

Pseudocopulation of an orchid by male ants: a test of two hypotheses accounting for the rarity of ant pollination

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Summary. The orchid *Leporella fimbriata* is pollinated by pseudocopulation with winged males of the ant *Myrmecia urens*. This recently studied interaction provides a unique opportunity to examine the two current hypotheses concerning the apparent rarity of ant pollination systems worldwide. The first hypothesis requires a series of specialized growth forms and floral characteristics regarded as adaptations to ant pollination. *L. fimbriata* does not possess them. The second considers the pollenicial effects of secretions from the metapleural gland of ants. These glands are absent in *M. urens* males and it may be that the occurrence of ant pollination requires the absence of metapleural glands in the vector.

Key words: Ant pollination – Orchid – Pseudocopulation – Metapleural gland

Bees and wasps are important pollinators of native and domestic plants throughout the world. Ants are closely related and are as morphologically, physiologically and socially advanced, yet, their role as pollinators is negligible (van der Pijil 1955; Faegri and van der Pijil 1971; Proctor and Yeo 1973; Beattie 1982, 1985). Two hypotheses have been advanced to explain the rarity of ant pollination and the recent discovery of pollination of an Australian orchid by pseudocopulating male ants provides a unique opportunity to examine the relevance of these hypotheses.

The first hypothesis states that because ants are smooth, small and flightless, little pollen can adhere to them and pollen transfer between plants does not occur because interplant distances are relatively large (van der Pijil 1955; Faegri and van der Pijil 1971; Proctor and Yeo 1973; Schubart and Anderson 1978; Armstrong 1979). Effective pollination by ants therefore, requires adaptive specializations of the plant which overcome these apparent shortcomings. The few possible cases of ant pollination have been examined to identify these adaptations and as a result, a syndrome of traits thought to be characteristic of ant pollinated plants has been assembled (Hickman 1974). Several traits concern the accessibility of flowers to small crawling insects and

the reduction of distance between flowers of different plants. They include a short, prostrate cushion or mat forming plant habit with interdigitation of branches from adjacent individuals and sessile flowers. Other traits include small flowers with low nectar volumes and few concurrently open flowers. These traits would promote outcrossing by forcing ants to move between flowers and between plants in order to harvest sufficient rewards. In addition, small pollen volumes per flower may discourage grooming behaviour which removes pollen from the ant integument. A corollary to this trait is that there should be few seeds per flower. This syndrome provides a convenient test of the first hypothesis as it leads to the prediction that a high proportion of these traits should be shared by all ant pollinated plants.

The second hypothesis is based on a series of recent studies demonstrating that pollen exposed to the ant integument for brief periods exhibits reduced viability and germination (Beattie et al. 1984, 1985). The detrimental effect is caused by contact with secretions from the metapleural glands. These secretions, which become distributed over the integument, are strongly antibiotic, and have an inhibitory effect on the spores and hyphae of entomogenous fungi (Beattie et al. 1986). It has been suggested that the disruption to pollen function, while probably coincidental, is likely to be a reason why ant pollination is rare. A fundamental prediction arising from this hypothesis is that ants which are pollinators will not possess metapleural glands, or plants pollinated by ants will possess mechanisms which avoid or overcome the deleterious effects of metapleural secretions on pollen.

Leporella fimbriata (Lindl.) George is a widespread monotypic terrestrial orchid from southern Australia. One to three red and green flowers 2–2.5 cm across are borne on erect scapes 12–30 cm in height. Flowers have no detectable scent and do not offer food rewards of any kind. Flowering scapes may form stands, reaching densities of 30 per m², but contact between scapes is rare. Pollen is shed as pollinia, each mass consisting of an estimated 100 000 grains. Pollination results in fruits which contain several thousand seeds. The species blooms unusually early, in the austral autumn (March to June).

Leporella fimbriata is exclusively and effectively pollinated by sexually attracted winged males of the ant *Myrme-*

Table 1. Summary of pollination data for *Leporella fimbriata* based on 350 h of field observation over 3 seasons (1984–1986) in Western Australia

| Category | Number of flowers | Number of pseudo-copulations ^a (by ants bearing pollinia) | Mean number of seeds per fruit |
|---|-------------------|--|--------------------------------|
| Observed flower visits by ants ^b | 57 | 33 (27) | 4865 ± 1316 ^c |
| <i>Control flowers</i> | | | |
| Ants excluded no hand pollination | 20 | 0 | 0 |
| Ants excluded hand pollinated | 20 | 0 | 4775 ± 1117 ^c |

^a Some recorded on video

^b only male *M. urens* were observed to visit this orchid

^c $n = 4$, $t = 0.104$, d.f. = 6, n.s.

cia urens Lowne (Table 1). The vector is 8–10 mm in length and typically approaches the flower upwind in circling and zig-zag flight patterns characteristic of insects orienting by scent. On reaching a flower, the ant grasps the labellum which is 8–12 mm wide, more or less flat with gentle curvature at the sides, and orients itself at right angles to the floral axis (see Peakall 1984 for photographs). The tip of the abdomen probes along the side of the labellum as the ant carries out vigorous copulatory movements. At the same time, pollen masses on the dorsal thorax which have accumulated during previous flower visits are held in contact with the stigma. As the ant prepares to depart, its body movements dislodge a fresh pollinium which adheres to the thorax by means of stigmatic secretions.

Petal tips removed from the flower attracted vectors but did not elicit a copulatory response. This suggested that the glandular tips are the source of attractant, probably a pheromone similar in effect to that emitted by the sexually active queen ant (see Jacobson 1972). As with other orchids, the texture, dark colouration, size and curvature of the labellum is thought to complete the mimicry, acting as a short range tactile and visual stimulus of mating behaviour (Kullenberg and Bergstrom 1973, 1976; Stoutamire 1983).

Successive pollination events involving a single vector and different scapes were observed on a number of occasions. The mean flight distance, including flights between orchid flowers and other vegetation, was short, (3.1 ± 4.5 m, $n = 34$) but some were as long as 15 to 20 m. Pollen germinates on the stigma within 2 to 3 days of pollination. Fruit capsules become notably swollen at 6 to 10 days and dehisce 45 to 75 days later. The percentage of flowers pollinated in populations where ant pollination was observed varied from 11.1 to 47.6%.

Leporella fimbriata does not exhibit the syndrome of traits commonly regarded as adaptations for pollination by ants. Its form is not prostrate nor dense, branches do not interdigitate, and the relatively large flowers born on erect scapes are not small or sessile. In addition, most flowers in a population tend to open synchronously, large amounts of pollen are produced and the fruits contain thou-

sands of seeds. Although the vectors frequently groom, they are unable to dislodge the pollen masses. These data demonstrate that ant pollination is not confined to plants exhibiting the traits associated with the first hypothesis nor to habitats where environmental conditions favour a prostrate plant form. Rather, they suggest that plant form is not the determining factor in the evolution of ant pollination.

Absence of metapleural glands in ant vectors would support the second hypothesis. Indeed, dissection and scanning electron microscopy of several pollinators revealed that these glands are not present in *M. urens* males. It appears, therefore, that ants may function as pollinators of plants with specialisations very different to those associated with the first hypothesis. In the case of *L. fimbriata*, these specialisations include a flowering period which coincides with the emergence of the winged sexual castes, the production of attracting pheromones, and the possession of petals modified as pseudocopulatory organs. The utility of these adaptations, however, is apparently predicated upon the absence of metapleural glands and their pollenicial secretions. Metapleural glands are present in most ants, but are known to be absent in the males of some species, and absent from all castes in three genera (Holldobler and Engel-Siegal 1984), including the genus *Camponotus*, of which one species *C. compressus* is reported as a pollinator of coconuts (Patel 1938). Further research will reveal whether or not pollination by ants is confined to ant castes or genera which do not possess metapleural glands or plant species which have evolved mechanisms avoiding the affects of metapleural secretions.

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References

- Armstrong JA (1979) Biotic pollination mechanisms in the Australian flora – a review. *New Zealand J Bot* 17:467–508
- Beattie AJ (1982) Ants and Gene Dispersal in Flowering Plants. In: Armstrong JA (ed) *Pollination and Evolution*. Royal Botanic Gardens Press, Sydney
- Beattie AJ (1985) The evolutionary ecology of ant-plant mutualisms. Cambridge Univ Press, Cambridge
- Beattie AJ, Turnbull CL, Knox B, Williams E (1984) Ant Inhibition of Pollen Function: A Possible Reason Why Ant Pollination is Rare. *Am J Bot* 71:421–426
- Beattie AJ, Turnbull CL, Hough T, Jobson S, Knox B (1985) The Vulnerability of Pollen and Fungal Spores to Ant Secretions: Evidence and some Evolutionary Implications. *Am J Bot* 724:606–614
- Beattie AJ, Turnbull CL, Hough T, Knox B (1986) Antibiotic Production: A possible Function for the Metapleural Gland of Ants (Hymenoptera: Formicidae). *Ann Entomol Soc Am* 79:448–450
- Faegri K, Pijil L van der (1971) *The Principles of Pollination Ecology*. 2nd Ed. Pergamon Press, Oxford
- Hickman JC (1974) Pollination by Ants: A low Energy System. *Science* 184:1290–1292
- Holldobler B, Engel-Siegal H (1984) On the metapleural gland of ants. *Psyche* 91:201–224

- Jacobson M (1972) *Insect Sex Pheromones*. Academic Press, London
- Kullenberg B, Bergstrom G (1973) The Pollination of Ophrys orchids. In: Benz G, Santesson J (eds) *Chemistry in Botanical Classification*. Nobel Foundation, Stockholm
- Kullenberg B, Bergstrom G (1976) The Pollination of Ophrys orchids. *Bot Notiser* 129:11-19
- Patel JS (1938) *The Coconut, A Monograph*. Government Press, Madras
- Peakall R (1984) Observations on the Pollination of *Leporella fimbriata* (Lindl.) A.S. George. *J of the Austr Nat Orchid Soc* 8:44-45
- Pijil L van der (1955) Some Remarks on Myrmecophytes. *Phytomorph* 5:190-200
- Proctor M, Yeo P (1973) *The Pollination of Flowers*. William Collins, Glasgow
- Schubart HOR, Anderson AB (1978) Why Don't Ants Visit Flowers? A Reply to D.H. Janzen. *Biotropica* 10:310-311
- Stoutamire W (1983) Wasp-pollinated species of *Caladenia* in South-western Australia. *Aust J Bot* 31:383-394

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