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Pollen waste and unrelated traits in a fig–fig wasp symbiosis: a new behaviour suggesting a host shift

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Abstract

In a fig–fig wasp symbiosis, we have discovered that male fig pollinators (*Alfonsiella fimbriata* Waterston) bite into the dehiscent anthers of *Ficus natalensis leprieuri* Miq., thus scattering the pollen grains throughout the syconium. Female pollinators are the only ones to transfer pollen to conspecific trees, and collect pollen actively from the anthers only. Thus, this male behaviour appears to be antagonistic to the pollination process. We compare different wasp pollinating behaviours between fig species exhibiting dehiscent and non-dehiscent anthers and conclude that this male behaviour is new and not required with spontaneously dehiscent anthers. These findings could suggest a host shift of *Alfonsiella fimbriata*. **To cite this article:** G. Michaloud et al., *C. R. Biologies* 328 (2005).

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Résumé

Dans une symbiose figuier–pollinisateur, nous avons découvert que les mâles de l'espèce pollinisatrice (*Alfonsiella fimbriata* Waterston) mordent dans les anthères, qui sont déhiscentes, dispersant ainsi le pollen dans la figue de *Ficus natalensis leprieuri* Miq. Les pollinisateurs femelles étant les seuls à transférer le pollen qu'ils collectent activement et uniquement à partir des anthères, ce comportement des mâles paraît mal adapté. Nous comparons différents comportements de pollinisateurs associés à des espèces de figuiers dont les anthères sont déhiscentes et non déhiscentes, et concluons que le comportement observé est nouveau, et inadapté à la déhiscence des anthères. L'absence de concordance entre les caractères analysés pourrait suggérer un changement d'hôte chez *Alfonsiella fimbriata*. **Pour citer cet article :** G. Michaloud et al., *C. R. Biologies* 328 (2005).

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1. Introduction

Among the many known relationships between plants and pollinators, the species-specific and obligatory mutualism between figs (Moraceae, *Ficus*) and pollinating wasps (Hymenoptera, Agaoninae) is often considered as an example of coevolution due to the precise morphological, physiological, and behavioural co-adaptations [1–6]. The fig (syconium) is a closed urn-shaped inflorescence that may contain both male and female flowers, and that may be actively or passively pollinated, depending on the species.

In ‘monoecious’ fig species, the fig has both male and female flowers, and the female wasps enter the fig when female flowers are receptive, lay eggs in some ovules and pollinate others at the same time. Thus, the pollinated ovules develop seeds and the oviposited ones are transformed into galls with the larval development of the young wasp. A few weeks later, the adult stage of this new generation of wasps coincides with the maturation of the seeds and pollen. The female wasps are the only ones able to transfer pollen to conspecific fig trees.

In these fig species, we distinguish three types of pollinating wasp behaviour in relation to differences in the anther structure. In ‘type one’, the anthers do not open spontaneously, and the males must sever them to allow the female wasps to access to pollen for collection. The behaviour of the male wasps is therefore essential for pollination. In the ‘type two’, the anthers do not dehisce spontaneously and only the female wasps split open the anthers, with the base of the antennae and mandibles, and widen the slit along the line of dehiscence to collect pollen. In the ‘type three’, the anthers dehisce spontaneously, which allows the females to actively collect the pollen grains from the anthers. In none of these three types of behaviour, are the pollinating females able to collect pollen outside of the anthers. In the last two types, the male wasps have no role in the pollination activity, and thus if they sever the anthers, it will affect the collection of pollen by females and therefore the pollination process.

Our studied fig species, *Ficus natalensis leprieuri* Miq., is ‘monoecious’ with spontaneously dehiscent anthers. Therefore, the female wasps (*Alfonsiella fimbriata* Waterston) [7] can actively load their two thoracic pockets with pollen [5]. However, we discovered that the flightless male wasps of *A. fimbriata*, were biting into the spontaneously dehiscent anthers [5], thus scattering the pollen grains throughout the syconium. Since females of *A. fimbriata* cannot collect pollen outside the anthers, this male behaviour appears to be antagonistic to the pollination process. This situation has never been reported elsewhere in the pollination literature and should increase the cost for the fig-tree reproduction without any apparent gain for the wasps.

Thus, we propose to answer the following questions. (1) Does the behaviour of the male wasp lead to a cost for the fig tree pollination? To answer to this question, we compared the average quantities of pollen wasted by male wasps with (i) the quantities produced and (ii) the quantities collected for pollen transfer by the female pollinating wasps. (2) How can we explain the male wasps’ behaviour? To answer to this question we will (i) consider whether this behaviour could be due to a feeding habit; or (ii) be adapted to a male flower structure existing in another fig species. As coevolution often results in correlated traits [8], and may be predictive of the pollination mode among figs and fig wasps [9], we will make a comparative analysis of different cases occurring in other fig–fig wasp symbiosis.

2. Materials and methods

Our observations took place in northeastern Gabon (Makokou field station, IRET), in the botanic garden, where this riparian fig species is colonised only by a single female of the studied pollinating species and no parasite at all (foundress of *A. fimbriata* always died within the syconia and dead bodies could easily be identified. In the natural riparian habitat, a mean of 1.2 foundresses were observed, SD = 0.4 (SD will be represented by \pm in the text and Table 1; $n = 180$

Table 1

Basic data: mean syconium production in *Ficus natalensis leprieuri* when colonised by a single female of *Alfonsiella fimbriata*

Sample	N (syconia)	Female flowers			Male flowers		
		Pollinators		Infertile		Seeds	Bladders
		males	females				
1	18	9.4 ± 3.5	71.0 ± 14.6	159.4 ± 33.5	38.4 ± 29.9	51.8 ± 45.4	34.1 ± 7.9
2	19	7.4 ± 10.8	45.2 ± 14.8	71.0 ± 28.2	41.2 ± 26.9	53.5 ± 31.2	16.5 ± 7.8

analysed syconia). When the pollinating wasps were coming out of their galls within the syconia some of them were cut into halves to allow us to collect male wasps while biting into the dehisced anthers in order to analyse the body and the digestive tracts of 12 of them.

To estimate the quantity of pollen missing per anther we collected at random from each of two trees, two samples of 20 syconia at fruit stage with mature pollen. We isolated each syconium, unopened, in a cloth-covered vial in order to collect the emergent wasps and monitor them; the flowering structure was also analysed (Table 1). Since each anther is made of four loculi [10], we divided each of them into two parts in order to note accurately the presence or absence of pollen. Thus, each anther was divided into eight parts, each one representing 12.5% for calculations.

To estimate the quantities of pollen produced per syconium, we made a thorough count under microscope of pollen grains of 24 virgin flowers belonging to six syconia. In the analysis of brood structure, we refer to normal female biased sex ratio [11]. The observed mean sex ratio (number of males divided by total number of individuals) was 0.12 ± 0.05 ($n = 45$ broods analysed), and 0.11 ± 0.07 ($n = 47$) for trees 1 and 2 from which our two fig samples originate.

3. Results

The analysis of the 12 males observed biting into the anthers and spreading pollen around showed abundant pollen grains on the external parts of their body, but no trace in their digestive tracts, thus suggesting that this was not a feeding behaviour.

The count of pollen grains under microscope of 24 virgin flowers provided a mean of 9698 ± 3995 pollen grains per anther. This result multiplied by the mean number of male flowers per sample (Table 1) gave an

estimate of 330 702 pollen grains produced per syconium in sample 1 and 160 017 in sample 2.

To estimate the average quantities of pollen wasted by male wasps, we analysed the anthers of two syconia containing only males (91 and 93, respectively) and no female wasp at all (they contained 23 and 32 anthers, respectively). We found an average of 43% and 87% of pollen missing. Also, another one of the analysed syconia from sample 1 had an unusual male-biased sex ratio with 52 male and only 19 female pollinators, and had 88% of its pollen removed from the 15 anthers counted.

In the analysis of syconia containing broods with normal female-biased sex ratios (see *Material and methods* section above), the average quantities of pollen removed from anthers were $56\% \pm 19\%$ for sample 1 ($n = 18$ syconia analysed) and $64\% \pm 11\%$ for sample 2 ($n = 19$).

Therefore, it appears that the proportion of pollen removed from anthers when males are alone, or in greater abundance than females, can be higher than in normal female-biased sex-ratio situations. To estimate the quantity of pollen grains collected by female pollinators, we first made a thorough count of pollen grains (stained with methyl blue) on 12 females with both pollen pockets being full (469 ± 124 pollen grains). We then estimated the average proportion of pollen stored by females in their two thoracic pollen pockets by dividing each of them into four parts in order to note accurately the presence or absence of pollen. The average pollen pocket load per female was 56% and 48% for samples 1 and 2, respectively ($n = 1332$ and 860 emergent female wasps analysed). Multiplying these proportions by the above average of 469 pollen grains and by the average number of female pollinators born per syconium (Table 1) provided an estimation of the quantity of pollen grains removed by females per syconium: 18 647 in average for sample 1 and 10 175 for sample 2 (respectively 6% and 7%

of the average quantities of pollen produced per syconium, only).

Subtracting these 6% of pollen dedicated to pollination from the above quantities that are removed from anthers (56% and 64% for samples 1 and 2, respectively), we find that 50% to 58% of the pollen produced per syconium must be wasted by males, and that therefore an average of 44% and 36% of the pollen of each analysed sample remains untouched, which constitutes a buffer against the pollen wasted by males.

4. Discussion

Our results show that the pollen wasted by males was not consumed and did not lead to a pollen shortage for the pollination process, which might explain why this apparently maladaptive male behaviour has not been counter selected. Moreover, our estimates show that the average quantities of pollen produced per syconium were 16 to 18 times what is collected by females for pollination, although the male:female flower ratio ranges between 0.12 and 0.09 (for samples 1 and 2, respectively), thus fitting with other active pollinated fig species, which ratios ranged from 0.15 to 0.01 [9]. This confirms the remark made by Kjellberg et al. [9] that producing more pollen in actively pollinated fig species would probably not increase the quantity of pollen dispersed by the wasps. Indeed, we see that the limited number of pollinating females born per syconium, and the low filling of their pollen pockets we observed on average (56% and 48% for samples 1 and 2, respectively) explains the low proportion of pollen dispersed by the wasps (in preparation). In our study, this pollen overproduction could play a buffer role in the waste of pollen by the male behaviour. Thus, owing to this overproduction, the males' behaviour does not affect the pollen transfer and the pollination process. However, it does represent a cost, as the trees could produce less pollen in the absence of pollen waste.

Our analysis shows that biting into the anthers was not an act of feeding (feeding occurs during larval stages, only), but the origin of this male behaviour remains a question. Coevolution often results in the existence of traits that are correlated [8,9]. Therefore, in this study of fig–fig wasp symbiosis, the male behaviour of biting into the anthers, should a priori be

correlated to anthers that are not dehiscent, which is not the case. The status of *Alfonsiella fimbriata* is also puzzling for Wiebes [12], who compares the classification of the African *Ficus*-section *Galoglychia* with that of the genus *Alfonsiella*. It seems to him that the fig–fig wasp relationship within this *Ficus*-section is not as specific as it is in others. Also, recent phylogenetic analysis by Kjellberg et al. [13] puts forward some discrepancies between wasp and *Ficus* classification within *Ficus*-section *Galoglychia*, subsection *Chlamydodora* (Mildbr. & Burret) C.C. Berg, to which *Ficus natalensis leprieuri* belongs. They concluded that “there are some situations which show that co-speciation is not an obligate rule”, and suggested a host shift of some fig pollinating species. Frank [14] considers that in fig and in fig wasps, behavioural differences “may be good characters for phylogenetic inference, or at least that a congruence between established phylogenies and behavioural differences may be observed”.

To understand the absence of congruence between the male wasp behaviour and the presence of spontaneous dehiscent anthers, we compared the different fig–fig wasp symbiosis known to involve non-dehiscent and dehiscent anthers in actively pollinated fig species. We found three main categories (Table 2).

1. Male wasps cut the stamens or (and) detach the ripe anthers; females push their heads into the median slit of the non-dehiscent anthers, keep the anther sacs open by their antennal scapes, crumble the pollen with their mandibles and perform the pollen lifting movement to load their pollen pockets.

2. Only female wasps split open the non-dehiscent anthers with the base of the antennae and with their mandibles; widen the slit along the line of dehiscence and crumble pollen; then actively load pollen into the pollen pockets. Males do not take part in this process.

3. Anthers spontaneously dehisce, and female wasps directly and actively load the pollen into their pollen pockets. Males do not take part in this process.

The results of this comparative analysis of the fig–fig wasp relationships show a good correlation between the anther structure and the wasp behaviour. When anthers are spontaneously dehiscent, only the active pollen loading by female wasps is necessary. In our studied fig species, *F. natalensis leprieuri*, the pollinating behaviour of female *Alfonsiella fimbriata* consists of active pollen loading, only, and thus per-

Table 2

Fig and fig wasp species involved in the three different categories of fig–fig wasp symbiosis with non-dehiscent and dehiscent anthers described in the text

Category	Fig species	Fig wasps species	References
1	<i>Ficus sur</i> (syn. of <i>F. capensis</i>)	<i>Ceratosolen capensis</i>	[23]
	<i>F. sycomorus</i>	<i>C. arabicus</i>	[24]
	<i>F. racemosa</i>	<i>C. fusiceps</i>	[25]
	<i>F. fistulosa</i>	<i>C. hewitti</i>	[26]
2	<i>F. vogelii</i>	<i>Allotriozoon heterandromorphum</i>	[27]
	<i>F. aurea</i>	<i>Pegoscapus jimenezii</i>	[14]
	<i>F. citrifolia</i>	<i>Pegoscapus assuetus</i>	[14]
	<i>F. costaricana</i>	<i>Pegoscapus estherae</i>	[14,28]
	<i>F. hemsleyana</i>	<i>Pegoscapus tonduzi</i>	[14,28]
	<i>F. ingens</i>	<i>Platyscapa soraria</i>	[29]
	<i>F. religiosa</i>	<i>Blastophaga quadriceps</i>	[14,30]
3	<i>F. pertusa</i>	<i>Blastophaga (valentinella) sylvestrii</i>	[31]
	<i>F. ottoniifolia supsp ottoniifolia</i>	<i>Courtella camerunensis</i> and <i>C. gabonensis</i> (in Gabon)	[5,17]
	<i>F. ottoniifolia supsp multinervia</i>	<i>C. gabonensis</i>	[7]
	<i>F. burttidavayi</i>	<i>Elisabetiella bajnathi</i>	[32,33]
	<i>F. natalensis natalensis</i>	(a) <i>Elisabetiella stukenberg</i> (South Africa); (b) <i>Alfonsiella longiscarapa</i> (South Africa, Zimbabwe; male behaviour not described); (c) <i>E. socotrensis</i> (South Africa); (d) <i>E. stuckenbergi</i> (Zimbabwe); (e) <i>A. brongersmai</i> (Zimbabwe; male behaviour not described)	(a, b) [34]; (c) [7]; (d) (e) and (b) in Zimbabwe [35]

fectly fits with the observed dehiscence of the anthers. In contrast, the male behaviour is unnecessary with the dehiscence of the anthers, and does not correspond to either of the different situations above described in fig pollination processes: males cut the stamens or (and) detach the ripe anthers, when anthers are not dehiscent, but never bite into the pollen sacs with their mandibles, as male *A. fimbriata* do. To our knowledge, this behaviour is new among fig–fig wasp relationships.

This comparative examination of male flower structures in relation to the behaviours of pollinating species finds no adaptive explanation for biting into the anthers of *F. n. leprieuri*. According to the definition of coevolution by Janzen [8], we have a trait (the pollinating male behaviour that consists in biting in the anthers) in one organism, *Alfonsiella fimbriata*, which should correspond to non-dehiscent anthers in the other organism (*F. natalensis leprieuri*). Instead, in our study, the corresponding trait in the other organism, *F. n. leprieuri* (the host fig), exhibits dehiscent anthers, which is not related. This unexpected situation could suggest a host shift of the pollinating wasp species *Alfonsiella fimbriata* from an unknown *Ficus* species (bearing most probably non-dehiscent anthers)

to *F. n. leprieuri*. A host shift situation has once been reported among figs and fig wasps [15,16]: “*Ceratosolen galili* shifted by horizontal transfer from an unknown presumably extinct, ficus species to *F. sycomorus*...”. This former pollinating wasp uses *F. sycomorus* as host for reproduction, but does not pollinate.

The origin of the behaviour we describe could also come from an ancestor involved in a passive pollination system. In such a case, if anthers were not spontaneously dehiscent, female pollinators could not be passively covered with pollen, and the males’ behaviour that consists in biting into the pollen sacs and spreading pollen around would be required and efficient. However, the observed active pollen-loading behaviour of the female pollinator, would, in turn, be an interrogation from an evolutionary point of view, as well as the presence of the pollen pockets. But in the above speculation, male and female behaviours remain antagonistic. Moreover, the only existing co-cladogenesis on the fig breeding system and pollination behaviour, which includes the genus *Alfonsiella* [17], does not show evidence of an ancestor involved in a passive fig pollination system. In addition, according to Kjellberg (personal communication), the genus *Alfonsiella* is only associated with active polli-

nation fig systems. In conclusion, the present case does not lend itself to any obvious adaptative explanation.

Our finding on the co-occurrence of non-correlated traits in two coexisting species may contribute to explain the above-mentioned ‘discrepancies’ between fig pollinating species and *Ficus* classification [13], and the numerous exceptions to the usually admitted one: one species relationship between fig species and fig wasp species [7,18–22]. With the heavy human pressure generating plant population extinctions, such situations might even become more common.

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