Deceptive Behavior in Plants. I. Pollination by Sexual Deception in Orchids: A Host–Parasite Perspective

Nicolas J. Vereecken

Abstract Sexually deceptive orchids attract male insects as pollinators by mimicking the reproductive signals emitted by the targeted females. Since this mimicry system involves the imitation of female mating signals of certain insects, and since mating signals, especially sex pheromones, generally act on a species-specific basis, theory holds that each sexually deceptive orchid is usually pollinated by only one or a few male insect species. While these orchids rely exclusively on their specialized pollinators for their own reproduction, the male insects derive no benefit from this interaction. In this chapter, I will argue that incorporating questions relevant to the field of animal-centered host–parasite interactions into investigations on the evolutionary ecology of orchid pollination by deception will provide important insights at both the proximate (or mechanistic) and at the ultimate (or evolutionary) levels.

1 Introduction

Despite the popular belief that plant pollination by insects epitomizes the ideal mutually beneficial partnership, observational evidence indicates that flowering plants sometimes exploit insects in complex and quite devious ways. This is particularly true in the Orchidaceae, where approximately one-third of all orchid species (i.e., ca. 10,000 species worldwide) achieve insect-mediated cross-pollination without providing a floral reward of any kind to their pollen vectors (Dafni 1984, 1987; Ackerman 1986; Nilsson 1992; Schiestl 2005; Jeraskova et al. 2006). Whereas a large proportion of deceptive orchids achieve cross-pollination by emitting generalized pollinator attractants that innately evoke the presence of a reward to a wide taxonomical range of insects, other species have narrowed their pollinator spectrum by evolving a much more specialized and fine-tuned imitation of specific rewarding models. Such instances fall

N.J. Vereecken

Behavioural and Evolutionary Ecology, Free University of Brussels (U.L.B.) CP 160/12, Av. F.D. Roosevelt 50, B-1050 Brussels, Belgium; Institute of Systematic Botany, University of Zürich, Zollikerstrasse 107, CH-8008 Zürich, Switzerland
e-mail: nicolas.vereecken@ulb.ac.be
e-mail: nicolas.vereecken@systbot.uzh.ch

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28 into the category of Batesian mimicry *sensu stricto* (Wickler 1968; Wiens 1978;
 29 Pasteur 1982), where the orchid (i.e., the *mimic*) impersonates another species (i.e.,
 30 the *model*) and thereby attracts its pollinator(s) (i.e., the *operator*) (Schiestl 2005;
 31 Ayasse 2006).

32 As research efforts proliferate in different areas of expertise in ecological
 33 research, scientists inevitably develop compartmentalized research agendas, and
 34 barriers to effective communication between these disciplines unfortunately
 35 become more and more apparent (Brooks and McLennan 1991; Bush et al. 1997;
 36 Waser and Price 1998; Wyatt 2003). In this chapter, we will argue that incorporat-
 37 ing questions relevant to the field of animal-centered host–parasite interactions into
 38 investigations on the evolutionary ecology of orchid pollination by deception will
 39 provide important insights at both the proximate (or mechanistic) and at the ulti-
 40 mate (or evolutionary) levels. Although several examples of Batesian food-decep-
 41 tive mimicry have been reported in the literature (Dafni and Ivri 1981; Nilsson
 42 1983; Dafni 1987; Johnson 1994, 2000; Galizia et al. 2005; Johnson and Shelah
 43 2006) (see also the chapter by Jeraskova et al.), here we shall limit ourselves mostly
 44 to orchid pollination by sexual deceit, i.e., the imitation of female insects by orchid
 45 flowers, since research in this field has been particularly prominent over the past
 46 decade. This chapter aims to encourage investigations of mimicry systems from a
 47 behavioral perspective, by pointing out specific gaps in our knowledge and possible
 48 avenues for future research that will help to fill them.

49 2 Sexual Deception: Parasitism of Insect Sexual Behavior

50 2.1 Why Parasitism?

51 The term *parasite* in the broadest sense refers to organisms that benefit from their
 52 interactions with other organisms (i.e., the *hosts*) by deriving advantages (habitat,
 53 nutrients, motility, or other services) at the latter's expense (Barnard 1990; Combes
 54 2001; Poulin 2007). But why should sexually deceptive orchids be classified as para-
 55 sites? The flowers of so-called sexually deceptive orchids do not produce nectar,
 56 pollen or any form or edible reward that their pollinators could collect during their
 57 floral visits. Pollinator attraction is almost exclusively mediated by the emission of
 58 specific signals emitted by these flowers, in particular female sex pheromone com-
 59 pounds in their odor bouquet (Schiestl et al. 1999). The male insects are therefore
 60 drawn to the orchid flowers as they patrol for mates, and subsequently attempt
 61 copulation or a precopulatory routine with the female decoys on the flowers, unwit-
 62 tingly taking up the orchid's pollen masses (the *pollinia*) in the process. Cross-
 63 pollination is then ensured as the insect transfers the pollen grains contained in the
 64 pollinia onto the flower of a nearby orchid during another *pseudocopulation*
 65 (Correvon and Pouyanne 1916, 1923; Pouyanne 1917; Coleman 1928; Kullenberg
 66 1961). In short, these orchids lure male bees with the false promise of sex, and

Deceptive Behavior in Plants. I. Pollination by Sexual Deception in Orchids

exploit the males' drive for specific reproductive signals to ensure their pollination. 67
 Since there is exploitation of the male bees' sexual behavior at the core of these 68
 interactions, pollination by sexual deception should therefore be viewed as asym- 69
 metrical or one-sided, with the orchid relying exclusively on its duped pollinator 70
 for its own reproduction, while the male insects derive no benefit from this interac- 71
 tion. From the plant's perspective (i.e., the parasite), the pollinator (i.e., the host) 72
 can therefore be viewed as an ephemeral resource that is used to facilitate cross- 73
 pollination and thereby maximize its overall reproductive success. 74

2.2 The Cost of Parasitism

75

A central issue related to host–parasite interactions and epidemiology is the level 76
 of harm or virulence caused by a parasite to its host. Although it has become 77
 commonplace to view parasites as having a negative impact on their hosts' fitness, 78
 investigations into host–parasite interactions have helped to develop an alternative 79
 and much more subtle picture of the extent to which parasites may affect their hosts. 80
 The available data reveal that host–parasite interactions fall along a continuum, from 81
 one end where the parasite has no negative fitness impact on its host(s) whatsoever, 82
 all the way to the other extreme, where the parasite causes the death of its host(s) 83
 (Poulin 2007). In light of all this, where do orchid–pollinator interactions stand 84
 along this host–parasite “harmfulness” continuum? To date, we only have a very 85
 limited knowledge of the costs, if any, that are incurred by the host species. 86
 However, it seems quite clear that, given the taxonomic range of orchid pollinators, 87
 each with their own ecological and behavioral peculiarities, no general statement 88
 can be made regarding the overall or optimal host exploitation strategy by these 89
 parasites. Since deceptive orchids, and sexually deceptive ones in particular, are 90
 known to be limited in their reproductive success by access to their hosts (Darwin 91
 1862; Kullenberg 1961; Neiland and Wilcock 1995, 1998; Ayasse et al. 2000; 92
 Tremblay et al. 2005; Vandewoestijne et al. 2008), it is expected that selection 93
 should favor host exploitation strategies at a rate that makes these intimate interactions 94
 sustainable across generations, each in their own particular way. Like all parasites 95
 involved in highly specific interactions, sexually deceptive orchids face a major 96
 constraint: a fitness impact on its host that was too strong, e.g., death caused during 97
 pseudocopulation in an extreme theoretical case, would severely compromise the 98
 orchids' chances of reproducing. Hence, it is expected that the orchids' parasitic 99
 strategy should allow the local persistence of their host population, ensuring their 100
 own survival, while adapting to the local mating preferences of their associated 101
 host(s) for female sex pheromone signals. 102

Although quantitative measurements on the level of harm incurred by the hosts 103
 are lacking at this stage, evidence from field observations and a selection of recent 104
 studies may help to sketch trends observed in several orchid genera. At first glance, 105
 it can be postulated that the orchids' trickery is likely to cause a waste of time and 106
 energy for male insects that are otherwise patrolling for mates during their reproductive 107

period. Pseudocopulations with the orchid flowers typically last between a few seconds and as long as a few tens of minutes (Vereecken, pers. obs.), and can therefore potentially cause a decrease in the number of mating opportunities for males that are visiting the orchid flowers instead of searching for access to freshly emerged females. This situation is notably exemplified in the West Palearctic genus *Ophrys*, where the hosts—male bees, wasps and sometimes even beetles—hatch first and generally outnumber (on a daily operational basis) receptive females during the reproductive period. The female insects usually mate only once after their emergence and before they initiate the construction of their nest and oviposition, and males sometimes compete quite intensively with one another to mate with their freshly emerged partners at the nesting/emergence site or at “rendezvous” spots (Alcock et al. 1978; Paxton 2005). In this climate of male–male competition over mates, it can therefore be assumed that male insects attempting copulation with the female decoys on the orchid flowers might miss out on occasions to engage in competitions over mates and sometimes even fail to reproduce altogether during their relatively short lifetime.

Recent studies carried out in Australia on sexually parasitic orchids have shown for the first time that the orchid parasitism might reduce or inhibit the mating opportunities of their hosts. In a series of experiments, Wong and Schiestl (2002) provided evidence that the hosts (males of the Thynnine wasp *Neozeleboria cryptoides*) learn to avoid their associated orchid parasite (*Chiloglottis trapeziformis*) after subsequent and unsuccessful copulation attempts, and that the hosts’ wingless females experience a significant decrease in attractiveness when they are “calling” for mates from inside an orchid patch (Wong and Schiestl 2002). The female wasps are only capable of restoring their original attractiveness towards the hosts as the distance between their calling spot and the parasite colony increases (Wong et al. 2004). In another recent study on the ichneumonid host *Lissopimpla excelsa* and its orchid parasites *Cryptostylis erecta* and *C. leptochila* from Australia, Gaskett et al. (2008) confirmed Coleman’s (1928) earlier findings that the hosts regularly ejaculate in the flowers during pseudocopulations. Such a wastage of sperm can potentially lead to transient gamete depletion, which might in turn compromise the opportunities of the hosts to transfer their sperm during subsequent matings with genuine females (Damiens and Boivin 2006; Gaskett et al. 2008).

The mimicry systems described above illustrate how the orchid parasites not only channel both time and energy away from the search for genuine mating partners by patrolling males, but can also impact on their hymenopteran hosts’ fitness in much more dramatic ways, notably by causing sperm wastage (see also Blanco and Barbosa 2005). As we have hypothesized above, each host–parasite association might be characterized by a balance between the host exploitation strategy that maximizes the parasites’ overall fitness and how it affects the hosts’ reproductive output (Fig. 1). In a meta-analysis of literature records on the mean reproductive success in sexually deceptive orchids and the associated vigor of the behavioral responses of the male insects to the orchid flowers, Gaskett et al. (2008) have suggested that orchids that trigger more intense pollinator behavior (high sexual arousal, e.g., by causing ejaculation) have a higher reproductive output than

Deceptive Behavior in Plants. I. Pollination by Sexual Deception in Orchids

other species where pollinator visits are brief (Fig. 1). Studies are now needed to test this hypothesis by including more species within each sexually deceptive orchid genus, but they represent an interesting parallel to experiments across many types of host–parasite interaction where parasite virulence correlates positively with parasite reproduction or dissemination rates (Turner et al. 1995; Ebert 1998, 2000).

Research on the reproductive biology of sexually deceptive orchids is a very promising field in many respects (see Schiestl 2005; Peakall 2007; Waterman and Bidartondo 2008), and efforts should now be made to determine the level of harm/costs incurred by the hosts, e.g., by investigating the flowers for the presence of host sperm in other genera of sexually deceptive orchids (see the method used by Gaskett et al. 2008), or by identifying other ways in which pseudocopulations can affect the hosts' reproductive output. By quantifying the costs, it will be possible to pinpoint the selection pressures at play on both sides of these host–parasite interactions, and we will gain important insights into the maintenance and the evolution of orchid mimicry.

Fig. 1a–d Classes of parasite virulence (measured by the intensity of host behavioral response) and the orchid parasites' overall associated reproductive success (in mean % of annual seed set within populations) in different genera of sexually deceptive mimicry systems. **a** The orchid parasite attracts its male insect host briefly without an attempt at copulation (*Pterostylis*; Taylor 1999; Lehnebach et al. 2005); **b** The orchid parasite attracts its male insect host and triggers inspection behavior or a precopulatory routine (*Caladenia*, *Chiloglottis*, *Drakaea*; Peakall 1990; Peakall and Handel 1993; Schiestl 2004; Dickson and Petit 2006); **c** The orchid parasite triggers a host copulation attempt only (*Ophrys*; Darwin 1862; Correvo and Pouyanne 1916; Kullenberg 1961; Ayasse et al. 1997; Neiland and Wilcock 1998; Ayasse et al. 2000; Vandewoestijne et al. 2008; Vereecken, unpublished data; *Geoblasta*; Ciolek et al. 2006); **d** The orchid parasite triggers host copulation attempt and ejaculation (*Cryptostylis*; Schiestl et al. 2004; Gaskett and Herberstein 2006; Gaskett et al. 2008). (Modified from Gaskett et al. 2008)

168 3 The Evolution of Color Versus Odor in Orchid Mimicry

169 In all cases of mimicry, the “ménage à trois” is subjected to specific selection pressures
 170 stemming from the nature of the interactions involved. From recent studies on the
 171 mating behavior of solitary bees and wasps, we now know that female insects
 172 attract patrolling males by releasing specific chemical compounds (either in blends
 173 or specific compounds) that are capable of triggering genuine copulation attempts
 174 by the male insects when tested for their attractiveness on dummies. Besides,
 175 comparative analyses of the orchids’ floral scent and the female insect sex pheromone
 176 have shown that the parasitic orchids use the same odor compounds as the females
 177 to deceive the males into pollinating the flowers (Schiestl et al. 1999, 2003; Ayasse
 178 et al. 2003; Schiestl 2004; Mant et al. 2005a; Vereecken and Schiestl 2008). In short,
 179 this interaction seems to constitute an illustrative case of mimicry that is primarily
 180 mediated by chemical signals.

181 At first glance, it might seem surprising that the showy, colorful flowers of a
 182 wide range of sexually deceptive orchid species do not use visual cues to lure their
 183 pollinators. What might this kaleidoscope of floral colors be used for? In a recent
 184 study on the Cretan species *O. heldreichii*, Spaethe et al. (2007) reported on the
 185 synergistic effect of scent and floral perianth color in pollinator attraction, which
 186 illustrates that although the mimicry is primarily based on sex pheromone mimicry,
 187 visual cues can also enhance the flowers’ attractiveness. These authors proposed that
 188 selection may have favored the spectral resemblance between the pinkish perianth of
 189 the flowers of *O. heldreichii* and the overall reflectance of co-occurring, nonorchid
 190 species which the females of the pollinator, the long-horned bee *Synhalonia rufa*
 191 (= *Tetralonia berlandi*), forage on right after their emergence. This scenario makes
 192 sense when we consider that in a variety of solitary bee species, mating takes place
 193 shortly after the emergence of neighboring “rendezvous” flowers (Alcock et al.
 194 1978; Westrich 1990; Paxton 2005), which, as Spaethe et al. (2007) showed, some-
 195 times include species whose inflorescences have a similar spectral reflectance. It
 196 seems therefore that some orchid species within the genus *Ophrys* have evolved a
 197 multicomponent floral mimicry based on the chemical mimicry of virgin female bees
 198 and the visual mimicry of the spectral reflectance of “rendezvous” flowers where
 199 mating takes place during the reproductive period of the bees’ life cycle (Fig. 2).

200 To date, the extent to which these results may be applicable to other species
 201 within the 250+ species-rich genus *Ophrys* and in other orchid genera remains
 202 poorly understood. Ongoing investigations on the adaptive significance of perianth
 203 color polymorphism and its influence on pollinator visitation rates indicate that
 204 even within the orchid genus *Ophrys*, certain species might incorporate visual cues
 205 in pollinator attractiveness, while others clearly don’t. In the Mediterranean species
 206 *Ophrys arachnitiformis* for instance, preliminary results suggest that (i) there is no
 207 differentiation in either relative or absolute amounts of behaviorally active com-
 208 pounds produced by the flowers between different color morphs of the orchid, and
 209 (ii) that neither the presence/absence nor the color of the perianth influences visita-
 210 tion rates of the pollinators to either odorless controls or dummies scented with
 211 odor extracts of *Ophrys* flowers (Vereecken and Schiestl, unpublished manuscript).

Deceptive Behavior in Plants. I. Pollination by Sexual Deception in Orchids

Fig. 2 A schematic view of the selection pressures at play and the nature of the signals involved in *Ophrys* mimicry systems. The orchid flowers hijack the communication channel used by males and females during their courtship, and some *Ophrys* taxa have even evolved a multicomponent mimicry that also incorporates signals involved in the localization of females by males on so-called “rendezvous” flowers. The *dashed lines* represent the involvement of signals of nonorchid flowering plants in the species interactions: the female bees use these signals to locate their foraging resources, the male bees use them to locate the “rendezvous” flowers, and some orchids mimic these signals along with the chemical signals of female bees to attract their pollinators

Hence, it can be postulated that floral color polymorphism in *O. arachnitiformis* is barely subjected to selection imposed by its pollinator, contrary to the results found by Spaethe et al. (2007), and that mate-searching flights of the hosts are primarily driven by odor signals, with no intervention of visual cues of any kind (Vereecken and Schiestl, unpublished manuscript).

More in-depth investigations into the chemical basis of *Ophrys*-pollinator investigations have been performed recently with the orchid *O. exaltata sensu lato*. An initial series of experiments showed that the females of the solitary bee *Colletes cunicularius* use population-specific ratios of specific chemical compounds, mostly alkenes (monounsaturated, straight-chained hydrocarbons with a carbon chain length of 21–25). These experiments have also demonstrated that patrolling males in this bee species are more attracted by sex pheromone mimicking compound mixtures of females from other populations (i.e., allopatric) over local ones (i.e., sympatric) (Vereecken et al. 2007b). Following on from this study, Vereecken and Schiestl (2008b) have undertaken to investigate whether the parasitic orchids released patterns of the key odor compounds matching those emitted by the sympatric females of their male hosts. Contrary to theoretical expectations that the parasitic orchids should imitate the chemical signals of the sympatric female bees as closely as possible (i.e., a “perfect match”), Vereecken and Schiestl (2008) found that the

scent composition of the orchid flowers was consistently slightly different from the local female bees' sex pheromone in any given population. The parasitic orchid scent, being different from the "model" signal, was even found to be actively preferred by the male hosts when both the orchid scent and the bee sex pheromone were assayed for their attractiveness. Vereecken and Schiestl (2008) have interpreted their results as a case of imperfect chemical mimicry driven by the predilection of hosts for odor blends released by "exotic" (pseudo)females. It remains to be tested whether the male host preferences can potentially change during the reproductive season, or even from one year to the next (see e.g. Kasumovic et al. 2008), and how this phenomenon might translate into selection for floral scent evolution in their associated parasitic orchids.

Collectively, these results alone demonstrate that we can enhance our understanding of the roles of different floral traits and the factors driving their evolution if investigations are performed from a behavioral perspective, by attempting to approach interspecific interactions from a different angle of view, in this case by deciphering the relevant signals in the insects' reproductive biology. Such background data are often decisive in subsequent investigations aimed at assessing whether the parasitic orchids have succeeded in impersonating the female insects by hijacking chemical communication channels only, or if pollinator attraction is mediated by a combination of other signals.

4 Host Specificity in Sexually Deceptive Orchids

4.1 *Defining Host Specificity*

The term host specificity relates to "the extent to which a parasite taxon is restricted in the number of host species used at a given stage in the life cycle" (Poulin 2007). For orchids that have co-opted male insects as pollinators, host specificity can therefore be viewed as the taxonomical spectrum of insects that can act as pollinators during their flowering season. Since sexually deceptive orchids have evolved the imitation of female mating signals of certain insects, and since mating signals, especially sex pheromones, generally act on a species-specific basis (Thornhill and Alcock 2000; Wyatt 2003), theory holds that each parasitic orchid is usually pollinated by only one or a few male insect species (Kullenberg 1961; Paulus and Gack 1990).

4.2 *The Determinants of Host Specificity*

Several important issues need to be discussed before making statements on host specificity in sexually deceptive orchids. The only data available in the literature are lists of insects that have been observed pseudocopulating (Fig. 3) with the

Deceptive Behavior in Plants. I. Pollination by Sexual Deception in Orchids

Fig. 3 Pseudocopulating male of *Andrena flavipes* (Kirby) (Hymenoptera, Andrenidae) on flower of the sexually deceptive orchid *Ophrys bilunulata* Rossi. (Photo: NJ Vereecken)

orchid flowers. Based on these pollinator records, interactions between the orchid parasites and their male insect hosts may appear to be relatively species-specific, but such data should be analyzed with caution (see Poulin 2007).

First, it should be considered that high levels of host specificity can be the direct outcome of inadequate sampling effort (Poulin 2007). Pollination events or flower visits are relatively rare under natural conditions, since most sexually deceptive orchids are severely limited in their reproductive success by access to pollinators (Tremblay et al. 2005). Hence, the likelihood of observing a pseudocopulation event under natural conditions during a quick visit in a population of these parasitic orchids is certainly much lower than one would expect. Not only that, but a great number of these orchids also have wide geographic range across which no pollinator record is available. Consequently, two parasitic orchids might each have a single pollinator host, but detailed investigations across their geographic ranges and over the years sometimes reveal that these orchids are instead exploiting a broader range of insect hosts (see, e.g., Lorella et al. 2002; Tyteca et al. 2006; Vereecken and Patiny 2006; Bower 2006; Vereecken et al. 2007a). The real range of hosts that can be exploited by a given parasite species is illustrated by Combes' (2001) "filters" concept (Fig. 4), which shows the mechanisms restricting the number of potential hosts. Unquestionably, the first mechanism that determines host-parasite interactions is the "encounter" filter: parasites must live in the ecosystem of their hosts and have contacts with them at specific stages in their life cycle. Any orchid parasite that does not satisfy this condition, e.g., by being deprived of access to its male insect hosts, will not reproduce. Experiments performed with picked inflorescences of *Ophrys* species transferred from southern France outside their home range provide evidence that the fresh, unpollinated flowers can be attractive to

Fig. 4 A schematic view of “encounter” and “attraction” filters that determine the spectrum of pollinators attracted by a sexually deceptive orchid species. Not all male insects respond adequately to the signals released by the orchid flowers: only those that perform stereotyped pseudocopulations on the flower labellum and withdraw pollinia are considered “potential pollinators.” The diversity of potential pollinators is further restricted by the encounter filter: only those insect species that co-occur with the orchids can act as pollinators. (Modified from Combes 2001)

novel pollinator taxa such as males of *Andrena flavipes* and *A. bicolor* in England for *O. lupercalis*, a Mediterranean orchid previously reported to be pollinated only by males of *A. nigroaenea*. Similar observations were made in Australian parasitic orchids by Bower (2006), who, by performing pollinator choice experiments under natural conditions, showed that novel pollinators might be attracted when picked inflorescences of a single orchid are translocated to allopatric populations. The second factor that determines the formation of the host spectrum is the “attraction” (or “compatibility”) filter, which, in the present case, relates to the ability of the parasitic orchids to successfully (1) attract male insects, and (2) trigger copulation attempts on the flower labellum, (3) resulting in pollinia removal or deposition. This succession of events is not systematically performed by all male insects initially attracted by the orchid flowers; some insects can be observed pseudocopulating (Fig. 3) on the flowers, but the mismatch between their body size/corpulence and the floral architecture hinders pollinia removal or deposition (Fig. 5).

Second, the apparent species-specificity of orchid–pollinator interactions can be an artefact of incorrect species identification. Besides situations where the insect hosts have been assigned to another species by mistake (see the discussion in Schiestl and Vereecken 2008), the problem lies in the taxonomical interpretation of host–parasite associations. Consider the situation depicted in Fig. 6, where a parasitic orchid is reported to have a low host specificity compared to its congeners,

Deceptive Behavior in Plants. I. Pollination by Sexual Deception in Orchids

Fig. 5 The sexually deceptive orchid *Ophrys lupercalis* is pollinated by males of *Andrena nigroaenea* (Hym. Andrenidae) (left). The flowers of this parasitic orchid are also attractive to males of other wild bee species, such as *A. minutula* (right). The right photograph illustrates Combes' (2001) "compatibility" filter concept: the male *A. minutula* is attracted by the flowers and makes an attempt at copulation on the flower labellum, but there is a mismatch between its body size and the floral architecture of *O. lupercalis*, preventing these small-sized male bees from withdrawing the orchid's pollen masses. (Photos: NJ Vereecken)

Fig. 6a–b A schematic view of taxonomic considerations that might affect estimates of host specificity in sexually deceptive orchids. **a** The orchid parasite species *a* has a low host specificity and exploits the range of host species *a–d* as pollinators across its home range; **b** the orchid parasite species *a* may also prove to be a complex of *n* cryptic parasite taxa, each highly host-specific and associated with *n* different insect taxa

e.g., because its pollinator records encompass *n* host taxa. With the growing incorporation of modern analytical techniques into studies on species interactions, different schools of thought have emerged: while some scientists might still consider this orchid parasite to be a single species with a lower host specificity, others, helped by analytical tools that are sometimes capable of identifying cryptic taxa,

would tend to regard this species as a group of host-specific cryptic taxa, each associated with a single host (see Bower 2006). These contrasting standpoints can potentially lead to extreme levels of taxonomical confusion and affect our estimates and understanding of host specificity in these groups of parasitic orchids. As is observed in different areas of the field of host–parasite interactions, some authors would even go as far as to suggest that new species should be proposed every time an alternative host species is found to be interacting with a parasitic orchid for the first time (see Paulus and Gack 1990; Delforge 2005). Preliminary field experiments with fresh orchid inflorescences tested for their attractiveness to different pollinator taxa in sympatry and allopatry indicate that individual flowers of a single orchid species can successfully attract male bees of different species as hosts (Vereecken, unpublished data), which suggests that lower levels of host specificity may indeed occur.

More experimental investigations of host specificity are now needed to help to sketch a more detailed picture of host spectra in each group of sexually deceptive orchids. From these and parallel studies on the behavioral and chemical ecology of the (more or less species-specific) hosts, it will be possible to investigate the selection pressures exerted on the floral traits, and possibly to assess the extent to which the attraction of different insects in different regions can lead to the evolution of divergent combinations of phenotypic traits (e.g., different ratios of key odor compounds) in the parasitic orchids under study (see, e.g., Aigner 2006; Herrera et al. 2006).

4.3 The Species Specificity and Evolution of Chemical Signals

As we have seen above, sexually deceptive orchids owe their high level of host specificity primarily to the nature of the signals involved in their mimicry system. Mating signals, and female sex pheromones in particular, are thought to rank among the most species-specific communication channels in the insect world (Thornhill and Alcock 2000; Wyatt 2003). Theoretically, the parasitic orchids' fine-tuned mimicry system should therefore not allow for cross-pollination between different orchid taxa that have evolved towards the exploitation of male insects belonging to different species.

Investigations into the chemical communication of orchid–pollinator interactions have indeed reported that orchids attracting different male insects as pollinators have odor bouquets consisting of different ratios of identical or structurally similar odor compounds (Borg-Karlson et al. 1993; Schiestl and Ayasse 2002; Ayasse et al. 2003; Stökl et al. 2005; Mant et al. 2005a; Véla et al. 2007). An exception to this premise is found in the Australian orchid pair *Chiloglottis trapeziformis* and *C. valida*, which are pollinated in a highly specific manner by the male thynnine wasps *Neozeleboria cryptoides* and *N. monticola*, respectively. In their recent study, Schiestl and Peakall (2005) have demonstrated that these two parasitic orchids attract their specialized host via the emission of a single odor compound, 2-ethyl-5-propyl-1,3-cyclohexandione (“chiloglottone”). Assortative pollinator attraction between these two orchids is nevertheless maintained to a large extent by the mating preferences of the male hosts

Deceptive Behavior in Plants. I. Pollination by Sexual Deception in Orchids

for different heights and the corresponding differences in floral heights between *C. trapeziformis* and *C. valida* (Schiestl and Peakall 2005).

Despite the evidence that different sexually deceptive orchid species associated with different male insect hosts have distinct odor bouquets, observations from the field, particularly in the Mediterranean genus *Ophrys*, indicate that hybridization in this group of orchids does occur in natural populations where two or more species grow in sympatry and bloom at the same period of the year (see, e.g., Stebbins and Ferlan 1956; Danesch and Danesch 1972). This phenomenon suggests that cross-attraction and interspecific gene flow may indeed occur. Furthermore, behavioral bioassays performed with the male insects have conclusively demonstrated that although pollinators are more attracted by the floral scent of the parasitic orchid they are associated with, heterotaxic visits occur and might under certain circumstances lead to successful pollination and the formation of natural hybrids (Stokl 2007; Cortis et al. 2008; Vereecken et al., unpublished manuscripts). Reproductive isolation in *Ophrys* is thought to be primarily mediated by host specificity, and post-mating barriers have been reported to be relatively weak compared to other European orchid genera where pollinator specificity is low (Cozzolino et al. 2005) and post-mating barriers generally keep co-occurring species reproductively isolated (Moccia et al. 2007; Scopece et al. 2007).

The investigations into the ecology and the evolutionary consequences of hybridization in sexually deceptive orchids challenge the commonly held view that these host–parasite interactions are strictly species-specific, and that “each [sexually deceptive orchid] species [...] attracts different sets of [...] pollinator species” (Grant 1994). From the recent studies on the topic, it has become apparent that, despite the evolution of a highly specific host exploitation mechanism, parasitic orchids have retained the genetic and signal variation required to adapt to fluctuating pollinator assemblages and selection pressures, and have evolved a higher flexibility in host specificity than previously thought. These observations make sense when we consider that the reproductive success of sexually deceptive orchids is typically limited by access to suitable hosts (see Tremblay et al. 2005 for a review). As a consequence, any mechanism, such as the ability to co-opt alternative host species, that contributes to conferring a higher reproductive output on its bearer should be favored by selection across generations and should lead to a more adaptive and flexible host exploitation strategy overall. This, in turn, could help these parasitic orchids when they face situations where their “official” host is temporarily unavailable or locally extinct.

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4.4 Signal Evolution Above the Species Level

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Most sexually deceptive orchid species usually display conservative patterns of pollinator attraction (i.e., they attract closely related pollinator taxa) (Mant et al. 2002; Vereecken and Patiny 2005), along with a weak differentiation in pollinator-attracting scents (see above; Mant et al. 2005b). Consequently, it has been suggested that pollinator shifts through minor changes in floral odor bouquets could be the driving

406

force for speciation (here, prezygotic reproductive isolation) in these parasitic orchids (Schiestl and Ayasse 2002). Furthermore, it is postulated that reproductive isolation between sympatric species can be strengthened when pollinator shifts involve sister species of insects that are reproductively isolated by using of specific ratios of similar compounds for their female sex pheromone, as is observed in mining bees of the genus *Andrena* (Schiestl and Ayasse 2002; Stökl et al. 2005).

In their study on the Australian *Chiloglottis*–*Neozeleboria* interactions, Mant et al. (2002) have found that sister orchid species tend to be pollinated by insects related taxonomically, which they interpreted as a case of phylogenetic conservatism in orchid–pollinator interactions. However, by incorporating an array of nonpollinating *Neozeleboria* species in their phylogeny of *Chiloglottis* host wasp species, Mant et al. (2005b) found that the host species exploited by the orchids did not form a monophyletic group, and that nonhosts clustered within the host species. Hence, they hypothesized that the parasitic *Chiloglottis* orchids species have diversified through repeated switches to congeners and alternative wasp species with similar traits to the ancestral pollinator. The host records in the three species of the *Ophrys insectifera* species group suggest that another scenario might be applicable here, namely that the parasitic orchids have not adapted to sister insect host species with similar mating signals to pollinators, but rather to unrelated insects (a sawfly, a mining bee and a digger wasp in this case) that presumably use similar chemical communication channels during their courtship (Vereecken et al., unpublished manuscript). Future studies should investigate whether the male insect hosts in groups of closely related sexually deceptive orchids are attracted by overlapping patterns of identical odor compounds in the floral odor, or if different odor compounds mediate the specific interactions between orchids and their pollinators.

5 Transitions to Parasitism by Sexual Deception in Orchids

To date, sexual deceit is thought to be exclusive to the family Orchidaceae, where it has evolved independently on multiple occasions and on different continents, with representatives found across Australia (ten genera: Coleman 1928; Stoutamire 1975; Peakall et al. 1987; Jones 1988; Peakall 1990; Bower 1996), Central and South America (seven genera: Van der Pijl and Dodson 1966; Dod 1976; Singer 2002; Singer et al. 2004; Blanco and Barbosa 2005; Ciotek et al. 2006), South Africa (genus *Disa*; Steiner et al. 1994), and the West Palaearctic (Delforge 2005; Schiestl 2005; Ayasse 2006; Jeraskova et al. 2006). Pollination by sexual deception is thought to be a derived pollination strategy within the family Orchidaceae (Van der Pijl and Dodson 1966; Van der Cingel 1995; Alcock 2005). Based on recent advances in molecular phylogenetic analyses and investigations into the chemical ecology and behavioral ecology of orchid–pollinator interactions, it is now hypothesized that this most unusual mode of pollinator attraction in the plant world is derived from food deception (see e.g. Bateman et al. 2003), another common pollination strategy in orchids (see also the chapter by Jeraskova et al.).

Deceptive Behavior in Plants. I. Pollination by Sexual Deception in Orchids

A recurrent idea in studies on the evolution of host–parasite interactions is that pre-adaptations must precede the emergence of an alternative kind of species interaction (Rothschild and Clay 1952). As we have seen above the signals involved in the attraction of male insects by the parasitic orchids in the genus *Ophrys* include the emission of patterns of alkenes (monounsaturated alkanes) (reviewed by Schiestl 2005), a specific class of chemical compounds that are otherwise present in the cuticles of a wide array of insect and plant species, where they avoid dehydration (Hadley 1981). An important first step towards an understanding of the evolution of these compounds has been made by Schiestl and Cozzolino (2008), who mapped the alkene production of flowers onto the phylogeny of a selection of European orchid species in the subtribe Orchidinae. Their results show that the emission of these compounds is detectable in the floral odors of most orchid species investigated, which suggests that the production of alkenes is a pre-adaptation to sexual deception, as defined in the case of *Ophrys* (Schiestl and Cozzolino 2008). Furthermore, their results show that the flowers in a group of non-*Ophrys* orchids that are primarily pollinated by male bees, notably in the genus *Serapias* and in *Anacamptis papilionacea*, also emit high amounts of alkenes. Collectively, these data suggest that the emission of these compounds in important amounts may have initiated the attraction of male insects as specialized flower visitors and facilitated the evolution of pollination by pseudocopulation in their sister (and presumably more derived, see Bateman et al. 2003) genus *Ophrys* (Schiestl and Cozzolino 2008), and that selection for pollination by males has resulted in increased production of alkenes.

If alkenes are considered pre-adaptations to the evolution of parasitism by sexual deceit as we know it in *Ophrys* (Schiestl and Cozzolino 2008), then they must have provided fitness gains to the parasite precursors before being favored by natural selection (Poulin 2007). Undoubtedly, male insects are not regarded as being the most effective pollinators of flowering plants *a priori*, since they are usually short-lived and they only occasionally interrupt their patrolling bouts for mates to collect nectar on the flowers, sometimes inadvertently collecting small amounts of pollen in the process. In contrast, female insects, and female bees in particular, spend a considerable proportion of their life cycles visiting flowers and collecting pollen, thereby contributing to pollen transfer from one flower to the next as they forage on different flower patches (Proctor and Yeo 1972; Michener 2007). So what would be the advantage, if any, from the plants' perspective, of relying on male insects for their pollination? First, male insects, and again bees in particular, focus almost exclusively on looking for mates in a highly specialized manner (Alcock et al. 1978; Paxton 2005), which provides the parasites-to-be with an opportunity to exploit hosts with a high degree of specificity in pollen transfer. Second, male insects are thought to promote outcrossing through their long-distance patrolling flights for mating partners (Williams and Dodson 1972; Peakall 1990; Peakall and Beattie 1996). These are potentially important aspects for the reproductive biology of orchids, since such patterns in pollen flow both within and among populations could considerably improve seed quality and decrease pollen loss (see, e.g., Johnson et al. 2004). It is therefore expected that there are indeed fitness advantages

N.J. Vereecken

associated with the stepwise evolution of floral signals that could ensure the specific attraction of male insects as pollinators by orchid parasite precursors.

Although significant advances have been made in our understanding of the evolution of signals and orchid–pollinator interactions over the past decade, we still have a very fragmentary view of several important aspects of the behavioral ecology and the host specificity of these parasitic orchids. For example, there is a dramatic lack of data on the chemical ecology and the evolution of many groups of sexually deceptive orchids, including those in the genus *Ophrys* which have been the focus of intense scrutiny over the past few years. The roles of chemical and visual cues in the attraction of the male hosts have received very little attention so far, despite the potential avenues of research provided by the extraordinary kaleidoscope of their floral colors and the associated chemical repertoire of their floral odor bouquets. The status of the current lists of pollinator records calls for repeated observations of orchid pollination under natural conditions, both in different regions across the orchids' home range and outside their natural habitat in order to properly characterize the host spectrum of all known parasitic orchids. Several orchids in different genera are pollinated by male insects without attempted copulations with the flowers, which might represent transitional stages in the evolution of sexual deceit from food deception. Finally, comparisons of the reproductive biology between congener species or genera of orchids that differ in the degree of intensity of host behavioral response (or virulence, see Fig. 1) might provide important insights into the factors that drive the evolution of sexual deception and its ecological consequences, from the most primitive forms to the most elaborate, where copulation attempts with the flowers and male insect ejaculation are observed.

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