

# Functional significance of the dark central floret of *Daucus carota* (Apiaceae) L.; is it an insect mimic?

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## Abstract

In *Daucus carota* L. (Apiaceae) the florets comprising the central umbellet of inflorescences are usually pink or dark purple, presenting a marked contrast to the surrounding umbellets, which are generally white. The number of dark florets varies, and some inflorescences have no dark florets. It has been proposed that the dark florets function as an insect mimic, and in so doing serve to attract insects to the flower. In contrast, other authors, Darwin included, suggest that they are functionally redundant. The present study examined whether the dark florets attract insects, and also whether this effect can be replicated by replacing these florets with an insect. At the study site in Portugal the predominant insect visitor was the beetle *Anthrenus verbasci* L. (Dermestidae), which is similar in size and shape to the dark florets. Large inflorescences and those with more dark florets attracted more beetles than small inflorescences and those with fewer or no dark florets. Inflorescences with the dark florets removed attracted fewer beetle visitors compared with intact inflorescences. Inflorescences in which the dark florets were replaced with one or a cluster of five dead, freeze-killed *A. verbasci* attracted more beetles than inflorescences from which the dark florets had been removed. Replacement of the dark florets with a relatively large Meloid beetle resulted in the attraction of markedly fewer *A. verbasci*. We conclude that the dark florets can act as an insect attractant for some insect groups by acting as an insect mimic, and that they are adaptive, in contrast to the speculations of Darwin.

*Keywords:* *Anthrenus verbasci*, carrot, Dermestidae, floral evolution.

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## Introduction

In the Carrot and some allied Umbelliferae, the central flower has its petals somewhat enlarged, and these are of a dark purplish-red tint; but it cannot be supposed that this one small flower makes the large white umbel at all more conspicuous to insects . . . That the modified central flower is of no functional importance to the plant is almost certain. It may perhaps be a remnant of a former and ancient condition of the species' Darwin (1888, p. 8).

Many angiosperms have generalized pollination systems with floral rewards that are readily accessed, so their flowers are visited by an array of insects from taxonomically diverse origins (Ollerton 1996; Waser *et al.* 1996;

Cresswell 1998). The flowers of *Daucus carota* (wild carrot) belong to this group, and are typical of those of the Apiaceae (the umbellifers), comprising a compound umbel held at the end of a tall stem (0.6–1.5 m tall). The umbel is formed from many umbellets, each of which is composed of several individual florets. As in most umbellifers the petals are white and the inflorescence forms a conspicuous horizontal convex disc that becomes concave with age. *Daucus carota* is unusual among the Apiaceae in that the florets of the central umbellet are pink or purple in colour and they are raised above the level of the surrounding florets (approximately 10% of individuals do not possess these dark florets; Westmoreland & Muntan 1996; Lamborn & Ollerton 2000).

The purpose of the dark central florets has been the subject of speculation and experimentation ever since Darwin's suggestion that they probably serve no current

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function. Detto (1905) suggested that the apparent presence of an insect on a flower would discourage other animals and that the dark central flower reduces flower damage from herbivores. In contrast, Rothschild (1972) argued that the dark florets might increase insect pollinator visitation. Using cage experiments, Eisikowitch (1980) demonstrated that inflorescences with dark florets attracted more *Musca domestica* (Diptera) (i.e. more *M. domestica* landed on them) than inflorescences with no dark florets, and *M. domestica* are known to be attracted to black spots painted onto a contrasting pale background (Chapman *et al.* 1999). Similarly, the attraction of various fly species to dark spots on flowers has been recorded in a range of other plants (Dodson 1962; McDonald & van der Walt 1992; Johnson & Midgley 1997). Westmoreland and Muntan (1996) experimentally removed the dark florets from inflorescences of *D. carota* at sites in eastern USA (where *D. carota* is naturalized) and found that this reduced visitation by Syrphidae and mordelid beetles, but that the responses of other insect groups varied between sites. Most recently, Lamborn and Ollerton (2000) experimentally manipulated inflorescences in the UK, but found no consistent effect on insect visitation or fruit set. Overall, there is little consistency between studies.

If the dark florets are adaptive, how might their presence attract insects? Yeo (1972) suggested that they might mimic the presence of an insect, and thus indicate either the availability of food or the presence of a conspecific, which might offer a mating opportunity. Both arguments have been used to explain the attraction of *M. domestica* to black spots (Chapman *et al.* 1999). In some plants, such as *Cryptostylis* and *Ophrys*, spp., reproductive mimicry occurs, whereby flowers or parts of flowers specifically mimic a female insect to attract males (pseudocopulation) (Dafni 1984). Conversely, one might expect the presence of another insect to signify increased competition for floral resources or the presence of a potential predator, in which case one would predict that fewer insects would visit inflorescences with dark florets.

In the present study, we examined how both natural variation and experimental manipulation of the dark florets affect insect visitation to *D. carota* in a population in Portugal where the predominant insect visitor is the beetle *Anthrenus verbasci*. These beetles are of very similar size and shape to the dark florets. We specifically assessed whether the dark florets could act as insect mimics by replacing them with beetles.

## Materials and methods

### Study site

Experiments were conducted at Quinta de Sao Pedro Field Study Centre in Lisbon, Portugal, in June 2006. The site

consists of 4 ha of grassland and open woodland; the study plant *D. carota* occurs in the grassland areas.

### Study species

*Daucus carota* is a biennial herb that occurs naturally throughout much of Europe, Asia and North Africa, and was introduced to North America in the 17<sup>th</sup> century. It occurs in meadows and field margins, particularly in disturbed areas and on calcareous soils, and it flowers from May to August. The primary umbels consist predominantly of hermaphrodite flowers, with some staminate flowers towards the center (Proctor *et al.* 1996; Fig. 1). The dark central florets are invariably hermaphrodites (Koul *et al.* 1989). Hermaphrodite flowers are protandrous, with stigmas only becoming receptive after all anthers have withered, which presumably minimizes selfing (Koul *et al.* 1989; Proctor *et al.* 1996).

The structure of the umbel provides a horizontal platform on which insects can graze, often for extended periods, and is typical of the 'small-fly pollination syndrome' proposed by Faegri and van der Pijl (1966). Both nectar and pollen are readily accessible and the flowers are typically visited by a broad range of Diptera, Hymenoptera, Coleoptera, and other generally small insects (Eisikowitch 1980; Westmoreland & Muntan 1996; Lamborn & Ollerton 2000). Bohart and Nye (1960) recorded 334 species of insects from 37 families on *D. carota* over a period of 4 years in Utah, USA, with considerable variation between years, whereas Hawthorn *et al.* (1956) listed 250 visiting insect species, also in the USA. Using data compiled from a number of sources, Knuth (1908) describes between 27 and 70 insect species visiting *D. carota* at various sites across Europe.



**Fig. 1** An inflorescence of *Daucus carota* and the beetle *Anthrenus verbasci* (inset).

At the study site, *D. carota* was abundant, with a population of many hundreds of plants. *Daucus carota* was also common in the surrounding area. By far the most frequent visitor to *D. carota* inflorescences was the beetle *Anthrenus verbasci*, which comprised approximately 97% of insect visitors, the remainder (in order of decreasing frequency) were various other beetles (primarily Cerambycidae and Meloidae), Diptera and Hymenoptera. *Anthrenus verbasci* are small, dark, rounded beetles (1.7–3.5 mm in length) and are similar in size and shape to the dark central florets of *D. carota* (diameter 2–3.2 mm) (Fig. 1). *Anthrenus verbasci* appear to graze primarily on pollen.

### Observations and experiments

Only *D. carota* growing in unshaded areas were used in the experiments, and the height and area of each inflorescence (estimated from the diameter because the inflorescences are circular) were recorded. The abundance of *A. verbasci* was recorded in response to natural variation in the number of dark central florets by recording the number of beetles on 100 randomly chosen inflorescences. Observations were made between 10.00 and 14.00 hours.

A further 100 inflorescences, selected to include only inflorescences with dark central florets, were randomly assigned to one of two groups: controls were left intact and the dark central florets were removed from the remaining inflorescences. All insect visitors were removed and scattered in long grass near the center of the study site. On the following day, the number of *A. verbasci* visiting each inflorescence was scored four times at 2-h intervals between 10.00 and 16.00 hours, and the mean number per inflorescence was used in subsequent analyses.

Finally, 200 inflorescences, excluding those that had been manipulated in the previous study, were randomly assigned to one of four groups: (i) dark florets removed and a drop of colorless glue (queen bee marking glue; E.H. Thorne, Wragby, Lincs, UK) was applied to the center of the inflorescence; (ii) dark florets removed and a single freeze-killed *A. verbasci* was glued to the center of the inflorescence; (iii) dark florets removed and a cluster of

five *A. verbasci* was glued to the center of the inflorescence; and (iv) dark florets removed and a single Meloid beetle was glued to the center of the inflorescence. The treatments were set up in the evening and observations were made on the following day. As above, the number of *A. verbasci* visiting each inflorescence was then scored four times at 2-h intervals between 10.00 and 16.00 hours.

The weather throughout the experimental period was uniformly warm and sunny.

### Results

The mean number of dark central florets per umbel was  $3.25 \pm 1.7$  (mean  $\pm$  standard deviation,  $n = 100$ ), and 18 out of 100 inflorescences had no dark central flower. The response of beetles (abundance) to this natural variation in floral characteristics was examined using General Linear Model (GLM) with Poisson errors and log-link function; the inflorescence area, height and number of dark florets acted as covariates. Beetles were more abundant on larger inflorescences ( $\chi^2_1 = 8.46$ ,  $P = 0.004$ ) and on those with more dark florets ( $\chi^2_1 = 204$ ,  $P < 0.001$ ; Fig. 2; Table 1). Inflorescence height did not contribute significantly to the model, although height, area and the number of dark florets were positively correlated with one another (Pearson product-moment correlation

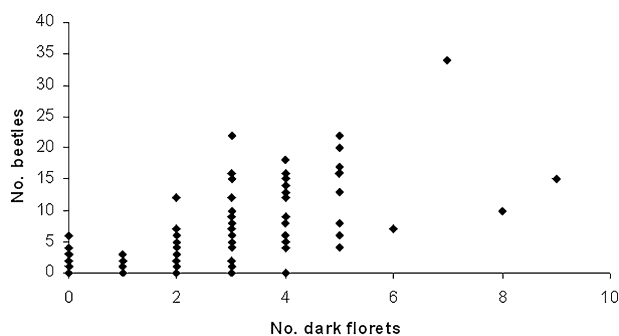


Fig. 2 Number of *Anthrenus verbasci* per inflorescence according to the number of dark central florets ( $n = 100$ ).

**Table 1** Results from the General Linear Model (GLM) analysis of the number of beetles attracted to inflorescences using Poisson errors with log-link function

Parameter	Parameter estimate (B)	SE	$\chi^2$	d.f.	P
(Intercept)	0.840	0.143	34.6	1	0.000
Height	-0.002	0.0016	1.46	1	0.227
Area	$4.97 \times 10^{-5}$	$1.71 \times 10^{-5}$	8.46	1	0.004
No. dark central florets	0.282	0.0197	204	1	0.000

Explanatory factors were inflorescence height (cm), area (mm<sup>2</sup>) and the number of dark central florets.  $r^2 = 0.448$ . SE, standard error.

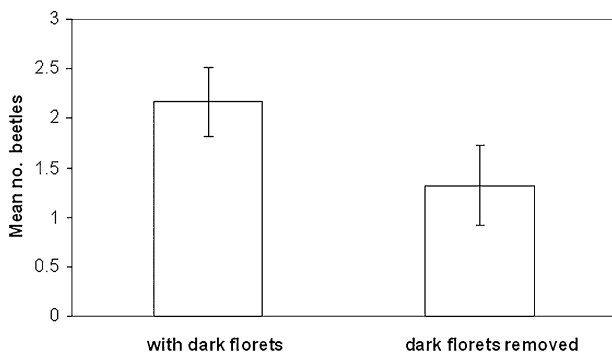


Fig. 3 Mean number of *Anthrenus verbasci* ( $\pm$  standard error) on inflorescences from which the dark florets had been removed compared with control inflorescences ( $n = 50$ ).

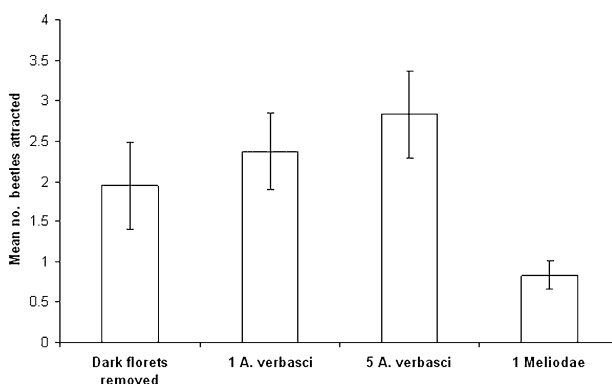


Fig. 4 Mean number of *Anthrenus verbasci* ( $\pm$  standard error) attracted to inflorescences from which the dark florets had been removed, to those in which the dark florets had been replaced by one dead *A. verbasci* or five dead *A. verbasci* or one dead Meloidae ( $n = 50$  per treatment).

coefficient: florets and height,  $R = 0.018$ , n.s.; florets and area,  $R = 0.269$ ,  $P = 0.007$ ; height and area,  $R = 0.401$ ,  $P < 0.001$ ,  $n = 100$ ).

The removal of the dark florets resulted in inflorescences attracting significantly fewer beetles than control inflorescences (Mann–Whitney,  $W = 2026.0$ ,  $n = 100$ ,  $P = 0.025$  [adjusted for ties]) (Fig. 3).

The replacement of dark florets with freeze-killed *A. verbasci* enhanced attraction of *A. verbasci* (Kruskal–Wallis test,  $H_3 = 18.6$ ,  $P < 0.001$  [adjusted for ties]) (Fig. 4). Pairwise comparisons using Mann–Whitney  $U$ -tests revealed which treatments differed significantly. Compared to flowers with the dark florets removed (controls), the addition of a single *A. verbasci* had no significant effect ( $P = 0.117$ ), but adding five *A. verbasci* attracted significantly more beetles ( $P = 0.020$ ). Flowers with a single Meloid beetle attracted significantly fewer beetles than flowers with either a single *A. verbasci* ( $P = 0.001$ ) or five *A. verbasci* ( $P < 0.001$ ).

## Discussion

The dark central florets of *D. carota* enhanced attraction of the beetle *A. verbasci*, which was by far the most frequent visitor to *D. carota* at our study site. More beetles were attracted to inflorescences that naturally had more dark florets, and removal of the dark florets reduced the attraction of *A. verbasci* compared with the controls. The dark florets and *A. verbasci* are strikingly similar in size and shape, and the positive effects of the presence of the dark florets on insect recruitment could be replicated by replacing them with one or more dead *A. verbasci*. In contrast, the presence of a much larger beetle appeared to repel *A. verbasci*.

Why might *A. verbasci* be attracted to dark florets or flowers with conspecifics on them? In bumblebees, naïve bees use the presence of conspecifics on flowers as a cue that the flower type is likely to be rewarding (Kawaguchi *et al.* 2006, 2007). However, once they are experienced, bumblebees switch to avoiding flowers on which conspecifics are feeding, presumably to avoid competition for the floral resources. It is possible that the *A. verbasci* in our study were behaving similarly, and it would be fascinating to compare the behavior of naïve and experienced beetles with regard to flower choice. Mating was not observed during our study, but it appears likely that aggregation increases mating opportunities. Aggregation may also reduce the probability of predation by providing a dilution effect. Many other adult insects aggregate, for a diversity of reasons (e.g. Turner 1975; Landolt & Phillips 1997; Darvill *et al.* 2007).

The avoidance of inflorescences with large beetles on them is readily explained by the fact that these beetles might be predatory, they might provide competition for floral resources, or at the very least they are likely to cause considerable disturbance to smaller organisms as they forage on flowers. Experienced bees are known to avoid inflorescences on which other bees are foraging unless the inflorescence is very large (Goulson 2003; Kawaguchi *et al.* 2006, 2007). Both the attraction to inflorescences with dark florets/dead conspecifics and the avoidance of inflorescences with large beetles on them is likely to be based on visual cues. Lamborn and Ollerton (2000) found no difference between the scent produced by dark florets and the more abundant white florets. In addition, the freeze-killed *A. verbasci* would have rapidly dried on the flower and because they were glued to the flowers the day before the observations were made they are likely to have been desiccated by the time of the observations. Thus, it seems unlikely that they were producing significant quantities of volatiles that might act as attractants. Mulligan and Kevan (1973) argued that the contrast between white and dark central florets acts as a long distance visual signal to insect pollinators.

Given the similarity in size and shape, it is tempting to conclude that the dark florets of *D. carota* have evolved to mimic *A. verbasci*, and by so doing they attract more *A. verbasci* and thus increase the likelihood of pollination. Johnson and Midgley (1997) studied dark spots on the petals of *Gorteria diffusa* (Asteraceae) and concluded that they mimic the main pollinator, the bee fly *Megapalpus nitidus* (Bombyliidae), and by so doing enhance visitation. However, other studies of insect visitation to *D. carota* at different localities record few or no visits by *Anthrenus* spp., suggesting that the pollinators of this species are highly variable from site to site (Knuth 1908; Hawthorn *et al.* 1956; Bohart & Nye 1960; Eisikowitch 1980; Westmoreland & Muntan 1996; Lamborn & Ollerton 2000). Lamborn and Ollerton (2000) also found large differences in insect visitors between years at the same site. Our study did not assess pollen transfer or fruit set, but small beetles such as *Anthrenus* spp. are unlikely to be highly effective pollinators, even at high density, because they do not often move between inflorescences, instead they tend to graze on pollen for several hours on a single inflorescence (*D. carota*, Goulson, pers. obs.). Thus, it seems unlikely that *D. carota* should have evolved this structure to attract this particular insect species. However, given that the dark central florets have been found to enhance visitation by Syrphids and mordelid beetles (Westmoreland & Muntan 1996), *M. domestica* (Eisikowitch 1980) and now by *A. verbasci*, it seems probable that their origin is adaptive, and that Darwin (1888) was probably incorrect in asserting that they are of 'no functional importance'.

*Daucus carota* has a vast range and, as far as is known, dark florets occur throughout its distribution, so it seems likely that they evolved in a single ancestral population of *D. carota* in the distant past, and presumably at this time pollination by one or more of the insect visitors present was enhanced by the production of the dark florets. Since then, as the species spread through much of the old world, the trait has most likely been maintained by localized and erratic positive selection. Dark florets are unlikely to be costly because they are small and are distinguished from white florets only by the enhanced production of anthocyanins, so if at certain times and places they do not enhance pollination (e.g. Lamborn & Ollerton 2000) there will not be strong selection against their production. Nonetheless it is interesting that some inflorescences have no dark florets. It may be that at some times there is selection against plants that produce dark umbels; for example, if pollinators are attracted to umbels with dark florets or to conspecifics on them when they are naïve, but avoid them once they become experienced (following the behaviour of bumblebees described by Kawaguchi *et al.* 2007), then the advantage conferred by the dark florets is likely to change over time as the insect population becomes more

experienced. It must be noted that the present study provides only a snapshot of the insect visitors to *D. carota* at one place and time, and visitations are highly likely to differ between sites, at different times of the season, and from year to year. In addition, we did not assess the efficacy of *A. verbasci* as a pollinator; it would greatly aid the interpretation of the present study if further work were to evaluate the relative importance of different pollinating organisms in *D. carota*.

It is increasingly recognized that most insect-pollinated plants are rather generalized in the insects that they attract and that pollinate them (Waser *et al.* 1996; Goulson 1999). Indeed, generalization is predicted when the abundance of different pollinator groups is unpredictable over time. For plants belonging to generalized pollination syndromes it is likely that some floral characters will be poorly adapted to current pollinator availability at any particular point in time and space. Thus, it is to be expected that studies conducted on the same species in different places may arrive at markedly different conclusions with regard to the adaptive value of particular traits.

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