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The pollination of *Arum maculatum* L. – a historical review and new observations

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ABSTRACT

Previous accounts of the complex trap pollination mechanism in *Arum maculatum* L. (Araceae) are briefly reviewed; they conflict in some details and are incomplete. Our own study showed that the species is self-incompatible; it traps female owl-midges *Psychoda phalaenoides* as the main pollinator, and papillae on the spathe and column surfaces stop them escaping. A fluid, consisting of a dilute sugar solution, surrounds the stigmas in most plants. This is not taken by the flies but acts as a site for pollen deposition and germination.

One pollen-bearing fly can carry over 150 pollen grains and can effect full pollination of the female flowers but, in our study sites, the numbers of flies were limited and some inflorescences failed to set fruit owing to lack of pollination. Experimental removal of parts of the inflorescence led to a reduction in the numbers of flies caught and in the number of inflorescences setting fruit, contrasting with previous work. It is concluded that all parts of the trap mechanism are essential to ensure full fruit set. In addition, the more flies that are caught, the more likely a plant is to act as a pollen donor to other plants.

INTRODUCTION

Lords-and-Ladies, *Arum maculatum* L., is one of Britain's most distinctive native plants. It grows in woodlands and shady hedgerows where the first signs of its presence are the broad glossy emerald leaves as they emerge through the sparse February ground flora. In late April or early May a pointed shoot growing from the centre of the leaf rosette unfurls to become the bizarre inflorescence for which the plant is famed. The species belongs to the huge, mainly tropical family, Araceae and is the only common British member of the genus. The centre of radiation of the genus *Arum* is in the Eastern Mediterranean (Prime 1960, 1980) and Britain and Ireland form the northern and western limit of its range. Bown (1988) gives a general, and beautifully illustrated, account of the whole family.

Arum maculatum spreads vegetatively to form clonal colonies, but these are restricted to a small local patch, up to about 1 m in diameter (Prime 1960). Reproduction and dispersal in the species is mainly by seed. The inflorescence of *A. maculatum* consists of a group of 20–40 female flowers at the base, then a whorl of hairs derived from sterile flowers, followed by 60–100 male flowers, another set of hairs and the whole is topped by a spadix (Fig. 1). A spathe surrounds this and remains fully furled around all the flowers up to the base of the spadix, acting as a trap for insects. This most unusual inflorescence, along with other peculiar features of the plant, has attracted considerable interest which culminated in the publication of the classic monograph, *Lords-and-Ladies*, by Prime (1960, reprinted 1981). Prime readily acknowledged that much remains to be discovered, but since 1960 very little work appears to have been done.

FUNCTION OF THE INFLORESCENCE PARTS IN POLLINATION

PREVIOUS ACCOUNTS

In past accounts there was some confusion over the working of the trap mechanism and the importance of the various parts of the inflorescence in pollination. Prime (1960) described in detail the events surrounding pollination, his account consisting of an amalgamation of past work and

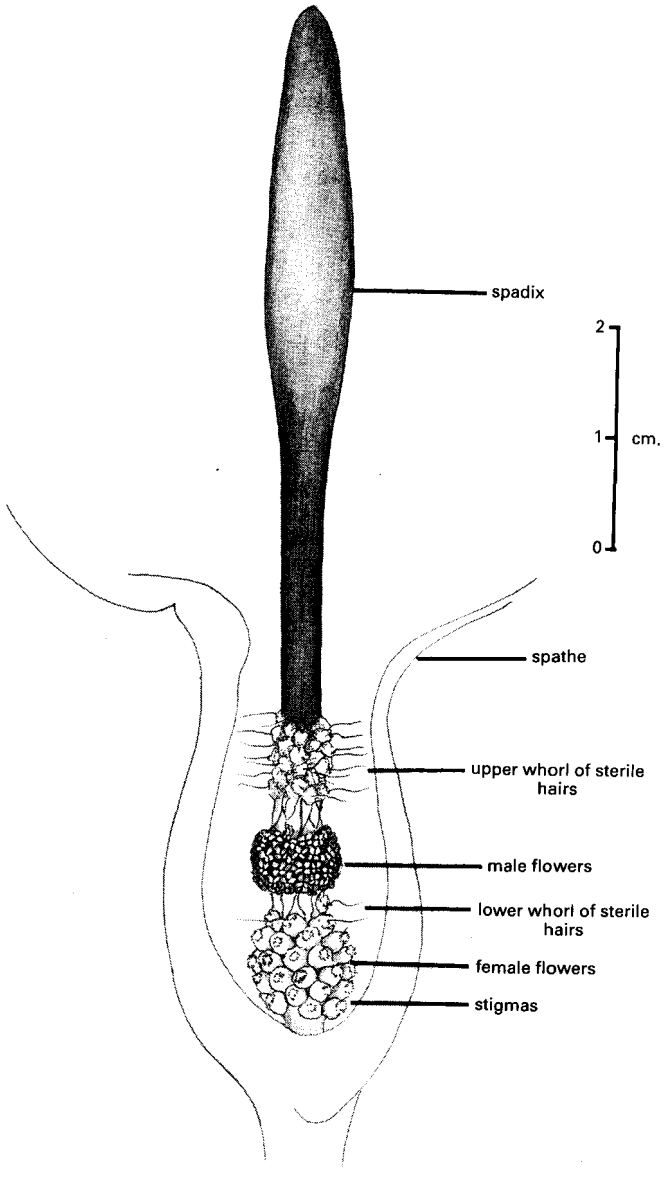

FIGURE 1. Inflorescence of *Arum maculatum* with spathe chamber cut open.

some of his own observations. The following is a summary of his account: as the spathe unfurls the female flowers are receptive and the spadix produces a "foul and urinous" smell from compounds volatilised by respiratory activity in the spadix. The smell attracts flies which breed in dung and, in particular, females of a single species of owl midge, *Psychoda phalaenoides* L. It is not clear where these flies alight, from Prime's account, but, by implication, they alight at the base of the spadix. The flies crawl downwards into the spathe chamber and, once inside, the upper whorl of trap hairs makes it impossible for them to fly out (though he suggests that they could crawl out up the spathe since the hairs do not reach the chamber wall). Through walking around the chamber, they may deposit any pollen they are carrying on to the receptive stigmas. Usually by the following morning

the smell of the spadix is gone, the stigmas are withered and a small drop of "nectar" (see later) is secreted by the female flowers, which the flies take. Pollen is shed by the male flowers, some of which is picked up by the flies, and the trap hairs begin to wither. Prime suggested that the flies then escape by crawling up the spathe wall.

Unknown to Prime until after he had written his account, Knoll (1926) had studied *Arum nigrum* in detail in Dalmatia, and this was brought to the attention of British botanists by Dormer (1960). Differences from Prime's account include the fact that the insects land on the spathe (though this is not entirely clear) and fall into the chamber (not crawl) as a result of its slippery surface. This surface has downward pointing papillae covered with oil droplets, to half way down the spathe chamber. The insects cannot climb the spathe or up the central column, owing to similar papillae on the column just above the female flowers. The upper whorl of hairs is therefore not relevant in preventing escape of the trapped flies, but stops larger insects, which may damage the inflorescence, from entering. "Nectar" is secreted throughout the female phase as well as the male phase and shedding of the pollen is accompanied by a crumpling of the epidermal cells of the column, allowing the insects to crawl up the spadix, rather than the spathe, to escape.

Although Knoll's work applied specifically to *Arum nigrum* and not *A. maculatum*, Meeuse (1961), Proctor & Yeo (1973) and Faegri & van der Pijl (1979) all quoted his account with the proviso that some of the details may not apply to *A. maculatum*, and ignored Prime's. Popular accounts in newspapers, newsletters and floras have variously combined these accounts and invented new variations of their own! *A. nigrum* is larger than *A. maculatum* and the lower whorl of trap hairs is similar to the upper whorl, whereas in *A. maculatum* the lower whorl has fewer hairs (often only two or three, Fig. 1) (Knoll 1926; Proctor & Yeo 1973 and personal observations). *A. nigrum* appears to attract many dung-feeding flies (all those small enough were found in the chamber (Knoll 1926)) whereas *A. maculatum* specifically attracts female *Psychoda phalaenoides* and, in places, *P. grisescens* Tonnoir (Proctor & Yeo 1973).

OBSERVATIONS FROM THE PRESENT STUDY

This investigation was set up to clarify the working of the trap mechanism. It was done mainly in a mature hedgerow on the edge of a playing field in Oxford (v.c. 23), where *Arum maculatum* was abundant (site A). Three further sites, one in an exposed hedgerow by fields (site B), another in a damp hollow near some young beeches (site C) and a third by paths in scrub woodland (site D), were used for comparison. Sites B, C and D were in the Chiltern region near Reading (v.c. 22). A fifth site, in a wooded garden in Cumbria (v.c. 69) was used in 1990 (site E).

The self-incompatibility system was tested using nine inflorescences in site A in 1990. These were covered in semi-opaque paper bags, before opening, on 5 May 1990, and were examined each day after that. When open, two were cross-pollinated artificially using a small paint-brush with pollen from two inflorescences from other plants several metres away, on 10 May. The pollen was dusted on to as many of the female flowers as possible through a hole cut in the spathe chamber wall. Damage to the chamber was minimised and it was difficult to reach the flowers on the opposite side of the column to the hole. Two other inflorescences were artificially self-pollinated in the same way on 14 and 15 May, but using pollen from the same inflorescence. The other five were left unpollinated. Checks on the inflorescences were made regularly thereafter until a final recording of fruit and seed set on 21 June 1990. 15 further inflorescences were bagged and left undisturbed in site E between 1 and 7 May 1990 and checked regularly until 22 July 1990.

Observations of the trap mechanism and the visiting insects were made using porous plastic windows inserted into the chamber wall of 30 inflorescences of *Arum maculatum* in late April and early May 1988 in site A and 35 inflorescences in early May 1990 in site E. Approximately 120 individuals of *Psychoda phalaenoides* were seen through these, over a period of several days in varying weather conditions.

To examine the surface of the spathe and column a series of transverse sections were taken through the spathe chamber wall and the column and examined under a light microscope.

The fluid around the stigmas (the "nectar" of Prime and others) was extracted from approximately 150 flowers on 13 inflorescences using microcapillaries. Measurements of the concentration of sugar, measured as a standard sucrose equivalent, were made on extracts from 5–10 flowers combined using Bellingham and Stanley pocket refractometers adjusted to read small volumes (Corbet 1978; Lack 1982). Extracts from five further inflorescences, one of which had reached the

male phase and the fluid had many pollen grains in it, were analysed for their amino acid content using the method of Yarwood (1989) which can detect trace quantities.

Pollen germination was tested by placing fresh pollen on 1) fresh stigmas, 2) in the stigmatic fluid, 3) in fluid from cut stems and 4) in tap water. Germination was recorded after twelve hours.

RESULTS

The two inflorescences which were artificially cross-pollinated set 20 out of 35 fruits (57%) and 27 out of 39 fruits (69%). These fruits had 1–5 seeds (most 2 or 3) with a mean of 1·8 seeds and 2·6 seeds respectively (excluding fruits that did not set). It was clearly noticeable that most of the fruits which failed to set on the crossed plants were those behind the column from the hole through which pollinations were made. The artificially selfed inflorescences produced 0 out of 34 fruits (0%) and 6 out of 30 fruits (20%) (mean seed number 2·5). None of the bagged and undisturbed inflorescences set any fruit. In many of the selfed and undisturbed inflorescences the fruit started to swell and only stopped about two weeks after inflorescence opening, when they withered. These results show that, normally, *A. maculatum* is strongly self-incompatible (confirming Prime (1960)). The few fruits set on one selfed inflorescence must have arisen either from a weak self-compatibility in the one plant or from contamination of the self pollen load on the paint brush with a few grains from another plant.

Most spathes opened in mid- to late morning, but there was some variation in the timing of flowering events and some opened at almost all times of the day. The smell was normally apparent immediately. Most of the *Psychoda phalaenoides* entered the chambers around dusk or in the early part of the night (before midnight) during the warm dry weather in which observations were made. When the weather is wetter or cooler they may be more active in daylight hours. They almost invariably landed on the spathe and fell into the trap, usually after slipping several times; only two, out of 55 seen entering, crawled in. Once inside, the flies can and did climb the central column, past the lower whorl of hairs and the male flowers to the upper whorl of hairs. These hairs are very close together and appeared to have a slippery surface, and this prevented the flies from manoeuvring between them and escaping. On the second day no smell was apparent and copious pollen was shed from the anthers which fell into the spathe chamber and on to any insects inside, and the hairs withered. The spathe remained impossible for the flies to climb, but they climbed the spadix past withered hairs to escape.

The sections through the spathe showed that papillae cover the open spathe and spadix and extend down on the spathe to half way up the female flowers (as described by Knoll (1926) for *A. nigrum*), with a transition zone, of approximately 5 mm, of progressively smaller papillae. The papillae pointed at 90° to the wall of the spathe and spadix. Papillae on the spadix extended down to the top of the upper whorl of hairs.

The stigmatic fluid was detected in only about two-thirds of inflorescences and varied in quantity up to about 0·3 μl per flower. It was not apparent when the spathe first unfurled, but appeared after about three hours and before most of the *Psychoda* were caught. It surrounds the feathery stigma, when present, and appears to be resorbed soon after the trap hairs wither. The concentration of sucrose equivalent was between 9% and 12·5% in all samples. The amino acids leucine, isoleucine and/or methionine were detected in the fluid which had pollen in it, but the other four fluid samples had no detectable amino acids. The sugar is only slightly more concentrated than that in the fluid which exuded from cut stems, mainly arising from the phloem – 8% sucrose equivalent was recorded from each of three cut stems.

Despite several periods of observing *Psychoda* inside the spathe chamber we never observed them taking the stigmatic fluid (contrary to Prime's (1960) claim) and many inflorescences had fluid and *Psychoda* present. *Psychoda* species are not known to feed during their adult lives (P. Withers, pers. comm. 1990). We must conclude either that the fluid has no function in *A. maculatum*, or that its function is nothing to do with a food reward for the insect visitors. It was often noticeable that, in an inflorescence's male phase, much pollen was trapped in the fluid and many grains had germinated. Observations on the germination of pollen grains showed that they germinate readily in the stigmatic fluid, including that from the same inflorescence, and on the stigmas and in tap water, although not in the fluid from cut stems.

Baker *et al.* (1973) analysed the contents of stigmatic exudates of 39 species of various plant families (in California and Costa Rica) and summarised previous accounts. They found amino acids

in exudates from 38 of the 39 species as well as lipids and other substances. They interpreted the function of the exudates as, in some plants, nutritional for the pollinating insects and, in others, as direct aids in the pollination process i.e. as sites for pollen germination and as a sticky fluid to make pollen adhere to the insects. They, and Eisikowitch *et al.* (1990), studying the highly specialised *Asclepias syriaca*, found that pollen germinated in exudate of up to 20% sucrose but not in higher concentrations. Eisikowitch *et al.* (1990) showed that the tubes burst in concentrations of 5% or less. The concentrations required for pollen germination, therefore, are much lower than those found in normal nectar, which acts as a food reward (Corbet 1978).

It seems that the stigmatic fluid in *A. maculatum* is not nectar in any recognised sense, but that its function is as a trap for pollen grains, as a *Psychoda* crawls over the inflorescence, and as a site for pollen germination. It may also help pollen to adhere to a *Psychoda* if some is brushed on to it in the spathe chamber.

Fluid is present around the stigmas of other members of the Araceae (a large quantity in some), and, in some, appears to act as a food source for visiting pollinators, though very little study has been done (Bown 1988). In *Arum hygrophilum* in Israel, Koach (1985) reported that *Psychoda cinerea* Banks males are trapped and may live longer inside *Arum* because of high humidity maintained by the stigmatic fluid (5% sucrose) and possibly from nutrition.

THE IMPORTANCE OF THE TRAP MECHANISM IN POLLINATION

Despite the elaborate trap structure and apparent effectiveness of the mechanism in *Arum maculatum*, the importance of it for pollination in the species was brought seriously into question by Schmucker (1925), whose experiments were reported by Prime (1960). Schmucker (1925) removed the spadix and/or the spathe from plants of *A. maculatum*, but found no effect on fruit or seed set from any of these mutilations (Table 1). The only detrimental effect on fruit set that he found was from removal of the upper whorl of hairs in addition to the spathe and spadix, and this he attributed to a wound response. Meeuse (1978) studied several members of the Araceae and found that damage to the male flowers had an inhibitory effect on flowering (perhaps hormonal). He did not refer to Schmucker (1925), but his observations back up the possibility of a wound influencing fruit set. Although Schmucker's (1925) conclusions were most unexpected, no further work on this appears to have been done. The implication from Schmucker's work was that the trap mechanism was a vestige from the species' evolutionary past, important perhaps in other members of the genus, but not in *A. maculatum*.

This investigation was set up to see whether we could duplicate and elaborate on Schmucker's experiments. Three aspects of the trap mechanism were studied:

1. whether various treatments to the trap mechanism had an effect on numbers of insects caught;
2. what effect the treatments and the numbers of insects caught had on seed and fruit set of the inflorescences; and
3. how many pollen grains an individual *Psychoda* may carry.

TABLE 1. NUMBER OF FRUITS AND SEEDS SET BY *ARUM MACULATUM* IN SCHMUCKER'S EXPERIMENTS (from Schmucker 1925)

	Sample size	% setting seed	Mean number of fruits per spike
Open pollinated	47	38	15
Spathe removed	31	32	12
Spadix removed	33	43	14
Spathe and spadix removed	43	26	10
Spathe, spadix and hairs removed	29	17	5

METHODS

Inflorescences of *Arum maculatum* were treated in the following ways:

1. Spathe removed
2. Spadix removed
3. Spathe and spadix removed
4. Hole cut in the spathe chamber wall
5. Open-pollinated (control)

It was found that earwigs sometimes entered the chamber through the hole cut for treatment 4; all inflorescences in this treatment were checked two days after flowering for any damage, and damaged inflorescences were not used. All treatments were made before 07.00 hours and before the spathe unfurled. Treated inflorescences were at least 1·5 m apart, and were labelled with plastic tags. Sample sizes varied mainly owing to problems of diseased, damaged or otherwise unusable inflorescences and are given in the results.

Treatments 1, 2 and 5 were carried out on inflorescences in site A which opened before 11.00 hours on 13 May 1988. The insects from each inflorescence were collected after 22.30 hours the same day, by placing a cotton wool plug soaked in ethyl acetate over the entrance to the chamber before extracting the insects. This ensured that the majority of the insects that the spike would catch had been caught.

Further flower spikes were chosen at random between 24 April and 8 May 1988 and subjected to one of the five treatments. They were then left to mature undisturbed over the next nine weeks. Their condition was checked regularly and any inflorescence that was damaged or diseased was discarded from the sample groups. The maturing fruits were collected during June and July as they began to turn yellow and mature, but before any frugivores (mainly blackbirds, Snow & Snow 1988) ate them. The number of seeds, fruits and aborted fruits (unswollen ovaries) were recorded.

A direct measure of the effect of number of insects caught on fruiting success was made between 25 April and 12 May 1989. Insects were collected from open pollinated inflorescences towards the end of the female phase, on the second morning of spathe opening between 07.00 and 08.30 hours. Each study inflorescence was checked to see that the anthers had not dehisced and no insect had escaped. Inflorescences were chosen to show a range of numbers of insects caught. The insects were collected by placing a glass sample tube over a hole cut in the spathe chamber wall. No ethyl acetate was used in case of an effect on fruit maturation. The insects were then counted and the inflorescence left to develop. Checks were made after two days that intruders had not entered through the hole and damaged the inflorescence and further checks were made regularly for any damage. Numbers of fruits and seeds set were measured as described above. In 1990, to investigate whether numbers of insect visitors limited fruit set, 28 spikes in site E, which were left open to insects, were artificially cross-pollinated through holes in the spathe chamber with pollen from three other plants, as described in the self-incompatibility test.

15 individual *Psychoda phalaenoides* were caught as they entered an *Arum* spathe chamber, in site E. The number of pollen grains that they were carrying was counted.

RESULTS

Removal of the spathe or removal of the spadix resulted in fewer insects being caught than in intact inflorescences (Table 2, both comparisons $P<0.001$, Kolmogorov-Smirnov test). There was no difference between these two treatments.

In site A, the percentage of spikes that matured any seed (no fruits were set without seeds)

TABLE 2. NUMBERS OF INTACT INFLORESCENCES OF *ARUM MACULATUM* AND THOSE WITH SPATHE OR SPADIX REMOVED WHICH HAD CAUGHT PARTICULAR NUMBERS OF *PSYCHODA* APPROXIMATELY TWELVE HOURS AFTER OPENING

	Sample size	Numbers of *Psychoda* trapped									
		0	1	2	3	4	5	6	7	8	>8
Intact	25	3	2	1	0	2	2	3	2	1	9
Spathe removed	18	13	3	2							
Spadix removed	24	19	4	1							

TABLE 3. PERCENTAGE OF SPIKES OF *ARUM MACULATUM* THAT SET ANY SEED AND THE MEAN NUMBER OF SEEDS SET IN EACH OF FIVE TREATMENTS

	Site A		Sites B, C, D		All sites
	Sample size	No. setting seed (%)	Sample size	No. setting seed (%)	Mean no. seeds*
Open pollinated	143	57 (40)	111	72 (65)	33·0
Spathe removed	68	12 (18)	48	4 (8)	23·4
Spadix removed	57	10 (18)	38	8 (21)	33·1
Spathe and spadix removed	30	0	23	1 (4)	16
Hole in chamber wall	50	10 (20)	18	8 (44)	13·1

* excluding those which set no seed

differed considerably between the test groups (Table 3). Those that had been manipulated in any way all had a smaller proportion of spikes setting seed than open pollinated inflorescences (all $P<0.01$, $^{N}_{N}{}^{2}$ tests). There were no significant differences between any of the treatments except for those from which both spathe and spadix were removed. Only one of these set any seed, significantly less than other treatments (all $P<0.05$, $^{N}_{N}{}^{2}$ tests). The percentage of open pollinated inflorescences which set seed was greater in sites B, C and D, pooled, than in site A ($P<0.001$, $^{N}_{N}{}^{2}$ test) but differences between manipulated and open pollinated inflorescences were similar to those at site A.

Of those spikes in site A that matured at least one fruit (Table 3), there was no significant difference in the number of seeds set by spikes with either the spathe or spadix removed compared with the open pollinated group. It seems that, if it is fertilised at all, all potential fruits are likely to be fertilised. Those spikes with a hole in the chamber wall, however, set fewer seed ($P<0.002$, modified t-tests, not assuming equal population variances). Pooled results from sites B, C and D showed almost exactly the same pattern as site A.

Table 4 shows the results obtained from all four sites together for percentage of potential fruits matured (sample sizes were too small for meaningful comparisons from site A separately). Removal of the spathe and cutting a hole in the chamber wall reduced percentage fruit set ($P<0.01$, Kolmogorov-Smirnov test) but removal of the spadix did not.

Fruiting success did not appear to be related to number of insects caught (Table 5). 82% of the inflorescences that caught any insects set seed and it seems that just one pollen-bearing insect was necessary for full fruit set to occur.

Of the 28 artificially cross-pollinated inflorescences, 27 (96%) set fruit.

The numbers of *A. maculatum* pollen grains recorded on individual *Psychoda* were (in increasing order) 0, 0, 2, 56, 70, 84, 93, 101, 111, 124, 127, 133, >150, >150, >150. The first two of these fifteen and, perhaps, the third (20%) were probably visiting their first *Arum* inflorescence, whereas the others had clearly come from another one.

TABLE 4. NUMBERS OF INFLORESCENCES OF *ARUM MACULATUM* IN VARIOUS TREATMENTS (PERCENTAGES IN BRACKETS) WHICH MATURED PARTICULAR PROPORTIONS OF POTENTIAL FRUITS

Those which matured no fruits excluded from these results.

		Percentage of potential fruits matured					
	Sample size	<20	20–40	40–60	60–80	80–99	100
Open pollinated	129	3 (2)	11 (9)	16 (12)	22 (17)	58 (45)	19 (15)
Spathe removed	16	1 (6)	5 (31)	4 (25)	3 (19)	0	3 (19)
Spadix removed	16	0	1 (6)	2 (12)	4 (24)	8 (47)	1 (6)
Hole in chamber wall	19	8 (42)	4 (21)	3 (16)	0	2 (11)	2 (11)

TABLE 5. NUMBERS OF FRUITS AND SEEDS SET BY PLANTS OF *ARUM MACULATUM* WHICH HAD CAUGHT PARTICULAR NUMBERS OF *PSYCHODA PHALAENOIDES*

Number of *P. phalaenoides* caught	Sample size	No. setting any seed	Mean no. of seeds set*	Mean % fruit set*
0	1	0	—	—
1	6	5	31	65
2	3	1	47	100
3	4	3	34	60
4	5	5	25	66
5	2	1	54	100
6	2	2	19	57
7	0	—	—	—
8	3	2	28	71
>8	8	8	31	72

* excluding those which set no fruits or seeds

DISCUSSION

In all sites, less than 100% of inflorescences set fruit, and in site A in 1988 only 40%. Some inflorescences in all study sites caught no insects and others caught one or very few, and the failure to fruit was related to the availability of *Psychoda phalaenoides*. This was further confirmed by the fact that all but one of the artificially crossed inflorescences set fruit. All the evidence from this investigation leads us to the conclusion that fruit set, in any one year at least, is limited by the numbers of pollinating insects. Fruits set in one year can, however, affect fruit set in the next year (a well-known phenomenon in fruit trees), so a definitive test for what limits fruit set would require following the same plants through two seasons. Possible limitation of fruit set by pollinator availability is recorded in a few species, but only definitively (i.e. as described above) in one, another aroid, *Arisaema triphylla* (Zimmerman 1988). Prime (1960) stated that, from preliminary observations, about 10% of *Arum maculatum* tubers died each year, but that flowering had no apparent effect on the probability of death.

Any disruption to the trap mechanism led to many fewer insects being caught (frequently none) and to lower numbers of inflorescences setting any fruit or seed. In fact, because of the precision of the trap mechanism and the function of all parts of the flower spike and spathe, it was surprising that inflorescences that had parts removed ever caught any insects. On those from which the spathe was removed the spadix was still, clearly, an attractant and one *Psychoda* was observed crawling around the cut edge of the spathe before slipping down and being trapped. On those from which the spadix was removed it is possible that the flies were attracted by the pale colour of the spathe since they appeared to be attracted by light surfaces (personal observation).

Although most spikes which had their spathe, spadix or both removed did not set any seed, of those that set at least one, there was very little difference in numbers of fruit set between the mutilated and intact inflorescences. Only those with the hole cut in the chamber wall set many fewer fruits. It seems that one pollen-bearing *Psychoda* may well be adequate to fertilise all the female flowers successfully so long as it has travelled from another clone; an individual fly can certainly carry enough pollen grains. Since the flies are normally trapped in the chamber for 18–24 hours, and move about during this time, there is plenty of opportunity to deposit the pollen on all the female flowers. In those chambers in which a hole was cut, the flies normally found their way out very quickly and flew off, so it is not surprising to find big reductions in fruit and seed set in these plants, since the flies will not have crawled over all the female flowers. *Psychoda* species live as adults for up to seven days (P. Withers, pers. comm. 1990) and this means that a significant proportion of flies trapped in any one inflorescence (perhaps up to 25%) are likely to be first-time visitors; our results for numbers of pollen grains carried confirm this. Others may come from another inflorescence in the same clone, so the pollen that they are carrying is not viable. These are likely to be the reasons for the lack of any fruit set by some inflorescences which trapped small numbers of insects.

Pollinator availability seems to be the main limiting factor in fruit set in this study, but other

factors may also be important. Some decay of fruiting spikes was noted, particularly in 1988 which was a wet, cool summer, but these were not included in the results. Resource limitation, often important in limiting fruit set (Stephenson 1981), did not appear to play any part in this study, though observations over two years would be needed to confirm this. Predation was not important in our study areas but Snow & Snow (1988) noted that many flower spikes of *A. maculatum* in their Chiltern study sites were eaten by deer before setting any fruit.

The results presented here are in clear contradiction of the results of Schmucker (1925). By chance, it appears that our site A was similar to his site in the overall proportion of open pollinated spikes setting fruit (38% of his spikes set fruit, 40% of ours) and, therefore, is likely to be comparable in pollinator availability and associated factors. This suggests that there are differences in the experimental methods used. Schmucker (1925) was not totally clear about his methods but stated that the treatments were made on spathes that were just about to open. He probably waited until just as the spathes opened to do the tests since this is likely to cause the least damage. We know from our study, however, that this stage may well be too late to prevent pollination. The spadix may smell before the spathe opens and those spathes which had only opened a fraction were sometimes found to have caught insects, though this was only noticeable if the chamber was cut open. We must, therefore, contest Schmucker's conclusion that the trap mechanism is not important for fruiting in *A. maculatum*, since our results show clearly that all parts are important.

It does seem that, for fruit set, it is not important how may insects are caught and that just one *Psychoda phalaenoides*, bearing pollen from another plant, may be adequate for full seed set, but this is only part of the pollination story. The other part, successful dissemination of pollen, is much harder to study and we can only make some suggestions about this in *A. maculatum*. Since pollinating insects are trapped by the *Arum* inflorescences for some hours, it is likely that almost all of the pollen that is taken out of one inflorescence by any one *Psychoda* will be deposited on the next one it visits – pollen carry-over will be minimal. One trapped *Psychoda* will probably mean that a significant number of seeds are fathered on only one other plant, or even none if the next inflorescence it visits is part of the same clone. The more *Psychoda* that are trapped, therefore, the more inflorescences will receive pollen from that individual plant and the more successful that plant will be as a father. This is true in most plants (Bertin 1988) and it suggests that successful trapping of as many *Psychoda* as possible will be important to ensure pollen dispersal.

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