POLLINATION STRATEGIES OF DECEPTIVE ORCHIDS – A REVIEW

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ABSTRACT

Orchids can be classified in terms of their pollination into rewarding species, which produce nectar in their flowers that serves as a reward for pollinators and deceptive species, whose flowers do not contain nectar and save energy for other purposes. This paper concentrates on the latter. Deceptive orchids attempt to deceive their pollinators by being similar to some non-orchid rewarding species, but not providing a reward. Each of these strategies has its advantages and disadvantages in terms of their effect on future fitness of a plant and/or population and subsequently its survival as a species. In summary, the literature indicates that deceptive strategies may lower reproductive success, but may be compensated for in that they cost less in terms of energy. This should be taken into consideration when developing management strategies for these species, which is often done by non-orchid specialists. This article is intended for such non-specialist audience and includes a description of the main types of deceptive strategies used by orchids, as well as examples of the most typical species.

Keywords: deceptive orchids; Orchidaceae; pollination; pollination strategies; reproductive success

Introduction

Pollination is the transfer of pollen from stamen to stigma. It is one of the reproduction options used by plants (Dressler 1981; Štípková and Kindlmann 2021). There are several ways in which plants can be pollinated: either self-pollination or cross-pollination and eventually geitonogamy. Both cross-pollination and geitonogamy are types of reproduction that require a mediator, such as water, wind or an animal. Orchids usually use animals, especially insects (e.g., wasps, hoverflies or butterflies) as pollinators. Plants must therefore be able to attract a pollinator and potential pollinators are usually mainly foraging for food if they land on a flower (Dressler 1981).

Orchids have evolved highly specialized flowers for attracting pollinators (Dressler 1981), which can be classified into those that produce nectar (rewarding species), those that do not produce nectar (deceptive species), which in this way save energy for other purposes (Gijbels et al. 2015). Orchids with deceptive flowers make up approximately a third of all orchids (van der Pijl and Dodson 1966; Dressler 1981; Ackerman 1986; Tremblay et al. 2005; Renner 2006; Christenhusz and Byng 2016) and are the group of plants with the most species with deceptive flowers (Jersáková et al. 2006).

Pollination strategies of deceptive orchids are very diverse. The characteristics of the flowers have been determined by selection, which was mediated by pollinators (Micheneau et al. 2009). Features attractive to pollinators include scent, length of the spur and colour of the flower, or presence of a reward (Micheneau et al. 2009). This implies that for the plant it is advantageous to offer some form of a reward to the pollinator and to advertise the fact by developing visually attractive flowers (Roberts 2007).

The more pollinators attracted by a plant, the more successful is the transfer of genes to the next generation (Trapnell and Hamrick 2006). This is important for the survival and evolution of species, and it is why plants produce flowers. Flowers are visually attractive to pollinators foraging for a source of energy (Trapnell and Hamrick 2006).

This review concludes that deceptive strategies may reduce the number of flowers pollinated and consequently plant fitness, but this may be compensated for in terms of energy saved for other uses. This should be taken into consideration when developing management strategies for these species, which is often done by non-orchid specialists. This article is intended for such non-specialists and includes a description of the main types of deceptive strategies used by orchids, as well as examples of the most typical species.

Deceptive orchids and their ability for deceit

The goal of orchids with deceptive flowers is to attract pollinators. This was achieved by evolving flowers that are attractive in terms of their colour, scent or morphology (Dafni 1984). Orchids produce flowers of various shapes that resemble those of plants that are attractive to pollinators or those of a plant that grows close by and produces a reward (Jersáková et al. 2006). A common strategy of deceptive orchids is to produce structures that imitate anthers or pollen (Jersáková et al. 2006). Other species use chemicals, such as pheromones or volatile

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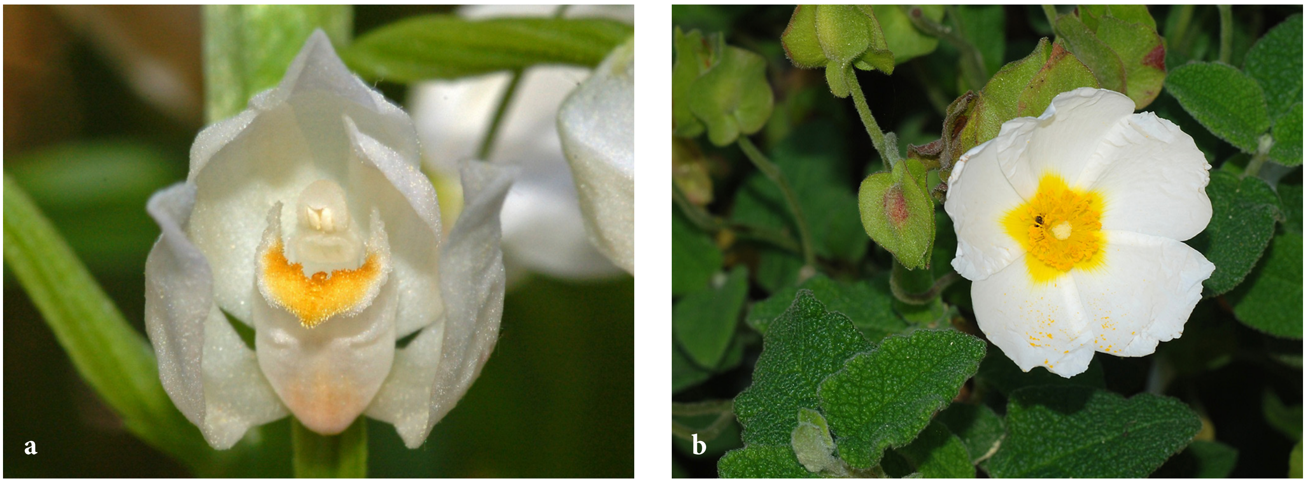

Fig. 1 *Cephalanthera longifolia* (a) and *Cistus salviifolius* (b) (Source: wikimedia.org).

substances, namely essential and ethereal oils, aldehydes or alcohols, to attract pollinators (Brodmann et al. 2008; Stökl et al. 2011). There are many such signals and some are very specific and it is assumed that this wide range of signals evolved because pollinators are more likely to avoid common deceptions than rare ones (Schiestl 2005).

Two-thirds of orchid species are rewarding, which means that they produce nectar for pollinators. Nectar is the most frequent and common kind of reward offered to pollinators by plants (Roberts 2007). Rewarding species usually produce more seeds (Trapnell and Hamrick 2006) and more fruit than deceptive species (Neiland and Wilcock 1998; Schiestl 2005; Molnár et al. 2015). Several studies involving different species of orchids report that species that provide rewards have higher reproductive success (the ratio of the number of fruits to the number of flowers produced per plant per season) than those that do not (Kindlmann and Jersáková 2006; Hobbhahn et al. 2017). A review of over 100 orchid species concludes that the reproductive success of deceptive orchids is only half of that of rewarding species (Neiland and Wilcock 1998), which clearly indicates that rewarding orchids are more successful at reproducing than deceptive orchids (Hansen and Olesen 1999).

Similarity of deceptive orchids to nectar-producing plants

Some deceptive orchids mimic a nectar-producing ("nectariferous") plant growing in the same area. This is referred to as Batesian mimicry, which in this case means that the flower of the deceptive orchid mimics the flower of another plant that offers a reward (Dafni 1984; Jersáková et al. 2006). Imitating flower tries to confuse potential pollinators foraging for nectar by being similar in colour or shape to that of a rewarding flower (Johnson et al. 2003). The orchids that are mimicked by other plants (rewarding in this case) are called "magnetic" plants, because they enable other species to mimic them as rewarding plants (Johnson et al. 2003). E.g., the deceptive orchid *Disa pulchra* is very similar morphologically to *Watsonia lepida*, a nectar-producing plant belonging to the *Iris* genus (*Iridaceae*) (Fig. 1). Both species are pollinated by the same insects (Duffy and Johnson 2017). The more similar an orchid is to a nectariferous species, the more likely it is that it will attract pollinators (Johnson et al. 2003).

An example that this issue may not be as simple is the deceptive orchid *Cephalanthera longifolia* (*Bino* et al. 1982: Widmer et al. 2001), whose flowers are supposed to imitate those of *Cistus salviifolius*, a member of the Rock rose family (*Cistaceae*) – see Dafni and Ivri (1981b). Dafni and Ivri (1981b) found that *C. longifolia* produces more seeds in places where *C. salviifolius* also grows. Because both species have the same coloration, they checked the possibility of floral mimicry. By doing that, however, Dafni and Ivri (1981b) observed that orange papillae on the labellum of *C. salviifolius* successfully imitate pollen of *C. longifolia* (= it can be considered as a "pseudopollen"). In addition, they found that the flowers of *C. longifolia* attract pollinators even in the absence of *C. salviifolius*. By putting these two observations together, Dafni and Ivri (1981b) hypothesize that the attractivity of C. *longifolia* to pollinators in the absence of the "magnet species", *C. salviifolius*, can be explained by the attractive value of the "pseudopollen" alone. The strength of this argument would be increased, however, in the situation, where *C. longifolia* coexists with a differentially coloured *Cistus* species (which also produces pollen). Would this *Cistus* also cause an increase of attractivity of *C. longifolia* for pollinators? This is a matter for future research.

Sexual deception

The strategy of using the flower as a sexual dummy to fool a specific pollinator is less common than the food-deceptive strategy (Tsiftsis and Djordjević 2020). There are about twice as many families that use food-deceptive strategies than those that use sexual deception (Jersáková et al. 2006). Sexually deceptive orchids are highly specialised and typically pollinator-specific (Peakall and Handel 1993; Cozzolino and Widmer 2005; Mant et al. 2005; Schiestl and Schlüter 2009; Gaskett 2011).

Flowers of several species of the genus *Ophrys* mimic the form and movement of the female of their specific pollinator (Kullenberg 1950) (Fig. 2 and Schiestl 2005).

The pollinator lands on the flower and tries to copulate with it, during which the pollinium of the flower sticks to it and is subsequently transported to the next flower it visits (Ayasse et al. 2000). Flowers of these orchids do not only use visual signals, but also scent to attract their pollinators (Schiestl 2005). A flower of *Ophrys sphegodes* attracts males of its pollinator both by looking and smelling like a female. They do this by secreting the same chemical substances as a real female. That the pollination of these orchids is entirely dependent on one particular species of insect would appear to indicate that their reproductive success is very low, but this not the case. The specific pollinator can visit the same plant a second or even a third time, because the chemical composition of scent produced by this orchid differs between plants (Ayasse et al. 2000). Correct positioning of the pollinator is necessary for pollinium removal, which reduces the probability of geitonogamy (Ayasse et al. 2000). The orchid *Caladenia huegelii* is also pollinated by wasps, which emit pheromones when close to the flower of this orchid, which is thought to indicate that the pollinator is responding as if about to copulate with a female and that two thirds of the males that land on a flower will attempt to copulate with it (Phillips et al. 2015). Scopece et al. (2010) report a higher percentage of pollination of orchids using sexual deception than non-rewarding orchids and sometimes even rewarding orchids.

Fig. 2 *Ophrys insectifera* (Source: wikimedia.org).

Scent

A relatively newly explored pollination strategy of deceptive orchids is the so-called chemical mimicry, which is to produce a scent that attracts pollinators (Brodmann et al. 2008). For example, the orchid *Epipactis veratrifolia* is pollinated by several species of hoverflies (Stökl et al. 2011), including *Ischiodon scutellaris* (Kumar and Rawat – see Fig. 3). The flowers of this orchid smell just like aphids, which is attractive for insect predators like hoverflies, the larvae of which feed on aphids. This results in some of the pollen of the flower adherring to the hoverfly and being transported to other plants of this orchid (Ivri and Dafni 1977; Kumar and Rawat 2011; Stökl et al. 2011; Jin et al. 2014).

Fig. 3 *Epipactis veratrifolia* (a) and one of its pollinators, *Ischiodon scutellaris* (b) (Source: wikimedia.org).

Fig. 4 *Orchis israelitica* (a) and *Bellevalia flexuosa* (b) (Source: wikimedia.org).

Epipactis helleborine, emits volatile aldehydes and alcohols. Brodmann et al. (2008) studied whether the social wasps that pollinate this orchid are attracted by visual signals or scent. Pollinators visited more frequently covered flowers that produced scent than visible flowers, which did not (Brodmann et al. 2008). The scent of *Orchis israelitica* also attracts pollinators, but only over long distances, as when the pollinator is close to the plant, it is attracted by the colour of the flower (Galizia et al. 2005).

Mimicry of anthers and pollen

Another strategy used by orchids is to falsely signal the presence of pollen (Lunau 2000). Flower colour and pattern have a significant role in this pollination strategy. Pollen absorbs ultraviolet radiation and thus protects DNA from damage (Heuschen et al. 2005). Pollinators recognize parts of a flower that absorb UV radiation. Parts of the petals of *Cattleya walkeriana* absorb UV radiation and falsely signal the presence of pollen to pollinators (Aguiar et al. 2020). This was first recorded for a plant, the colour of the centre of the flowers of which is yellow, not the whole flower. *Dactylorhiza sambucina* is an example of such a species (Kropf and Renner 2005). There are few examples of this kind of mimicry in the above species, but it occurs more frequently in other families (Heuschen et al. 2005; Pohl et al. 2008).

Some orchids deceive their pollinators by having flowers with structures that morphologically resemble anthers (Dafni 1984). This visual deception tricks pollinators into to visiting the flower. *Orchis israelitica* imitates the rewarding plant *Bellevalia flexuosa*, which is a member of the Liliaceae (Fig. 4). Anthers of the rewarding plant are a dark colour and there are many dark dots in the centre of the flower of the deceptive orchid, which imitate these anthers (Dafni and Ivri 1981a). Both species are pollinated by bees, which are attracted to visual signals, which in this case are in flowers similar in colour and size (Galizia et al. 2005).

Shelter

The flowers of some deceptive orchids appear to provide shelter for their pollinators. This strategy is rare in orchids, with only one documented genus, *Serapias* (Vöth 1980; Dafni et al. 1981; Jersáková et al. 2006; Vereecken et al. 2012). A possible reason is that it is very costly in terms of the investment in resources. The flower must be big enough to provide a refuge for the pollinator. For example, bees, which pollinate the orchid *Serapias vomeracea*, stay overnight in orchid flowers. These bees usually nest in holes in the ground and the flowers of this orchid have structures that simulate such holes (Dafni et al. 1981), Fig. 5.

Bees, which spent the afternoon flying from flower to flower of this orchid, often overnight in a flower. In addition, the flowers are warmed by the morning sun and the

Fig. 5 *Serapias vomeracea* (Source: wikimedia.org).

Fig. 6 *Caladenia nobilis* (Source: chookman.id.au).

bees may also stay in a flower for two nights (Dafni et al. 1981). Compared with *Serapias lingua*, which uses sexual deception to attract pollinators, the percentage fruit set of *Serapias vomeracea* is higher (Pellegrino et al. 2017).

Nectar

Some of the deceiving orchids produce a small amount of nectar, which they supposedly produce to attract insects and pollinators (Phillips et al. 2020). *Caladenia nobilis* (see Fig. 6) is an example of such an orchid. Some of its flowers contain a small amount of nectar, which contains mainly saccharose and also fructose and glucose (Phillips et al. 2020). This orchid is pollinated by only one species of insect and by producing nectar it increases its attractiveness and chance of being pollinated (Phillips et al. 2020).

Jersáková et al. (2008) report how pollinators react to nectar. Adding saccharose to the flower of the deceptive orchid *Dactylorhiza sambucina* increased its production of fruits. In the case of the deceptive orchid *Disa pulchra*, more flowers were pollinated (Jersáková and Johnson 2006).

Nectar is the main reward of orchids because it attracts pollinators, which feed on nectar (Gijbels et al. 2015) and in facilitating the transfer of pollen by pollinators it enhances the reproductive success of orchids. The nectar produced by orchids is composed predominantly of carbohydrates and amino acids (Gijbels et al. 2015), with the carbohydrate concentration ranging between 3.5% and 71% (Brzosko and Mirski 2021). The composition of nectar differs between genera and even in some deceptive orchids (Phillips et al. 2020; Brzosko and Mirski 2021). The reason for this is unknown. It is likely, however, that either the pollinator is an important factor (Micheneau et al. 2009; Brzosko and Mirski 2021), or the composition of the nectar influences the sexual, social and foraging behaviour of pollinators (Wróblewska et al. 2019).

Conclusion

The most frequently used strategy of deceptive orchids is to closely resemble an orchid that produces nectar (Jersáková et al. 2006). The least used deceptive strategy is providing shelter for pollinators (Jersáková et al. 2006), even though it results in higher reproductive success in terms of higher fruit production, than orchids using insect sexual deception (Pellegrino et al. 2017). Although deceptive strategies may result in fewer flowers being pollinated and indicate a lower plant fitness, this may be compensated for by saving energy.

This should be taken into consideration when developing management strategies for orchids, which is often done by people who are not orchid specialists, which are the main target of this review.

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