A comparison of the pollination ecology of *Arum maculatum* and *A. italicum* in England

A. DIAZ

School of Conservation Sciences, Bournemouth University, Dorset House, Talbot Campus, Fern-Barrow, Poole, Dorset, BH12 5BB

and

G. C. KITE

Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AB

ABSTRACT

Britain is considered to have two native species of *Arum*; the common Lords & Ladies, *A. maculatum* L., and the Rare Lords and Ladies, *A. italicum* Miller subsp. *neglectum* F. Towns. Currently *A. italicum* subsp. *neglectum* occurs only as thinly scattered populations spread across southern England and the Channel Islands. This study investigates whether part of the reason for the rarity of *A. italicum* subsp. *neglectum* in Britain is because it has different pollinator requirements to that of its very common close relative, *A. maculatum*. Results indicate that although the inflorescence odour composition of the two species are different, they attract similar suites of insects. Most insects caught by the plants were female *Psychoda phalaenoides* L., but both *A. maculatum* and *A. italicum* subsp. *neglectum* also caught substantial numbers of females of another species of midge, *Smittia pratorum* Goetghebuer. Both *P. phalaenoides* and *S. pratorum* were found to carry *Arum* pollen between plants but *S. pratorum* generally carried much smaller pollen loads than *P. phalaenoides.* The main pollinator of *Arum italicum* subsp. *italicum* Miller was also found to be *P. phalaenoides.* In conclusion, as female *P. phalaenoides* are readily available throughout the flowering period of *A. maculatum* and *A. italicum*, pollinator limitation is unlikely to be a reason for the rarity of *A. italicum* subsp. *neglectum* in Britain.

KEYWORDS: *Arum italicum*, *Arum maculatum*, *Psychoda phalaenoides*, *Smittia pratorum*, pollination ecology, odour chemistry.

INTRODUCTION

Plant species of the genus *Arum* have evolved a fascinating range of pollination systems centred around a general theme of using an odour to lure pollinators into elaborate inflorescences and then often imprisoning them to increase their effectiveness as pollinators. Important details vary, such as the nature of the odour, and not all species appear to trap their pollinators (Boyce 1993). Britain is believed to have two native species of *Arum*: *A. italicum* and *A. maculatum* (Prime 1961; Stace 1991). In Britain *A. italicum* occurs as two sub-species, *A. italicum* subsp. *neglectum* and *A. italicum* subsp. *italicum*, but only *A. italicum* subsp. *neglectum* is considered as native (Boyce 1993). Its current distribution is confined to scattered and dwindling populations across southern England and the Channel Islands (Prime 1960). In contrast, *A. maculatum* occurs frequently throughout England and Wales. It has been suggested that the reason for this difference in distribution may be that *A. italicum* is more sensitive to freezing (Prime 1960; Chatters 1994) as it is at the northern limit of its range in Britain (Stewart & Pearman 1994). This study investigates whether there is also a difference in pollinator requirement.

The pollination ecology of *A. maculatum* has been the subject of a number of studies and these indicate that the most frequent insects captured are female owl midges of the species *Pyschoda phalaenoides* (Prime 1960; Lack & Diaz 1991; Kite 1995). By contrast, there has been no detailed

study of the species of insect caught by *A. italicum* in Britain. There is some indication that the two species produce different floral odours (Kite *et al.* 1998). This study compares the pollination ecology of *A. maculatum*, *A. italicum* subsp. *neglectum* and *A. italicum* subsp. *italicum* in southern England. It aims to investigate the relationship between scent production, total insect capture and reproductive success. It also investigates which of the species captured are actually acting as pollinators.

METHODS

STUDY SITES

Five sites were used in this study (Table 1). Three of these sites, E-Meon (Hampshire), Arundel (W. Sussex) and Dancing Ledge (Dorset), contained sympatric populations of *A. maculatum* and *A. italicum* subsp. *neglectum*. A fourth site at Ridge (Dorset) contained a naturalised population of *A. italicum* subsp. *italicum*. *Arum maculatum* did not occur at this site and so comparisons were made with a nearby population of *A. maculatum* at Wareham (Dorset). Each site contained a population of at least 200 plants of each *Arum* species present. All sites other than Dancing Ledge were in deciduous woodland. The Dancing Ledge site consisted of a system of stone walls on exposed sea cliff grasslands where both species of *Arum* occurred mostly in the shelter of the walls or nearby scrub.

PSYCHODA AVAILABILITY

Although the flowering times of *A. maculatum* and *A. italicum* can overlap in Britain, peak flowering time for *A. maculatum* is usually from the last week of April to the first week of May while that for *A. italicum* is the last two weeks of May. The availability of *Psychoda* was monitored at each site from mid-April 2000 to mid-June 2000 to establish if *Arum* populations were experiencing differences in pollinator availability. To do this, ten 10 cm^2 sticky traps were positioned at random but at a height of 25 cm above the ground within each study site. Traps were constructed out of sheets of stiff yellow plastic fly traps and were functional even in wet weather. Trap points were visited each week through the study period to count the number of *Psychoda* caught and to set fresh traps. This method did not measure total *Psychoda* abundance, but provided an index with which to assess the relative abundance of *Psychoda* before, during and after the flowering period of each *Arum* species studied.

INFLORESCENCE ODOUR ANALYSIS

The spadix appendix odour of selected inflorescences of each species was collected in the field, with minimal disturbance to the plant, by the technique of headspace trapping. A plastic sleeve made from a forensic sample bag (Keygrowth Marketing) was attached to the end of an odour trap (100 mm long x 3 mm diameter; SGE Ltd) packed with 100 mg of 35/60 mesh Tenax TA (Jones Chromatography) and inserted over the spadix of an odorous inflorescence. Air was then drawn past the appendix and through the trap at a rate of 25 ml/min by means of a portable constant flow pump (DuPont Air Sampler Model P125A). The odour was collected during the female phase of inflorescence opening: that is from about 18:00 h, soon after spathe opening, to about 07:00 h the following morning.

TABLE 1. LOCATION OF STUDY SITES.

Study Site	Taxon Surveyed	Location and Grid Reference
E-Meon	*A. maculatum* & *A. italicum* subsp. *neglectum*	East Meon Church, Hampshire (GR468122)
Arundel	*A. maculatum* & *A. italicum* subsp. *neglectum*	Offham Hanger, near Arundel, W. Sussex (GR502108)
Dancing	*A. maculatum* & *A. italicum* subsp. *neglectum*	Dancing Ledge, near Langton Matravers, Dorset (GR399076)
Wareham	*A. maculatum*	Wareham, east part of town wall, Dorset (GR392087)
Ridge	*A. italicum* subsp. *italicum*	Ridge village, Dorset (GR393086)

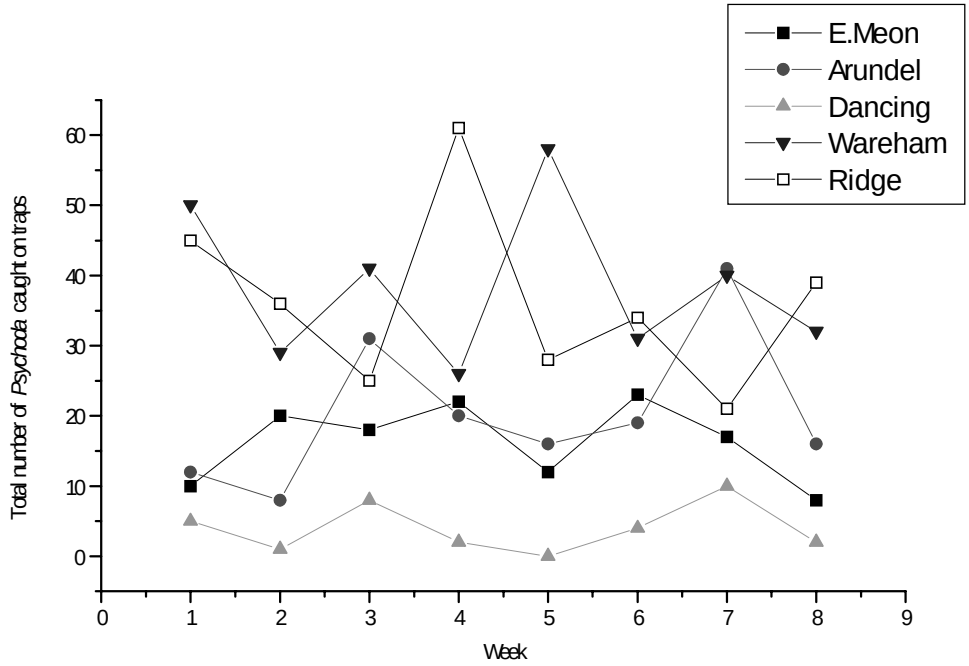

FIGURE 1. The total number of *Psychoda phalaenoides* caught per week on ten artificial traps in each study site. Week 1 started on the 14th of April 2000.

The compounds on the Tenax trap were analysed by thermal desorption-gas chromatography-mass spectrometry (TD-GC-MS: thermal desorption injector, SGE; GC, Perkin-Elmer Model 8500; MS, Finnigan-MAT Ion Trap Detector 800 series). The trap was inserted into the thermal desorption injector for 10 s where it was subjected to a flow of helium gas at 10 psi and 250°C. During desorption, the helium flow from the trap was directed onto a non-polar capillary column, the front end of which was looped through a polystyrene cup full of liquid nitrogen. The front end of the column was then removed from the liquid nitrogen and chromatography of the volatile compounds was carried out using an oven temperature programme of 40–260°C at 5°C/min. Electron ionisation (70 eV) mass spectra of the compounds eluting from the column were recorded by the ion trap detector (acquisition parameters: *m/z* range 38–400, automatic gain control set at *m/z* 38, scan rate 1/s) and the retention index of each component was determined by calibrating the retention time against a series of n-alkanes (Supelco UK Ltd) analysed in the same manner. Identifications were achieved in the first instance by comparison of the mass spectra and retention indices with those published by Adams (1995), obtained using the same column polarity and mass spectrometer. For components showing unsatisfactory matches, assignment was attempted by on-line searching of the NIST mass spectral database (Mikaya *et al*., 1999). The identities of some components were confirmed against standards purchased from the Aldrich Library of Rare Chemicals. Peak areas were determined from the total ion chromatogram and expressed as a percentage of the summed peak areas of all the component peaks, ignoring those components (either Tenax artefacts or air pollutants) that were also present in a control sampling of air at the study site.

INSECT CAPTURE AND SEED SET

Insects were collected from 30 inflorescences of each *Arum* species at each site. Collections were made over three separate days during the main flowering phase of each population. Only one

TABLE 2. COMPOSITION OF THE APPENDIX ODOURS OF INDIVIDUAL INFLORESCENCES OF WILD-GROWING *A. ITALICUM* AND *A. MACULATUM* DETERMINED BY TENAX TRAPPING IN THE FIELD AND TD-GC-MS

			Relative amount, % (tr = <1%)									
			A. italicum			*A. italicum*						
No.	RI	Component Assigned	subsp. *italicum*			subsp. *neglectum*					*A. mac.*	
1	703	3-methyl-2-butanone[c]	2	1	1	tr	tr	2	5	11	-	-
2	745	pentan-1-ol[c]	4	2	3	-	-	-	-	-	-	-
3	759	3-methyl-2-pentanone[c]	2	tr	3	tr	tr	tr	tr	2	-	2
4	823	butyl acetate[b]	-	-	-	-	-	-	-	-	-	2
5	890	2-heptanone[a]	2	1	1	2	tr	4	2	2	2	5
6	898	3,7-dimethyl-1-octene[a]	6	12	9	16	29	21	28	38	-	-
7	922	2,6-dimethyl-1,7-octadiene[c]	3	5	2	4	2	4	2	3	-	-
8	939	3,7-dimethyl-1,6-octadiene (β-citronellene)[a]	51	50	37	21	23	28	13	22	-	-
9	967	3,7-dimethyl-2-octene*	-	-	-	26	23	21	12	9	-	-
10	1004	*trans*-2,6-dimethyl-2,6-octadiene[a] **	-	-	-	5	5	8	3	2	-	-
11	1028	1-*p*-menthene[b]	-	-	-	tr	tr	tr	-	tr	-	-
12	1035	limonene[b]	1	1	8	-	tr	tr	-	-	-	-
13	1075	3,7-dimethyl-1-octen-7-ol[b]	-	-	-	tr	tr	tr	-	-	-	-
14	1086	*p*-cresol[a]	8	5	13	tr	tr	tr	tr	tr	5	tr
15	1093	2-nonanone[b]	1	tr	-	tr	tr	tr	-	-	-	-
16	1109	n-nonanal[b]	1	tr	-	-	-	-	-	-	-	-
17	1201	methyl salicylate[b]	4	4	8	-	-	-	-	-	-	tr
18	1210	n-decanal[b]	-	-	-	-	-	-	-	-	-	tr
19	1301	indole[a]	-	-	-	-	-	-	-	-	9	tr
20	1354	unidentified sesquiterpene	tr	2	tr	-	-	-	-	-	-	-
21	1368	citronellyl acetate[b]	tr	tr	tr	tr	1	tr	4	tr	-	-
22	1376	α-copaene[b]	-	-	-	-	-	-	-	-	1	tr
23	1404	unidentified sesquiterpene	12	15	13	11	9	6	20	4	1	7
24	1409	(Z)-caryophyllene[b]	tr	tr	tr	4	2	1	3	tr	2	2
25	1426	(E)-caryophyllene[b]	tr	tr	tr	7	3	3	7	1	13	5
26	1443	aromadendrene[b]	tr	tr	-	-	-	-	-	-	tr	tr
27	1464	α-humulene[b]	-	-	-	tr	tr	tr	tr	6	9	7
28	1475	allo-aromadendrene[b]	-	-	-	-	-	-	-	-	4	3
29	1489	unidentified sesquiterpene	-	-	-	tr	tr	-	-	-	7	8
30	1510	bicyclogermacrene[b]	-	tr	-	tr	tr	-	-	-	4	6
31	1531	δ-cadinene	tr	tr	tr	-	tr	-	-	-	4	5
32	1543	(Z)-nerolidol[b]	-	-	-	tr	tr	-	-	-	-	-
33	1575	(E)-nerolidol[b]	-	-	-	tr	tr	-	-	-	-	-
34	1716	unidentified sesquiterpene	-	-	-	-	-	-	-	-	14	16
35	1773	pentadecanol[b]	-	-	-	-	-	-	-	-	11	5
36	1788	1-octadecene[b]	-	-	-	-	-	-	-	-	3	11
37	1801	octadecane[b]	-	-	-	-	-	tr	-	-	2	2
38	1828	unidentified alkene	-	-	-	-	tr	tr	-	-	tr	3
39	1834	unidentified	-	-	-	-	-	-	-	-	tr	2
40	1906	n-nonadecane	-	-	-	-	-	tr	-	-	2	7
41	1987	1-eicosene[b]	-	-	-	-	-	-	-	-	4	tr
42	2000	n-eicosane[b]	-	-	-	-	-	-	-	-	2	2

RI = Retention index of component on BPX5
Component assignment criteria:
a = comparison of mass spectrum and retention index with standard. b = comparison of mass spectrum and retention index with published data (Adams 1995). c = comparison of mass spectrum with published data (Mikaya *et al.* 1999).
*Compound 9 was assigned as the reduction product of 10 by analogy with the occurrence of 8 and its reduction product 6. Compounds 9 and 6 had very similar mass spectra. No chromatographic or mass spectral data on authentic 3,7-dimethyl-2-octene was available.
** A standard of *cis*-2,6-dimehtyl 2,6-octadiene from the Aldrich Library of Rare Chemicals gave a RI of 986 but showed a minor component at RI 1003 with the same mass spectrum, which also matched 10. Compound 10 was therefore tentatively assigned as the *trans* form.

population was sampled on any one day. On each collection day, inflorescences in late female phase were examined at random until ten inflorescences were found that contained captive insects. A record was kept of how many inflorescences needed to be examined to find ten with captives. All insects caught were extracted from the inflorescence using a pooter (a suction tube attached to a collecting pot) and preserved in 70% alcohol for later identification. This method caused no damage to the inflorescence. The inflorescences were labelled so that success of seed set could be determined from berry formation over the following two months. Seed set was scored as simply either present or absent to avoid disrupting the infructescences of *A. italicum* subsp. *neglectum.*

COMPARISON OF POLLEN IMPORT

The number of pollen grains brought in by different insect species was counted by extracting freshly captured insects out of inflorescences (by suction, using a pooter) , stunning the insects with diethyl ether and then mounting them on microscope slides smeared with a small amount of gel. Cover slips were placed over the insects and gently pressed down to squash the specimens. Pollen grains carried per insect were then counted using a light microscope with a 100 × magnification. Insects were collected from ten plants per species on each study site. All collections were made during peak flowering phase.

RESULTS

PSYCHODA AVAILABILITY

The number of *Psychoda phalaenoides* captured on the sticky traps was not significantly related to season in any of the sites studied (Figure 1). This suggests that, within each site, *A. maculatum* and *A. italicum* experienced similar availability of *P. phalaenoides.* However, there were significant differences in *P. phalaenoides* capture per site (Kruskal Wallis H = 29·82, $P<0·001$), with the highest numbers captured at Wareham and Ridge and the lowest at Dancing Ledge. This indicates that *Arum* may experience different levels of pollinator availability at different sites.

APPENDIX ODOUR COMPOSITION

The appendix odour from three inflorescences of *A. italicum* subsp. *italicum*, five inflorescences of *A. italicum* subsp. *neglectum*, and two of *A. maculatum* were successfully trapped and analysed (Table 2). The results obtained for *A. maculatum* were similar to those reported previously for the species (Kite, 1995) in that the odour showed the presence of 2-heptanol, *p*-cresol and indole together with various sesquiterpenoids and long-chain aliphatic compounds. However, the odours of two inflorescences analysed in the present study showed a greater relative abundance of an unidentified sesquiterpene alcohol (compound **34** in Table 2), also reported by Kite (1995), which accounted for the largest relative peak area in the total ion chromatograms.

In contrast, the inflorescence odours of both subspecies of *A. italicum* were characterised by high relative amounts of acyclic monoterpenes and related alkenes (mainly compounds **6**–**10**) with indole being undetectable. This also concurs with the results obtained by Kite *et al.* (1998) for *A. italicum* in cultivation. Exact structural assignment of these compounds by GC-MS is problematic and the criteria for their assignments are given in Table 2, but certainly the compounds were not detectable in the odour of *A. maculatum*.

The odours of the two subspecies of *A. italicum* differed in the profile of acyclic monoterpenes and alkenes they contained. While 3,7-dimethyl-1,6-octadiene (β-citronellene, **8**) and its reduced form 3,7-dimethyl-1-octene (**6**), both assigned against authentic standards, were present at high relative abundance in both subspecies, *A. italicum* subsp. *neglectum* also contained 2,6-dimethyl-2,6-octadiene (**10**) and an alkene (**9**) that is likely to be its reduced form. Amongst other differences, the odours examined of *A. italicum* subsp. *italicum* could also be distinguished from those of subspecies *negectum* by the higher relative abundance of *p*-cresol in the former.

The major sesquiterpene (**23**) in the odour of both subspecies of *A. italicum* did not give any matches with mass spectra of sesquiterpenes included in the NIST 98 (Mikaya *et al.* 1999) or Adams (Adams 1995) libraries. This compound also occurred in the odour of *A. maculatum*, but the major unidentified sesquiterpene alcohol (**34**) in the odour of *A. maculatum* was not detected in the analyses of *Arum italicum*. These sesquiterpeonoids will require isolation for structural characterisation.

TABLE 3. NUMBER OF INFLORESCENCES, IN LATE-FEMALE PHASE OF FLOWERING, EXAMINED AT EACH VISIT TO OBTAIN TEN INFLORESCENCES THAT HAD CAPTURED AT LEAST ONE INSECT. EACH SITE WAS VISITED THREE TIMES FOR EACH SPECIES OF *ARUM* PRESENT

	E-Meon	Arundel	Dancing	Wareham	Ridge
A. maculatum	12	14	22	10	-
	15	10	16	15	-
	13	12	20	11	-
A. italicum	11	13	15	-	14
	10	14	20	-	11
	12	15	23	-	13

INSECT CAPTURE

The number of inflorescences sampled per site and per species of *Arum* to obtain ten inflorescences that had caught insects are given in Table 3. Results differed significantly between sites (Kruskal-Wallis H 6·92, $P = 0{\cdot}075$ for *A. maculatum* and H = 9·03, $P = 0{\cdot}029$ for *A. italicum*) but not between species of *Arum* (Mann Whitney U = 57·5, $P = 0{\cdot}5989$) (Table 3). The number of inflorescences that captured insects was far lower at Dancing Ledge than at the other sites, as was the maximum and average number of insects caught per inflorescence.

All insects captured were Diptera (true flies) and the vast majority belonged to the sub-order Nematocera (thread horn flies). The few non-Nematocera caught were insects belonging to one of many different families of Diptera from the sub-order Cyclorrhapha (blow flies, house flies, fruit flies, hover flies). Most insects captured by all taxa of *Arum* on all sites were female *Pyschoda phalaenoides*, Nematocera belonging to the family Psychodidae. (Figure 2, 3 and 4). The second most abundant group of insects captured by *A. maculatum* and *A. italicum* subsp. *neglectum* on all sites were female *Smittia pratorum* Goetghebuer. These are Nematocera belonging to the family Chironomidae. By contrast, the population of *A. italicum* subsp. *italicum* studied was found to capture very few *S. pratorum* but instead captured considerable numbers of *Psychoda grisescens* Eaton and a range of species of Nematocera belonging to the family Ceratopogonidae. Species of Nematocera from families other than Pyschodidae, Chironomidae and Ceratopogonidae were captured by *Arum* only infrequently and so are presented together as "other Nematocera" in Figures 2, 3 and 4. The composition of the "other Nematocera" did not differ between taxa of *Arum* and consisted of insects from the following families: Sciaridae, Mycetophilidae and Bibionidae.

COMPARISON OF POLLEN IMPORT

The only species that were found to carry pollen grains into any of the taxa of *Arum* studied were *P. phalaenoides* and *S. pratorum*. Of these two species, *P. phalaenoides* was the most frequent importer of pollen for all *Arum* taxa and also brought in a far larger average number of pollen grains per fly than did *S. pratorum* (Table 4).

SEED SET

A comparison of the relationship between seed set and insect capture found that success of seed set was significantly less likely if capture of female *Psychoda phalaenoides* did not occur (Figure 5) (Mann Whitney U = 905, $P < 0{\cdot}0001$ for *A. maculatum*; U = 38, P = 0·003 *for A. italicum* subsp. *neglectum* and U = 484; P = 0·0002 for *A. italicum* subsp. *italicum*).

DISCUSSION

The differences in the profile of the major compounds trapped from the odours of *A. maculatum* and *A. italicum* is remarkable given that both mainly attract *P. phalaenoides*. This difference in the chemical composition was noted before in a preliminary chemical survey of the odours of *Arum* species in cultivation (Kite *et al*., 1998). This earlier study found that the odour profile of *A. italicum* was closer to that of Mediterranean species of *Arum* (such as *A. nigrum* Schott) than to *A. maculatum*, even though *A. italicum* is thought to be more closely related to *A. maculatum*

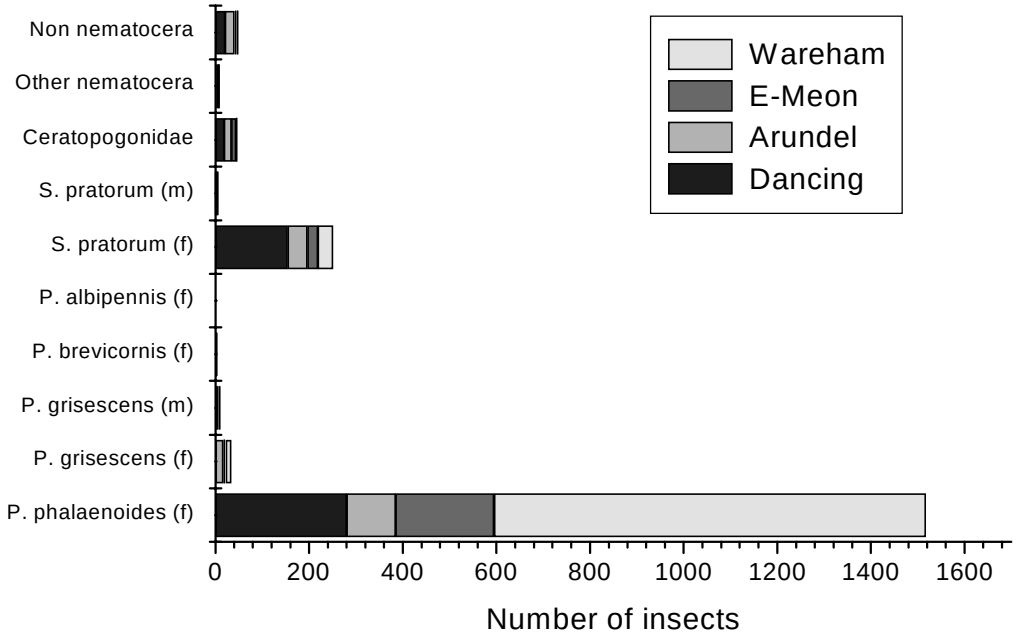

FIGURE 2. The total number of invertebrates captured by *A. maculatum* inflorescences in each of the study sites.

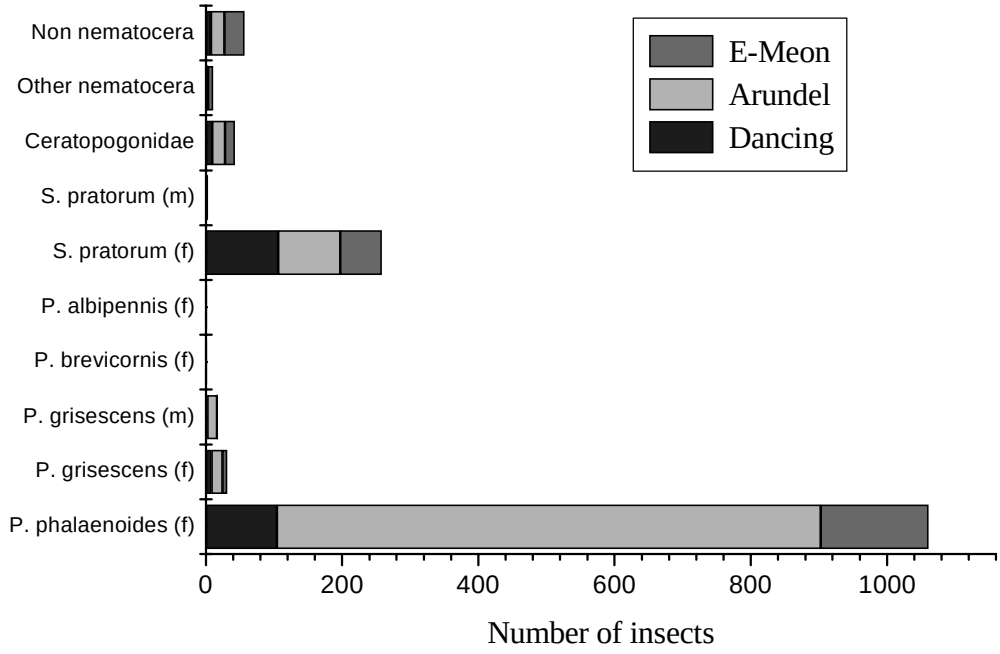

FIGURE 3. The total number of invertebrates captured by *A. italicum* subsp. *neglectum* in each of the study sites.

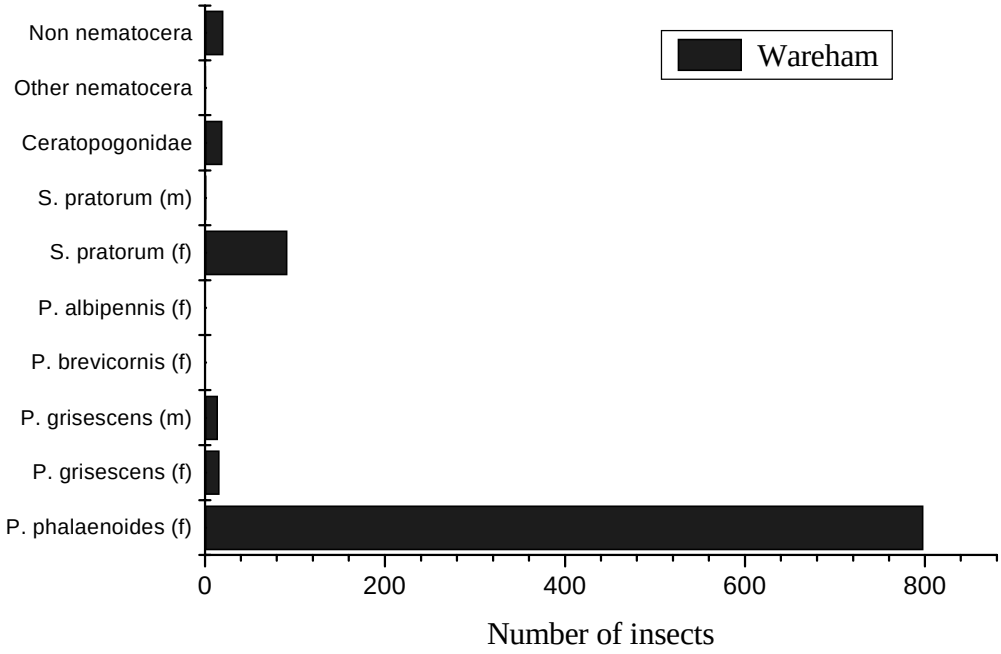

FIGURE 4. The total number of invertebrates captured by *A. italicum* subsp. *italicun* in the Ridge study site.

(Boyce 1993). Inflorescences of these Mediterranean species have been observed to attract a variety of insects that breed on dung, including flies (Diptera: Sphaeroceridae) and beetles (Coleoptera: Staphylinidae), but not *Psychoda* (Drummond & Hammond 1991; 1993). Consequently, Kite *et al.* (1998) questioned an observation by Méndez and Obesco (1992) that *Psychoda* was the main pollinator of *A. italicum*. Clearly, though, our present work supports Méndez and Obesco (1992) and shows that, in southern England at least, *P. phalaenoides* is the chief pollinator of both *A. maculatum* and *A. italicum*. Further work is currently being carried out to establish what insects pollinate *A. italicum* and *A. maculatum* plants in France and Spain.

Previously, p-Cresol was suggested as being a possible attractant for *Psychoda phalaenoides* since it was detected as a common component of the odour of *A. maculatum* and of cow dung, one breeding habitat of *P. phalaenoides* (Kite 1995). *p*-Cresol, particularly in combination with indole and 2-heptanone, was later shown to attract *Psychoda* species in a field behavioural assay (Kite *et al*. 1998). *p*-Cresol and 2-heptanone were two of the components common to the odours of *A. maculatum* and *A. italicum* and so could be responsible for attracting *Psychoda* to both, although it was only present in trace amounts in the odour of *A. italicum* subsp. *neglectum*. Indole could not be detected in either subspecies of *A. italicum*. Another common component is the uncommon sesquiterpene (number 23 in Table 2) that will require isolation for identification. The true attractants may not, of course, be among either the major odour components that are more readily detected by GC-MS or those components common to both species.

This study found that a second species of insect, *Smittia pratorum,* also functioned as a pollinator of *Arum maculatum* and *A. italicum* subsp. *neglectum* in Britain. *Smittia* are terrestrial chironomids whose larvae develop in wet soil (Frouz 1997). It is possible that *S. pratorum* may be attracted to *Arum* to feed on the stigmatic exudate as species in this genus have been reported as feeding on the stigmatic exudate of *Pseudowintera colorata* (Winteraceae) (Lloyd & Wells 1992). *A. italicum* subsp. *italicum* was not recorded as catching *S. pratorum* in this study but instead caught greater numbers of *Psychoda grisescens* than the other two taxa. Only one population was studied and further work is clearly required to establish whether there are consistent differences in insect capture between *A. italicum* subsp. *italicum* and the other two taxa studied.

TABLE 4. A COMPARISON OF THE NUMBER OF POLLEN GRAINS CARRIED INTO *ARUM* INFLORESCENCES BY *PSYCHODA PHALAENOIDES* AND *SMITTIA PRATORUM*

		Psychoda phalaenoides			
Taxon	Site	Number of flies examined	% flies with pollen	Mean No. pollen grains per fly	Max No. pollen grains per fly
A. maculatum	E-Meon	85	69	65	346
	Arundel	114	79	51	244
	Dancing	98	65	57	268
	Wareham	224	85	55	290
A. italicum subsp. *neglectum*	E-Meon	89	70	58	261
	Arundel	280	72	71	304
	Dancing	40	58	60	335
A. italicum subsp. *italicum*	Wareham	102	75	53	321
		Smittia pratorum			
A. maculatum	E-Meon	12	8	3	3
	Arundel	10	10	5	5
	Dancing	61	5	11	31
	Wareham	9	0	0	0
A. italicum subsp. *neglectum*	E-Meon	22	4	4	4
	Arundel	35	6	11	20
	Dancing	32	9	6	19
A. italicum subsp. *italicum*	Wareham	1	0	0	0

The finding that both male and female *Psychoda grisescens* were captured by *A. maculatum* and *A. italicum* agrees with a previous study of *A. maculatum* (Edwards 1940) and is interesting given that *Arum* scent is thought to mimic egg laying sites. Little is known of the ecology of *P. grisescens* other than that it breeds in dung and in the fungus *Coprinus atramentarius* (Satchell 1947; Withers 1988). One possible explanation for the capture of both male and female *P. grisescens* is that males and females fly together and that as the males pursue the females they are inadvertently lured into *Arum* inflorescences.

This study has found that the vast majority of *Arum* pollen imported into inflorescences of *A. maculatum*, *A. italicum* subsp. *neglectum* and *A. italicum* subsp. *italicum* was being carried in by *Psychoda. phalaenoides*. This finding, together with the results from the study of seed set, indicating dependence on visits by *P. phalaenoides*, confirm that *P. phalaenoides* is the main pollinator for *Arum*, at least in Britain. The very high frequency with which *P. phalaenoides* are carrying *Arum* pollen is a testimony to the remarkable effectiveness of a deception which is good enough to lure in *P. phalaenoides* but not so good as to stimulate egg laying. The study found that *P. phalaenoides* not only carry *Arum* pollen more frequently than *S. pratorum*, they also generally carry a greater number of pollen grains per insect. Scanning electron microscopy reveals that the reason for this appears to be that pollen can more easily lodge on the much hairier body of *P. phalaenoides*.

In conclusion, this study has found that scent production appears to differ between the three *Arum* taxa studied but that this caused no differences in the types of insect captured by *A. maculatum* and *A. italicum* subsp. *neglectum* and only small differences between these and *A. italicum* subsp. *neglectum*. In particular, there was no difference between taxa in their ability to capture their main pollinator, *P. phalaenoides*. Female *P. phalaenoides* are readily available throughout the flowering period of *A. maculatum* and *A. italicum* and so results from this study indicate that pollinator limitation is unlikely to be a reason for the current rarity of A. *italicum* subsp. *neglectum* in Britain.

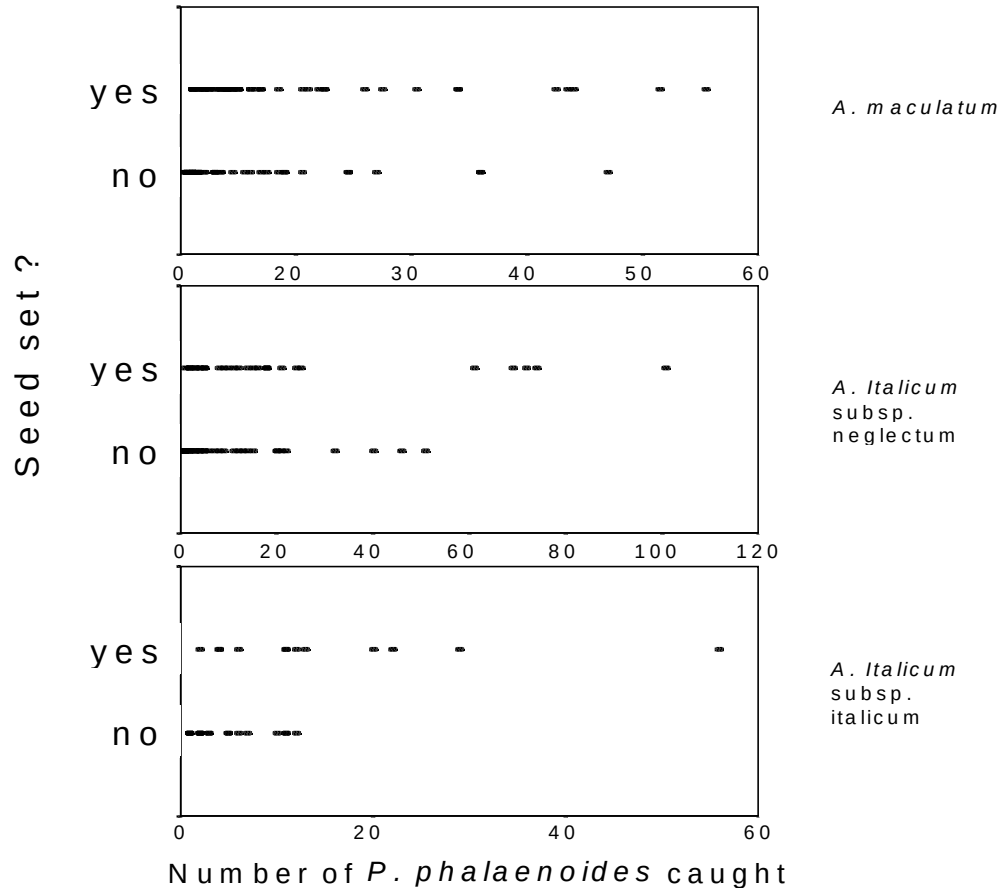

FIGURE 5. The relationship between number of *Psychoda phalaenoides* caught by plants in each taxa of *Arum* and success of seed set.

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