ARTICLE ADDENDUM

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Private channels in plant-pollinator mutualisms

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Volatile compounds often mediate plant-pollinator interactions, and may promote specialization in plant-pollinator relationships, notably through private channels of unusual compounds. Nevertheless, the existence of private channels, i.e., the potential for exclusive communication via unique signals and receptors, is still debated in the literature. Interactions between figs and their pollinating wasps offer opportunities for exploring this concept. Several experiments have demonstrated that chemical mediation is crucial in ensuring the encounter between figs and their species-specific pollinators. Indeed, chemical messages emitted by figs are notably species- and developmental stage-specific, making them reliable cues for the pollinator. In most cases, the species-specificity of wasp attraction is unlikely to result from the presence of a single specific compound. Nevertheless, a recent paper on the role of scents in the interaction between *Ficus semicordata* and its pollinating wasp *Ceratosolen gravelyi* showed that a single compound, 4-methylanisole, is the main signal compound in the floral scent, and is sufficient by itself to attract the obligate pollinator. Mainly focusing on these results, we propose here that a floral scent can act as a private channel, attracting only the highly specific pollinator.

Mutualisms are interspecies interactions in which each participant gains net benefits from interacting with its partner. Like many other interspecies interactions, mutualisms are usually mediated by chemical signals. For instance, floral scents act as pollinator attractants in numerous plant species.[1-3] We studied the chemical compounds that mediate a set of interactions which has become a model system for understanding the evolution of mutualisms: the interactions between Ficus (Moraceae) and their species-specific pollinating fig wasps (Chalcidoidea: Agaonidae). In this 'nursery pollination mutualism', the pollinators can breed only in receptive figs of their host tree, which depends in turn on the wasp as its sole pollinator. Each pollinator species is usually associated with a single Ficus species. Fig trees mainly grow in tropical regions, and many species can co-occur in the same forest. In these regions, the density of individual species is often quite low.[4] Therefore, signals emitted by each species must be efficient at long distances and specific, to allow the attraction of the associated pollinator. In all of the Ficus species that have been studied so far (approximately 40 of a total of roughly 800 species worldwide), figs have been shown to release volatile compounds when they are receptive (i.e., at the stage when pollination can occur).[5-10] Behavioral tests have been performed with pollinators of several species, confirming for these species the role of fig scent in pollinator attraction (Soler et al. in prep).[5-7,9,11] In the floral scents of the fig species studied, at least two to five major compounds account for the majority of the total volatiles emitted by receptive figs.[8,10,12-15] These major volatiles emitted by receptive figs are generally compounds that are not rare in floral fragrances. The species-specificity of wasp attraction is thus usually not likely to result from the presence of only one single specific compound.[10,13] However, Chen and co-workers,[16] focusing on *Ficus semicordata*, found that a single benzenoid compound, 4-methylanisole, is sufficient to attract its pollinator. Though 4-methylanisole occurs in floral fragrances, having been documented in floral scents of plants from 17 families (of the 90 families included in the review by Knudsen et al.),[17] it usually accounts for only a fraction of total volatiles, and this was the first time that this benzenoid compound has been reported in the floral scent of a Ficus species.[7,10-12,18] To our knowledge, no previous study has shown that 4-methylanisole is attractive to pollinators of any plant, or that this compound could by itself mediate the specificity of any mutualistic interaction.

Raguso (2008)[3] defined a 'private channel' as the potential for such exclusive communication via unique signals and receptors. Moreover, according to Schaefer et al.[19] private channels must fit three major criteria: (1) the identification of an intended (effective mutualist) receiver; (2) sensitive signal detection by this receiver, and finally (3) poor detection by unintended (less effective) receivers. Chen et al.[16] showed that a single compound, 4-methylanisole, accounted for more than 90% of the volatile compounds emitted by receptive figs of *F. semicordata*. This compound is also known not to be produced by the two other sympatric Ficus species in which floral odours have also been studied, nor by any Ficus species whose scent has been analyzed (Soler et al., in preparation).[10,13] Moreover, Chen et al.[16] found that the species-specificity of the attraction of *Ceratosolen gravelyi*, the pollinating wasp of *Ficus semicordata*, was due mainly, if not entirely, to this single major compound. Indeed, based on behavioural (olfactory) tests, they showed that the specialized pollinating wasp detects 4-methylanisole and is attracted by it, even at low concentrations (wasp response tested in concentrations ranging from 1.22×10^2 ng/100 μl to 1.22×10^6 ng/100 μl). The last criterion for a private channel proposed by Schaefer et al.[19] i.e., poor detection by unintended receivers, is the only one which has not been clearly demonstrated by Chen et al.[16] In the case of fig/fig wasp mutualisms, the unintended receivers correspond obviously to the parasites of the mutualism. Indeed, many fig species harbor numerous species of chalcidoid wasps that mature within ovaries in fig inflorescences, like the pollinator, but do not carry pollen. Each of these non-pollinating fig wasps is assumed to be associated specifically with a single Ficus species[20] and to use fig scents as cues to detect the host species, as do pollinating fig wasps.[21] However, in the case of the *F. semicordata/C. gravelyi* mutualism, no non-pollinating fig wasps have been observed ovipositing during the period when figs are at the receptive stage. This situation is quite unusual in Ficus species (Proffit M, unpublished data; Rasplus J-Y, personal communication). The apparent absence of 'eavesdropping' parasites at the time when pollinators are attracted to the figs suggests that the last criterion of a private channel—poor detection by potential receivers other than the specific pollinator—also holds in this case, although this has not been experimentally demonstrated.

The study by Chen et al.[16] is, to our knowledge, the first that attempted to test the existence of a private channel in a fig/fig wasp interaction. Nevertheless, this is not the first case of a putative private channel in a nursery pollination mutualism. Indeed, examples have been highlighted in the interactions between *Yucca filamentosa* (Agavaceae) and its moth pollinator *Tegeticula cassandra* (Prodoxidae)[22] and in the interactions between *Peltandra virginica* (Araceae) and its pollinating fly *Elachiptera formosa* (Chloropidae).[23] Similarly, the existence of private channels has been suggested for several species in the family Eupomatiaceae, pollinated by beetles.[24] In contrast, Svensson et al.[25] showed that in the Breynia (Phyllanthaceae)/Epicephala (Gracillariidae) interaction, pollinators are attracted by common volatile compounds, supporting the hypothesis that no private channel exists in this case. In a review of the role of scents in plant-pollinator interactions, Raguso[3] highlighted the putative examples of private channels, but noted that their existence is still debated, notably in the case of non co-specialized plant-pollinator interactions. Nevertheless, some studies have suggested that private channels do exist in this class of interactions. Most examples concern the Orchidaceae. For instance, Eltz et al.[26] showed that carvone oxide and ipsdienol are volatile floral rewards emitted by Neotropical orchids pollinated by male euglossine bees, which collect volatile substances for courtship displays. However, probably the best-known examples are Ophrys spp., temperate-zone terrestrial orchids whose flowers mimic the female pheromone of the pollinator to attract males, which pollinate flowers by pseudo-copulation.[27-29] In his review of the role of scents in plant pollinator interactions, Raguso[3] also proposed that floral filters do not need to rely upon exclusive olfactory signals or receptors. Indeed, few studies have determined whether pollinator-attractive compounds could alone assure species-specificity (private channel), or whether specificity is mediated by more complex 'floral filters', of which scent is only one component. These latter may integrate mechanical or other kinds of barriers, as seems to be the case in the interaction between the dwarf palm *Chamaerops humilis* and the weevil *Derelomus chamaeropsis*.[30]

In the literature about private channels in chemical mediation of mutualisms, two points still seem unclear. One is a semantic point: do cases in which specificity is ensured by specific ratios of several more common compounds constitute a private channel, or is this concept restricted to cases in which specificity is ensured by a single rare compound? The literature on private channels emphasizes cases of the latter type. A related question is whether specificity is sometimes ensured not by a single rare compound, but by a combination of rare compounds. While all the putative cases of private channels that have attracted attention concern emission of and attraction to a single rare compound,[3,16,18] the limited number of studied cases does not allow drawing firm general conclusions. Nevertheless, we might think that a hypothetical private channel constituted by several rare compounds might be more difficult to evolve (if it requires the acquisition of several biosynthetic pathways by the plant, and of specific receptors by the insect) or counter-selected (owing to greater costs).

We propose here that in the mutualism between *F. semicordata* and *C. gravelyi*, despite the existence of mechanical barriers to flower visitation (as in all Ficus species), available information on the chemical communication between plant and pollinator constitutes a strong case for the mediation of a highly specific interaction through a private channel, which acts largely alone as a floral filter that prevents 'cheaters' from finding and exploiting a potential resource. An interesting long-term consequence of such an adaptation in a highly co-specialized plant-pollinator interaction is that it might reduce evolutionary flexibility, preventing host shifts, and perhaps making it difficult for the mutualists to evolve counter-adaptations to a new parasite that 'decodes' the private channel. Private channels may be isolated adaptive peaks, even more difficult to escape than they are to reach. This could explain their apparent infrequent occurrence in nature.

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