

Does bee or wasp mimicry by orchid flowers also deter herbivores?

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Abstract General visual bee mimicry and specific chemical mimicry by flowers to solitary female bees or wasps are well known in several orchid genera, for example, the Mediterranean genus *Ophrys*, the Australian genera *Cryptostylis* and *Chiloglottis*, and the South-African *Disa*. This mimicry has been shown to attract solitary male bees or wasps, which are their species-specific pollinators. The visual and chemical signals are considered to be a type of deceptive pollination mechanism based on mimicry for the exploitation of perceptual biases of animals. We propose that in addition to this unique pollination mechanism, these plants exhibit another, rarely mentioned and practically forgotten, non-exclusive function of bee or wasp mimicry (Batesian mimicry). This mimicry may deter large mammalian herbivores, and possibly also insects from the plants and especially from their flowers by a type of visual and olfactory deceptive aposematism. While visiting the flowers, bees and wasps may add a Müllerian effect to this defense. We extend this hypothesis to many other rewarding flowers that are bee or wasp pollinated and propose that abundance of pollinating bees or wasps may deter herbivorous mammals and insects from the plants during their peak flowering season.

Keywords Batesian mimicry · Bees · Defense · Herbivory · *Ophrys* · Wasps

Introduction

Most observational, experimental and theoretical studies of plants mimicking animals have focused on types of mimicry that increased pollination (Wickler 1968). The first and best-known case is the mimicry of the bee orchids belonging to the genus *Ophrys*. *Ophrys* flowers generally resemble bees in size, shape and color and are pollinated by species-specific solitary male bees attracted to the flowers (Kullenberg 1950, 1956, 1961; Wiens 1978; Dafni 1984; Ayasse et al. 2000; Schiestl et al. 2000; Schiestl 2005; Jersáková et al. 2006). Accumulating evidence indicates that the chemical-olfactory mimicry of female bee pheromone, first described by B. Kullenberg (Vereecken et al. 2009), and not the visual one (as originally proposed), is the species-specific deceiving attractant of the solitary male bees to *Ophrys* flowers (Kullenberg 1950, 1956, 1961; Pijl and Dodson 1966; Dafni 1984; Ayasse et al. 2000; Schiestl et al. 2000; Schiestl 2005). The flower fragrance mimics exactly the structure and composition of the specific sexual pheromone exerted by the females of the pollinating male bees (Schiestl 2005). An experimental examination showed that the specific chemical mimicry and not the general color polymorphism of *Ophrys* flowers functions in the species-specific pollinator attraction (Vereecken and Schiestl 2009), and that the variation in the visual stimulus prevents recognition of the deceptive flowers by the male bees that could lead to lack of pollination (Schiestl 2005). In the orchid genus *Cryptostylis*, there is even a visually contrasting difference between the deceptive orchid flower, which reflects UV seen by hymenoptera, and the red, green and white orchid flower to which the hymenoptera eye is less sensitive (Gaskett and Herberstein 2010). Moreover, the orchid flower visual details, including their hairy surfaces are too delicate for the limited spatial resolution of the bee eye (e.g., Spaethe and Chittka 2003), but

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observable for sharper sighted herbivorous mammals. Thus, concerning pollination, the general visual bee mimicry of *Ophrys* flowers remains partly unexplained, and we think that it deserves further consideration.

We propose that in addition to pollination, bee and wasp mimicry exhibit a rarely mentioned and practically forgotten, non-exclusive function of defensive Batesian mimicry. This mimicry may deter large mammalian herbivores, and possibly also insects from the plants and especially from their flowers. We extend this hypothesis to many other rewarding flowers that are bee or wasp pollinated and propose that abundance of pollinating bees or wasps may deter herbivorous mammals and insects from the plants during their peak flowering season.

Anti-herbivory animal mimicry by plants

The role of defensive, anti-herbivory animal mimicry by plants has received very little attention and in order to indicate its possible function and occurrence, we review in this section previous hypotheses and experiments. Only a few such cases were proposed to operate and out of these only two have been tested. Several types of defensive animal mimicry by plants have been proposed: (1) insect egg mimicry (Benson et al. 1975), (2) ant mimicry (Lev-Yadun and Inbar 2002; Lev-Yadun 2010), (3) aphid mimicry (Lev-Yadun and Inbar 2002), (4) caterpillar mimicry (Rothschild 1974, 1984; Lev-Yadun and Inbar 2002), (5) animal leaf tunneling damage mimicry (Smith 1986; Lev-Yadun 2003; Soltau et al. 2009), (6) animal leaf chewing damage mimicry (Niemelä and Tuomi 1987) and (7) carrion and dung odors of various flowers, an olfactory mimicry of a danger of predators and parasites (Lev-Yadun et al. 2009).

The best-known case of defensive animal mimicry by plants is of butterfly egg mimicry by *Passiflora* plants. It has been proposed to reduce egg laying by *Heliconius* butterflies, but may also operate for other plant and butterfly taxa (Benson et al. 1975; Gilbert 1980, 1982; Shapiro 1981a, b; Williams and Gilbert 1981). Both Shapiro (1981a) and Williams and Gilbert (1981) showed that butterflies refrain from laying eggs on plants that mimic such eggs. Another well-known type of animal mimicry by plants that was experimentally tested is the case of leaves with white variegation lines, which has been proposed to mimic tunneling to reduce colonization by other insects and possibly also deter large herbivores that may refrain from consuming damaged tissues (Smith 1986; Brown et al. 1991; Lev-Yadun 2003, 2006, 2009; Lee 2007; Soltau et al. 2009; Schaefer and Ruxton 2009, 2011; Yamazaki 2010). Soltau et al. (2009) painted white variegation on non-variegated leaves of *Caladium steudneriifolium* (Ara-ceae) and found that it reduced insect herbivory.

Ant mimicry in the shape of dark spots and short lines along stems, branches, petioles and inflorescences was proposed by Lev-Yadun and Inbar (2002) with some further discussions by Lev-Yadun (2006, 2009), Lev-Yadun and Gould (2009) and Schaefer and Ruxton (2009, 2011). Similar probable ant mimicry has recently been proposed to exist in flowers of many *Passiflora* species (Lev-Yadun 2010). The potential defense by ant mimicry is obvious. Ants bite and sting and are aggressive, and many herbivores will avoid them. Indeed, ants have become models for a variety of arthropods that have evolved to mimic them (Edmunds 1974). Plants may benefit if ants protect them from insect and mammalian herbivory (Madden and Young 1992; Jolivet 1998). In a field experiment, removal of ants and aphids resulted in an increase of 57 % in species richness, and their abundance increased by 80 % (Wimp and Whitham 2001). Many plant species invest resources in attracting ants, providing them with shelter, food bodies and extrafloral nectaries (Huxley and Cutler 1991).

Aphid mimicry, especially by dark anthers of wind-pollinated grasses, was proposed by Lev-Yadun and Inbar (2002) and discussed by Lev-Yadun (2006, 2009) and Lev-Yadun and Gould (2009). Lev-Yadun and Inbar (2002) described aphid mimicry in *Paspalum paspaloides* (= *P. distichum*), where the dark anthers are the size, shape and color of aphids and they sway in the wind like swiveling aphids. Similarly, the stems of *Alcea setosa* are also covered with dark flecks that look like aphids. Similar morphologies were found in several wild grasses growing in North Carolina (USA; Lev-Yadun unpublished). It has been proposed by Lev-Yadun and Inbar (2002) that plants that look infested may be left untouched by both grazers and other aphids or insects. Several studies have shown that early infestation by aphids and other homopterans has a negative impact on host plant preferences and larval performance of other insect herbivores. Finch and Jones (1989) reported that large colonies of the cabbage aphid *Brevicoryne brassicae* and the peach aphid *Myzus persicae* deter ovipositioning by the root fly *Delia radicum*. Inbar et al. (1999) demonstrated that homopterans (whiteflies) not only alter adult cabbage looper (*Trichoplusia ni*) host selection, but also actually reduce the feeding efficiency of their offspring. Aphids respond to crowding by enhanced dispersal (Dixon 1998), and it is thus also probable that they may avoid previously infested or infestation-mimicked hosts. This clear zoological data set supports the hypotheses about the potential defensive value of aphid mimicry, but experimental data are needed to fully accept this hypothesis.

Defensive caterpillar mimicry by plants was first proposed by Rothschild (1974, 1984) for stipules along the branches of *Passiflora caerulea* that look like caterpillars, slugs or snails climbing along the stems, and later for immature pods of several annual legumes (*Lathyrus*

ochrus, *Pisum humile* and *Vicia peregrina*) that have conspicuous reddish spots arranged along the pods, causing them to look like aposematic lepidopteran caterpillars (Lev-Yadun and Inbar 2002; Lev-Yadun 2006, 2009; Lev-Yadun and Gould 2009). Unpalatable caterpillars with stinging and irritating hairs, functional osmeteria or body-fluid toxins often advertised their presence by aposematic coloration (Cott 1940; Bowers 1993). Therefore, Lev-Yadun and Inbar (2002) suggested that by mimicking aposematic caterpillars with red ‘spiracle spots’, wild legumes may reduce immature pod predation by large herbivores and possibly also by certain insects.

Mimicry of feeding damage by caterpillars has been proposed as the reason for the formation of lobed leaves in some Moraceae (Niemelä and Tuomi 1987) and further discussed by Brown et al. (1991), by Lev-Yadun and Inbar (2002), by Lev-Yadun et al. (2004) and by Lev-Yadun (2009). Dirzo (2002) proposed that leaf ends in certain palms mimic being chewed.

Lev-Yadun et al. (2009) proposed that carrion and dung odors of various flowers that have traditionally been considered an adaptation for attracting the flies and beetles for pollination also have another, overlooked, anti-herbivore defensive function. They suggested that such odors may also deter mammalian herbivores, especially during the critical period of flowering. It was based on the fact that carrion odor is a good predictor of the proximity of carnivores. Similarly, dung odor predicts feces-contaminated habitats that may present high risks of parasitism and pathogens. These were two new types of repulsive olfactory aposematic mimicry by plants: (1) olfactory feigning of carcass (thanatosis), a well-known behavioral defensive strategy in animals (see Edmunds 1974; Ruxton et al. 2004) and (2) olfactory mimicry of feces, which also has a defensive visual parallel in animals (see Hinton 1973; Eisner and Eisner 2000; Eisner et al. 2005; Weiss 2006; Forbes 2009).

For recent discussions on the specific factors involved in the potential defensive role of animal mimicry by plants, see Lev-Yadun and Inbar (2002), Lev-Yadun (2006, 2009), Lev-Yadun and Gould (2009), Lev-Yadun et al. (2009), and Schaefer and Ruxton (2009, 2011).

A related phenomenon, the use of aposematic insects to defend plants from large herbivores, was proposed by Rothschild (1972, 1986), when various poisonous aposematic insects aggregate on poisonous plants, adding to the plant’s aposematic odor and possibly also to its warning coloration.

Floral bee mimicry as anti-herbivory defense

Concerning the pollination-mimicry hypothesis, we propose that the visual and chemical bee-mimicking signals

can be considered also to belong to a different type of deception based on exploitation of perceptual biases of animals (e.g., Schaefer and Ruxton 2009). Here, we present the question of whether the visual bee and wasp mimicry of orchid flowers or the exploitation of perceptual biases of animals toward aggressive bees and wasps can serve also as a sophisticated anti-herbivory defense. The emerging evidence on various types of odor mimicry by orchids (Schiestl and Ayasse 2001; Brodmann et al. 2008, 2009) and the plethora of deception types by plants (Wickler 1968; Wiens 1978; Schaefer and Ruxton 2009, 2011) strongly indicate that very sophisticated anti-herbivory bee or wasp mimicry can be expected.

In the genus *Ophrys*, the combination of non-species-specific visual bee mimicry with the species-specific role of chemical-fragrance mimicry of the female bee pheromone for attracting pollinating solitary male bees may indicate an additional, non-reproductive cause for the evolution of such special floral bee-mimicking morphology (but see Schiestl 2005). Following the hypotheses that plants employ defensive animal mimicry described above, we propose re-considering and experimentally testing the almost forgotten century-old anti-herbivory role of visual bee mimicry discussed by Rolfe (1910) and briefly mentioned by Pijl and Dodson (1966). Mr. E. Kay Robinson, in a letter to the newspaper “Daily News”, was the first to propose that bee mimicry was not for pollinator attraction, but to deter grazing cows (Rolfe 1910). While Rolfe (1910) dismissed the defensive hypothesis, which was later practically forgotten, we think that it may also be a part of the explanation for the visual bee or wasp mimicry by orchid flowers, especially in the view that olfactory mimicry is the dominant species-specific pollinator attractor. We propose that many large herbivores and some herbivorous insects may be deterred by visual bee or wasp mimicry, and that defensive mimicry of bee pheromone in *Ophrys* flowers should also be considered in this context, especially in deterring herbivorous insects. This proposed defensive mimicry is not exclusive and probably plays a secondary role to pollination. In this connotation, Wickler (1968) mentioned, without giving the reference that Brown expressed in 1831 an opinion that *Ophrys* species scare off insects with their bee-mimicking flowers.

The potential benefit from bee or wasp mimicry is obvious. Bees and wasps may be aggressive and sting, and so deter herbivores (Breed et al. 2004). In this respect, a variety of arthropods (e.g., flies, spiders, butterflies) are known to mimic bees or wasps as defense from predators (Cott 1940; Wickler 1968; Edmunds 1974; Plowright and Owen 1980; Rothschild 1984; Howarth and Edmunds 2000; Bain et al. 2007; Chittka and Osorio 2007; Penney et al. 2012). Plants thus may benefit from defensive bee or wasp mimicry if herbivores consider them to be occupied

by bees or wasps and refrain from eating them, especially their flowers. While *Ophrys* and other bee- or wasp-pollinated taxa mimic solitary bees and wasps (Wickler 1968; Dafni 1984; Schiestl 2005; Jersáková et al. 2006; Gaskett and Herberstein 2010), and the worst bee attacks are of bees such as the honeybee that form large colonies (Breed et al. 2004), there is no need for perfect mimicry to deter enemies (e.g., Howarth and Edmunds 2000; Chittka and Osorio 2007; Janzen et al. 2010; Penney et al. 2012) and imperfect bee and wasp mimicry should not be different (see Kauppinen and Mappes 2003; Penney et al. 2012). From other systems of bee mimicry, we know that the mimicry does not have to be perfect for human eyes but rather for the eyes and perception of the target animal (Bain et al. 2007) even though the human eye was found to be a good judge (Penney et al. 2012). The fact that bees and wasps are actually found on orchid flowers, and that while male bees are stingless wasps do have stings, and that it is not always possible or easy to distinguish between stingless and sting owning bees, adds a Müllerian effect to this visual defense.

There are four potential components of bee or wasp mimicry: (1) visual (shape and color), (2) chemical (odor), (3) movement and (4) sound production. Out of these, plants are known to mimic or exploit the first three. The visual aspect of bee or wasp mimicry has been discussed above, and there are no sufficient data about defensive bee or wasp mimicry by plants to discuss it. Therefore, we discuss below the potential role of plant movement in combination of visual bee and wasp mimicry in defense from herbivory.

The visual role of plant movement as a way of communication (and deception) between flowers and pollinators has been studied in two cases of attraction. In the first case, some orchid species belonging to the genus *Oncidium* induce attacks by territorial male *Centris* bees when the inflorescences move in the wind because the male bees mistake them for rival males. During the attacks of the pseudo-rivals, the male bees transfer the pollen (Dodson and Frymire 1961; Dodson 1962 cited in Wiens 1978). In the second case, Warren and James (2008) showed that movement (“waving”) of the inflorescences of *Silene maritima* increases pollination success. Thus, following such examples from pollination biology, there is no theoretical reason to dismiss the possibility that plant movements also take part in visual defense from herbivory (see also Yamazaki 2011).

In order to specifically propose that bee mimicry may defend plants, it is essential to demonstrate that bees indeed deter herbivores and thus defend plants. Vollrath and Douglas-Hamilton (2002) and King et al. (2007, 2009, 2011) showed in a series of field experiments that even the largest living terrestrial herbivore, the African elephant, is

deterred by (1) honeybee attacks, (2) just the recorded sound of bee buzzing and (3) the sight of empty beehives. Elephants refrained from attacking local *Acacia* trees and crops growing on local farms in the proximity of beehives. Moreover, at the opposite end of the herbivore size scale, caterpillars are also deterred by wasp buzzing (Tautz and Markl 1978) and exposure to honeybee buzz reduced caterpillar damage in soybean plants (Tautz and Rostás 2008). Therefore, we propose that visual and olfactory bee or wasp mimicry by orchid flowers may serve not only pollination, but also defend them from herbivory by both large herbivores and insects.

The common occurrence of eight bee-mimicking *Ophrys* species in heavily grazed areas in Israel (Feinbrun-Dothan and Danin 1991) is another indirect support for our hypothesis; as it has been found that a well-defended and possibly aposematic geophyte, *Anemone coronaria*, which is poisonous and has red flowers, benefits from heavy grazing that also reduces competition with grasses (Perevolotsky et al. 2011).

Can pollinating bees deter herbivores?

We extend our hypothesis to many other plants that produce highly rewarding bee-pollinated flowers and propose that the sight and sound of massive pollinating bee activity may deter herbivore insects and vertebrates from plants, especially their flowers, in the critical peak flowering season. The well-known deterrence of caterpillar feeding and movement by wasp and bee buzz (Tautz and Markl 1978; Tautz and Rostás 2008) and the great fear of bees by African elephants (Vollrath and Douglas-Hamilton 2002; King et al. 2007, 2009, 2011) are strong indications of such defense. If experiments show that pollinating bees deter herbivores, some of the costs of attracting bees by flowers should be regarded as defense rather than pure costs of reproduction. However, this hypothesis still deserves significant field observations and experimental work.

Additional testing of the defensive (anti-herbivory) role of bee and wasp mimicry

As discussed above, defensive bee and wasp mimicry are well known, and therefore, there is no need to test this principle. It should, however, be tested specifically for deceptive orchids, and in general when they are abundant on flowering plants. (1) Grazers and relevant herbivorous insects have to be inspected to see whether they regularly avoid such orchids, (2) visually mimicking plastic models should be used to study grazer responses when seeing them, (3) olfactory signals when known should be

examined (with and without) the visual aspect, (4) the innate and learning components of deterrence should be tested in mature versus very young grazers, (5) increasing and decreasing signal strength by changing plant densities and external application of volatiles should also be done, (6) the biochemical and molecular aspects of herbivore responses to these signals should be studied, (7) the fitness of the orchids as expressed in seed set and plant demography should be studied over many years under various grazing pressures, (8) all these should also be done with non-mimicking flowers that according to our hypothesis are protected by an abundance of bees and wasps.

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