A One-sided Affair: a Look at Orchid's Two-Faced Ways

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Summary

***Orchidaceae* are a family of plants that are known for tricking their pollinators through means of deceptive pollination and sexually deceptive mechanisms. A deceptive flower is one that offers no reward to its pollinator, but still attracts pollinators by mimicking a plant or an insect that does offer a reward. Sexual deception occurs when a plant sends a signal to its pollinator, tricking the insect into thinking the plant is available for sex, despite the pollinator being biologically unable to successfully copulate with the plant. Orchid fertilization is of interest to evolutionary biologists who aim to uncover how these rewardless plants continue to be pollinated by reward-seeking pollinators. The use of phenotypic variation, strong olfactory cues, and adapted plant parts to lure in insects are some of the ways in which orchids achieve success. Other findings suggest that orchids have adapted to ensure cross-fertilization, as opposed to self-fertilization, in order to produce more viable offspring. In this review I will explore how the use of deception, rewardlessness, and pheromones allow for the continued reproductive success of several orchid species.**

Introduction

What is deceptive pollination?

A deceptive flower is one that offers no reward to its pollinator, but still attracts pollinators by mimicking a plant or insect that does offer a reward (Dafni, 1984; Baker, 1978; Paegri, 1979). For centuries, deceptive pollination has been an area of focus because it is a relationship that one would not expect to survive under natural selection. The deception that occurs between plant and pollinator requires further study to uncover the mechanism behind the survival of this relationship. *Orchidaceae* are a family of plants that are known for tricking their pollinators. In fact, one third of the family does not produce any nectar; 10,000 species practice deception through mimicry; and 400 species of orchids go a step further and sexually deceive male pollinators (Ledford, 2007; van der Pijl and Dodson, 1966; Ackerman, 1984). Thus orchids are a perfect model species to use when studying deceptive pollination.

Sexual deception occurs when a plant sends a signal to its pollinator, tricking the insect into thinking the plant is available for sex, despite the pollinator being biologically unable to successfully copulate with the plant. Because orchids are pollinated by reward-seeking insects, and most orchids offer no reward, it is a mystery as to how orchids continue to succeed in pollination. Research indicates that although non-rewarding plants (orchids) suffer from low pollination rates, they continue to enjoy reproductive success (Ledford, 2007). At first this may seem to be the opposite of what we know to be true about nature, but this review aims to resolve our instinctive disbelief surrounding the continued success of orchids. The uncovering of the means by which orchids continue to stay reproductively successful would no doubt cause Darwin's jaw to drop, being that he referred to orchids as having adapted to near perfection (Darwin, 1876). In this review I will explore how the use of deception, rewardlessness, and pheromones allow for the continued reproductive success of several orchid species.

Darwin's Look

Charles Darwin is known best as an advocate for natural selection. While on one has yet disproven his theory of natural selection, we have come to find instances where outwardly it does not exactly hold up. It is not until we look deeper that we can apply his theory to observed cases of what seems to be "not-so natural selection." In his book, *The Various Contrivance by Which Orchids Are Fertilised by Insects* (1876), Darwin spends over two-hundred pages uncovering the mechanisms by which orchids are fertilized.

Darwin acknowledges that orchids seem to have tremendously specific relationships with their pollinators. He connects his natural selection theories to the dual-purpose protective devices by arguing that, due to specificity between plant and pollinator, some orchids species cannot ensure fertilization and therefore may be rendered extinct. Thus, Darwin explains that whatever has kept these species around shows that they have been favored in some other way (Darwin, 1876). He concludes his book by marveling at the perfection by which orchids have adapted to engage in cross-fertilization, noting that species like *Cephalanthera grandiflora* and *Neottia nidus-avis* self-fertilize because they fail at cross-fertilization. However, he leaves us with an understanding that cross-fertilization is worth the risk due to its production of more viable offspring (Darwin, 1876). The adaptive nature of these plants throughout evolution is responsible for their reproductive success.

Mechanisms for fertilization

Cross-fertilization is not the safest way to go about reproduction; yet, we observe it in most of the orchid family as the primary means for reproduction. Darwin does not offer much explanation for the continued success of orchids that rely solely on cross-fertilization by their specific pollinators. However, the contrivances by which they have been successful are now, decades later, beginning to unfold. We are starting to find that aside from the aforementioned adaptations that make orchids well-suited for cross-fertilization and allow them to only host a small range of pollinators, there may in fact be several other ways by which orchids have adapted to ensure pollination.

For example, Darwin talks in detail about the composition of orchid's pollen. The pollen is durable: it attaches to its pollinators, ensuring transplant on a new flower (Darwin, 1876). However, he reports that in order for the pollen to even attach to an insect, the mechanism by which the insect lands on the flower must be the same each visit. This leads him to question the adaptation of orchids' flower parts. Darwin describes the adaptation that has occurred in many

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orchids through time, causing the protective devices (upper sepal and petals) to double as a guide to pollinators, ultimately forcing them to visit the front of the plant (Darwin, 1876). The labellum is another structure that Darwin explains as a functional part of ensuring pollination. It acts as a landing place for pollinators and, because it stands in front of the reproductive mechanism, the rostellum, it often forces an insect to bump into pollen. In *Epipactis palustris*, for example, it forces the insect to brush up against the rostellum. In other species, if the labellum is touched, it causes the whole flower to close, providing the insect with only one route of exit. That route includes running into the rostellum (Darwin, 1876). Darwin outlines the adaptive nature of the structure of orchids, giving us an understanding of how orchids are pollinated. Understanding the mechanism of pollination is important; however, understanding why orchids evolved this way must also be investigated.

How do orchids pull it off?

The use of olfactory cues is the most important of several mechanisms plants use to deceive pollinators. For example, some orchids give off scents that mimic those of nectar-producing plants signaling pollinators to visit the flower even when no nectar is present as a reward (Proctor, 1996). Darwin mentions that orchids may use their strong scent to aid in attracting insects (Darwin, 1984), but he never proposes that the scents are deceitful in nature. In spite of his oversight, we now can observe that this type of mimicry allows orchids to more effectively lure reward-seeking insects.

Sexual deception occurs in much the same way through the emission of scents, or pheromones, that mimic those of a female pollinator. However, but it can also be carried one step further. In order for orchids to cause *psuedocopulation* (Correvon & Pouyanne, 1916; Pouyanne, 1917; as cited by Ayasse *et al*, 2003) to occur with male pollinators, they need more than mere attractants; often an orchids' contour resembles that of a female pollinator's (Proctor, 1996). In *Ophrys speculum*, parts of the flower, especially the lip, feel like females insects. These parts of the flower mimic female body hairs and antennae to the point that they cause males to engage in mating-type behavior (Proctor, 1996). Schiestl (2004) looked at the ways in which orchids mimic the body type of their pollinators. He compared male wasps' preference for female wasp body type and concluded that males prefer medium-sized females versus small ones, and that similarities between medium-sized body type and the orchid's labella were present. These results suggest that an orchid's labella may have evolved to be longer and broader, like the body of a female wasp, in order to aid successful deception (Schiestl, 2004). Darwin had only begun to breach the surface of how and why these mechanisms have adapted in orchids.

In addition to having similar texture, orchids give off a strong scent which is said to attract male pollinators from long distances (As reviewed by Proctor, 1996). The attractive scents are thought to mimic wasp sex pheromones (Schiestl et al, 1999). Also, male wasps have been found to show a preference for higher levels of pheromones (Schiestl, 2004). Therefore, if orchids produce a stronger scent and have a labella resembling a female wasp, wasp-wasp copulation success will be reduced (Schiestl, 2004). Clearly, orchids are talented when it comes to manipulating their pollinators.

Additionally, each species of orchid has a small range of specific pollinators with which it interacts, and each plant thus seems to have a unique mechanism for deception. For example, the fly orchid has a close relationship with its pollinator, the *Argogorytes* wasp: the wasp which will not visit any other plant, except by mistake, because the fly orchid's upper lip matches the shape and texture of a female's back. The fly orchids conveniently have a flowering season that spans the time of emergence of the male wasps (Proctor, 1996). Thus, the orchids take full advantage of *Argogorytes,* displaying one more way in which orchids manipulate their pollinators.

The scents released by orchids are of particular interest. It has been suggested that each sexually deceptive species has its own unique perfume that is pollinator specific (Ledford, 2007). Schiestl and Francke (1999) placed the antennae of the insects between two electrodes and observed the chemicals that elicited a stimulatory response. By isolating different compounds that make up orchid pheromones and analyzing each individually, they concluded that plant and wasp sex pheromones are similar. In addition, the 14 orchid pheromone compounds that excite male *A. nigroaenea* are also used to make up a protection device located on the surface of many plants (Schiestl *et al,* 1999). Not only does this allow us to understand the attraction principle occurring between pollinators and orchids, but this also points to evolutionary implications (Ledford, 2007). As Darwin suggested, while we may not understand the function of a part of nature, chances are good that it has a purpose (Darwin, 1984). It is not until we look deeper that we can find the function and perhaps, as in this case, a dual purpose.

Comparative analysis of the chemical makeup of the pheromones released by the insects to those of the plants has been performed using various techniques, including gas chromatography and mass spectrometry. As expected, in general the chemical makeup of these "love potions" in both the insects and the plants have been found to be quite similar (Mant *et al,* 2007; Schiestl *et al*, 2007). More specifically, Ayasse *et al.* (2000) found that the esters and aldehydes present in the active signaling compounds of the orchid pheromones seem to be what is attracting pollinators. They show that these compounds vary less in signaling compounds than in non-signaling compounds (Ayasse *et al.,* 2000). The results show that bee and wasp pollinator species undoubtedly have little way of distinguishing the difference between the scents of their female lovers and their orchid mistresses.

Why haven't pollinators caught on?

Pollinators have built-in mechanisms for saving energy and obtaining the maximum benefit out of every visit to a plant. For example, they have been known to avoid flowers that smell like they were recently visited because they know that there will be less nectar available. Pollinators are generally energy-efficient and they will avoid plants that offer little or no benefit to them. Why then does the relationship between orchids and their specific pollinators continue to exist?

As previously discussed, orchids use mimicry to con insects into landing on their flower and eventually pollinating them. Why have the seemingly intelligent pollinators not learned from their mistakes? One possible answer is that orchids come in a variety of shapes, colors, and sizes. Therefore, in addition to having deceptive chemicals, it is nearly impossible for pollinators to learn from their mistakes and avoid the next orchid plant because it most likely will not resemble the previously visited one (Ledford, 2007; Proctor, 1996). The orchids appear to be one step ahead of the insects' evolutionary tools for success. Thus, one must ask, what is the effect on the pollinators?

Besides luring their pollinators into a situation of pseudocopulation, are the orchids hindering the insects' chances for real copulation? Wong *et al*. (2002; 2004) shows that not only are orchids deceiving their wasp pollinators, the plants are actually harming them. After examining pheromone amounts and copulation attempts between plant-insect and insect-insect, they concluded that a male wasp will choose pseudocopulation over actual copulation with a female wasp when the two options are in close proximity with one another (Wong *et al,* 2002; 2004). While Wong and his colleagues do not offer an explanation for this result, one might speculate that the pheromones released from the orchids are stronger and/or more abundant than those of the female wasps. Alternatively, wasps that choose to attempt to mate with the flowers over the females may be immature, inexperienced wasps that would prefer to attempt sex and fail then to have not attempted at all (Ledford, 2007). A future study could examine the relationship between wasp maturity and quantity of pseudocopulation occurring. This would provide more insight on a pollinator's motives for pseudocopulation.

Where is the benefit in trickery?

Because of the slight variations in each individual orchid species and the specificity for a certain pollinator species, we assume that pollination attempts are quite limited in nature. From this, we can also speculate that the reproductive success of orchids will be minimal; however, in reality, it is plentiful enough to keep these plants around. Knowing that orchids offer no benefit to their pollinators because they do not produce any nectar, the obvious benefit to the plant is conservation of energy. Research with nectar supplementation in *Barlia robertiana* has shown that seed paternity is higher in rewardless plants (Smithson & Gigord, 2001), suggesting that evolution actually favors the rewardless nature of orchids. Another study looked at the orchid species *Tolumnia variegate* and its fitness response to an increase in seed set and fruit production: the results suggest that limited pollination is actually being selected for because fitness does not increase as a result of increased pollination (Calvo, 2007). The reoccurring theme is that orchids seem to go against what we would expect to see in nature; therefore, scientists are continuing to uncover unexpected evolutionary trends. There is, however, a twist that can help to further understand the backwardness of orchids' continued reproductive success. This idea will be highlighted in the following section.

What Darwin overlooked…

Darwin would have predicted the near-immediate extinction of the deceptive species of orchids, and he would have speculated that pollinators would have figured out the orchids' scam of rewardlessness and push them into non-existence by refusing to pollinate them. Why, then, hasn't this happened?

In addition to saving energy by not producing nectar and by producing more durable pollen rather than mass quantities of pollen, orchids make up for their limited amount of pollination by instilling mechanisms that increase its quality. Darwin was right in his expectation of pollinators realizing their predicament and avoiding deceitful orchids, but what he did not expect was that the educated avoidance of pollinators would lead to the orchid's increased reproductive success. To investigate the way in which this occurs, a catch and release study was done with *Zaspilothynnus trilobatus* Turner wasps. Results showed that, after being tricked by a rewardless plant, wasps will travel up to 132 meters away before visiting another plant (Peakall, 1990). These results suggest that orchids are both tricking wasps enough to attain pollinators and increasing their reproductive quality by limiting inbreeding: by offering no reward to the insects, pollinators are more likely to fly a greater distance before landing on another plant in hopes of avoiding the deceitful plant species.

Orchids counter the pollinators' long distance flight plan by varying not only their shapes, sizes, and flower color, but also their odor. Orchids use pheremones to lure male pollinators with the false promise of sex, and pheremone content varies from plant to plant to ensure high-quality reproductive success. Ayasse *et al.* (2000) studied the sexually deceptive orchid, *Ophrys sphegodes*, for its flower-specific odor variation. They found that orchids ensure cross-pollination by varying their olfactory cues to the pollinators, which most often causes pollinators to visit different species, plants, and flowers. They also found that bees remember the odor of a given flower, ensuring that they do not visit the same flower more than once (Ayasse *et al.,* 2000). Taken together, these results indicate that the orchids hold the key to an inbreeding-preventive mechanism that Darwin failed to recognize as evolutionarily favorable.

To further prove Darwin wrong, Johnson (2000) compared the reproductive success of a non-rewarding orchid, *Disa pulchra*, to a morphologically similar nectar-rewarding iris plant species, *Watsonia lepida*. He proposed *D. pulchra* is a mimic of the iris because both plants share a common pollinator, the long-tongued fly. He found that flies do not discriminate between the orchid and the iris, but they do spend less time on the rewardless orchid (Johnson, 2000). This leads to speculation that the less time a pollinator spends on the orchid, the less chance there is for self-pollination to occur. Digging deeper, Johnson (2000) found that viable seed counts from outcrossed fruits were greater than seed counts from self-pollinated fruits. This result reinforces the evolutionary theory that an orchid's deceitful methods, although potentially limiting to the quantity of reproduction, can greatly improve reproductive quality. Cross-fertilization usually produces more viable offspring than self-fertilization and thus enhances the liklihood of maintaining fitness.

Orchids and the future

Several questions remain to be answered regarding *Orchidaceae* and their unique relationship with pollinators. One question revolves around the idea of speciation. Because each orchid seems to have a unique scent for its specific pollinator, new studies are finding that even a small change in the scent of an orchid species could attract a new and different pollinator. This change in pollinator species could therefore cause the reproductive isolation needed to qualify that particular species for speciation. New research is heading in this direction.

After looking at Pemberton and Wheeler's (2006) study that questions the existence of a mutualism between the orchid bee, *Euglossa* *viridissima*, and perfume orchids, we can deliberate on the existence of any orchid-pollinator relationships acting as mutualisms. Pemberton and Wheeler (2006) concluded that no mutualism exists between orchid bees and perfume orchids; even though the orchids rely on the bees, the bees can survive without the orchids. Future research could focus on identification of the potential existence of orchid-pollinator mutualisms in nature. This then begs the question, what affect, if any, do orchids have on other plants in nature? There are plenty of unanswered questions surrounding orchids and the means by which they continue to thrive.

Conclusion

This review has outlined several of the advances made since Darwin's book on the uncommon evolution of orchids, but is by no means a comprehensive report on the entire subject. These more recent findings suggest that orchids have adapted not only to ensure cross-fertilization, as opposed to self-fertilization, but also to enjoy greater amounts of reproductive success with less effort. Orchids do not have to produce nectar in order to lure pollinators to visit; instead, they adapt their protective devices and already present scents to do the work. Orchids are a fabulous example of how small changes in already existing processes can benefit an organism in nature. As Darwin spends his last page raving about the perfection of orchid adaptations, I too will describe orchids as being nothing short of evolutionary geniuses.

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