (xenogamous treatment) or self-pollen (geitonogamous treatment). A control group was labelled and left to open pollination. The level of autogamy was obtained by bagging a total of 39 individual cyathia from the five plants. When fruits reached full size (early May), bags were removed and the capsules produced were counted and opened to record the number of viable seeds in them.

Censuses of flower visitors

During the flowering peak of 1995 (from 21 March to 6 April) we made direct observations of lizards and insects visiting the flowers of *E. dendroides* in a total of 27 (site A) and 50 plants (site B), all haphazardly selected and labelled. We recorded the visits to each plant during periods of 15 min, from a minimum distance of 2 m. Censuses started at about 0900 h and lasted until 1600 hours (GMT), encompassing the time during which both lizards and insects are active. All plants at site A were observed for an average of eight days, and the 15-min period during which a plant had to be watched was arbitrarily determined each day. Plants on site B were not observed as often, but all censuses were done simultaneously with censuses done in site A by another person. The total observation time per plant varied from 60 to 150 min at site A and from 15 to 75 min at site B. Total time spent watching plants was 58.25 h at site A and 26.25 h at site B. In 1996, censuses of flower visitors at both sites were again made, from 9 April to 12 April, mainly to confirm the observed patterns found in 1995. A total of 28 plants from site A and 38 from site B were observed during 7.75 h and 9 h, respectively. In 1996 censuses were also done at dusk to discover any possible nocturnal pollinator of the plant.

For each animal visit to a plant we recorded: (1) the type of visitor, (2) the number of inflorescences visited (often we could not observe the total number, so data represent the minimum number of cyathia visited), and (3) total time spent on the plant. When the visitor was an insect we categorized it in one of seven groups: hemipterans, lepidopterans, hymenopterans – in the particular case

of *Ancistrocerus ebusianus* visits, we recorded the species name as it is easily distinguishable from the other wasps – and among the flies we distinguished Calliphoridae, Syrphidae and other Diptera – which included species in the families Sarcophagidae, Anthomyiidae, Muscidae, Scathophagidae and Ephydriidae.

The quantitative component of the plant-pollinator interaction (NFV, defined as the total number of flowers of an individual plant visited by the population of a pollinator per time unit, *sensu* Herrera 1989) was calculated, separately for lizards and insects, multiplying their abundance (frequency of visits) by their flower visitation rate (number of cyathia visited per minute).

A number of plant variables which might be relevant criteria used by lizards and/or insects when visiting inflorescences were measured on the plants at site A. These traits were: (1) plant height, (2) plant width, (3) total number of cyathia, (4) number of cyathia with available nectar, and (5) plant orientation (predominant direction of branches and inflorescences). Two additional variables measured the opportunity for lizards to reach the cyathia: (6) height of the lowest branch (lizards climb the trunk usually using the lowest branches), and (7) level of access to the plant, a qualitative variable that indicates the percentage of the shrub perimeter contacting any sort of substrate, whether ground, rocks or other plants. An index from 0 to 4 was given to each individual plant: 0 = the lizard has to climb the trunk to reach the branches, 1 = 1–25%, 2 = 26–50%, 3 = 51–75%, 4 = 76–100% of canopy perimeter contacting the substrate. From site B, data on plant size and fecundity were also recorded for comparison.

Lizards as pollen vectors

To evaluate the pollen load that *P. lilfordi* carries among flowers, we captured several individuals and examined the pollen attached to their snouts. Three lizards were caught while there were lapping nectar, by means of a slipknot at the end of a 1 m pole, and other seven individuals were trapped into plastic trays placed under *E. dendroides* shrubs. The pollen grains were collected on a piece of transparent tape, stuck around the snout and immediately removed, and were counted under a dissecting microscope (at 30–40 \times).

In addition, we wanted to determine the potential pollen load that lizards could carry after visiting a known number of cyathia, both before and after contacting the sticky nectar. For this, we first held six individuals and rubbed their snouts against the stamens of five cyathia. Pollen from each lizard was collected on separate tapes. We then repeated the operation but previously rubbing the snout of each lizard with five nectar glands. The number of grains in each treatment was later recorded.

Reproductive success

Experiments on selective exclusion of pollinators were not possible in this study because of the difficulty of excluding insects without affecting the visits by lizards to the shrubs. However, the fact that, within the same plant population, lizards were abundant at one site and very rare at the other – and no plant variables measured differ between sites – allows us to estimate the effect of each type of pollinator on plant reproductive success.

Reproductive success was determined both in 1995 and in 1996. The first year, we examined fruit set (number of fruits produced/number of cyathia) in a total of 15 individuals, haphazardly chosen from each site. From each plant 50 cyathia were labelled on 23 March, and the number of fruits produced was recorded on 4–5 May. To know not only the number of seeds produced (three per capsule, except on very few occasions) but also the quality (viability) of the seeds, we opened the capsules of 10 of those individuals from each site and dissected, using forceps, a random sample of 50 seeds from each site. Each seed was classified as viable (with the locule filled with white endosperm), aborted (the endosperm was dry and yellowish and did not fill the locule) or attacked

by the wasp larva *Bruchophagus* sp. (Eurytomidae). Attacked seeds were added to the viable ones as larvae can grow only on seeds full of endosperm. The total number of viable seeds produced may still be underestimated as some larvae might have promoted seed abortion at an early stage. The following year, on 7 May, we again recorded the fruits produced in 25 haphazardly chosen cyathia from each of 10 plants at each site. From each individual, 25 capsules were opened, and a random sample of 25 seeds was dissected. We could therefore evaluate the variation of viable seed production in each site. Total flower crop was recorded for each plant.

Lizard density at the two sites

We carried out lizard censuses to corroborate observations that population densities of this animal varied between sites A and B. A straight-line transect was covered on foot, at both sites, scanning ahead and recording the number of individuals seen before they flushed, and the length of the transect was walked at a constant speed during 10 min. We recorded the animals sighted in a strip 3 m wide. We did the censuses on warm, sunny and windless days, between 1000 hours and 1230 hours (GMT) – the period of greatest lizard activity during the day. The transects were walked on four different days during the flowering period of *E. dendroides*.

Density of vegetation at the two sites

The different lizard densities found between sites A and B could be due to different densities of *E. dendroides* shrubs and/or to different vegetation cover (used by lizards as a refuge). To explore this possibility, we measured the number of *E. dendroides* shrubs and the number of meters without tall (> 50 cm) vegetation in a total of 10 transects, 15 m long and 2 m wide, at each site.

Data analysis

All analyses were performed using the SAS statistical package (SAS 1987). Procedure NPAR1WAY was used to do Wilcoxon's tests and procedure CORR was employed to calculate the correlations among variables. Analyses of variance were done with the procedure GLM. Both logarithmic and angular transformations were used to normalize data before analyses. All means are accompanied by their standard deviations, unless otherwise indicated.

Results

Breeding system

There is no autogamy in *E. dendroides* as none of the individual bagged cyathia developed a fruit (Table 1). This is because the flowers are protogynous, the stigma being no longer receptive when stamens dehisce. Pollen was not limiting, and self- and cross-pollen produced similar fruit sets ($F_{2,11} = 0.33$, $P > 0.05$) and seed sets ($F_{2,11} = 0.50$, $P > 0.05$) (Table 1). Considering that each ovary contains three ovules, the average seed/ovule ratio was 0.28 (± 0.23) and did not differ among treatments either ($F_{2,11} = 0.50$, $P > 0.05$). There is, presumably, some pollination by wind as some buds that were included in the same bag and were not hand-pollinated developed into fruits and produced viable seeds (A. Traveset unpublished work).

Table 1 Fruit set (proportion of flowers that set fruit, seed set (viable seeds/flowers) and seed:ovule ratio (ovules = flowers \times 3) in the different treatments of the hand-pollination experiments. Data are from five *Euphorbia dendroides* plants at site A. Geitonogamous crosses could not be performed in one plant because none of its stamens were dehiscing when stigmas were hand-pollinated. The number of flowers monitored in each plant for each treatment ranged from 9 to 25. No significant differences were found among the three pollination treatments for any of these three reproductive parameters

Treatment	No. flowers monitored	Fruit set $\bar{x} \pm SE$	Seed set $\bar{x} \pm SE$	Seed/ovule $\bar{x} \pm SE$
Geitonogamy	55	0.39 \pm 0.16	0.57 \pm 0.20	0.19 \pm 0.07
Xenogamy	104	0.45 \pm 0.13	1.05 \pm 0.32	0.35 \pm 0.11
Control	120	0.55 \pm 0.13	0.83 \pm 0.39	0.28 \pm 0.13
Autogamy	39	0	0	0

Table 2 Differences in patterns of flower visitation between lizards and insects. Flower visitation rate (FVR) refers to the number of cyathia visited per minute. NFV represents the quantitative component of the plant-pollinator interaction (defined as the total number of flowers of an individual plant visited by the population of a pollinator per time unit). Data are from 27 plants observed in 1995 in site A. Ranges are given in parentheses

Variable	<i>Podarcis lilfordi</i> $\bar{x} \pm SE$	Insects $\bar{x} \pm SE$	Wilcoxon's test χ^2_1	<i>P</i>
No. visits/min	0.09 \pm 0.02 (0–0.32)	0.03 \pm 0.002 (0–0.12)	6.93	**
FVR	0.99 \pm 0.18 (0–3.33)	0.12 \pm 0.03 (0–0.61)	21.44	***
Visit duration (s)	154 \pm 12 (60–298)	47 \pm 12 (2–284)	25.50	***
NFV	0.15 \pm 0.04 (0–0.96)	0.009 \pm 0.003 (0–0.05)	16.33	***

** $P < 0.01$, *** $P < 0.001$

Flower visitation patterns by lizards and insects

The patterns of flower visitation by the two types of pollinators were compared at site A, where lizards were abundant (Table 2). The frequency of lizard visits was found to be associated with total flower crop ($r_s = 0.57$, $P = 0.003$, $n = 27$ plants) and with the number of cyathia producing nectar ($r_s = 0.53$, $P = 0.004$, $n = 27$) but not with the variables describing plant size, even though the total number of cyathia produced was directly correlated with both plant height ($r = 0.51$, $P = 0.01$, $n = 27$) and canopy width ($r = 0.57$, $P = 0.003$, $n = 27$). Neither plant orientation, accessibility to the cyathia, nor height of the lowest branch appeared to influence the number of lizards visiting the shrubs (all $P > 0.05$). Flower visitation rate by lizards also increased with flower crop ($r_s = 0.59$, $P = 0.002$, $n = 25$) and with the number of cyathia with available nectar ($r_s = 0.54$, $P = 0.004$, $n = 25$). Lizards spent 1–5 min on a plant, this time being independent of the plant traits measured. Up to five individuals were ob-

Table 3 List of the insect species that visited the flowers of *E. dendroides* in Cabrera island during 1995, and percentage of visits made by each category of insects censused

Order	Species (Family)	Visits
Diptera	<i>Calliphora vicina</i> (Calliphoridae)	8.0%
	<i>Calliphora vomitoria</i> (Calliphoridae)	
	<i>Lucilia sericata</i> (Calliphoridae)	
	<i>Episyrphus balteatus</i> (Syrphidae)	19.2%
	<i>Eupeodes corollae</i> (Syrphidae)	
	<i>Scaeva pyrastris</i> (Syrphidae)	
	<i>Fucellia tergina</i> (Anthomyiidae)	
	<i>Anthomyia confusanea</i> (Anthomyiidae)	21.0%
	<i>Hebecnema fumosa</i> (Muscidae)	
	<i>Lispe pygmaea</i> (Muscidae)	
<i>Scathophaga stercoraria</i> (Scathophagidae)		
<i>Sarcophaga bolivari</i> (Sarcophagidae)		
	Unidentified species (Ephydriidae)	
Hymenoptera	<i>Ancistrocerus ebusianus</i> (Eumenidae)	36.6%
	<i>Anthophora balearica</i> (Anthophoridae)	11.3%
	unidentified species	
Hemiptera	<i>Spilostethus pandurus</i> (Lygaeidae)	3.3%
Lepidoptera	<i>Cynthia cardui</i> (Nymphalidae)	0.5%

served at the same time on one shrub, and only one labelled plant in this site had no records of lizards. A lizard could lap nectar from many cyathia (up to 67 in our censuses) in a single visit to a plant.

The frequency of insect visits (all groups pooled) to flowering plants was significantly lower than that of lizards (Table 2) and independent from it ($r_s = 0.17$, $P > 0.05$, $n = 27$). Insect visits increased with the number of cyathia producing nectar ($r_s = 0.44$, $P = 0.003$, $n = 25$) though they were only marginally correlated with total flower crop ($r_s = 0.37$, $P = 0.07$, $n = 25$). The other plant traits had no apparent influence on the frequency of insect visits. Flower visitation rate by insects also increased with flower crop ($r_s = 0.47$, $P = 0.02$, $n = 25$). The time that an insect stayed on a plant ranged from 2 s to *c.* 5 min, and was independent of all plant traits measured. Usually, insects contacted only a few cyathia at each visit, but occasionally visited over 50. No flower visitors were observed at dusk, indicating that at least in Cabrera all pollinators of *E. dendroides* are diurnal.

Altogether, the quantitative component of the plant-pollinator interaction (NFV), representing a composite measure of visitation frequency and rate, was far greater for lizards than for insects at site A (Table 2). Lizards, overall, visited plants 3 times as often as insects did, stayed on the plant about 3 times longer, and contacted about 8 times more cyathia per minute than did insects.

At least 18 different species of insects visit the flowers of *E. dendroides* in Cabrera (Table 3). All are potential pollinators as they contact both anthers and stigmas. Except for *A. ebusianus* and for the syrphid group, more commonly observed in site A than in site B (see next section), all other groups were equally abundant in the two sites examined.

Table 4 Frequency of visits and flower visitation rate (FVR) by lizards and insects in the two study sites during the two halves (periods 1 and 2) of the flowering season of 1995. Wilcoxon's tests were used to compare (1) areas within each period and (2) periods within each area, for lizards and insects separately. Means with the same letter are not significantly different ($P > 0.05$). A total of 50 plants were observed from site B, although not all of them in both periods

Site	Period	<i>n</i>	Time of observ. (min)	<i>P. lilfordi</i>		Insects	
				No. of visits/min	FVR	No. of visits/min	FVR
A	1	27	1425	0.10 ^a	1.23 ^a	0.008 ^c	0.02 ^c
	2	27	2070	0.09 ^a	0.76 ^a	0.07 ^d	0.18 ^d
B	1	31	570	0.005 ^b	0.01 ^b	0.06 ^c	0.18 ^c
	2	30	1005	0.01 ^b	0.03 ^b	0.03 ^c	0.05 ^c

Table 5 Number of individuals of each insect species found visiting the flowers of *E. dendroides* in the two study sites (A and B) during the first and second halves of the flowering season. Period 1 goes from 21 March to 29 March and period 2 from 30 March to 6 April 1995. Time of observation is in minutes [*n* = number of plants observed, *Dip*: Dipterans other than calliphorids (*Call*) or syrphids (*Syr*), *Hym*: Hymenopterans other than the wasp *Ancistrocerus ebussianus* (*A.ebu*), *Hemip*: Hemipterans]^a

Site	Period	Time obs.	<i>n</i>	Insect species					
				<i>Dip</i>	<i>Call</i>	<i>Syr</i>	<i>Hym</i>	<i>A.ebu</i>	<i>Hemip</i>
A	1	1425	27	3	0	2	0	7	0
	2	2070	27	20	7	34	9	62	5
B	1	570	31	12	4	2	11	5	0
	2	1005	30	10	6	3	4	4	2

^a An individual of *Cynthia cardui* (Nymphalidae, Lepidoptera) was observed on site A in period 1

Spatio-temporal variation in the frequency of visits

Since an increase in insect abundance was evident over the flowering season (as ambient temperature increased) we arbitrarily divided the observation period into two halves (21–29 March, and 30 March–6 April) to determine differences in their frequency of flower visitation and in the species composition with time.

Table 4 shows the frequency of flower visits by both lizards and insects at the two study sites and the two periods considered. The most striking difference between site A and B was in the number of lizard visits, over ten times more numerous in site A. This was due to the significantly larger population density of these animals in site A (0.33 ± 0.13 (SE) lizards/m²) compared to site B (0.11 ± 0.01 lizards/m²) (t -test, $F = 71.7$, $P < 0.001$, $n = 5$ censuses). Consequently, the number of cyathia that lizards visited per time unit was also much greater at site A than at B (Table 4). Insects increased in abundance as time progressed, though this was observed only in the censuses at site A ($X^2_1 = 26.1$, $P = 0.0001$) (Table 4). The species composition of insects was the same in both sites (Table 5). The increase in abundance over time was especially notable in *A. ebussianus*, in the

Table 6 Differences between the two study sites in plant traits and vegetation cover. Flower crop refers to the number of cyathia produced whereas vegetation cover refers to the number of meters without tall (>50 cm) vegetation in transects of 30 m². Mean and one standard error are given for each variable

Trait	Site A	Site B	<i>t</i> -test
Plant height (cm)	79.6 ± 4.8	86.2 ± 4.3	$F_{1,56} = 1.05$ ns
Plant width (cm)	123.5 ± 7.4	108.7 ± 4.4	$F_{1,56} = 3.22$ ns
Flower crop	788 ± 126	585 ± 72	$F_{1,36} = 1.89$ ns
<i>E. dendroides</i> shrubs/m ²	0.48 ± 0.04	0.44 ± 0.05	$F_{1,18} = 0.53$ ns
Vegetation cover	1.70 ± 0.33	3.82 ± 0.55	$F_{1,18} = 3.30$ **

** $P < 0.01$, ns = not significant

Table 7 Comparison of the frequency of visits, flower visitation rate (FVR) and quantitative component of the plant-pollinator interaction (NFV) between lizards and insects from the data gathered in the flowering season of 1996. Since period of observation for each plant was short this year, data from all plants observed in each daily census ($n = 3$ days at site A and $n = 4$ days at site B) were pooled

Site	Variable	<i>P. lilfordi</i>	Insects	Wilcoxon's test
		$\bar{x} \pm SE$	$\bar{x} \pm SE$	
A	No. visits/min	0.21 ± 0.02	0.18 ± 0.02	0.78 n.s.
	FVR	1.12 ± 0.28	0.86 ± 0.10	0.43 n.s.
	NFV	0.25 ± 0.09	0.16 ± 0.05	1.19 n.s.
B	No. visits/min	0.02 ± 0.02	0.36 ± 0.10	5.40 *
	FVR	0.03 ± 0.02	0.75 ± 0.19	5.40 *
	NFV	0.002 ± 0.002	0.32 ± 0.14	5.40 *

* $P < 0.05$

syrphids and in the diptera (other than syrphids and calliphorids).

Vegetation cover was the only trait found in this study that presumably accounts for the differences between the two sites in the frequency of flower visits by lizards. The shrubs of *E. dendroides* were similar in size, fecundity and density in both places (Table 6).

Due to the extremely low frequency of lizard visits at site B, NFV for the plant-lizard interaction here was 0.0009 ± 0.0004 (SE; $n = 50$ plants) cyathia visited by lizards per minute, *c.* 167 times lower than at site A (Table 2). In contrast, NFV for insects at site B was 0.009 ± 0.005 (SE; $n = 50$ plants), the same as in site A (Table 2). That is, lizards were about 17 times more important quantitatively for the plant-pollinator interaction than insects in site A, but in site B insects visited ten times more cyathia per minute than lizards.

In 1996, a less dramatic difference between insects and lizards was observed (Table 7), probably because censuses were carried out at the late-peak of the flowering season, when insects were more abundant. NFV was again greater for lizards at site A and the opposite occurred at site B. The relative frequency of each insect taxon visiting the flowers of *E. dendroides* differed somewhat from that in 1995. In 1996, syrphid flies were

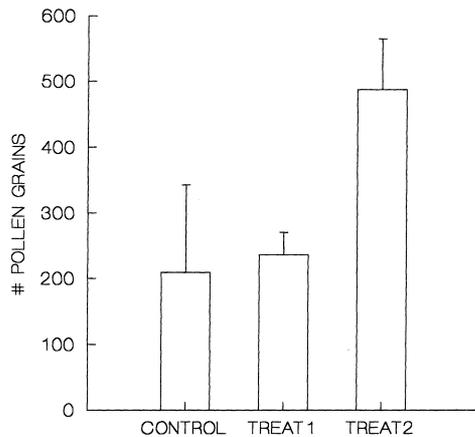


Fig. 1 Potential number of pollen grains carried by lizards in their snout after visiting the flowers of *Euphorbia dendroides*. Treatments consisted on rubbing lizards' snout against the stamens of five cyathia before (treatment 1) and after (treatment 2) contacting the nectaries. The number of pollen grains carried at the moment lizards were trapped (by means of slipknots) was used as control. Standard error bars are given

extremely abundant, representing 56% of the insect visits, whereas *A. ebusianus* only represented 18%. The other 26% of the visits were by other flies, bees and hemipterans.

Lizards as pollen vectors

The mean number of pollen grains carried by captured lizards (control group) was 209 ± 232 ($n = 3$). The lizards caught in traps bore much less pollen (an average of 47 ± 77 grains, $n = 7$) perhaps because they lost it within the tray when trying to escape and/or when feeding upon the tomato bait. Pollen was always more abundant (up to 50% more) in the ventral than in the dorsal part of the snout.

When we rubbed lizards' snouts against the stamens of five cyathia, pollen load increased to 236 ± 98 ($n = 8$, range: 121–409). Such increase was even greater when lizards got nectar in their snouts (488 ± 219 , $n = 8$, range: 203–818) ($F_{2,23} = 13.21$, $P = 0.0002$) (Fig. 1).

Influence of flower visitors on plant reproductive success

In both 1995 and 1996, fruit set was significantly greater at site A than at site B (Table 8). This estimate of reproductive success was significantly correlated to total flower crop, but only in 1996 ($r_s = 0.48$, $P = 0.04$, $n = 20$) and was not influenced by the other plant traits measured (all $P > 0.05$).

The average seed viability (proportion of seeds that were viable) was greater in site A than in site B (Table 8) both years. Variation among shrubs, however, (examined only in 1996) was great, and at least in this year

Table 8 Reproductive success of *E. dendroides* in the two years at the two study sites. Seed set (viable seeds/cyathia) was estimated as the product of: fruit set (fruits/cyathia) \times three (seeds/fruit) \times seed viability (viable seeds/dissected seeds)

Year	Site	Fruit set $\bar{x} \pm SE$ (n)	Seed viability $\bar{x} \pm SE$ (n)	Seed set $\bar{x} \pm SE$ (n)
1995	A	0.89 ± 0.02 (15)	0.68 (50) ^a	1.82
	B	0.73 ± 0.04 (15)	0.42 (50) ^a	0.92
		$\chi^2_1 = 8.46$ **	–	–
1996	A	0.82 ± 0.04 (10)	0.73 ± 0.06 (10)	1.78 ± 0.15 (10)
	B	0.68 ± 0.05 (10)	0.49 ± 0.13 (10)	1.03 ± 0.28 (10)
		$\chi^2_1 = 4.07$ *	$\chi^2_1 = 0.98$	$\chi^2_1 = 3.03$ [†]

* $P < 0.05$ ** $P < 0.01$ [†] $P = 0.08$ for the Wilcoxon's tests

^a Seeds from 10 individuals were pooled

there were no significant differences between sites. Seed set (viable seeds/cyathia) was only marginally greater at site A than at site B (Table 8). Such seed set was not associated with flower crop ($r_s = 0.06$, $P > 0.05$).

Discussion

E. dendroides depends on pollen vectors for reproduction, as shown by the lack of fruit set in bagged flowers. The species is self-compatible and geitonogamous pollination appears just as effective as outcross pollination. Pollen was not limiting, at least at site A (where hand-pollinations were performed) probably because pollinators were abundant here. Moreover, wind might also contribute to pollination, as has been found in other entomophilous species (e.g. Gómez and Zamora 1996).

P. lilfordi showed to be an effective pollinator of the plant. While searching for nectar, it collects large quantities of pollen from the anthers, mostly in the ventral part of the snout, moving it among cyathia and promoting both geitonogamy and cross-pollination. When the snout is impregnated with nectar, the amount of pollen carried is even greater (Fig. 1). Geckos (genus *Hoplodactylus*) have also been reported to collect considerable amounts of pollen, mostly on their throats, transporting it for many meters (up to at least 50 m) and for a long time (at least 12 h) (Whitaker 1987). *P. lilfordi* sometimes consumes the stamens of *E. dendroides*, so it may lower plant male fitness to some degree as well.

The fact that the plant flowers early in the year when temperatures are still low (minimum 10°C, maximum 16°C, on average) and few insects are flying, together with the low number of species blooming at that time (which might compete for pollinator attraction), are probably the main reasons that lizards spend a considerable amount of time searching for the copious and highly nutritious nectar on this shrub. *Rosmarinus officinalis* and *Globularia alypum* are the only two species present in the area that flower simultaneously with *E. dendroides*. Both plants (with entomophilous flowers) are also visited by *P. lilfordi*, but at a much lower frequency than *E. dendroides* (Sáez and Traveset 1995).

Pollination by lizards is probably a common phenomenon in a variety of places where these animals have been reported to feed on nectar (Elvers 1977; Evans and Evans 1980; Whitaker 1987; Dearing and Schall 1992; Eifler 1995) but little attention has been given to the possibility that they act as pollinators. In fact, pollination by reptiles may be a very ancient interaction, perhaps even older than pollination by beetles, as suggested by Hughes (1976, p. 57). Coprolites from the Permian and Jurassic periods indicate that reptiles were already browsing on flowers by that time (Schwitzer 1968; Harris 1945, 1956; cf. Elvers 1977; Faegri and Van der Pijl 1979).

A great spatial variation on a small local scale was found in the importance of the two kinds of pollinators (lizards vs. insects) for the reproduction of *E. dendroides*. Vegetation cover, twice as dense at site A, is presumably the main factor that causes the different lizard density at the two sites and, ultimately, the variability in frequency of visits to plants. Two other factors that have been suggested to cause local spatial variability in plant-pollinator interactions are plant population size (Sih and Baltus 1987; Sowig 1989; Jennersten and Nilson 1993; Conner and Neumeier 1995) and sunlight regime (Herrera 1995).

Differences in insect abundance on a very small spatial scale have been attributed to the existence of microhabitat selection by pollinators (e.g. Beattie 1971) and may be associated with differences in features of flower supply, plant traits and/or microclimatic aspects (e.g. Herrera 1988). Different causes probably apply to different species of insects, so for instance the abundance of the wasp *A. ebusianus* in site A might be associated to the presence of its prey (moth larvae) there. Temporal variation in insect abundance was also evidenced, both within the season (at least the wasp *A. ebusianus*, the syrphids and other Diptera increased their populations considerably during the season of 1995), and between years (at least the syrphids were much more abundant in 1996 than in 1995). The insect abundance on Cabrera is very low compared to that on the neighbouring island of Mallorca (about 300 times greater in size) during the same period (A. Traveset, personal observations). The species composition and the frequency of visits by insects on Cabrera appear to be even lower (30–40 times) when compared to other studies carried out in the mainland (Herrera 1989; Gómez and Zamora 1992).

When a diverse assemblage of pollinators visits a plant, the most abundant visitor species may or may not be that which transfers the greatest amount of pollen (e.g., Primack and Silander 1975; Galen 1989; Herrera 1989; Horvitz and Schemske 1990; Waser and Price 1990). In the present system, lizards maintain the strongest interaction with *E. dendroides* in site A, since they are the most abundant and temporally predictable pollinators besides carrying a greater quantity of pollen than do insects. In other studies that have compared flower visitation patterns and pollinator effectiveness

between insects and vertebrates (birds in all cases), it is also found that the latter are more effective when insects are scarce, in high elevations habitats (Cruden 1972) or in early-flowering periods, when temperatures are usually low (Waser and Price 1990; Vaughton 1992).

The differences in fruit and seed set between sites A and B are mainly attributed to the different frequency of visits by lizards in the two sites. Even though insects were also more abundant at site A, they represented a much lower fraction of the total visits to the cyathia than lizards. Plants with large flower crops were visited more frequently by both lizards and insects (and with a higher flower visitation rate) than plants with small crops, which might explain the greater fruit set found on the former (at least in 1996). Seed set (proportion of cyathia that develop into viable seeds), however, appeared to be independent of number of cyathia produced, being probably influenced by factors such as resource supply or genetic incompatibilities. This makes it unlikely, therefore, that there is pollinator-mediated selection on such plant trait. Fruit and seed set are usually influenced by a variety of factors, both biotic and abiotic, in addition to pollinator service. It is because of this diversity of factors that the importance of pollinators cannot be judged by simply comparing the pollinator assemblage and mean fruit production for different years (Schemske and Horvitz 1989; Campbell 1991).

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