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SPECIAL PAPER

ANT INHIBITION OF POLLEN FUNCTION: A POSSIBLE REASON WHY ANT POLLINATION IS RARE[1]

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ABSTRACT

Ant pollination systems are remarkably rare. We show that pollen exposed to ants for brief periods exhibits reduced viability, reduced percent germination, and shorter pollen tubes relative to control pollen. Pollination with ant-borne pollen also results in lower seed-set than pollination with untreated pollen. This disruption of pollination processes must have exerted a powerful selection pressure against the evolution of ant-pollination systems. It is suggested that the nest-building and brood-rearing habits of ants require that they secrete large amounts of antibiotics to combat pathogenic microorganisms. It is these secretions that disrupt pollen function. Bees and wasps exhibit very different nesting behavior, consequently there are no chemical barriers to their coevolving with flowers as pollinators.

THERE ARE ONLY about a dozen convincing examples of ant pollination throughout the world (Kincaid, 1963; Hickman, 1974; Wyatt, 1981; Beattie, 1982). A few more are suspected, including a bizarre case of an orchid pollinated by pseudocopulation with a male ant (Bates, 1979). The rarity of adaptations to pollination by ants is remarkable since their close relatives, the bees and wasps, are of primary importance as pollinators in most plant communities (Faegri and van der Pijl, 1971). This paradox has been the subject of much study and speculation by botanists and entomologists who point to the variety of interactions involving ants and other (mainly vegetative) plant structures, some of which are highly coevolved mutualisms (Wilson, 1971). Proximate explanations for the paucity of ant pollination systems include the evolution of physical barriers such as sticky tissues and glandular hairs which limit ant access to flowers (Kerner, 1878; Kevan and Baker, 1983), repellent floral nectars or floral parts (Stager, 1931; van der Pijl, 1954; Janzen, 1977; Baker and Baker, 1978; Feinsinger and Swarm, 1978; Schubart and Anderson, 1978; Rico-Gray, 1980; Stephenson, 1981) or the luring of ants away from flowers by means of extrafloral nectaries (Kerner, 1878; Bentley, 1977; Elias, 1983). But why should these mechanisms have evolved in the first place? And why should ants not disperse pollen when they routinely disperse other plant propagules as diverse as seeds, fruits, and sporangia (Janzen, 1974; Beattie, 1983)?

Several reasons have been suggested as to why ants make poor pollinators. However, most of them are based upon insufficient data. Firstly, it has been argued that pollen does not adhere to ants, but in fact many ant species are as hairy as bees, or covered with bristles or heavily sculptured and quite capable of carrying pollen (Cole, 1940; Sparks, 1941; Wyatt, 1981). Secondly, the objection has been raised that ants groom their bodies too frequently. However, bee pollinators also groom frequently, often while in flight from one flower to the next, removing all but the most inaccessible pollen (e.g., see Beattie, 1971). In addition, once stored in the "pollen basket," pollen loses much of its germinability (Kraai, 1962; Heinrich, 1979; Iwanami et al., 1979). Thirdly, worker ants do not fly and are generally assumed to have limited foraging areas, therefore it is thought that they cannot effect gene flow among the plants they service. There are several reasons for questioning this assertion: 1)

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Many ant species forage over far greater distances than those winged pollinators which are limited by small body size, the defense of territory or the aggregation of floral rewards (Elton, 1932; Wilson, 1971; Davidson and Morton, 1981; Linhart, 1973; Sudd, 1967). 2) Many plant species exhibit pollination systems in which there is a high frequency of inbreeding. This is often in part because the frequency distributions of pollinator flight distances are leptokurtic. The frequency distributions of ant foraging distances may be leptokurtic (Wyatt and Stoneburner, 1981) or platykurtic (Beattie and Culver, 1979). In any case, the pollen component of gene flow may be insignificant and compensated by effective seed dispersal (Levin and Kerster, 1974). 3) A low growth form or high density of plants often means that as many individuals are accessible to ants as they are to winged pollinators (Wyatt, 1981). Fourthly, it is often believed that ants do not forage systematically and selectively on plants. In reality, however, this behavior is commonplace and ants repeatedly ascend plants, from low herbs to tall trees, to harvest honeydew, prey, seeds and extra-floral nectar (Tevis, 1958; Berg, 1954; Brian, 1955; Wilson, 1971; Laine and Niemela, 1980; Lu and Mesler, 1981). Finally, ants are abundant and ubiquitous, and possess sensory systems equal to or exceeding those of bees and wasps (Wilson, 1971). All of these considerations force us to wonder why ants did not coevolve with the flowering plants as pollinators, as did their relatives, the bees and wasps. While it is true that one can point to many contemporary ant species which exhibit behavioral repertoires inappropriate to pollination, there seems to be no compelling reason why mutual adaptations between early angiosperms and ants could not have evolved into pollination systems as efficient and effective as bee-flower systems. In fact, while the fossil record reveals the presence of ants during the explosive radiation of the angiosperms in the late Cretaceous, there is as yet no evidence of bees during the same period (Wilson, Carpenter and Brown, 1967; Carpenter, 1977).

In our search for a more fundamental answer to this problem we found that myrmicacin (1-B-hydroxydecanoic acid) has been isolated from the metathoracic gland of the leaf-cutting ants *Atta sexdens* and *Acromyrmex subterraneus,* the seed-eating ant *Messor barbarus* and the omnivore *Myrmica laevinodis.* The secretion in which this molecule is found also contains either one of the plant hormones B-indolylacetic acid or phenylacetic acid (Schildknecht and Koob, 1970, 1971). It is an inhibitor of the growth and spore germination of a variety of bacteria and fungi (Schildknecht, 1976; Maschwitz, Koob and Schildknecht, 1970). Of even greater interest, a series of laboratory experiments have shown that myrmicacin, applied in minute quantities to pollen cultures, inhibits pollen germination and retards pollen tube growth (Iwanami and Iwadare, 1978, 1979; Iwanami et al., 1979, 1981; Nakamura, Miki-Hirosige and Iwanami, 1982). Since pollen growth is disrupted when subjected to ant secretions in the lab, does it suffer a similar fate when exposed to living, intact ants? We investigated this question with the possibility in mind that ants are not pollinators because they secrete substances that inhibit pollen function.

MATERIALS AND METHODS—Live ants were collected from the Brisbane Ranges National Park, 50 km west of Melbourne, Australia. In the lab, vials were prepared containing small quantities of pollen. In most experiments the species was *Prunus avium,* but some *Lycopersicon peruvianum, Rhododendron arboreum,* and native *Acacia retinodes* pollen was also used. An ant was introduced into each vial and left for 30 minutes, by which time a light dusting of pollen was evident on the integument. The ant was then removed and the pollen transferred to a culture slide for an incubation period of 18 hours. Percent germination and pollen tube growth were then recorded, the latter with the aid of a Zeiss Videoplan Image Analysis System. Sample sizes are given in Tables 1 and 2. Care was taken to ensure that pollen was exposed only to integument-borne secretions and not to substances from the mouth, anus, sting, or cloaca: at the start of each experiment ants were permitted to walk into the pollen vials under their own volition, and later, pollen was transferred to the culture slide in one of three ways: 1) The ant was grasped with fine forceps high up on a second leg. The ant invariably curled its body around the forceps to bite and sting. This in turn exposed the entire dorsal surface for application to the culture slide, free of oral or anal secretions. 2) The ant was allowed to wander, unmolested, back and forth across the culture slide. 3) Unattached pollen remaining in the vial was transferred to the culture slide with a fine, sterilized needle. Controls utilized identical pollen and vials, but with no ant treatment.

Culture slides were dipped twice in agarose medium (0.3 g agarose, 5 ml Brewbaker-Kwack 10% medium, 20 ml 30% sucrose, 25 ml distilled H_2O) according to the method of Williams et al. (1982). Pollen was transferred to slides within 20 minutes of solidification of medium. Slides were incubated for 18 hours

TABLE 1. **A.** *Percent germination of control versus experimental (ant-treated) pollen. Except where indicated all treatments are for pollen removed directly from the ant integument. In each trial four ants were used, yielding 4 culture slides per trial and a total of 120 ants. The term t_s is a test of equality of the control and experimental percentages (Sokal and Rohlf, 1981). In all cases the value for t_s is highly significant, $P < 0.001$, showing differences between control and experimental percentages. Numbers in ( ) indicate replicates using fresh batches of pollen, * indicates experimental values obtained by allowing ant to walk undisturbed over culture slide, ** indicates experimental values obtained from unattached pollen, *** indicates values obtained after 12 hours incubation, **** indicates values obtained after 36 hours incubation. Identification of ants to species level was impossible in some cases.* **B.** *Percent viability of control versus experimental pollen*

Ant	Control		Experimental		
Subfamily, genus and species	%	*n*	%	*n*	t_s
A. PERCENT GERMINATION					
Nothomyrmeciinae			[*Prunus avium* pollen]		
Nothomyrmecia macrops (#1)	75	800	56	465	11.55
(#2)	57	800	43	200	3.57
*	75	800	55	240	12.13
**	75	800	43	400	19.02
Myrmicinae					
Aphaenogaster sp. (#1)	75	200	47	200	5.84
(#2)	48	512	17	701	8.79
(#3)	67	801	47	801	8.33
(#4)***	61	801	33	800	11.38
(#5)****	60	800	34	800	10.54
**	67	801	33	800	13.88
Chelaner sp.	64	600	26	802	14.32
Meranoplus sp.	64	600	26	800	14.32
**	64	600	18	798	17.85
Pheidole sp.	67	801	44	800	9.35
**	67	801	31	800	14.74
Ponerinae					
Amblyopone australis	67	801	58	801	3.73
Rhytidoponera sp. 1	48	512	30	800	6.57
sp. 2	42	600	32	800	3.82
Myrmeciinae					
Myrmecia pilosula	64	600	8	628	22.31
sp. 2	65	800	51	400	4.65
Formicinae					
Oecophylla smaragdina	59	600	39	500	6.63
Dolichoderinae					
Iridomyrmex sp.	65	800	44	763	8.40
Myrmicinae			[*Rhododendron arboreum* pollen]		
Aphaenogaster sp.	48	512	17	701	11.68
Ponerinae					
Rhytidoponera sp. 1	48	512	30	800	6.52
Formicinae			[*Lycopersicon peruvianum* pollen]		
Oecophylla smaragdina	71	800	53	800	7.62
B. PERCENT VIABILITY					
			[*Lycopersicon peruvianum* pollen]		
Aphaenogaster sp.	92	1,506	63	780	16.43
Myrmecia pilosula *	92	1,506	78	860	9.24
			[*Acacia retinodes* pollen]		
Aphaenogaster sp. *	91	700	46	20	4.59
Myrmecia pilosula (#1)*	91	700	14	32	9.78
(#2)*	63	375	28	131	7.08

TABLE 2. *Statistics for pollen-tube lengths of experimental and control pollen. The data are shown as raw units taken from an eyepiece graticule. The conversion factor is: 1 eyepiece unit = 0.0125 mm*

Treatment	$\bar{x} \pm$ SE	n	t	P
1. Control	102.96 ± 1.90			
Aphaenogaster sp.	93.73 ± 2.07	800	3.29	<0.01
2. Control	102.96 ± 1.90			
Pheidole sp.	93.90 ± 2.02	800	3.28	<0.01
3. Control	87.33 ± 3.22			
Meranoplus sp.	51.22 ± 1.72	400	9.90	<0.001
4. Control	87.33 ± 3.22			
Meranoplus sp. (unattached pollen)	53.34 ± 1.82	400	9.20	<0.001
5. **Meranoplus* sp. (whole ant)	51.22 ± 1.72			
Meranoplus sp. (unattached pollen)	53.34 ± 1.82	400	0.85	n.s.

* To determine if the different methods of transferring pollen to culture slides after ant treatment yielded different results, the two *Meranoplus* treatments were compared.

at 22 C in a humid atmosphere, and on removal fixed in FAA.

Percent viability was determined by using fluorescein diacetate in 10% sucrose (f.d.), according to the method of Heslop-Harrison and Heslop-Harrison (1970). Pollen was exposed to ants in the usual way. The ant was then allowed to walk through several drops of saturated f.d. on a slide until pollen was apparent in the solution. After 3 minutes of further exposure to the air, a cover slip was placed over the solution and the pollen viewed by fluorescence microscopy; pollen with bright green fluorescence was viable, non-fluorescing grains were considered dead.

RESULTS—Percent germination and percent viability in treatments and controls are shown in Table 1. In every case germination and viability were significantly reduced by ant treatment. The figures for *Acacia retinodes* pollen are of special interest as the ants for these experiments were collected from *A. retinodes* trees.

The data on pollen tube growth are given in Table 2. In all cases the pollen tubes from ant-treated pollen were significantly shorter than controls.

As a final test, we examined the effect of treated compatible pollen on seed set, using wild tomato flowers (*Lycopersicon peruvianum*). In this case, the treated pollen was unattached pollen taken from vials which had contained ants for 30 minutes. In the first treatment 23 flowers were pollinated with pollen exposed to *Aphaenogaster* sp., with 20 control flowers. There was a significant reduction in seed set: (control pollen $\bar{x} = 71.55 \pm 5.92$, *Aphaenogaster*-treated pollen $\bar{x} = 51.13 \pm 5.79$, $t = 2.45$, df 41, $P = 0.02$). In the second treatment 21 flowers were pollinated with pollen exposed to *Myrmecia* sp., with the same 20 control flowers. Again there was a significant reduction in seed set: (control pollen $\bar{x} = 71.55 \pm 5.92$, *Myrmecia*-treated pollen $\bar{x} = 40.48 \pm 5.43$, $t = 3.87$, df = 39, $P = 0.001$).

DISCUSSION—It is clear from the data that pollen function is disrupted following contact with ants. However, we do not claim that this is the only reason why ants are not more commonly pollinators, nor can we assert that it is myrmicacin from the metathoracic gland which produces these effects. Identification of the origin and of the chemical structure of the disruptive secretion will require much more experimentation.

If the effect of ants on pollen is general, the question of its origin and function arises. Wheeler (1910) noticed that ants produced an "oleaginous" material which was spread over the body, possibly to prevent the growth of fungi and bacteria. A little later Bequaert (1922) reported that ants were remarkably free of fungal infection compared to other arthropods. More recently Maschwitz, U., K. Koob, and H. Schildknecht (1970) and Maschwitz (1974) reported that ants distribute antibiotic secretions over their bodies and larvae. We suggest that the secretions of ants which function to combat microorganisms, by chance also incapacitate pollen grains. The appearance of compounds which destroyed bacteria and fungi incidentally created a powerful selection pressure against the evolution of ant pollination.

It is possible that myrmicacin is the common denominator since it inhibits or disrupts the growth of bacteria and fungi on one hand, and pollen grains on the other. While this molecule

has been isolated from only four ant species, they represent a varied sample both geographically and biologically. *Atta sexdens* and *Acromyrmex subterraneus* are both fungus-growing ants from the neotropics. *Messor barbarus* is a seed-harvester, widespread in the European and north African Mediterranean zone. *Myrmica laevinodis* is an omnivore which eats all kinds of animal and plant products, with a large distribution to temperate Eurasia. As for its mechanism of action myrmicacin disrupts the flow of components to cell walls, the function of Golgi vesicles, and mitosis (Nakamura et al., 1982), and is consequently potentially capable of affecting both germination and pollen-tube elongation. Having presented this information on myrmicacin we must stress that this molecule is merely implicated in the adverse effects of ants on pollen, and that several other secretions, and several other glands besides the metathoracic may be involved, or even be more important. Collectively, ants have an astounding array of glands and secretory products (Wilson, 1971) many of which may contribute to the phenomena we have described here.

Finally, it may be asked why this originated among the ants but not among their close relatives, the bees and wasps? Ants differ fundamentally from bees and wasps in that their eggs, larvae, and pupae lie exposed in the nest, unprotected by either a wax cell as in the bees, or a paper one as in the wasps (Wheeler, 1910). That nesting in natural cavities, especially in the ground, is fraught with the danger of infection by bacteria and fungi, is clear from the variety of bactericidal and fungicidal agents found in the nest materials of closely related Hymenoptera such as bees. Indeed, some of these materials are also known to inhibit pollen germination (Michener, 1974), and the effects of bees on pollen may not be as benign as previously assumed. It is very likely that microorganisms have always been an important source of mortality in ant nests (Wheeler, 1910; Michener, 1974; Evans, 1974) and selection for defenses against them must have been very powerful right from the start. This is also suggested by this study, since three genera showing strong effects on pollen—*Nothomyrmecia, Myrmecia,* and *Amblyopone*—are the most primitive ants known. While the habit of nesting in natural cavities and not constructing specialized brood cells confers the advantage of greater mobility, it exposes the eggs, larvae, and pupae to pathogenic microorganisms. In the absence of physical barriers to these organisms, the smearing of antibiotic compounds on all the members of a colony seems to be a necessary and highly appropriate alternative type of defense. As a result the interactions between angiosperms and ants have become fundamentally different from those between angiosperms and bees and wasps. Coevolution was not precluded, but the ants coevolved primarily with non-floral structures, while bees and wasps became the most important group of pollinators.

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