ISRAEL JOURNAL OF BOTANY, Vol. 34, 1985, pp. 47–58

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NECTAR SECRETION PATTERNS IN SOUTHERN SPANISH MEDITERRANEAN SCRUBLANDS

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ABSTRACT

Most species in the scrublands of Andalucia (southern Spain) either secrete no nectar or are insignificant nectar producers. Although the 122 species studied belong to 23 families, the nectar secretion pattern is largely determined by three families: Cistaceae, Labiatae and Leguminosae. The amount of sugar secreted by nectariferous species is positively related to flower dry weight. The amount of sugar produced, for a given floral dry weight, is significantly higher for species with tubular corollas than for species with non-tubular ones.

Insects may visit flowers for a variety of non-energetic substances, such as sexual attractants (Dressler, 1968; Simpson & Neff, 1981) and trichomes or resins (Faegri & van der Pijl, 1979).. They may also seek resting sites (Daphni et al., 1981) or visit a non-rewarding flower that resembles a truly rewarding one (Daphni & Ivri, 1981). Nevertheless, food (pollen and nectar) is the most common reward offered by plants to insect pollinators. Pollen is thought to have been the original food sought by the most primitive anthophilous insects (Crepet, 1979; Kevan & Baker, 1983). Subsequent evolutionary changes have improved the energetic efficiency of the plant—pollinator relationship, and pollen has very often been replaced by nectar, a less "expensive" material (Baker, 1963; Baker & Hurd, 1968; Takhtajan, 1980). Nectar is a complex mixture of substances, consisting mainly of sugars. It is the floral reward most frequently offered by extant insect-pollinated plants to pollinators (see Kevan & Baker, 1983 for an extensive review).

The aim of this study was to determine the frequency of occurrence of nectar as a floral reward among the woody plant species of southern Spanish mediterranean scrub formations. The quantity of sugar secreted was investigated and related to floral attributes such as size and structure.

STUDY AREA AND METHODS

Data were collected mainly in six localities broadly distributed across the province of Andalucia, southern Spain (36—38°N, 3—7°W), during extensive regional studies on

Received July 17, 1984 and in revised form January 23,1985

the reproductive biology of scrub formations. Four of these sites were in mountainous parts of the region (Sierra de Algeciras, Sierra de Cazorla, Sierra Morena and Sierra de Ronda) and the remaining two near the coast (Donana National Park and Barbate). They encompass a broad variety of habitat types, ranging from coastal sclerophyllous scrub to heathland and mixed oak-pine forests (maximum elevation 1600 m). All major mediterranean scrub types in the region have been sampled. Site descriptions may be found in Polunin and Smythies (1981) and Herrera (1982).

Nectar secretion was investigated during 1982 and 1983 in 122 woody species which include all the major constituents of southern Spanish entomophyllous scrub. The presence or absence of floral nectar was determined for every species in the field (by bagging flowers for 24 h when necessary) and/or in cut flowering stems kept in sealed plastic bags for 24 h at room temperature under a natural light regime. Flowers on cut stems were examined under a dissecting microscope for the presence of nectar and the production quantified for 28 of the original 122 species, to which were added 14 non-woody species (bulbous and annual or perennial herbs). Nectar was extracted and its volume determined with 5-pl callibrated micropipettes. The concentration of diluted solids, mainly sugars (Baker & Baker, 1975, 1983; Harborne, 1982) was measured (on a weight-weight basis) with a temperature-compensated hand refractometer.

The main reason that nectar secretion was quantified from flowers on cut stems kept in plastic bags was that most species were found to have very concentrated nectar

TABLE I

Average sugar secretion, concentration and volume of nectar secreted in three plant species

Species		*Sugar secreted (mg/flower/day)*	*Nectar concentration (% w/w)*	*N*[4]	*Nectar volume (,ul)*	*N*
Lavandula latifolia	a[1]	0.28	56.0 ± 2.0[3]	13	0.5 ± 0.1	13
	b	0.20	33.4±1.5	12	0.6±0.1	14
Lonicera periclymenum	a	2.05	24.7 ± 0.1	4	8.3 ± 0.7	4
	b	2.33	21.4 ± 0.8	15	10.9 ± 0.8	15
Rosmarinus officinalis[2]						
Population 1	a	0.41	47.6 ± 2.0	15	0.9 ± 0.1	81
	b	0.45	21.4 ± 0.5	27	2.1 ± 0.1	73
Population 2	a	0.23	45.3 ± 3.7	9	0.5 ± 0.1	58
	b	0.27	20.9±0.4	10	1.3±0.1	23

[1] a - production by bagged flowers in the field; b - production by flowers on cut stems.

[2] Two populations of *Rosmarinus officinalis* were studied: (1) at 1000 m elevation, on limestone mountains under a regime of relatively high rainfall (1400 mm/yr), Sierra de Cazorla; (2) on dry (550 mm/yr) sandy soil, coastal area, Donana National Park.

[3] Mean ± SE.

[4] N - number of measurements.

in the field (commonly higher than 60%) so that manipulation and measurement of nectar was extremely difficult. This, together with the fact that in many species only minute volumes of nectar were secreted by individual flowers, made accurate quantification under natural conditions virtually impossible. In three control species for which nectar yield and nectar concentration were determined from intact and cut flowering stems, the absolute *weight of sugar* secreted per flower (volume X concentration) remained in the same order of magnitude regardless of the procedure (Table I). Flowering stems inside plastic bags secreted relatively dilute nectar (rarely exceeding 25%), this being compensated by larger volumes than in the field, probably due to the high relative humidity inside the bags (Corbet et al., 1979a). Note that neither volume nor concentration are used later for comparisons, but rather the parameter resulting from multiplying the two together (i.e. weight of sugar), which is only slightly affected by the method and is directly related to energetic profitability for insects. (See Cruden & Hermann, 1983, for a discussion on the measurement methods of nectar secretion.)

In the species with quantified nectar secretion the average dry weight of individual flowers (excluding the pedicel) was determined to the nearest 0.1 mg by weighing samples 'of 12—100 air-dried flowers. Weight was used subsequently as an indirect estimate of flower size in the analyses below.

RESULTS

Incidence of Nectar Production

The woody plant species examined for nectar production belonged to 23 families of which three (Cistaceae, Labiatae and Leguminosae) accounted for 58% of the total species, whilst the remaining 18 families each contributed less than 2% of the total (see Appendix A for a species list).

Three patterns of nectar secretion were distinguished (Table II). In 50 species (Class 0), floral nectar could not be ascertained in any of the populations examined.

TABLE II

Distribution of woody plant species of southern Spanish scrublands among nectar production classes: 0 — nectar not detected; 1 — nectar present in minute amounts (less than 0.5 μl), hardly detectable; 2 — nectar in amounts sufficiently large to make it easily detectable

	Nectar production class		
Family	*0*	*1*	*2*
Cistaceae	9	9	0
Labiatae	0	2	21
Leguminosae	24	2	6
Others	17	18	16
Total	50	29	43
%	41	24	35

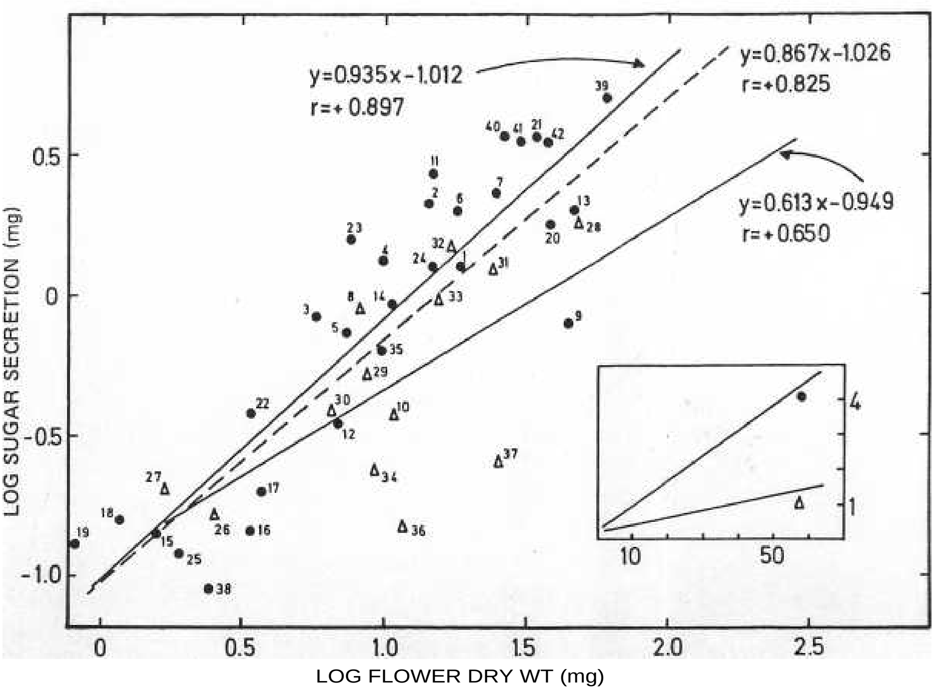

Fig. 1. Variation of sugar secretion with floral dry weight (both in mg) in a sample of 42 southern Spanish plant species. Species are identified by their numbers in Appendix B, where data used are shown in detail. Broken line — regression for all species combined, solid lines correspond to separate regressions for sympetalous (filled dots) and polypetalous (open triangles) species. Inset shows variation of sugar secretion with flower weight for untransformed data.

In 29 species (Class 1) nectar was present in such minute amounts (less than 0.5 µl/ flower/24 h) that it was detected only after close and careful examination. Only in 43 species was the presence of nectar easily ascertained, usually in large amounts (Class 2). Among the three main families, all species in the Labiatae were consistent producers, while the Cistaceae and Leguminosae were dominated by species with pollen flowers which did not secrete nectar, or which did so in minute amounts.

Sugar Secretion, Flower Size and Sympetally

Average values for sugar secretion and flower dry weights for 42 species (28 woody and 14 non-woody) are shown in Appendix B. A significant positive correlation exists between sugar production and dry weight of flower ($r = 0.745$, df = 40, $P < 0.01$, untransformed data). Log-transformed data have been used for clarity in Figure 1, but the significance of the relationship is insensitive to the transformation ($r = 0.825$, $P < 0.001$, for log-transformed data).

Twenty-nine of the 42 species included in the analyses have sympetalous, mostly tubular flowers, while flowers' in the remaining 13 species are polypetalous, with corollas having free and distinct petals, lacking a tube. Since species with tubular flowers tend to be distributed above the regression line and species with polypetalous flowers below it (Fig. 1), separate linear regressions were obtained for each of these groups. Regressions were compared by covariance analysis (F = 8.92, df = 1.39, P = 0.0054). For a given floral dry weight, the average amount of sugar produced is significantly higher for species with tubular flowers than for species with non-tubular ones, the difference becoming larger with increasing flower dry weight as illustrated by the divergence of respective regression lines (Fig. 1).

DISCUSSION

Frequency of Nectar Production

The present survey of 122 southern Spanish scrub species has revealed that only 35% may actually be considered nectariferous. Most of the remaining species offer no nectar at all. Others secrete negligible amounts of nectar per flower, where the nectar probably acts as a secondary attractant while pollen is the main reward (e.g. *Cistus* spp.). Thus, in terms of *number* of species and on a regional basis, nectar is not a widespread floral reward in southern Spanish entomophyllous scrub, and this observation agrees with the generalizations made by Southwick (1982) for the north temperate area as a whole.

Extensive areas of the study region may be considered sub-arid (annual rainfall below 600 mm; Lines Escardo, 1970). Thus, reduced water availability could explain the relative scarcity of species producing a large amount of nectar. Although the ability of a species to secrete nectar is clearly genetically determined, this ability may be realized only if environmental conditions render it possible (Percival, 1965). For example, watering may significantly increase nectar secretion with respect to non-watered individuals of *Delphinium nelsonii* (Zimmerman, 1983). Also, nectar secretion may vary from year to year within a population, depending on the amount of rainfall (see Cruden et al., 1983; Hiebert & Calder, 1983). If water stress operates against abundant nectar secretion, the low average rainfall and/or the high variability in precipitation between years in the study, area (Lines Escardo, 1970) could be expected to have selected against taxa which produce nectar as the sole reward to pollinators. Species that rely on a copious and constant production of pollen may have a higher or more constant seed-set than the nectariferous ones, and so perhaps have greater reproductive success.

Whichever hypothesis we select to explain the existence of a pollen-rich group of species, we must bear in mind that there exists a certain degree of phylogenetic constraint. Most species in the present study belong to just three families which are largely responsible for the patterns described above. The Cistaceae produce little or no nectar, and in those members of the Leguminosae present in the study area (mainly species of the tribe Genisteae), absence of nectar is the rule. Only the Labiatae may be considered truly nectariferous.

Sugar Secretion of Nectariferous Flowers

As shown above, large flowers are -energetically more rewarding than small ones. This result agrees with the findings of Opler (1983), obtained during an extensive survey of Costa Rican species with different pollination syndromes, and must be related to the fact that flower—visitor relative sizes and plant reward—visitor needs have to be adjusted for the system to work adequately (see Heinrich & Raven, 1972; Hickman, 1974; Pyke, 1978; Waddington, 1980; Heinrich, 1981; Cruden et al., 1983; among others). It may be asked here why, for the same flower weight, sympetalous species are more rewarding than polypetalous ones? Most of the sympetalous species in the study area possess shorter or longer tubular corollas, which restrict the range of visitors able to make a profitable foraging. We suggest that the relatively specialized vectors required to pollinate such flowers receive a superior "payment" for their services in the form of surplus nectar. In other words, tubular flowers must be more rewarding, or the vectors would leave them to visit easier ones (see Heinrich & Raven, 1972; Heinrich, 1981). At the same time, the tube may provide an exclusion mechanism for poor pollinators and robbers (Inouye, 1980, 1983; Herrera et al., 1984), and helps to control the problem of excessive nectar viscosity (Corbet et al., 1979a,b).

Appendix A

Entomophyllous scrub species for which the presence of flower nectar was determined. An index of secretion intensity (0, 1, 2) is indicated for every species. See text for details

Family	*Species*	*Secretion index*
Apocynaceae	*Nerium oleander* L.	0
Berberidaceae	*Vinca difformis* Pourret	2
	Berberis hispanica Boiss. et Reuter	0
Boraginaceae	*Lithodora fruticosa (L.)* Griseb	2
Capparidaceae	*Capparis spinosa* L.	2
Caprifoliaceae	*Lonicera arborea Boiss.*	2
	L. implexa Aiton	2
	L. periclymenum L.	2
	L. splendida Boiss.	2
	Viburnum tinus L.	2
Cistaceae	*Cistus albidus* L.	1
	C. crispus L.	1
	C. ladanifer L.	1
	C. laurifolius L.	1
	C. libanotis L.	1
	C. monspeliensis L.	1
	C. populifolius L.	1
	C. psilosepalus Sweet	1
	C. salvifolius L.	1
	Fumana ericoides (Cay.) Gand.	0
	F. thymifolia (L.) Spach ex Webb.	0
	Halimium atriplicifolium (Lam.) Spach.	0

Appendix A (Contd.)

Family	*Species*	*Secretion index*
	H. commutatum Pau	0
	H. halimifolium (L.) Willk.	0
	H. lasianthum (Lam.) Spach.	0
	Helianthemum croceum (Desf.) Pers.	0
	H. hirtum (L.) Miller	0
	H. origanifolium (Lam.) Pers.	0
Compositae	*Helichrysum picardii* Boiss. et Reuter	0
	H. stoechas (L.) DC	0
	Phagnalon saxatile (L.) Cass.	1
	Santolina rosmarinifolia L.	0
Ericaceae	*Arbutus unedo* L.	2
	Calluna vulgaris (L.) Hull	1
	Erica arborea L.	0
	E. australis L.	2
	E. ciliaris L.	2
	E. erigena R. Ross.	0
	E. lusitanica Rudolphi	0
	E. umbellata L.	1
Labiatae	*Ballota hirsuta* Bentham	2
	Calamintha sylvatica Bromf.	2
	Lavandula lanata Boiss.	2
	L. latifolia Medicus	2
	L. stoechas L.	2
	L. viridis L'Her.	2
	Marrubium supinum L.	2
	Origanum virens Offmanns et Link	2
	Phlomis crinita Cay.	2
	P. lychnitis L.	2
	P. purpurea L.	2
	Rosmarinus officinalis L.	2
	Stachys circinata L'Her.	2
	Teucrium fruticans L.	2
	T. polium L.	2
	T. scorodonia L.	2
	Thymus baeticus Boiss. ex Lacaita	2
	T. capitatus (L.) Hoffmann et Link.	2
	T. granatensi Boiss.	2
	T. mastichina L.	2
	T. tomentosus Willd.	2
Leguminosae	*Adenocarpus telonensis* (Loisel) DC	0
	Anthyllis cytisoides L.	2
	A. tejedensis Boiss.	2
	Calicotome villosa (Poiret) Link.	0
	Chamaespartium tridentatus P. Gibbs	0
	Chronanthus biflorus (Desf.) Frodin et Heyw.	0

Appendix A (Contd.)

Family	*Species*	*Secretion index*
	Coronilla juncea L.	0
	C. minima L.	0
	Cytisus baeticus (Webb) Steudel	0
	C. grandiflorus DC	0
	C. malacitanus Boiss.	0
	C. patens L.	0
	C. scoparius (L.) Link	0
	C. villosus Pourret	0
	Dorycnium rectum (L.) Ser.	2
	Echinospartum boissieri (Spach) Rothm.	0
	Erinacea anthyllis Link	2
	Genista cinerea (Vill.) DC	0
	G. hirsuta Vahl	0
	G. triacanthos Brot.	0
	G. tridens (Cay.) DC	0
	Lotus creticus L.	2
	Psoralea bituminosa L.	2
	Retama monosperma (L.) Boiss.	1
	R. sphaerocarpa (L.) Boiss.	1
	Spartium junceum L.	0
	Stauracanthus boivinii (Webb) Samp.	0
	S. genistoides (Brot.) Samp.	0
	Teline linifolia (L.) Webb et Berth	0
	T. mompessulana (L.) C. Koch	0
	Ulex minor Roth	0
	U. parviflorus Pourret	0
Liliaceae	*Asparagus aphyllus* L.	2
	Ruscus aculeatus L.	0
	Smilax aspera L.	0
Myrtaceae	*Myrtus communis* L.	0
Oleaceae	*Jasminum fruticans* L.	2
Plumbaginaceae	*Armeria velutina* Welw. ex Boiss. et Reuter	1
Primulaceae	*Coris monspeliensis L.*	1
Ranunculaceae	*Clematis cirrhosa* L.	0
	C. flammula L.	0
	C. vitalba L.	0
Rhamnaceae	*Frangula alnus* Miller	1
	Rhamnus alaternus L.	1
	R. lycioides L.	1
Rubiaceae	*Putoria calabrica* (L. fil.) DC	2

Appendix A (Contd.)

Family	*Species*	*Secretion index*
Santalaceae	*Osyris alba* L.	1
	O. quadripartita Salzm. ex Decne	1
Scrophulariaceae	*Antirrhinum majus* L.	2
Thymelaeaceae	*Daphne gnidium* L.	1
	D. laureola L.	1
	Thymelaea hirsuta (L.) Endl.	1
Umbelliferae	*Bupleurum fruticosum* L.	1
	B. spinosum Gouan	1

Appendix B

Data on flower weight and sugar secretion rate used in the analyses. Numerals identifying species in Figure 1 correspond to those shown below

Family/Species	*Flower type*'	*Average dry wt of flowers (mg) (N)*	*Daily sugar secretion*[2] *(mg/flower/day)*	*N1*	*N2*
Apocynaceae					
1. *Vinca difformis* Pourret	S	18.80(20)	1.25 ± 0.09[3]	25	26
Boraginaceae					
2. *Borago officinalis* L.	S	14.30(15)	2.14 ± 0.17	19	19
3. *Cynoglossum cheirifolium* L.	S	5.87(20)	0.85 ± 0.09	10	10
4. *Echium albicans* Lag. & Rodr.	S	10.10(20)	1.34 ± 0.16	15	15
5. *Lithodora fruticosa (L.)* Griseb	S	7.57(20)	0.73 ± 0.09	18	24
Caprifoliaceae					
6. *Lonicera implexa* Afton	S	18.51(20)	2.01 ± 0.19	15	15
7. *Lonicera periclymenum* L.	S	25.17(20)	2.28 ± 0.15	15	15
Caryophyllaceae					
8. *Silene colorata* Poiret	P	8.45 (20)	0.90 ± 0.19	15	15
Convolvulaceae					
9. *Convolvulus althaeoides L.*	S	44.13(15)	0.79 ± 0.12	15	15
Cruciferae					
10. *Moricandia moricandioides* (Boiss. Heywood)	P	8.19(20)	0.38 ± 0.04	10	10
Ericaceae					
11. *Arbutus unedo L.*	*S*	14.78(50)	2.74 ± 0.17	50	50
12. *Erica australis L.*	*.S*	6.81(40)	0.37 ± 0.04	16	27
Iridaceae					
13. *Gladiolus segetum* Ker-Gawler	S	47.51(12)	1.97 ± 0.24	10	10

Appendix B (Contd.)

Family/Species	*Flower type*[1]	*Average dry wt of flowers (mg) (N)*	*Daily sugar secretion*[2] *(mg/flower/day)*	*N1*	*N2*
Labiatae					
14. *Ballota hirsuta* Bentham	S	10.83(40)	0.92 ± 0.08	20	38
15. *Calamintha sylvatica* Bromf.	S	1.57(35)	0.14 ± 0.01	10	35
16. *Lavandula Janata* Boiss.	S	3.48(40)	0.11 ± 0.01	10	71
17. *Lavandula latifolia* Medicus	S	3.71(20)	0.20 ± 0.02	12	145
18. *Lavandula stoechas* L.	S	1.18(80)	0.16 ± 0.01	70	647
19. *Origanum virens* Hoffmanns & Link	S	0.82(50)	0.13 ± 0.01	10	34
20. *Phlomis crinita* Cay.	S	38.60(40)	1.79 ± 0.17	25	27
21. *Phlomis purpurea* L.	S	35.66(20)	3.64 ± 0.16	30	30
22. *Rosmarinus officinalis* L.	S	3.49(20)	0.38 ± 0.02	64	234
23. *Stachys circinata* L'Her.	S	7.78(20)	1.60 ± 0.17	10	10
24. *Teucrium fruticans* L.	S	15.38(20)	1.25 ± 0.06	71	81
25. *Teucrium polium* L.	S	1.92(50)	0.12 ± 0.01	10	87
Leguminosae					
26. *Anthyllis cytisoides* L.	P	2.58(20)	0.17 ± 0.01	10	55
27. *Anthyllis tejedensis* Boiss.	P	1.73(20)	0.18 ± 0.02	10	17
28. *Astragalus lusitanicus* Lam.	P	48.20(20)	1.77 ± 0.22	20	20
29. *Lotus creticus* L.	P	8.90(20)	0.52 ± 0.06	10	37
30. *Psoralea bituminosa* L.	P	6.64(20)	0.38 ± 0.03	15	15
Liliaceae					
31. *Asphodelus aestivus* Brot.	P	24.56(40)	1.24 ± 0.07	40	40
32. *Asphodelus albus* Miller	P	18.08(12)	1.40 ± 0.10	15	15
33. *Asphodelus ramosus* L.	P	16.06(20)	0.96 ± 0.08	20	20
34. *Scilla peruviana* L.	P	9.52(20)	0.23 ± 0.02	7	13
Oleaceae					
35. *Jasminum fruticans* L.	S	9.87(20)	0.63 ± 0.06	10	10
Rosaceae					
36. *Crataegus monogyna* Jacq.	P	11.86(20)	0.15 ± 0.01	10	29
37. *Pyrus bourgaeana* Decne	P	25.62(20)	0.25 ± 0.05	10	14
Rubiaceae					
38. *Putoria calabrica* (L.fil) D.C.	S	2.41(100)	0.09 ± 0.01	15	58
Scrophulariaceae					
39. *Antirrhinum majus* L.	S	61.96(12)	4.98 ± 0.52	12	12
40. *Digitalis obscura* L.	S	27.29(20)	3.66 ± 0.28	9	9
41. *Scrophularia sambucifolia* L.	S	31.16(20)	3.58 ± 0.44	16	16
Solanaceae					
42. *Atropa baetica* Willk.	S	37.83(12)	3.59 ± 0.46	8	8

[1] S -- sympetalous, P — polypetalous.

[2] N 1 = number of nectar measurements, N2 = number of individual flowers.

[3] Mean ± SE.

ACKNOWLEDGEMENTS

This study was supported by a grant from the Comision Asesora de Investigacion Cientifica y Tecnica to S. Talavera (Departamento de Botdnica, Facultad de Biologia, Universidad de Sevilla). I wish to thank P. Gibbs, C.M. Herrera and P. Jordano for reading and criticizing an early version of the manuscript.

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