

Pollination in small islands by occasional visitors: the case of *Daucus carota* subsp. *commutatus* (Apiaceae) in the Columbretes archipelago, Spain

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Abstract This study investigates the pollination ecology and related floral traits of the species *Daucus carota* subsp. *commutatus* in the isolated archipelago of Columbretes, E. Spain, where bees are absent. Two populations were studied: a small population found on a relatively large island (Grossa) inhabited nowadays by three people; and a larger population on a smaller uninhabited island (Foradada). The plant, found also in other rocky coastal enclaves of the west Mediterranean, is totally self-compatible, andromonoecious, exhibiting strong protandrous dichogamy and sequential flowering of umbel orders, with limited probability of self pollination at the plant level. Pollination on both study islands is carried out solely by flies, mainly by *Eristalis tenax* (Syrphidae), a long distance visitor and efficient pollinator, but irregular migrant to the archipelago; and *Lucilia sericata* (Calliphoridae), an abundant flower visitor but less efficient pollinator dependent on human and avian wastes for its larval

growth. The small population on Grossa appears not to suffer pollen limitation. Seed set is reduced, however, in the large population on Foradada, which we attribute to the low pollinator capital of this island, which is too small to attract and sustain migrant hoverflies and where no human and avian wastes are available to sustain blowfly growth. We conclude that in isolated environments with reduced or unpredictable pollinator capital, long distance migrant pollinators, such as *E. tenax*, play an invaluable conservation and perhaps evolutionary role for the native plants. Because these islands have been always practically uninhabited we argue that the absence of adequate local pollinator capital is perhaps compensated by the selection of particular floral traits, which differentiate the study subspecies from other conspecifics. Such traits are: the exposure of nectar during male versus female stage to enhance quick pollen flow; the extended stigma receptivity period (up to 10 days) resulting in a total flower life span of up to 22 days, enabling an adequate pollen deposition on stigmas even under low pollen transfer rates. In this respect, the low flower sex ratio (hermaphrodite: staminate) compared to other conspecifics studied elsewhere may be also relevant.

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as pollinators · Calliphoridae as pollinators ·
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Introduction

Due to existing geographical barriers (e.g., many small islands, archipelagos, and high mountains) and intense land use over millennia, the Mediterranean region probably has more isolated plant populations than most other areas (Blondel and Aronson 1999; Pérez-Bañón et al. 2003; Thompson 2005). This is especially true for small Mediterranean islands, where populations may develop under conditions of both geographical and genetic isolation. Although small Mediterranean islands possess specific characteristics and traits (Pérez-Bañón et al. 2003) and can be considered as natural laboratories for the study of evolutionary processes (Carlquist 1974), research on them has been limited mainly due to difficulties of access (Anderson et al. 2001).

Geographically isolated angiosperm populations on islands can often suffer pollen limitation and reduced seed set due to inadequate pollinators or limited pollinating faunas (McCullen 1990; Howarth and Mull 1992; Anderson et al. 2001; Pérez-Bañón et al. 2003). In turn, pollinator scarcity and reduced pollinator services may result in high selfing rates (Barrett 1996; Ramsey and Vaughton 1996; Fausto et al. 2001; Anderson et al. 2001; and references cited therein) or the evolution of alternative pollination modes (Barrett 1996; Gómez and Zamora 1996; Goodwillie 1999; Culley et al. 2002; Lázaro and Traveset 2005), particularly anemophily (Berry and Calvo 1989; Anderson et al. 2001). Small and isolated populations of species may lose genetic variability by random genetic drift and/or inbreeding (Fischer and Matthies 1998; Menges and Dolan 1998; Young et al. 1999), which may reduce fitness and consequently lead to local extinction (Ouborg et al. 1991; Van Treuren et al. 1991; Ouborg 1993; Oostermeijer et al. 1994, 2000; Groom 2001).

In a previous study we examined the pollination ecology of *Medicago citrina*, a predominantly bee-pollinated species, in the volcanic archipelago of Columbretes consisting of a few very small islands

(Pérez-Bañón et al. 2003). *M. citrina* was pollen limited in two islands due to the absence of permanent bee populations in the archipelago (Español 1958; García Marí et al. 1991). Although low, the levels of seed set found indicated that the species shows some adaptation to the isolated environment and scarcity of appropriate pollinators (e.g., easy tripping caused by flies, as well as by agents other than insects such as wind or high temperatures: Pérez-Bañón et al. 2003). Blowflies and hoverflies were the only flower visitors, with *Eristalis tenax* (Syrphidae) being the most effective pollinator. In this study, we assess the limitations *Daucus carota* subsp. *commutatus* (Apiaceae) is likely to face within the same insular community and identify possible adaptations of the species in the absence of bees.

Despite their more or less uniform floral structure, the members of the cosmopolitan family Apiaceae are known to display varied breeding systems (Bell 1971; Koul et al. 1989). Carrots (*Daucus carota* L.) have been described as obligate outcrossers pollinated by a wide range of insect groups including flies (hover-, blow-, stratiomyid, and other flies), sawflies, beetles, sphecids, and other wasps, and parasitic hymenoptera, as well as bees (Free 1993; Proctor et al. 1996; Lamborn and Ollerton 2000; and references cited in these studies). The widest range of visitors on carrot flowers was reported around the area of Logan, Utah, USA where Bohart and Nye (1960) during a 4-year survey recorded 334 insect species belonging to 71 families, with female solitary bees and honeybees being the most efficient, followed by sphecids wasps, hover and soldier flies (Stratiomyidae). In the same area, Hawthorn et al. (1956) counted ca. 250 species dominated by bees, wasps and flies. Westmoreland and Muntan (1996) found a wide range of insects visiting naturalized carrot populations in north America, the most common being ants, small flies (Chloropidae), and to a lesser extent hoverflies. In India, carrots were found to be pollinated by 24 insect taxa consisting mainly of Hymenoptera and Diptera, and to a minor extent by Coleoptera, Lepidoptera and Hemiptera (Koul et al. 1986).

In Europe, the species is pollinated by a wide diversity of insect taxa. As reported by Knuth

(1908), several authors observed 27–70 insect species in different sites in northern Europe. In central England, pollinator guilds include beetles, hoverflies, and true flies (Lamborn and Ollerton 2000). The great variety of insect visitors is presumably due to the open and easily accessible flowers of this species (Free 1993; Proctor et al. 1996).

Pollination of carrots in the Mediterranean nearly always involves solitary and honeybees. In Italy, carrot crops are pollinated mainly by solitary bees (viz. mainly by *Andrena minutula* and to a minor extent by other *Andrena* spp., *Halictus* spp., and *Anthidium manicatum*), and are less frequently visited by flies of the Syrphidae, Muscidae, and Calliphoridae families (Ricciardelli d'Albore 1986). Carrot crops were shown to depend on solitary bees for their pollination more than any other insect group, in keeping with all other Apiaceae species studied (Ricciardelli d'Albore 1986). While honeybees do not pollinate carrots in Italy (Ricciardelli d'Albore 1986), in Egypt they are as common as *Anthophora* spp. (Hussein and Abden-Aal 1982) and in Israel they contribute to carrot pollination along with beetles and 'many species of flies' (Eisikowitch 1980).

Being such a super generalist in attracting different pollinator guilds, *D. carota* subsp. *commutatus* is expected to suffer less pollen limitation than *Medicago citrina* in Columbretes where bees are absent and so it is likely to be better adapted to the extreme isolation of such a small archipelago. In this article we present a complete study of the pollination and reproductive success of the species performed in situ. We compare our results with previous studies on *D. carota*, both the wild and cultivated varieties, as well as other congeneric and familial species (Bell 1971; Lovett-Doust 1980; Koul et al. 1989; Free 1993; and references cited therein). Our main questions are: (i) Does *D. carota* subsp. *commutatus* perform well as to seed set in small and isolated environments without bees? (ii) What is the origin and how do non-bee visitors perform as pollinators? (iii) Does the species benefit from alternative modes of pollination such as anemophily? and (iv) Compared to other *Daucus* species in non-isolated environments are there any particular pollination traits characterizing this species?

We discuss our findings in relation to those of *Medicago citrina* (Pérez-Bañón et al. 2003) in the context of species management and the maintenance of biodiversity in isolated environments, especially in Mediterranean islands. The results presented here and those on *M. citrina* are part of a major study on the reproduction ecology of plants in insular ecosystems, with the aim of exploring the possible constraints associated with isolation and to pinpoint the vulnerability and risks related to their conservation (Pérez-Bañón 2000; Juan 2002).

Material and methods

The study species

Daucus carota L. subsp. *commutatus* (Paol.) Thell [= *Daucus gingidium* L. subsp. *commutatus* (Paol.) O. Bolòs and Vigo.] is a herbaceous, well ramified, biennial plant of up to 1 m high, bearing three to four pinnate leaves mainly as a basal rosette. Numerous compound umbels appear in a clear hierarchical order on each individual, encompassing one primary or central umbel (C), several primary lateral umbels (L₁), secondary lateral umbels (L₂), and tertiary lateral umbels (L₃) (Fig. 1). The compound umbels are made up of several umbellets symmetrically arranged

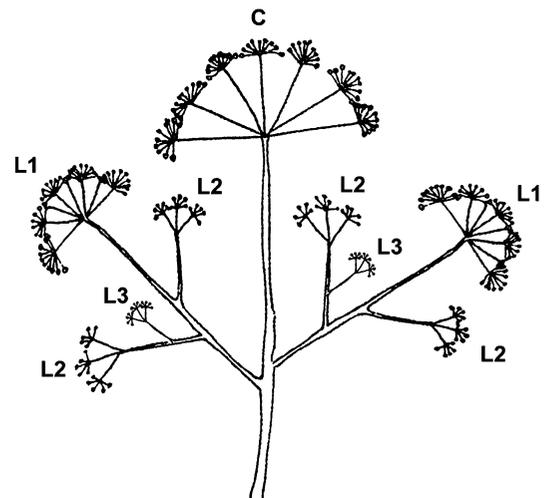


Fig. 1 Illustration of the umbel orders of *Daucus carota* subsp. *commutatus* (C: central; L₁: primary lateral; L₂: secondary lateral; L₃: tertiary lateral)

around the umbel stem, each comprising several minute flowers.

Like most of the species of the family Apiaceae (Bell 1971), *D. carota* subsp. *commutatus* is andromonoecious with hermaphrodite and staminate (male) flowers on the same individual. The gynoecium is inferior to the nectary and comprises two carpels within a binocular ovary, thus maximal reproductive yield is two seeds per flower. The style disc (or stylopodium) lies over the gynoecium and bears two floral styles. The upper surface of the ovary wall functions as a floral nectary, hereafter called the “nectary disc”.

Daucus carota subsp. *commutatus* occurs in *Crithmo-Limonion* communities of the coastal enclaves of Italy, France, Corsica, Sardinia, Morocco, and Algeria and probably other areas of the west Mediterranean. Human disturbances over recent decades have strongly affected the rocky coastlines this species occupies. In Spain, the species is restricted to the Mediterranean islands of the Balearic (Mallorca, Menorca and Ibiza) and Columbretes archipelagos (Fig. 2). In Columbretes, *D. carota* subsp. *commutatus* occurs on four islands: Foradada and Ferrera, where major populations are found (700–800 and ca. 300 individuals, respectively); Lobo, one of the islets around Foradada, with ca. 150 individuals; and Grossa, with a population of ca. 50 plants.

Nomenclature of plant taxa used throughout the paper is according to Pujadas (2003).

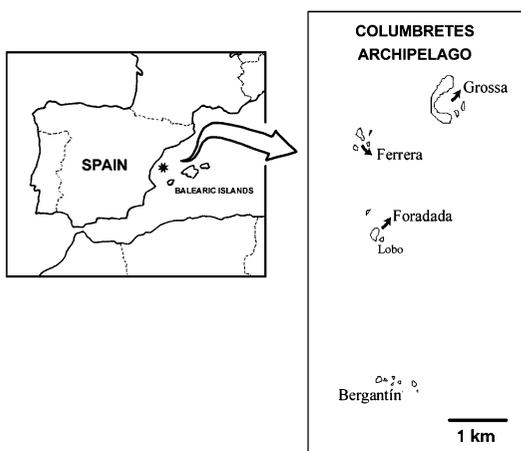


Fig. 2 Map of the Columbretes archipelago located SE of the Mediterranean coast of Spain

Study sites and populations

The fieldwork was carried out in the Natural Park of Columbretes archipelago located ca. 55 km east of the coast of Castellón (eastern Spain). This archipelago is a group of very small, dry, volcanic, uninhabited islands, except for Grossa that has been inhabited since 1851 by a few people (Serrano-Adell 1991; Fig. 2). The area is characterized by a Mediterranean climate with a mean annual temperature of 18.6°C and a mean annual rainfall of 315 mm. In addition to the climate, the vegetation on the islands is also influenced by the vicinity of the sea and the high levels of nutrients from the large populations of seagulls inhabiting the islands. The dominant vegetation of the study islands is low scrub composed of *Suaeda vera* Forssk., a nitrophilous nanophanerophytic plant, *Medicago citrina* (Font Quer) Greuter, a perennial woody leguminous shrub, *Lavatera* sp. pl., and *Lobularia maritima* (L.) Desv. subsp. *columbretensis* R. Fern., together with herb communities dominated by *Euphorbia terracina* L. and *Medicago littoralis* Rohde. A more detailed description of the archipelago and the study islands is available in Pérez-Bañón et al. (2003).

The study was carried out on two populations of different size, one small and one relatively large, located on the islands that were the easiest to access within the archipelago. These were the islands of Grossa and Foradada having the lowest and the highest population sizes of the study species in the archipelago, respectively (see above).

The pollination treatments, experiments and observations were conducted from May to July in 1996 and 1997 on both Grossa and Foradada islands. Systematic everyday observations, however, were conducted mainly on Grossa due to accessibility problems on Foradada.

Anthesis and flowering traits

Flower life span or duration of anthesis was recorded on Grossa in 1996. The flowers were selected at random on L_1 umbels ($n_{\text{plants}} = 5$, $n_{\text{flowers}} = 47$), marked in bud stage and followed on a daily basis until they withered.

Flowering phenology

Observations on the flowering phenology of the study species were carried out in 1996 on the total number of plants of the study populations throughout the flowering period (May–July). The total number of umbels in flower was counted. On Grossa, the counting was conducted directly on each individual ($n = 50$), but in Foradada the very sheer slopes prohibited direct counting on many plants and so direct counting was conducted only in a selected plot (10×5 m with 15 plants) and with a pair of binoculars in the rest of the population. Counting was carried out every 3–5 days during the flowering peak on Grossa, and every 6–10 days on Foradada when weather and sea conditions allowed access to the island.

The flowering phenology at the umbel level was studied on the L_1 umbels of two plants on Grossa during the flowering peak. Umbels were marked when every flower was in the bud stage. We counted the number of open hermaphrodite and staminate flowers every day until no buds were left.

Proportion of hermaphrodite to staminate flowers

This study was performed in 1997 based on preliminary results from 1996. Measurements were carried out in all study populations throughout their flowering period. Plants were marked and studied from the beginning to the end of their flowering ($n = 10$ on Grossa and $n = 9$ on Foradada). When in flower, the central umbel and two random umbels of each order were collected from each plant and their hermaphrodite and staminate flowers were counted.

Floral rewards

Nectar and pollen

Due to its high viscosity and secretion all over the nectary disc, nectar was not possible to retrieve and measure using calibrated microcaps (Petanidou and Smets 1995). Therefore, we assessed the pattern of nectar secretion together with that of

pollen presentation by simply observing the presence of nectar and pollen on the flowers. The flowers were selected on different L_1 umbels, marked in the bud stage and followed on a daily basis until they lost petals in May 1996 ($n_{\text{plants}} = 8$, $n_{\text{flowers}} = 25$). All of them were open to pollinator access.

Mating system

Pollen viability

Pollen viability was assessed using a test of pollen germinability (the hanging drop technique using the Brewbaker–Kwack medium; Dafni 1992; Kerns and Inouye 1993). Preliminary trails of several sucrose solutions (10–50%) showed that pollen germination was highest, albeit still low with 40% sucrose solution, which was subsequently used to prepare the Brewbaker–Kwack medium.

Forty-five flowers on L_1 umbels on eight plants were sampled for pollen directly from the anthers once per day (ca. at 12:00 h). One third of the sampled flowers had freshly dehisced anthers, the second third were flowers on their 2nd day of anthesis (i.e., with pollen exposed for 24 h), and the final third were on their 3rd day of anthesis (i.e., with pollen exposed for 48 h). The pollen of each flower was split in three samples, each one treated separately. We only tested pollen of the first three days of anthesis because no pollen remained on the flowers after this period (Pérez-Bañón and Petanidou, personal observations).

Each pollen sample (± 200 grains) was sprinkled and mixed well with a droplet of the Brewbaker–Kwack medium under a dissecting microscope. The droplets (=samples) were left hanging from the lid of a Petri dish at room temperature. After 24 h, pollen germination was stopped by freezing (Dafni 1992). Each sample was transferred onto a slide, permanently mounted and examined under a phase contrast microscope (two samples per flower and per day, selected at random). Only the pollen grains that successfully germinated and produced visible pollen tubes were considered viable. Pollen viability is expressed as the percentage of germinated

pollen grains. The results were averaged first by flower, then by day.

Stigma receptivity

The stigma receptivity of the flowers was assessed during two successive years using different techniques. In the year 1996 we used the method of pollen germination in vivo (Dafni 1992). This technique was applied in the field on 172 flowers on different L₁ umbels born on eight different plants of the Grossa population. These pollination treatments started in late May 1996 and continued for about one month. The flowers were marked at the bud stage and covered with a cylindrical metal cage ca. 20 cm in diameter and height, bearing fine gauze to prevent unwanted pollen deposit on the stigmas. All flower ages were employed from the 1st day until the 24th day, using five to seven flowers per day (age). The flowers were artificially cross-pollinated using fresh pollen from plants selected at random and located within a distance of 30–40 m from the recipient plant (one pollen donor for each flower). After 6–7 h the flowers were collected, fixed in ethanol 70%—acetic acid 45% (3:1 by volume) for 1 h and then transferred into ethanol 70%. Before observation, stigmas were acetolysed in 45% acetic acid at 60°C for 5 min, dyed with safranin O—aniline blue (Dafni 1992), and observed under a light microscope. We counted the total pollen grains deposited on the stigma together with the number of pollen grains that germinated and produced elongated tubes. We also noted the morphological changes of stigma vis-à-vis with its receptivity throughout the experiment.

Based on the relation between style morphology and stigma receptivity as resulted above, we carried out further observations in the year 1997 using 43 flowers born on eight different plants. The flowers were followed daily throughout their anthesis and the receptivity of stigma was estimated on the basis of the style size. The day style reached at least 150% of the length at its early male stage was taken as the starting day of stigma receptivity (see results). The duration of *Daucus* receptivity period was calculated as the average over all flowers followed.

Anemophily

In order to detect the possibility of pollen dispersal by wind in the windy environment of Columbretes we:

1. Scattered pollen ($n = 67$ grains) on a glass surface and inspected the pattern of pollen dispersion with a magnifying glass ($\times 30$).
2. Placed slides ($n = 13$) covered with silicon oil near to the umbels in flower of the Grossa population (28 May 1996, 21.00 h). The slides were positioned horizontally just under the umbels ($n = 7$), 10 cm off the perpendicular from an umbel at the side of the wind ($n = 4$) and opposite to the wind direction ($n = 2$). They were collected ca. 24 h later and observed under a light microscope.

Pollination tests

The reproductive success of the study species was assessed by performing a spontaneous self-pollination test and manual self- and cross-pollination treatments (see below). All treated umbels were enclosed in metal cages covered with fine gauze, which excluded insects but not the wind from having access to the floral stigmas. The cages remained closed after the pollination treatments until the beginning of fruit set. All treatments were carried out in the Grossa population in late May up to mid June 1996. Fruits were collected seven weeks later. Seed set was assessed under a dissecting microscope, as the percentage of seeded mericarps (seeds produced) of the hermaphrodite flowers over the total number of ovules contained in these flowers. The following pollination treatments were carried out:

Spontaneous self-pollination—This treatment was designed to determine the likelihood of spontaneous pollination in the study species. Two entire C umbels and another three L₁ umbels on five different plants with flowers at the bud stage were selected at random, each one separately marked, encaged and left undisturbed until fruit harvest (total number of hermaphrodite flowers encaged $n = 1,954$).

Manual self-pollination—Manual pollinations were carried out on three L_1 umbels each divided in two parts. In order to determine whether the species is self-compatible, 134 hermaphrodite flowers born on the one half of the umbel were self-pollinated. The flowers were individually marked in the bud stage and followed with a magnifier for several days. After the style had completely protruded, each flower was self-pollinated by hand once per day for four consecutive days, starting on the 7th–12th day after the commencement of anthesis. Selfing was carried out using one-day pollen from the same plant.

Manual cross-pollination—This treatment was carried out on the second half of the umbels used for manual self pollination. A total of 147 flowers were marked, followed individually until they were receptive and then crossed using 1-day pollen from neighbouring individuals (one pollen donor for each flower). Cross-pollinated flowers were used as a positive control for determining reduced seed set due to pollen limitation from insufficient pollinator visits or reduced compatibility of self-pollen.

Natural pollination—This involved no treatments in order to check the pollination levels under natural (free) pollination conditions, and thus to determine the pollination efficiency of flower visiting insects in nature. Natural pollination success was assessed in both the study islands, on Gossa using the same plants as in the above treatments.

In order to check whether reproductive success is related to/depends on the umbel order, seed set was estimated separately for each umbel order. The assessment was carried out in 1997 using five plants selected at random in each of the study islands. On every individual the central umbel and two umbels per order (L_1 , L_2 , and L_3) were selected at random. The total number of umbels studied per population were $n_C = 5$, $n_{L1} = 10$, and $n_{L2} = 10$ on both the islands; and $n_{L3} = 4$ and $n_{L3} = 0$ on Gossa and Foradada, respectively. The umbels were marked with waterproof paint at the bud/flowering stage, left to be freely visited by insects, and collected 7 weeks later. Seed set was assessed under a dissecting microscope, as the percentage of seeded mericarps over the total ovules contained in the hermaphrodite flowers within an umbel.

Assessing the role of pollinators

Visitation rate

All observations of pollinator visitation rates were carried out in a permanent plot in 1996 in the Gossa population. The plot, 2×2 m large, consisted of several individuals comprising a total of ca. 250 umbels depending on the blooming period.

Systematic surveys and insect visitor counts were performed from the 13th May until the 10th June by two observers recording the number of insects visiting the flowers/umbels in the plot for 15-min periods. Surveys and flower visitor collections continued until the end of the flowering period, albeit at a non-systematic basis, carried out during five observation visits to the archipelago from mid June to mid July. The counts were conducted four to five times per day from 9.00 h through to 20.00 h.

Due to accessibility difficulties, pollinator observations on Foradada were not systematic. On this island, sporadic observations and collections were carried out during our visits.

Pollinator efficiency

The pollination efficiency of flower visitors was assessed on the basis of the pollen transferred on the bodies of different insect species and the seed set resulting from insect visits.

Pollen loads on insects—Pollen adhering to the insect body of the main flower visiting species was collected and examined. The loads were sampled from insects captured after they had just visited an umbel of *Daucus carota* subsp. *commutatus* in or in the vicinity of the permanent study plot on Gossa during flowering peak. Immediately after their capture, insects were anesthetized in ethyl-acetate and the pollen from all body parts was removed with a sticky piece of fuchsin glycerine-jelly to be later examined in the lab (Beattie 1972). The pollen (both con- and heterospecific) was counted under a light microscope and identified by using reference material collected in the field.

Seed set resulting from floral visits by different insect species—In order to assess the relative

pollination efficiency of different insect species visiting *Daucus* flowers in setting fruits, we carried out the following experiment: On 16 May 1996, six L_1 umbels in bud stage were covered by metal cages with fine gauze. When in flower, one to two specimens of the major insect species visiting *Daucus* were inserted in the cages, each species in a separate cage, until all flowers in the cage started fruiting. The insects were replaced by new conspecifics captured in the neighborhood every day, the replacement carried out for up to 20 days until the last hermaphrodite flowers in the cages were no longer receptive. All species were replaced almost with the same frequency, with additional occasional replacements due to sudden insect death. Insect species employed were *Eristalis tenax* ($n = 27$), *Eupeodes corollae* ($n = 38$), *Episyrphus balteatus* ($n = 35$) (Syrphidae), *Calliphora vicina* ($n = 44$), and *Lucilia sericata* ($n = 44$) (Calliphoridae). Pollinator effectiveness was measured as the percentage of seeded mericarps over the total number of ovules of the hermaphrodite flowers within the umbel.

Following a previous experimental design (Pérez-Bañón et al. 2003), we assumed that this experiment would be appropriate to assess the relative pollination efficiency of insects, although we knew that caged pollinators may not show the same levels of efficiency as those under natural conditions and may act atypically, either making fewer visits when disturbed or visiting flowers by necessity in capture. This was to some extent counterbalanced by the regular replacement of insects in the cages. In addition, the daily replacement of insects kept somewhat constant the inflow of external pollen into the cage, as the main pollen source for the pollination of the hermaphrodite flowers, because self-pollen of the treated umbel was either gone or not viable.

Data analysis

Differences in percentages were tested using a *G*-test (test for goodness of fit) with a *posteriori* application of the William's correction (Sokal and Rohlf 1995). The *G*-test program was written by WN Ellis (University of Amsterdam). For other analyses we used the Statistica package.

Where needed, the data were tested for normality prior to statistical analysis using the Kolmogorov–Smirnov one-sample tests. In several cases the data were not normally distributed, and therefore non-parametric tests were applied, such as Kruskal–Wallis ANOVA (K–W) followed by separate Mann–Whitney *U*-tests (M–W) (Sokal and Rohlf 1995).

Statistical tests were carried out on the basis of the number of plants, not that of flowers born on them.

Results

Anthesis and flowering at the umbel, plant, and community level

The flowers of *Daucus carota* subsp. *commutatus* are strongly protandrous. Young stamens and petals are incurved at the beginning of anthesis, opening with anthesis advancement. Stamens stand vertically over the stigma when the anthers freshly dehisce and become fully expanded outwards after shedding their pollen. This position, however, cannot lead to self-pollination because stigmas are receptive much later, as it will be shown below. This early male stage lasts for 2.4 ± 0.08 days ($n = 47$, range 1–3). The flower petals appear 1.7 ± 0.11 days after the first anthers have been exposed, thereafter remaining for 12.3 ± 0.79 days ($n = 47$). However, our data on stigma receptivity (cf. below) show that flower anthesis may extend beyond petal shedding, as the stigmas remain receptive even after the 20th day of anthesis.

The creamy white flowers are minute and mainly actinomorphic, with five parts (sepals, petals, and stamens). Some of the external flowers on the outer umbellets of C and L_1 umbels however, have enlarged and irregular corollas. Hermaphrodite and staminate flowers are born on the same umbellet, always in the same order, with hermaphrodites at the peripheral (external) and staminate flowers towards the centre. The central flower of all umbellets in all umbels is always hermaphrodite. The central umbellet of all umbels regardless of their order is reduced to one or a few purple or white flowers.

When in full bloom, the umbels of all orders are spherical, with their central flowers purple in colour. Considering their pollination function (structure, behaviour of visiting insects), all umbels can be regarded as major “units of attraction” (Bell and Lindsey 1978). All individual plants bore a central umbel, several lateral ones of the first (viz. L_1) and second order (L_2), whereas the presence of a third lateral order (L_3) was not uncommon. Based on 19 plants counted, the ratio of C: L_1 : L_2 : L_3 umbels was 1.0: 17.7: 79.6: 41.7 (Table 1). At the level of a whole plant, the highest number of flowers tended to be born on lateral umbels (L_1 : $28.1 \pm 2.85\%$, L_2 : 61.5 ± 3.14 and L_3 : $8.1 \pm 2.07\%$), while central umbels bore only $2.3 \pm 0.68\%$.

Daucus carota subsp. *commutatus* flowers in early summer, with a peak between mid June and early July (Fig. 3). There is a clear sequential order in the flowering of umbels within each individual, with the central umbels flowering first, followed successively by lateral umbels of the first order (L_1), then the second (L_2) and finally the third (L_3). It is interesting that all umbels of the same order of an individual come into flower simultaneously. Anthesis is centripetal in all umbel and umbellets. Within each umbel, external hermaphrodite flowers of the outer umbellets are the first to come into flower, followed by the

inner staminate flowers. Figure 4 shows the sequence of flower opening for hermaphrodite and staminate flowers in an L_1 umbel. The overlap in anthesis among umbels of different orders is given in Fig. 5. Given the strong protandry and the strong separation between male and female phases, the probability that two phases coincide at the umbel level is low.

The percentage of hermaphrodite flowers (i.e., an alternative value for floral sex ratio) within an umbel depended on the umbel order (C, L_1 – L_3) in each of the study islands, with central umbels having higher percentage than lateral ones (K–W $H_{Grossa(3, 38)} = 27.34$, $P = 0.0000$; $H_{Foradada(3, 33)} = 22.92$, $P = 0.0000$; Table 1). This percentage decreased progressively with the order, and in general umbels L_2 and L_3 consisted mostly of staminate flowers. There was no difference in the percentage of hermaphrodite flowers among the populations of Grossa and Foradada at the umbel levels C, L_1 and L_2 , but there was for L_3 (M–W U tests: $U_{C(10, 9)} = 33$, $P > 0.05$; $U_{L_1(10, 9)} = 39$, $P > 0.05$; $U_{L_2(10, 9)} = 27$, $P > 0.05$; $U_{L_3(8, 6)} = 6$, $P = 0.020$).

Floral rewards to pollinators

Pollinators visit the flowers for both nectar and pollen. Based on the observations of 25 flowers

Table 1 Variation in floral traits between different umbel orders and populations of *D. carota* subsp. *commutatus*

Traits	UMBEL ORDER				
	Central		Laterals		
	(C)	Primary (L_1)	Secondary (L_2)	Tertiary (L_3)	Entire individual Mean \pm SE
<i>Island Grossa</i>					
	($n = 10$)	($n = 20$)	($n = 20$)	($n = 16$)	($n = 10$)
Total # flowers/umbel	4829 \pm 499	4895 \pm 313	3006 \pm 252	1223 \pm 135	462141 \pm 119574
Sex ratio (hermaphrodite : staminate)	4.6 \pm 2.12	0.6 \pm 0.09	0.2 \pm 0.02	0.2 \pm 0.03	0.3 \pm 0.03
# Of hermaphrodite flowers	2941 \pm 454	1704 \pm 190	485 \pm 53	176 \pm 18	95029 \pm 22650
% Hermaphrodite flowers	61.0 \pm 7.23	33.6 \pm 3.08	16.1 \pm 1.31	15.6 \pm 1.93	20.5 \pm 1.74
Total # umbels per plant	1.0 \pm 0.00	17.6 \pm 2.72	84.4 \pm 14.98	55.7 \pm 18.67	158.7 \pm 33.66
<i>Island Foradada</i>					
	($n = 9$)	($n = 18$)	($n = 18$)	($n = 12$)	
Total # flowers/umbel	4079 \pm 658	3709 \pm 382	2098 \pm 222	658 \pm 165	237389 \pm 40814
Sex ratio (hermaphrodite : staminate)	1.3 \pm 0.38	0.4 \pm 0.05	0.2 \pm 0.02	0.3 \pm 0.01	0.3 \pm 0.02
# Of hermaphrodite flowers	1859 \pm 176	1070 \pm 102	356 \pm 31	140 \pm 38	50747 \pm 8075
% Hermaphrodite flowers	49.5 \pm 5.35	29.6 \pm 2.11	18.3 \pm 1.12	21.0 \pm 0.97	22.0 \pm 1.24
total # umbels	1.0 \pm 0.00	18.2 \pm 2.03	69.2 \pm 9.04	17.9 \pm 6.44	104.3 \pm 14.95

For each umbel (C, L_1 – L_3) we give total number of flowers, flower sex ratio, and % of hermaphrodite flowers. Total number of umbels per plant is given separately. Average values are followed by SE; n is the number of plants or umbels (L_1 – L_3) used in the calculations

Fig. 3 Flowering phenology of the populations of *D. carota* subsp. *commutatus* studied in Columbretes

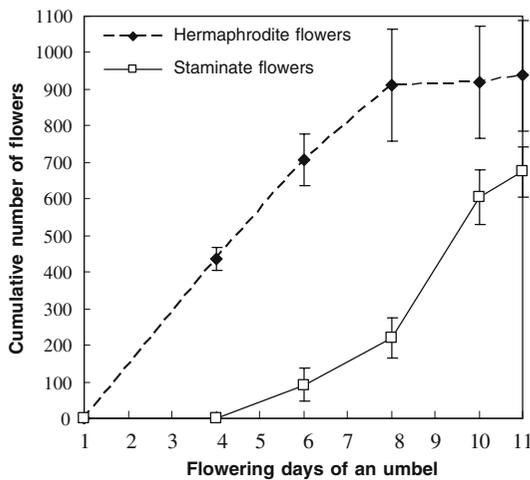
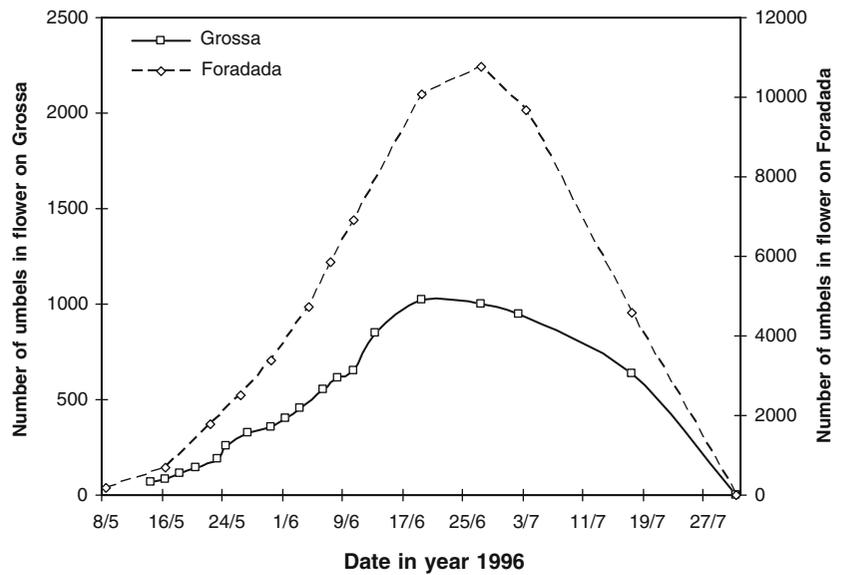


Fig. 4 Patterns of commencement of floral exhibition of hermaphrodite and staminate flowers within an umbel of *D. carota* subsp. *commutatus*. Values are means over two L_1 umbels selected at random

born on eight plants, pollen was presented in the beginning of all flower anthesis for 2.2 ± 0.16 days ($n = 8$) (see above). Nectar, secreted from the whole surface of the nectary disc, was also presented at the beginning of flower anthesis. Nectar was abundantly produced during the first three days, and continued to be secreted at much lower quantities for the following 3–4 days, thereafter remaining as a viscous candy on the nectary disc due to

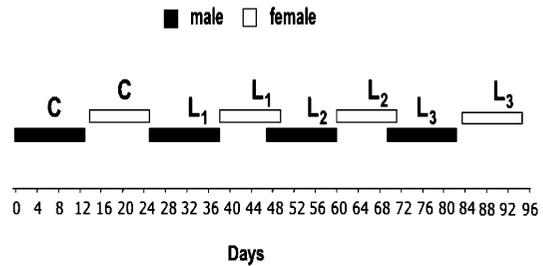


Fig. 5 Flowering phenology of an individual of *D. carota* subsp. *commutatus* based on combined data on flower life span, duration of stigma receptivity, and umbel phenology. We distinguish successive male and female phases of all hermaphrodite and staminate flowers born on umbels of all available orders (C– L_3) within a plant

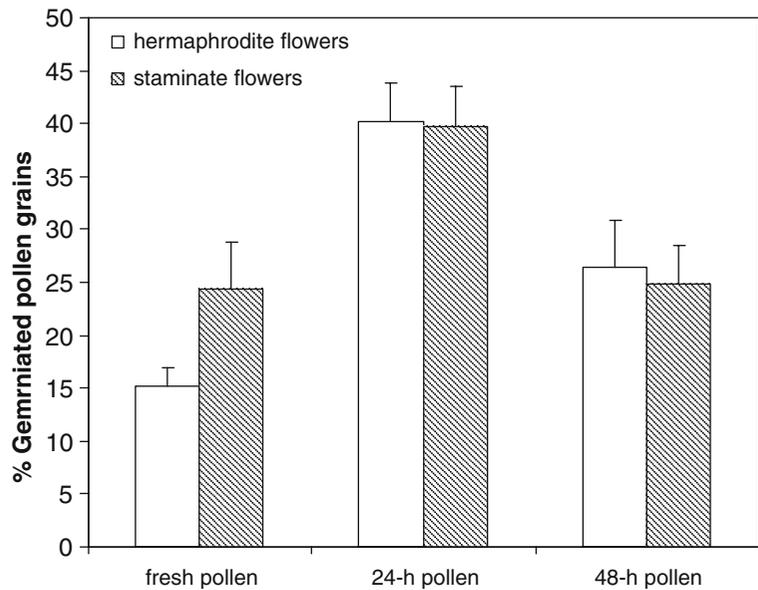
evaporation. In conclusion, both pollen and nectar were offered principally during the male phase of the flower.

Mating system

Pollen viability and stigma receptivity

Based on in vitro germination tests, both hermaphrodite and staminate flowers appear to have similar patterns of pollen viability (Fig. 6; $P > 0.05$). Surprisingly, the highest viability was found after it had been exposed for 24 h not in fresh pollen. This was true, however, only in hermaphrodite flowers ($H_{(2, 24)} = 11.59$, $P = 0.0030$), not the

Fig. 6 Pollen germination of *D. carota* subsp. *commutatus*. We give % of the pollen grains germinated in Brewbaker-Kwack medium. Results are distinguished according to the flower sex (hermaphrodite, staminate) and time of pollen exposure (pollen from anthers freshly opened, exposed for 24 h and 48 h). Bars stand for SE



staminate ones ($H_{(2, 24)} = 3.13$, $P > 0.05$). Pollen grains remain viable however, even after 48 h of exposure, although with a lower germination rate.

In vivo pollen germination tests determined the exact duration of stigma receptivity in the flowers. The starting period of stigma receptivity is manifested by a remarkable elongation of the styles up to 50% greater than the length of the early male stage. It starts between the 7th and 12th day of anthesis, in average at day 9.3 ± 0.22 of the flower anthesis and lasts for up to ten days or more (Fig. 7), in average for 7.4 ± 0.34 days (data from 1997). It is interesting that in all flowers examined the maximum pollen germination was observed on the third day after the stigma started to be receptive.

Anemophily

Of the total 67 pollen grains dispersed on a glass surface, 23.9% were dispersed individually, while the rest were clumped in aggregates. This dispersion pattern indicates that the pollen of *Daucus carota* subsp. *commutatus* can to some extent be wind-born. This was confirmed by pollen adherence on slides, of which 12.1% were dispersed as single grains, 7.9% in groups of ≤ 10 , and the final 80.0% in larger aggregates.

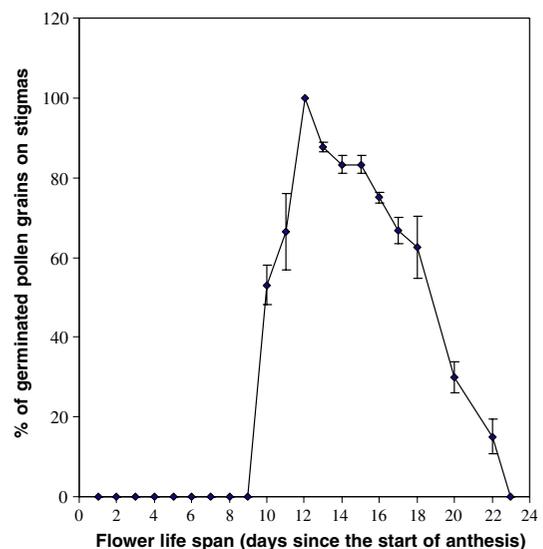


Fig. 7 Levels of stigma receptivity of hermaphrodite flowers of *Daucus carota* subsp. *commutatus* throughout anthesis. We give % of pollen germinated on the floral stigmas during the days following the commencement of flower anthesis (day 0). Data are daily averages over several flowers born on L_1 umbels of three different plants. Total number of flowers was 156

On the other hand, the absence of spontaneous pollination (see below) is indicative of an insignificant contribution from wind pollination to the reproduction of this species, even in a windy, island environment.

Reproductive success after pollination treatments

Seed set (% of seeded mericarps over the initial total number of ovules of the flowers treated, i.e., number of flowers treated \times 2) of flowers of L_1 umbels that were free-pollinated by insects was significantly higher compared with non-treated flowers that produced almost no seed (58.7% vs. 1.0%, respectively; G test, $P < 0.001$). Given that the flowers tested for spontaneous self-pollination were not wind proof, the resulted absence of spontaneous pollination implies there is need for animal-provoked pollination in *Daucus carota* subsp. *commutatus*.

Flowers on the L_1 umbel that were self- and cross-pollinated by hand set also very high seed yields (52.1% and 62.2%, respectively) which did not differ significantly from the above average seed set received after free pollination (G test, $P > 0.05$).

Seed set after free pollination appeared to depend on the order of the umbel in both Grossa and Foradada islands (Fig. 8). In both study populations, C and L_1 umbels set equally high percentage of seeds; in L_2 seed set was lower in both islands, whereas no seed was set by L_3

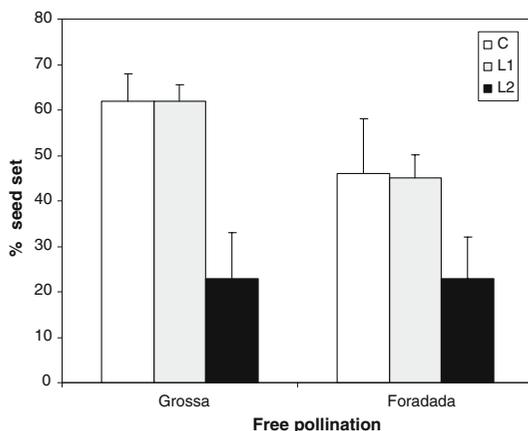


Fig. 8 Seed set (% of seeded mericarps over the total amount of ovules contained in the hermaphrodite flowers marked in bud stage) after free pollination of different umbel orders. We give results from two populations, Grossa ($n = 5$ plants) and Foradada ($n = 5$). Number of umbels employed in each population: $n_C = 5$, $n_{L_1} = 10$, $n_{L_2} = 10$, $n_{L_3} = 10$. There was no fruit set from L_3 umbels. Bars indicate SE

umbels. Between the two populations there was significant difference in seed set by the L_1 umbels (M–W $U_{(5, 5)} = 2.0$, $P = 0.0283$), but not by L_2 (M–W $U_{(5, 5)} = 12.5$, $P > 0.05$) and C ones (M–W $U_{(5, 5)} = 6.0$, $P > 0.05$). When considering the number of seeds produced by the umbels instead of the seed set percentages (Grossa: C = 3187 ± 440.8 , $L_1 = 1266 \pm 363.8$, $L_2 = 257 \pm 177.7$ ($n = 5$ plants); Foradada: C = 1674 ± 271.2 , $L_1 = 612 \pm 71.3$, $L_2 = 137 \pm 104.9$ ($n = 5$)), the two populations were found to differ in C umbels (M–W: $U_{(5, 5)} = 2.0$, $P = 0.0283$) but not as to L_1 and L_2 umbels (M–W $U_{(5, 5)} = 5.0$, $P > 0.05$, and $U_{(5, 5)} = 11.5$, $P > 0.05$, respectively).

Flower visitation rates and efficiency of pollinators

Based on the total number of insects observed in the permanent plot and paying at least one visit to a *Daucus carota* subsp. *commutatus* flower, the main and most frequent visitors at the Grossa population were flies of the families Calliphoridae (66.9% of the total visitor number). Syrphidae (15.6%), Stratiomyidae (6.7%), Scatophagidae (4.6%), and ‘other flies’ encompassing Anthomyiidae and Muscidae, etc. (6.2%) were less common flower visitors. Pollinator activity is illustrated in Fig. 9. As implied by our non-systematic surveys, carried out from mid June to mid July, *Daucus* flowers continued to be visited by the same insect species until the end of flowering. Among all fly species the most active one was the calliphorid *Lucilia sericata* that effectuated 64.0% of all visits registered in the permanent plot, while the large-sized *Eristalis tenax* (Syrphidae) were relatively irregular in visiting *Daucus* flowers (Fig. 10). Although we have no recorded data, from our sporadic observations and collections we found that flower visitors to *Daucus* flowers on Foradada were extremely less regular compared to Grossa. This applies mainly to all calliphorid species, especially to *Lucilia sericata* that were always present in the nearby island of Grossa (Pérez-Bañón and Petanidou, personal observations).

Pollen transfer ability on insect bodies is, on average, high for all flower visitors of *Daucus carota* subsp. *commutatus*, with *Eristalis tenax* scoring the highest (Table 2). With >80% of *Daucus* pollen carried on their bodies, visitors

Fig. 9 Comparative patterns of activity of different insect families visiting the umbels of *D. carota* subsp. *commutatus* in the permanent observation plot

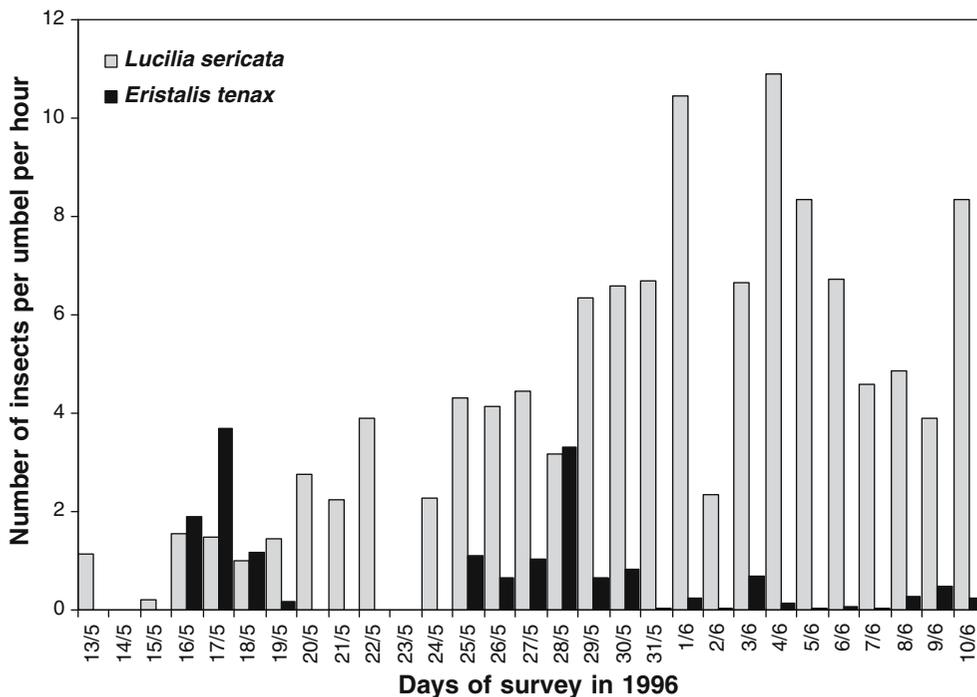
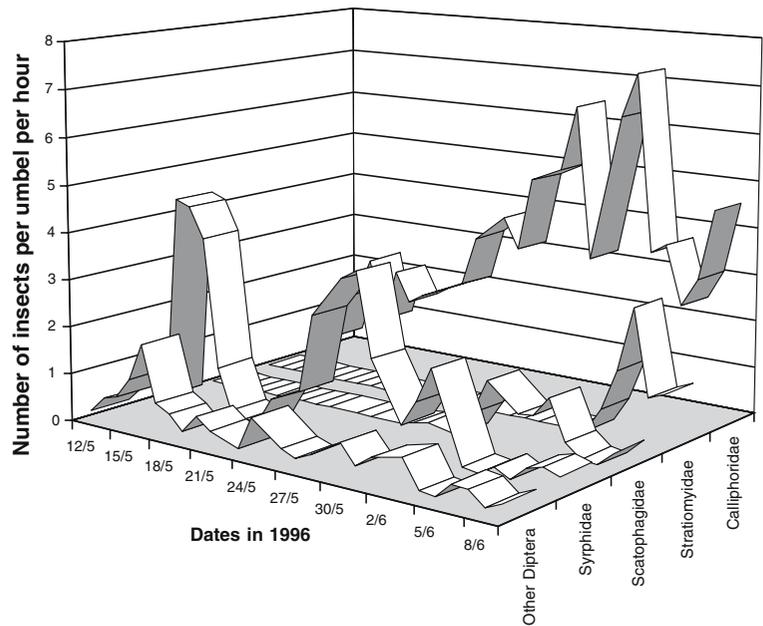


Fig. 10 Comparative abundance of individuals of the calliphorid fly *Lucilia sericata* and the syrphid fly *Eristalis tenax* visiting the umbels of *D. carota* subsp. *commutatus* in

the permanent observation plot. We give data of the most insect crowded surveys (9:00–11:00) throughout the field-work period in 1996

appeared to be constant to *Daucus* flowers. Other plant species contributing to insect pollen loads were *Lobularia maritima* subsp. *columbretensis*,

Sisymbrium irio, *Suaeda vera*, *Chenopodium murale*, *Sonchus tenerrimus*, *Phagnalon saxatile*, and *Erodium chium*.

Table 2 Quantitative and qualitative analysis of the pollen load adhered on the bodies of the main flower visitors of *D. carota* subsp. *commutatus* on Grossa islet

	Number of pollen grains on insect bodies				<i>Daucus</i> pollen (% of the total)
	Mean load	SE	Range	<i>n</i>	
Calliphoridae					
<i>Calliphora vicina</i>	1930	581.1	70–5249	20	84.2
<i>Lucilia sericata</i>	1493	381.5	218–3380	20	82.6
Syrphidae					
<i>Eristalis tenax</i>	4353	1221.2	335–14652	15	82.6
<i>Eupeodes corollae</i>	994	315.8	46–3534	15	88.3
<i>Epsyrphus balteatus</i>	1068	301.6	95–2374	15	90.4
<i>Scaeva pyrastris</i>	2435	712.8	241–5491	13	88.8
<i>Meliscaeva auricollis</i>	1539	494.6	44–4726	15	83.5
Scatophagidae					
<i>Scathophaga stercoraria</i>	2025	458.6	418–3398	7	86.2

The insects were captured in flight, after having visited a *Daucus* umbel; *n* is the number of insects examined

Fig. 11 Seed set of *D. carota* subsp. *commutatus* obtained per L_1 umbel and individual fly enclosed in cages. Seed set was calculated as % of the mericarps seeded over the total ovules contained in the hermaphrodite flowers of an umbel

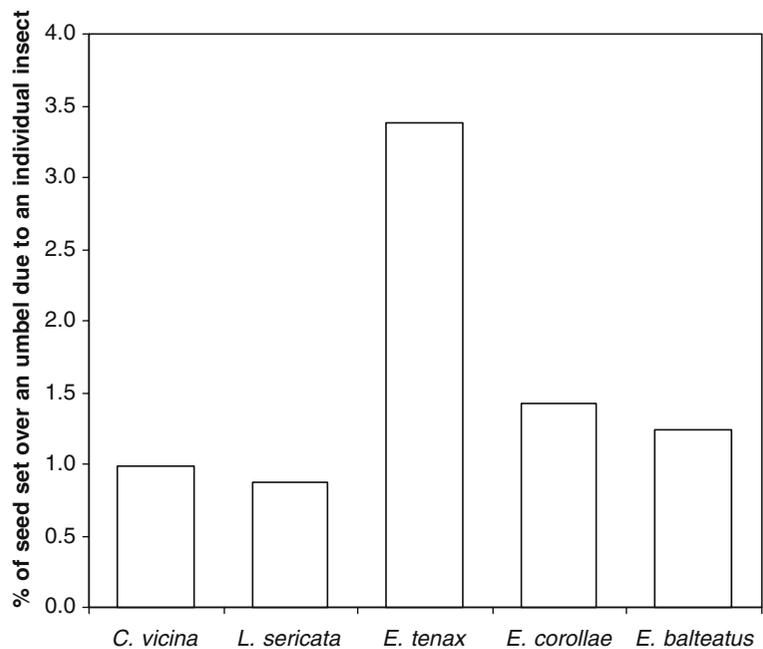


Figure 11 gives the pollinating efficiency of an individual fly visiting a *Daucus* umbel per day, in terms of % seed set of caged L_1 umbels, each one left to be pollinated by a different fly species. There was a significant difference in the seed set output among all the insect species included in the experiment (*G*-test, $P < 0.001$), with *E. tenax* (Syrphidae) being by far the most efficient pollinator of *D. carota* subsp. *commutatus*.

Discussion

Mating system and reproductive success of *D. carota* subsp. *commutatus*

In the archipelago of Columbretes, *Daucus carota* subsp. *commutatus* exhibits traits that are common for other *Daucus* or Apiaceae species found worldwide, such as andromonoecy,

strong protandrous dichogamy, and sequential flowering of umbel orders within a plant (Bell 1971; Lovett Doust 1980; Koul et al. 1989; Free 1993; Proctor et al. 1996). In fact, this species is totally compatible, but with a limited probability to self-pollinate in nature at the flower (due to strong protandry pollen is dispersed or/and loses in viability before stigma becomes receptive) and at the umbel level (Fig. 5). Our results confirm that the umbel constitutes a whole functional unit operating as a pollen donor at the beginning of umbel flowering as described by Bell and Lindsey (1978), with stigmas becoming receptive after all anthers have withered within the umbel and pollen dispersed. This strategy allegedly avoids the possibility of geitonogamy (Koul et al. 1989), yet the probability of self pollination within a plant, i.e., between umbels, is not insignificant, under the condition that pollinators are not limited. This is because although lateral umbels do not come into flower before the central umbel has started fruiting, there is some period of overlap between lateral umbels of successive orders, e.g., between L_1 – L_2 or L_2 – L_3 (Fig. 5). This shows that there is some probability of geitonogamous selfing at the plant level as first reported by Borthwick and Emsweller (1933) and Hawthorn et al. (1956). It seems to be true however, that most flowers of the Grossa population enjoy cross-pollination as also inferred by Fryxell (1957), Westmoreland and Muntan (1996), Lamborn and Ollerton (2000) and a wide range of studies reviewed by Free (1993). In the latter review, the author confirmed the rarity of spontaneous self pollination in the entire genus of *Daucus*, as verified in this study. Therefore, and because wind contributes very little to the transfer of *Daucus* pollen, animal agents are of vital importance to the pollination of the species in Columbretes.

As indicated by our cross-pollination results the study species does not suffer pollen limitation on Grossa, where seed yield was found to be as high as in wild and cultivated carrots studied elsewhere (Braak and Kho 1958; Koul et al. 1989). Interestingly, in all *Daucus* species studied, only C, L_1 , and L_2 umbels produce seeds (Koul et al. 1989).

Pollination services on Grossa were mainly offered by resident calliphorid and migrant syrphid flies (see also Pérez-Bañón et al. 2003). Such flies were relatively rare on the small island of Foradada offering scarce pollination services to the flowers of *Daucus*. This was probably the main cause for the lower seed set after free pollination found on Foradada compared to Grossa both the number of seeds produced (C umbels) and the percentage of seeds (L_1 umbels) over the total number of hermaphrodite flowers (Fig. 8).

Pollination trait particularities of *Daucus carota* subsp. *commutatus* in Columbretes

Beyond the aforementioned similarities between the mating systems of *Daucus carota* subsp. *commutatus* and other conspecifics, there are some interesting peculiarities regarding its pollination ecology in the Columbretes archipelago that require attention. These are:

1. Affluent floral rewards (both nectar and pollen) during the male phase of the flowers, with extremely limited nectar in the form of evaporated candy remaining on the nectary disc during the female phase. Strong protandry at the umbel level is interestingly related to abundant floral rewards offered to visiting insects by different flowers coming successively into the male stage. By having more alluring male than female flowers (see also Bell et al. 1984), the species seems to favour pollen dispersal by enhanced pollinator visitation at the umbel level throughout its male stage of anthesis, i.e., during the first half of the umbel flowering period (Figs. 4–5). The enhanced floral attractiveness during the male vs. the female phase is even more pronounced by petal shedding during the female phase (viz. around day 14, i.e., during the period of greatest stigma receptivity: Fig. 7).
2. Extremely long stigma receptivity period. By having floral stigmas that are receptive up to 10 days, *Daucus carota* subsp. *commutatus* has the most extended female stage of all *Daucus* or Apiaceae species known so far (Koul et al. 1989). According to these

authors, the stigma receptivity of two wild and two cultivated populations of carrots did not exceed 4–5 days. In fact, the extended receptivity period of the Columbretes populations of *Daucus* is exceptional, especially when the harsh Mediterranean summer conditions are considered (Petanidou et al. 1995). We believe this extended receptivity period is a trade-off to compensate for the low availability of appropriate pollinators (see above). In this respect, it will be very interesting to have data on the temporal characteristics of anthesis of other populations of the same species that enjoy a more typical ‘Mediterranean’ array of visitors including solitary and honeybees (see Introduction).

3. Low ratio of hermaphrodite: staminate flowers compared to other phylogenetically related species. With an average of 20.5–22.0% of hermaphrodite flowers per population, *D. carota* in Columbretes has a much lower percentage of hermaphrodite flowers than other carrot subspecies, which range between 47.4% and 55.2% (Koul et al. 1989). This percentage is also among the lowest of six Apiaceae species including carrots (Bell 1971), and comparable only to other hetero-generic Apiaceae species ranging between 15.6% and 21.3% (Lovett Doust 1980). Such a differentiated sex allocation pattern may be indicative of a shortage in resources in the habitats of *Daucus*. Indeed, habitat quality and inherent environmental factors may influence floral sex ratio in the Apiaceae: in Holland low temperatures were responsible for a lower percentage of hermaphrodite flowers in cultivated carrots (although this applied only to L₃ umbels: Braak and Kho 1958), whereas in England *Smyrniium olustrum* bore fewer hermaphrodite flowers in a copper mine spoil compared to a sheltered roadside coastal verge (Lovett Doust 1980). Under the evidence of the above it could be inferred that the lower percentage of hermaphrodite flowers observed in the two Columbretes islets may constitute the response to environmental pressures, at first place the extreme summer drought and the

precarious pollinator services depending on accidental migration (viz. hoverflies) and on discontinuous human presence (viz. blowflies).

Pollination services on small islands: do flies alone suffice?

The geography of effective pollinators in the Mediterranean (see Introduction) indicates the importance of bees for the pollination of *Daucus* in this region. *Daucus* flowers towards summer, in a period that floral resources are scarce but bees still active (Petanidou 2004; Petanidou et al. 1995; Petanidou and Ellis 1996; Petanidou and Lamborn 2005). By flowering then, *Daucus* could benefit from bee presence, as elsewhere (Free 1993; Proctor et al. 1996; Lamborn and Ollerton 2000). This is not the case in Columbretes, however, where bees are absent, and so pollination depends entirely on the availability of local (viz. blowflies) and migrant (viz. hoverflies) pollinators, a case that is unique in the literature in which pollination is accomplished exclusively by flies. Evidently, such plasticity in the dependence on quite different pollinator guilds makes carrots very successful in occupying isolated environments.

The available flies seem to accomplish a great pollinator job in Columbretes, especially on Grossa. The most efficient representatives are *Eristalis tenax* and *Lucilia sericata*. Regarding the amount of pollen it carries on its body, *E. tenax* is a pollinator that is more efficient than *L. sericata* (Table 2), whereas the latter is a rather permanent flower visitor (Fig. 10). While *L. sericata* is more sedentary on the flowers, *E. tenax* is a long distance visitor, therefore it is likely to be the main cross pollination agent of *Daucus* in the archipelago. Both these characteristics would qualify *E. tenax* as the super pollinator of carrot if it was not a migratory species depending chiefly on wind drifts, with a non-permanent presence on the islets (Fig. 10; Pérez-Bañón et al. 2003). On the other hand, Calliphoridae constitute a safe local pollinator resource, but like *L. sericata* they are sedentary and very short distance fliers, thus

Table 3 Fruit- or seed-set (%) after free pollination in all natural populations of *Medicago citrina* and *Daucus carota* subsp. *commutatus* in small islets of the Columbretes archipelago

Islet	Size of the islet (ha)	Population size (# plants)		Fruit/seed set after free pollination (%)		
		<i>Medicago</i>	<i>Daucus</i>	<i>Medicago</i>	<i>Daucus C</i>	<i>Daucus L₁</i>
Grossa	ca. 20	100	50	15.7 ± 2.81	62 ± 6.0	62 ± 3.6
Foradada	1.6	500	700–800	9.8 ± 0.86	46 ± 12.0	45 ± 5.0
Ferrera	1.5	400	300	9.4 ± 0.96		

For each site we give the population and the islet size. Unless specifically mentioned otherwise, the data are from year 1998. (Combined data are from this study, Juan 2002, and Pérez-Bañón et al. 2003)

their activity may bring about geitonogamy rather than long distance dispersal of pollen. Another shortcoming of the pollination by blowflies is that their population numbers rely on human wastes and bird excrements on the islands, therefore they are anthropogenic and avian by-products. This may partly explain the lower seed set of free-pollinated plants on Foradada, an island that, unlike Grossa, is neither inhabited by humans nor hosts a substantial bird colony (Fig. 8). Our personal observations confirm that human litter and avian excrement zones on Grossa were the incubating areas for calliphorids, which supplied the *Daucus* population with flower visitors.

That *Daucus* populations appear to manage well on remote small islands opens the question of pollination plasticity under difficult conditions in terms of sufficiency and efficiency of local pollinators in such areas. Based on our collective data from two species in the same archipelago (*D. carota* subsp. *commutatus* and *Medicago citrina*; Pérez-Bañón et al. 2003), we conclude that, in general, small islands provide reduced pollinator services to their plants, the reduction depending on the size of the island rather than the size of the plant population (Table 3). This may be attributed rather to the reduced resources small islands afford to sustain a sufficient number of pollinators than to Alle effects (Groom 1998; Oostermeijer et al. 2000). Yet, by being limited in size such islands are unable to attract migrating insects that are passing by, which are necessary for the pollination of the native plants. Under such conditions any available pollinator regardless its population size is of extreme importance for the local flora.

This study, together with a previous one of ours (Pérez-Bañón et al. 2003) brought evidence that

in small islands where bees are absent, *E. tenax* individuals landing accidentally on the island are invaluable for the viability and the long term persistence of the local flora. Indeed, these animals appear to be relatively efficient and long distance pollen dispersers, a role that is normally played by bees in the Mediterranean (Petanidou and Lamborn 2005). In this sense, nature conservation management plans in small archipelagos, such as Columbretes, should consider sustaining the populations of migrating pollinators of *E. tenax* at the source sites, i.e., at the nearby mainland. This is crucial, as numerous Mediterranean coastland areas are under continuous threat by development, which is a major risk for the populations of migrant insects originating from these areas.

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