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TABLE 3. COMPARISON OF BODY-TEMPERATURE OF WOODLICE WITH AIR TEMPERATURE IN A HUMID ATMOSPHERE

Temperature of air in box (°C.)	Body-temperature of woodlice in box (°C.)
17·6	17·5
19·5	18·2
18·2	17·7

Summary of Conclusions

1. The higher the temperature, the greater the rate of water loss.

2. This loss of water may be reduced by the formation of aggregates.

3. Under moist conditions woodlice are photonegative and hydropositive in their responses.

4. Under dry conditions the hydropositive response predominates.

5. In a saturated atmosphere, the body-temperature is practically the same as that of the surroundings.

6. In an unsaturated atmosphere, the body-temperature is lower than that of the environment.

AN INVESTIGATION OF THE EFFICIENCY OF THE POLLINATION MECHANISM IN LORDS-AND-LADIES

(*Arum maculatum*)

BASED ON WORK BY A. LAMB
(*Awarded Coles Prize for Biology*, 1956)

Introduction.

Arum maculatum, commonly known as Lords-and-Ladies or Cuckoo Pint has a highly specialised pollination mechanism, depending on the visits of small midges which are attracted by the putrid smell of the inflorescence. Details of the structure of this inflorescence are too well known to require more than a brief description here. It is borne on a fleshy axis, and consists of a band of female flowers round the base of the axis, above these a band of male flowers, and above these again a band of sterile male flowers with long stiff hairs directed obliquely downwards. All the flowers are reduced to their simplest possible form; just ovaries and styles, or simple stamens, as the case may be. The upper part of the axis ends in a blunt, fleshy structure, dull purple in colour, called the spadix, and it is the smell of this which is said to be responsible for attracting the midges. The bands of flowers are enclosed in a chamber formed by a single large, sheathing bract, the spathe. This forms a "waist," level with the sterile male flowers, and above these it folds back to expose the spadix (hence the common name "Jack-in-the-Pulpit").

Midges, attracted by the spadix, can pass down to the chamber where the flowers are situated, but the downwardly directed hairs in the waist of the spathe prevent them from getting out again, so that they are detained until these hairs wither. This withering occurs only *after* the male flowers have discharged their pollen, so the insects leave bearing pollen with them, and presumably carry this to some other inflorescence which they enter while the stigmas of the female flower are still receptive—i.e. before the male flowers ripen. Thus self-pollination is prevented by the female flowers ripening first, and cross-pollination is effected if the midges leaving on inflorescence are attracted to another one in which the stigmas are still at the receptive stage. The object of these investigations was to confirm these points, and to try and gain some ideas of the efficiency of this elaborate device, as judged by the proportion of seeds set.

Factors Influencing the Planning of the Experiments

If we are to gain real insight into the working of this pollination mechanism, we must be able to answer the following questions:

1. Is it, in fact, the putrid smell of the spadix that attracts the midges which visit these flowers? Are there any other factors likely to play an important part in attracting the insect visitors?

2. Can the mechanism work in any other way than that suggested? Might not the trapped midges achieve self-pollination?

3. What is the efficiency of the mechanism, and how may this be affected by factors that could vary under natural conditions?

Experimental Work.

1. A simple trap (working on the same principle as a lobster pot) was made from a small, closed, cardboard box by inserting a glass funnel through a hole in one side. This was "baited" with some freshly cut spadices and left in a suitable place. It was soon found to have trapped a number of midges, thus confirming that they must be attracted by the smell of the spadix, since in this case they could not see it. This does not rule out the possibility that the colour may also play some part in attracting them, and it is interesting to note in this connection that a number of other flowers visited by flies of this type have a similar dull purple colour.

Although it seems that the smell of the spadix is primarily responsible for the attraction, there is the possibility that this may be enhanced by trapped flies which die before they escape.

2. As explained in the introduction, the female flowers of the inflorescence ripen first, so the possibilities of self-fertilisation would rest upon whether any of these still remain receptive when the pollen is first shed from the male flowers growing above them. Clearly, any insects trapped in the inflorescence at this time could effect self-pollination, but the pollen is just as likely to drop from the male flowers onto the stigmas below without the assistance of insects. All that is needed, then, to test whether self-pollination is possible is to enclose a number of inflorescences before they open, thus excluding all insects, so that cross-pollination cannot take place.

3. Methods of estimating the efficiency of the pollination mechanism also depended upon a comparison between controls and plants in which various means were adopted to check insects taking part in pollination. These are so close to the technique mentioned in 2 above, that the experiments are best described together.

The area of shrubbery in front of Francis House was found to have large numbers of *A. maculatum* plants, evenly distributed. Three sets of 25 of these were used for testing each of three treatments, while 50 plants were used as controls. The plants used for any one treatment were chosen from all over the area and not confined to one part of it; they were distinguished from plants receiving other treatments by tying pieces of coloured tape loosely round the bases of the stalks. The results of each treatment were assessed by counting, on each inflorescence, the number of developing ovaries and those which had not developed (presumably due to failure of pollination). These counts were made while the developing berries were still green, because, if left till a later stage, many of the unfertilised ovaries drop off and no proper comparison can be made.

The first method of trying to check insect visits was to use Mylol, a proprietary preparation containing the insect repellant dimethyl phthalate in an ointment base. It was found that this could not be applied directly to the spadix, as it caused it to shrivel. It was therefore smeared on sticks put into the ground near the plants and on the surrounding undergrowth. The Mylol was renewed every two days and immediately after showers of rain during the week's flowering period. Even so it did not prove wholly effective in preventing insect visits.

In the second set of 25 plants the young inflorescences were enclosed in transparent plastic bags until the spathes unrolled; the bags were then removed and the spadix of each plant cut out with a scalpel just above the band of sterile male flowers. The principal attraction for the visiting insects was thus removed, but in spite of this a small number of the midges found their way into the "flower chamber" of these plants, confirming that the attraction of the spadix is not solely responsible for their visits.

Finally, another 25 inflorescences were enclosed in Cellophane bags before the spathes unrolled, and this time they were left in the bags, so that there was no possibility of any insect visits.

Results

For reasons of economy of space, the full tables of results are not reproduced here, but the percentages of unfertilised carpels under the different treatments are compared in frequency classes:

PERCENTAGES OF CARPELS NOT DEVELOPING IN LORDS-AND-LADIES PLANTS

% of carpels unfertilised per plant	Frequency of occurrence per 25 plants			
	Plants "protected" with Mylol	Plants with spadix removed	Inflorescences enclosed	Controls*
0—10	1	0	0	15
10—20	1	1	0	7
20—30	2	1	0	2
30—40	3	3	1	½
40—50	4	6	0	½
50—60	4	4	0	0
60—70	5	3	0	0
70—80	3	2	0	0
80—90	1	3	0	0
90—100	1	3	24	0

*For controls, numbers per 50 plants are halved.

Discussion

From the results of the controls it is clear that under normal conditions the percentage of carpels which do not develop is low: the mean value for the 50 plants was 11 per cent. The pollination mechanism is evidently highly efficient, and a comparison with the results obtained from the enclosed inflorescences shows that it depends almost entirely on the visits of insects. In this group 10 out of the 25 plants had one or two of the carpels developing (the total number of carpels ranging between 17 and 42), while in one specimen 15 out of 22 developed. In the remaining 14 plants none of the carpels developed. There must, then, be a small possibility of self-fertilisation or parthenocarpy. Extensive self-pollination is probably prevented by the fact that the stigmas of the female flowers are past their receptive stage by the time that the stamens dehisce, but self-incompatibility may also play a part.

Neither "protection" with Mylol, nor removal of the spadix were fully effective in keeping the insect visitors away, and even a few flies might carry enough pollen grains to effect fertilisation of a number of carpels. Nevertheless, the mean percentage of carpels not developing in these two cases was 51 and 56 respectively (compared with 11 per cent. for the controls). This emphasises the importance of the adjustment between the conditions of the habitat and the type of insects attracted. *A. maculatum* grows most abundantly in deep shade, where insects such as bees would rarely go, but midges are plentiful. Were the plants to grow in sunnier situations the number of visiting midges might be seriously curtailed, with drastic consequences to the percentage of seeds produced. It would be interesting to compare the percentage seed-set of plants growing on recently cleared ground with those in their normal habitat.

POLLEN AND POLLINATION IN RHODODENDRONS

BASED ON INVESTIGATIONS CARRIED OUT BY A. RIDGE

The release of pollen from the stamens of flowers is usually achieved by the formation of a longitudinal split down each side of the anther. The walls curl back (by a mechanism similar to that operating in fern sporangia) and the pollen is either shaken out and dispersed by wind or exposed to contact with the hairy bodies of insects visiting the flower. In members of the heather family (Ericaceae), however, no such split occurs, but instead a pore is formed at the top of each anther lobe. This is very easily observed in Rhododendron flowers, where the anthers are particularly large. At first sight it is difficult to understand how the pollen grains should ever be dispersed from these stamens, for the anthers are held erect with the pores at the top so that gravity can play no part. Furthermore, the filaments, although long, are too firm to allow the operation of anything akin to the censer mechanisms used in seed dispersal, where seeds are thrown out by centrifugal force. Again, so far as insect dispersal is concerned, one would imagine that only the topmost pollen grains in the anther would be exposed to contact with visiting insects, and those below, it seems, must be left behind. However, if one pokes the top of a ripe anther with a pencil point, the pollen is found to stick to it, and is drawn out as a sticky thread when the pencil point is moved away. It was with a view to finding more about the detail of this mechanism that the following observations were made.

Microscopic Examination of the Pollen

The actual grains appeared triangular in outline; probably they remain in the form of tetrads with the four nuclei resulting from meiosis arranged as at the four corners of a tetrahedron. Each