LIARS AND CHEATS: THE STORY OF ORCHID DECEPTION

CAROL SIEGEL

"Whenever, therefore, people are deceived… it is clear that the error slid into their minds through the medium of certain resemblances to the truth."
-Socrates

WE HUMANS ARE NO STRANGERS to deception. Psychologists say we start lying when we are two years old and lie every hour or two after that for the rest of our lives. Some deception is rather innocent. We dye our hair, wear padded bras, or take twenty pounds off our weight on our driver's licenses. We slip in false teeth, make our resumes look more glorious, or pretend we like a friend's awful haircut. Other deception is less innocent. We cheat on our taxes, step out on our mates, or fool nice people out of millions like Bernie Madoff. We are often not exactly what we pretend to be.

We humans may be the masters of deception in the animal kingdom, but, in the plant kingdom, nothing holds a candle to the orchid. Fully one-third of the approximately 30,000 orchid species promise pollinators a reward and deliver nothing at all. In the Western Palearctic (Europe, Middle East, North Africa), deception may occur in as many as half of all orchid species. In Australia, most terrestrial orchid genera are deceptive. World-wide, it is estimated that 38 genera of orchids are involved in food deception, and 18 genera of orchids exploit sexual deception. With 10,000 cheating orchid species, deception is neither rare nor unusual. In no other plant family is lying more of a way of life than it is for the orchids. Although non-rewarding flowers have evolved in at least 32 angiosperm families, it is thought that more than 85% of deceptive plant species world-wide are orchids. For orchids, it is very often a reward decoy and not the real McCoy which is offered. As Michael Pollan says in his introduction to *Deceptive Beauties*, "The deception and exploitation of animals has become something of an orchid family specialty."

This unusually high occurrence of non-rewarding plants falls into several broad categories:

- Sexual Deception
- Rendezvous Attraction
- Batesian Mimicry Of Food Plants
- Generalized Food Deception
- Brood Site Imitation
- Prey Imitation
- Pseudoantagonism
- Shelter Imitation

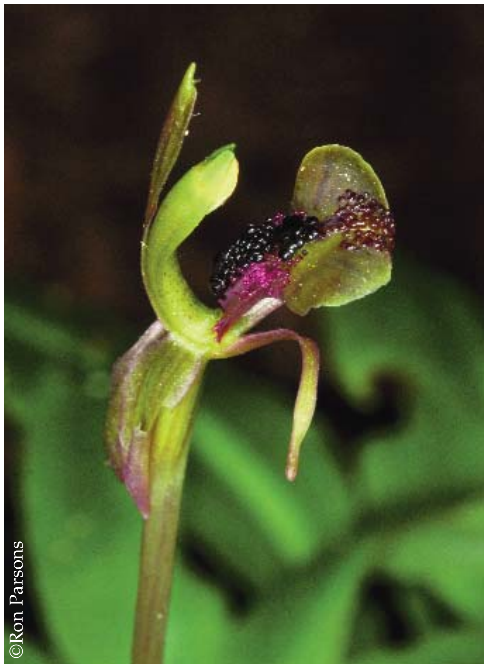
Sexploitation and the Unrewarding Orchid Sex Trade

Perhaps the most bizarre orchid deception involves male insects who are so aroused by the scent, look, and feel of an orchid that they try to mate with it. Called "pseudocopulation," or false copulation, it is only false for the insect. It is real for the orchid. The insect does not score, but the orchid does. In the course of the insect's frustrating amorous attempts, pollinia is picked up and delivered, and orchid sex is completed.

Sexual deception has evolved at least six times in different lineages. It occurs in at least 18 orchid genera including many examples in the genus *Ophrys* in Europe, some *Disa* species in South Africa, and at least nine genera of terrestrial orchids in Australia, altogether comprising about 400 species. However, Florian Schiestl says that this pollination syndrome is probably more widespread since new cases have been described in some genera of neo-tropical Maxillariinae and Pleurothallidinae. In the last group, sexual deception may be prevalent, Schiestl says, in the large genus

Chiloglottis reflexa and pollinator Peak

Chiloglottis aff. *valida* and two pollinators.



Chiloglottis trapeziformis attracts its wasp pollinator with chemical mimicry.

Chiloglottis seminuda and wasp pollinator.

Chiloglottis trapeziformis and a male pollinator.

Lepanthes with more than 800 species. Anecdotally, evidence also exists for four other orchid genera.

John Alcock describes pseudocopulation in fascinating detail with nine species in the genus *Drakaea* (the Hammer Orchids). In Australia, the Caladeniinae, which include *Drakaea*, rely on a family of parasitic wasps called *Thynninae* which lay their eggs into the larvae and pupae of beetles and other insects. Males are extremely good fliers, but the females don't fly. The lip of the orchid *Drakaea glyptodon* looks like the wingless female thynnine wasp *Zapilothynnus trilobatus*. The flightless female spends her whole life underground looking for root-feeding beetle grubs. For four days of her life, she climbs out of the ground and alights on a shrub and emits her pheromone love call from glands in her head. Competition for females is intense, and males can't be picky. Within two minutes, catching her enticing fragrance, a male thynnine wasp pounces on her, lifts her into the air and takes her for a lengthy honeymoon, copulating mid-air with her and regurgitating food he has collected into her mouthparts.

Orchids exploit the desperation of the highly competitive males. The *Drakaea* species have evolved a scent that supposedly mimics the receptive female wasp. Responding to the olfactory cues, the male wasp tries to take the dummy orchid "female" for a little mid-air lovemaking; the unsuspecting amorous wasp is tilted forward onto the column by a see-saw like hinge on the lip and comes in contact with the pollinia or stigma. The *Drakaea* species are mainly maroon in color, glossy with lots of warty protuberances, but it is the odor that is the main attractant. Botanist Warren Stoutamire describes how thynnine wasp males followed his car and came in through an open window to locate drakaeas on the floor. Despite the fact that males sometimes fall for dummy flowers, alighting quickly on anything resembling a female results in an advantage over the long range. As Alcock says, "Extreme sexual enthusiasm generates a net reproductive gain for males despite the occasional error." In more than half of 60 experiments by Alcock and Darryl Gwynne, perched females attracted a male in less than two minutes. A male who hesitated would always miss out. Eager males had a real reproductive advantage. Orchids exploit this eagerness.

Thynnid wasps pollinate other Australian orchids in similar ways including *Spiculaea ciliate* (the Western Australian Elbow Orchid). Although *Spiculaea ciliate* has a hinged labellum rather than a hinged lip, it operates in much the same way as drakaeas. It depends on a scented decoy although it has a different scent and is pollinated by a different species of thynnine wasps. Stoutamire showed that the scent comes from the abdomen of the insect, not the head. He removed the head of the female, and it was still attractive to the wasp males. The male, in attempting to mate with the decoy, finds himself slammed against the column with his wings trapped in the column's hooded appendage. After struggling to get out, he has bright yellow pollinia attached to his chest. His attempts to copulate frustrated, he flies off carrying as many as a million grains of pollen in each pollinia. He falls for another dummy orchid female, crashes again into the column, and completes a sex act for the orchid, if not for himself.

Breakthroughs achieved by applying electrophysiological tools in combination with analytical chemistry have allowed the breakdown of individual compounds in the deception scent bouquet and have shown the extraordinary degree to which orchids mimic their pollinator females. Peculiarly, the Australian *Chiloglottis trapeziformis* attracts its wasp pollinator, *Neozeleboria cryptoides*, with a single compound, Chiloglottone, that represents an as yet unknown class of substances. The female wasp's sex pheromone is a single hydrocarbon

2-ethyl-5-propylcyclohexan-1, 2-dione. *Chiloglottis trapeziformis* also produces this compound, matching the particular molecule exactly. This pheromone, dispensed on a bead on the head of a pin, is sufficient to attract the excited male wasps to attempt to copulate with the head of the pin. Male wasps deal with this one species of orchid and select against any orchid that does not match this pheromone in every way.

In another example of mimicry, *Ophrys sphegodes* and its bee pollinator *Andrena nigroaenea* both have evolved similar compounds to attract male bees. Scientists extracted hydrocarbons from the cuticle of the female bees, and they found 15 compounds that attracted male bees. The decoy lip of *sphegodes* had the same 15 compounds. The relative amounts of each compound were also the same for the orchid and the bee. No wonder the orchid drives the male *Andrena* bees crazy. When experimenters placed extracts from female bees on a dead female bee and then did the same with the decoy orchid lip, male bees pounced on both in exactly the same way. They could not tell the difference between a female and an orchid. The suggestion is that the waxy coat, which used to waterproof only, became modified because the scent attracted pollinators. *Ophrys sphegodes* now only produces a false pheromone scent and does not waste resources on making other scents.

For most insects, pseudocopulation is an unrewarding and unsatisfying affair, and insects don't ejaculate. This saves sperm for encounters with real females. However, the insects pollinating *Cryptostylis* species frequently ejaculate and waste their sperm on the lip of the orchid. Anne C. Gaskett *et al.* studied *Cryptostylis erecta* and *Csy. leptochila* and their shared male "dupe" pollinator *Lissopimpla excelsa*. Blobs of ejaculate were observed on both orchids, visible to the naked eye. *Cryptostylis* has an extremely high percentage of pollination and ensures pollinia transfer by the vigorous copulation its mimicry provokes.

Sometimes preventing males from delivering sperm to a female can benefit the *Cryptostylis* orchid. Interestingly, many sexually-deceptive orchid pollinators are exclusively solitary and haplodiploid species from 11 hymenopteran families. If a female insect is deprived of mating by orchid deception, she can still produce male offspring but no female offspring. If the orchid reduces sperm quantity to the female, she will produce more males than females. This generates a supply of naive male insects to fall once again for the trick of pseudocopulation. With a surplus of males in another generation, choosiness is lowered, making pseudocopulation more likely. For the insect to survive, all it takes is normal sexual reproduction some of the time.

Botanists argue as to whether this is really deception since the insect gets sexual stimulation. Although philosophical botanists like to argue these sorts of questions, most botanist feel that deception is involved because the insect is getting a different reward from the

The term "pseudocopulation" was coined by Pouyanne after observing that only male bees were attracted to *Ophrys speculum*.

Ophrys sphegodes produces a false pheromone scent to attract male bees.

one promised, which is sex with a female of his own species. There seems to be a continuum, a transition from no rewards at all to the desired reward sought and promised. Possibilities range from 0-100% and are more subjective and subtle than it seems at first glance. Deception is complicated.

In *Ophrys* species, several authors have noted that sexual deception partly relies on the fact that the male bee pollinators emerge two weeks earlier than females, that females mate only once, and that there are many more males than females. This temporary excess of males results in a low threshold of stimulation, and males will mate with things that only vaguely resemble females. Inexperienced males do not have a complete picture of what a female should look like. The arrival of real females usually reduces the visits to most sexually deceptive orchids, but there are some exceptions. Some male bees will continue to prefer orchid decoy ladies. For example, males of *Andrena* bee species continue to

The ridge on the lip of *Oph. bombyliflora*'s resembles *Eucera* bee female genitals.

try to copulate with *Ophrys lutea* even after their own females have emerged. *Campsoscolia* males, too, continue to be deceived by flowers of *Ophrys speculum* even after they have had sex with their own females. Likewise, males of *Lasioglossum marginatum* keep trying to initiate sex with flowers of *Orchis galilaea* even when there are lots of females, and oddly some ichneumonid wasps *Lissopimpla excelsa* actually seem to prefer to copulate with *Cryptostylis* species when offered a choice between them and real wasp females. It is thought that some flowers produce a supernormal stimulus, volatile olfactory chemicals that are not exactly the same as the female but which are super-stimulating.

With *Ophrys* species, as a general rule, odor is the most important long-distance attractant and excitant, but short-range, visual and tactile clues orient the bee for copulation. Bertil Kullenberg laid the foundation for a great deal of knowledge of *Ophrys* species. He found male digger wasps were attracted to the scent of *Oph. insectifera* while still several meters away but that visual clues worked only at a very short distance. Visual stimuli are secondary for attraction, but the orchid flower is sometimes amazingly realistic. Many common names of *Ophrys* species reflect their visual resemblance to insects like *Oph. sphegodes* (the Early Spider Orchid), *Oph. insectifera* (the Fly Orchid), and *Oph. apifera* (the Bee Orchid). Usually the sepals and petals are colored and the petals smaller, sometimes triangular or rectangular in shape. The lip has no spur but is velvety and rigid like a bee body. The surface of the lip often has an elaborate pattern or shield-like area with a hairy margin. There is sometimes a blue, shiny mirror look to the lip which mimics the female's folded wing. At the apex of the lip is often a small or large appendage which can be mistaken for the female abdomen. There can also be two eyelike knobs at the lip base with the column forming a basal stigmatic cavity. There is a ridge on the lip that resembles the ridge surrounding the insect genitals as in *Oph. bombyliflora*'s resemblance of Eucera bee female genitals. In *Oph. scolopax*, hairs on the fringe of the lateral lobe of the lip stimulate the bee like the bristles of the wing and resemble the longer hairs of the hind legs, abdomen, and thorax of the female Eucera bee. Even the convexity of the lip gives an abdomen-like appearance. It is fascinating to note that the development of bilateral symmetry (a flower being the same on the left and the right but different on the top and the bottom) in orchids opened up the possibility of mimicking the morphology of pollinators because the symmetry of insects is also bilateral. If the orchid had radial symmetry like a daisy, the mimicking of an insect would have been near-to impossible.

The visual similarity of *Ophrys* species to female insects differs considerably in different species. *Ophrys insectifera* and *Oph. speculum*, pollinated by *Scoliid* wasps, are more exact copies of the female of their pollinator than *Oph. fuciflora* and *Oph. kotschyi* which are pollinated by bees. Some hymenoptera need a detailed mimic of their female, and some need only a suggestion. Van der Cingel claims that visual clues seem more beneficial for *Anthophoridae, Megachilidae, Sphecidae*, and *Scoliidae* whereas olfactory cues are more important to *Andrenidae* and *Colletidae*.

The hairs on the lips of *Ophrys* species help position the male with its head toward the column (cephalic position) or the head away from the column (abdominal position); *Oph. lutea* mimics the way the insect copulates with its own females. The process of pseudocopulation usually takes just a few seconds, but author Jean Claesssens observed *Argogorytes mytaceus* trying to copulate with *Oph. insectifera* for 35 minutes. Revisit rate is extremely low with very low fruit set.

Flies can also be duped by orchids. Exploitation of mating behavior has been an important factor in the evolution of Telipogoninae, a Neotropical subtribe. It contains 126 species in four genera. Flowers offer no reward but mimic female flies. The common name of these orchids is "La Mosca," "the fly," which they strongly resemble. Most of them have an insect-like swelling or callus on the lip. For example, parts of the lip of *Trichoceros* species closely mimic the spiny abdomen of the bristly female of tachinid carrion flies, and male carrion flies attempt to copulate with these flowers. The labellum, sepals, and petals are yellowish to cream-colored with dark red veins and a column that is hairy and usually purple. Calaway H. Dodson reported that the males of *Paragymnomma* species are attracted visually to *Trichoceros antennifer.* While olfactory cues are usually most important in sexual deception, this orchid ostensibly relies on visual stimuli. Leendert Van der Pijl and Dodson stated of the flower, "It is commonly so lifelike that it appears as though it could easily fly away." The shiny stigmatic surface at the apex of the false flower "abdomen" reflects sunlight as does the genital opening of the female fly. This is a fly signal for female mating receptivity. Amorous males who attempt to copulate with the orchids pick up pollinia on their legs. The long stipe then bends into a good position to attach to the stigma of the next orchid visited. Tachinid flies are particularly distinctive in size, color, and spininess of the abdomen, and orchids mimic the specific fly species leading to a very distinctive pollinator-flower relationship. Fly mimics are also found in the genus *Telipogon*.

Sexual deceit remained puzzling to prudish Victorian scientists at a time when the "legs" of pianos were covered for modesty. Darwin was puzzled by it. As a result, it was not until 1916 that it was figured out. A. Pouyanne, who was President du tribunal de Sidi-Bel-Abbes in Algeria, observed *Ophrys speculum* (the Mirror Orchid) for many years. He noticed that only male bees paid attention to the orchid and females paid no attention. When presented with a bouquet of the flowers, the females flew away "as if they were pursued with an unpleasant or annoying object." He asserted that the large blue spot in the center of the lip mimicked the wings of the females resting on a plant. He thought that the males were attempting to copulate with the flower and coined the term "pseudocopulation."

The publication went largely unnoticed until M. J. Godfrey confirmed it in 1923 in France where patrolling males were seen to visit *Oph.* x*arachnitiformis* in the same amorous way. There was an increased interest in the subject (sometimes called "Pouyannian mimicry"). This was followed by a string of publications in Australia from 1927 to 1938 in which Edith Coleman described her extensive research in the pollination of *Cryptostylis* species spp. by male *Lissopimpla excelsa*.

Pouyanne did many ingenious experiments. He cut off whole flowers and put them on the ground, and males tried to copulate with the flowers even when they were facing down. He even wrapped them in a bundle of newspapers with the same result. He cut off the lips and threw the lips on the ground and the bees tried to copulate with just the lips. He showed the importance of scent alone in exciting males to pseudocopulation.

Evolution of Sexual Deception in Orchids

How did sexual deception evolve? A number of species of the large genus *Caladenia*, from southern Australia, dupe insects. This genus gives us a good idea about how elaborate female decoys evolved. Alcock says that they may have originated visually in the form of widely separate rows of small, pale calli (thickened fragrant protuberances on the lip) as in *Caladenia vulgata*. Later, the scent-producing calli may have gotten darker, larger and closer together as in *Caladenia wanosa.* In *Caladenia discoides* (the Bee Orchid) and *Caladenia macrostylis* (the Leaping Spider Orchid), the lump of calli begins to look more convincing although still a very generalized decoy. In *Caladenia multiclavia* (the Lazy Spider Orchid), we see evolution into something like the genus *Drakaea* with a lip decoy packed with calli sitting on a flexible hinged labellum. There seems to be a progression from a flower petal that looks like a petal to one that resembles a female decoy.

It is suggested that at some time in the past, protocalli on the lip produced attractive odors to advertise nectar. If one of the volatile floral components accidentally mutated to bear a slight resemblance to an insect sex pheromone, the flower, with that mutation, might have had a reproductive advantage. The orchid might have attracted insects looking for mates as well as nectar. Further mutations that lead to higher reproductive success and a closer match to insect pheromones might have been selected.

Others suggest that orchids possess waxes for protection and waterproofing. The cuticular hydrocarbons found in the waxy coats of some orchids are similar to those in the cuticle or exoskeleton of some insects. If an orchid produced a waxy substance that incidentally attracted sexually-motivated male bees, it might have a reproductive advantage. Over time, the waxes that changed to produce good chemical mimics of female pheromones might attract more males and have better reproductive success.

Sexual deception leads to extremely loyal pollinators with a chemical attractant often aimed at a single species. Christian Ziegler points out that can lead to fine-tuning for better and better mimicking, evolving amazingly accurate imitations of pheromones. Once the orchid flower has started to mimic the chemical attract of an insect species, fine-tuning can happen quickly. Sometimes the flower can produce even more pheromone than the female insect leading to the occasional preference for the flower over the real female.

Alcock notes, "In some cases, the pollinator and the deceptive orchid appear to be in an arms race, with the orchids evolving better and better attractant scents and the pollinators evolving better and better discriminating capacity. Because females of each wasp and bee species have their own unique pheromonal blend, deceptive orchids are more or less forced to mimic the lures of one species. Doing this, they attract one species of insects which becomes the sole or chief pollinator and are unlikely to deposit pollen on another species which would be wasteful."

Irene Palmer, Darwin expert, points out that the evolution of complex flowers such as members of the *Ophrys* family is probably the result of just such an arms race between an insect and an orchid. Their flowers closely resemble the bees or wasps which pollinate them. They have had to keep pace with male insects' capacity to learn to detect differences between a real insect and an orchid flower which is mimicking a female insect. The flowers constantly evolve and change just to remain attractive to the insect. This is called the "Red Queen Effect;" the idea is based on Lewis Carroll's *Through the Looking Glass*. In the story, the Red Queen dragged Alice through the countryside, going faster and faster. When Alice expressed her astonishment, the queen told her, "It takes all the running you can do to keep in the same place."

Rendezvous Flowers or Cruising for Females

Robert Dressler, in 1981, suggested that rendezvous attraction might have been the first step in the evolution of pseudocopulation. Males tend to hang out around flowers where they might meet feeding females with which to have sex. Some orchids exploit the sex drive of male bees during mate-seeking flights. Male bees, patrolling flowers for females foraging on nectar and pollen, are sometimes deceived by orchids with similar colors, shapes, or scents as plants that females visit. This has been reported in the European species *Cephalanthera rubra* and *Anacamptis papilionacea* as well as in the African *Disa obtusa* and *Ceratandra grandiflora*. In *Cephalanthera rubra,* male *Chelostoma fuligunosum* bees inspect *Campanula* flowers for females during feeding. *Cephalanthera rubra* imitates these flowers but offers no nectar. Females of this bee species collect pollen from the bellflowers for their brood and males look for them around and in these flowers for a "rendezvous." The orchids cleverly start to flower about two weeks before the bellflowers do and at the same time that the *Chelostoma* males emerge from the outer cells in the nest burrow which is much earlier than the females.

Dressler felt the next stage in pseudocopulation evolution might involve the flowers emitting signals that release certain aspects of male sexual behavior. This step is represented by the East Mediterranean species *Orchis galilaea* pollinated exclusively by *Lasioglossum marginatum* males. The males land on the dark spots on the lip which suggests that the strong, musk-like scent of the lip is similar to the female pheromones. This intermediate stage is also present in the South Australian species *Caladenia patersonii* pollinated by tiphid males. In this species, sexual deceit is mixed with generalized food deception as the flowers are pollinated by insects of both sexes including bees and syrphid flies looking for food.

Sugarless Orchids and Food Fraud

Don't get me wrong—not all orchids are liars and cheats. A good 20,000 orchid species are "honest" and actually provide rewards to the pollinators who visit. These orchids trade nectar for pollination services. Nectar is a sugary solution usually produced from secretory tissue on the lip or in elongated labella spurs and is the reward that is advertised and desired. (Orchids don't usually offer pollen as a reward, as many other flowers do, since orchid pollen is packed in bundles as pollinia and delivered all at once as a sticky mass. If the insect were to consume the pollinia, nothing would be left for reproduction.) The remaining third of orchids are deceit flowers offering no reward. The greatest majority of the liars imitate the bright colors and sweet scents of flowers that offer nectar rewards. Insects are not rocket scientists, are often inexperienced or naïve and fall for the trick. The orchid trades lies for pollination services and quite often succeeds.

The presence of nectarless genera such as *Dactylorhiza* and *Orchis* has long puzzled botanists. In 1793, Christian Konrad Sprengel was the first to notice the empty spurs of *Orchis* species and claimed that he never found "sap" in the spur of *Datrr. majalis* and called this kind of flowers "Scheinsaftblume," a sham nectary flower. He could not understand why there was no nectar. In 1873-4, Federico Delpino supported Sprengel's claim and noted that these kinds of orchids were only visited by young, inexperienced bumblebees. He noted that, with time, they learned to avoid these flowers.

Sprengel's discovery was greeted with disbelief by Charles Darwin. In 1877, he rejected the idea of floral deception because he said that insects, particularly bees, were too intelligent to fall for "so gigantic an imposture." When studying orchids with no nectar in their spur, he supposed that the insects could pierce through to the inner wall of the flower and suck out the liquid. He observed little puncture bites in the membrane of the inner spur wall of *Datrr. maculata* and postulated that the insects were sucking sugary juices from the inner cellular space. Muller and others agreed. The overwhelming evidence now is that Darwin was wrong and that there are many orchids which deceive potential pollinators. The time it takes for the bee to fruitlessly search for nectar is enough time for the pollinia to stick firmly to the insect and to move into the best position to be picked up by the stigma of the next flower visited.

Hermann Ziegenspeck, in 1936, analyzed the papillae in the spur and thought they were food hairs or tis-

Anacamptis israelitica is a nectarless deceiver.

Calypso bulbosa var. *occidentalis* dupes naïve bumblebees twice.

Dendrobium infundibulum blooms at the same time as rhododendrons.

sues. However, E. Daumann, in 1941, argued that although all parts of the flower contained sugar, especially glucose, there was no sugar in the spur papillae of unrewarding orchids. He found that only a small percentage of bumblebees made holes in the spurs and that the inner cellular space was simply filled with air, not a sugary solution. It was Amots Dafni and Y. Ivri who suggested that the pollination of nectarless *Orchis* species might be based on the visual and perhaps olfactory mimicry of nectariferous flowers.

Food deception often relies on mimicry which falls into several classes: **Batesian mimicry**, **guild mimicry**, and **generalized mimicry**. H.W. Bates, a friend of Charles Darwin, described the form of mimicry that bears his name. Batesian mimicry requires three things: a model, a mimic- sometimes called an operator, and some advantage gained by the mimic. The model is the species being imitated. The mimic is the species doing the imitating. The advantage is what the mimic gets out of the deception. Bates, who described animals in Brazil, emphasized predator avoidance as a benefit. For him, the model was the poisonous monarch butterfly. The mimic was the innocuous bland-tasting viceroy butterfly which got the advantage of deterring predators by mimicking the monarch.

Batesian mimicry usually involves relatively rare species that benefit from an adaptive resemblance to a more common model or "magnet" species. Orchids are unusual in having lots of species but relatively few plants, usually spaced far apart. A pollinator might not find it worth its while to consistently be faithful to these orchids. It is sometimes better for the orchid to imitate an abundant rewarding flower with faithful pollinators. On the other hand, the orchid must not trick the pollinator so often that the pollinator wises up and being relatively rare makes it harder. As Christian Ziegler says, "Orchid's small numbers ensure their survival. If deceptive orchids were more common, the ruse would not work since they depend on the ubiquity of honest flowers."

It has been shown that flowers of some mimics bear such a close resemblance to the particular model species that the pollinators cannot distinguish between the two. Flower color appears to be the most critical factor. Food deception mimicry relies most often on pollinators that use color rather than scent as the primary cue. Bees can be deceived by mimics that match flower color even when they differ substantially in scent.

An example of Batesian mimicry occurs in the South African orchid *Disa pulchra* which closely resembles the nectariferous iris *Watsonia lepida*. John Alcock points out that both have a spike of about twenty showy pink flowers and are difficult to tell apart. A long-tongued horse fly, the iris pollinator, also has a hard time telling the two apart. Sometimes, it sticks its proboscis into the orchid and comes away with pollinia at the base of its proboscis but with no nectar for his trouble.

Disa ferruginea also relies on Batesian mimicry for food deception. This nectarless orchid is entirely dependent on the butterfly *Meneris tulbaghia*. There are two color-forms of this mimic, a red-flowered one studied by Steve Johnson in the southwestern Cape that imitates flowers of *Tritoniopsis triticea* and an orange one from the Langeberg Mountains that mimics *Knipho fiauvaria.* Butterflies cannot seem to distinguish between the rewarding models and the non-rewarding mimics when they are in a mixed stand. Interestingly, the orange form of the orchid has a shorter spur than the red form, which matches the shorter proboscis length of the butterfly in the terrain of the orange orchid form.

In Israel, the nectarless deceiver *Anacamptis israelitica* blooms simultaneously with its nectariferous model *Bellevalia flexuosa* which it strongly resembles. *Anacamptis israelitica* blooms interspersed with its model which outnumbers it by twenty to one. The two species share the same pollinators, *Eucera clypeata* and possibly *Anthophora* spp. *Bellevalia* serves as a magnet species to attract the bees to the orchid, and, when the two bloom together, the orchid fruit set increases from 2.8% to 27.2%. There is clearly an advantage to the mimic orchid.

Traunsteinera globosa, the Globe Orchid, mimics *Scabiosa columbaria* and some other species of composite-like flowers. Inflorescences of the nectarless *T. globosa* have a striking similar pink color, habitat, and blooming season as the *S. columbaria.* The tips of the hood parts of the *globosa* are knobbed shape like the stigma of the *columbaria* which emerge from the flower in an upright position.

There are many cases of Batesian mimicry in the genus *Cephalanthera*. *Cephalanthera rubra* and *Ceph. damasonium* mimic bellflowers, and *Ceph. longifolia* mimics rockroses. In the case of *Ceph. longifolia*, the pollinator receives a substitute for pollen in the form of orange papillae on the lip, "pseudopollen." This seems to work as an intoxicant for the bees. Botanists question whether this facsimile food and other forms of pseudopollen are a reward for the pollinator (Mullerian mimicry). This is an example of the gradual transition from a zero reward to some sort of reward, though not that which is expected.

Pseudopollen is found in several orchids and mimics real pollen. *Calypso bulbosa*, a very rare orchid, dupes naïve bumblebees twice. First it lures them to its mock stamens with its pseudopollen, and then it appears to have nectar in a dry nectary. Bumblebees rarely make a second visit to this orchid, having been deceived twice on the same flower which might be one reason why this orchid is increasingly rare. Although pseudopollen and other substances like it have been seen to be collected from orchids, there is no evidence that they provide nutrition to the insects.

In the Himalayas, many large-flowered, nectarless dendrobiums deceive bumblebees by mimicking rhododendrons. At that elevation, bumblebees, which can fly in the cold up to 19,000 feet (5791 meters), are the dominant plant pollinator. The female queen bumblebee, the only survivor of her colony, remains dormant underground, emerging in the spring before the rains begin, gathering nectar and pollen for her growing brood. Naïve and unschooled, with no mentors, she can be fooled early in the season by any orchid that looks as though it might have food. It takes her two-six flights to learn her foraging route. Early generations of male bumblebee offspring emerge in the spring before the monsoonal rains. The dendrobiums bloom in the spring at the end of the dry season, just in time to entice the naïve males as well. The bumblebees do not have a developed caste system or communication, and thus they all act individually as pollinators. Each one has a learning curve, and while the bumblebees are learning and making mistakes, the orchid is being pollinated.

Large honeybees fill the bumblebee Himalayan niche as a mid-altitude pollinator in peninsular India and Sundaland. The honeybees have sentinels that almost immediately alert the colony to a new mass flowering at the tops of the trees. The dendrobiums concurrently bloom with a mass blooming of its own. This "feeding frenzy" gets nectarless dendrobiums pollinated as part of the excitement of the general feeding frenzy.

Some *Tolumnia* species deceive the large female bees of the genus *Centris* by mimicking the flowers of *Malpighiaceous* vines. These tricky species include *Tolu. guianense, Tolu. quadriloba, Tolu. haitiensis,* and *Tolu. conpressicaulis*. These female bees gather waxes and oil from the paired sepaline glands of *Malpighiaceae* and place it on their hind legs where it is absorbed by the capillaries and carried to the brood cells, often mixed with pollen as food for the larvae. These energy-rich oils and waxes are highly sought by the female *Centris* bees, and they actively but fruitlessly visit the tolumnias looking for this food source.

Epidendrum radicans (and its similar cousins *Epi. secundum* and *Epi. ibaguense*) also invite butterflies for a dinner that is never served. These species are similar in that they have different color forms and overlapping habitats with similarly-colored morphs of *Asclepias curassavica* and *Lantana camara*, both of which produce nectar. Hummingbirds, butterflies, and skippers are misled by the similarity in color and do the reproductive work with no reward. This type of deception where two or more of the rewarding species resemble each other is sometimes called "guild mimicry."

Guild Mimicry

When a nectarless orchid imitates a whole group of orchids as the model, it is called "guild mimicry."

The most outstanding example of guild mimicry occurs with the orchid *Disa draconis* in southern Africa and its pollinator the mega-nosed fly or "Pinocchio fly" (*Moegistorhynchus longirostris*). His proboscis, the longest mouthpart of any known fly, protrudes four inches from its head, five times the length of its bee-sized body. In flight, the outstanding proboscis dangles between the insect's legs and trails behind its body. This weird organ enables it to reach deep pools of nectar inaccessible to less superbly endowed pollinators.

Evolution has left this amazing pollinator and its guild of unrelated long-spurred plant species dependent on one another, examples of extreme specialization. The plant guild of the mega-nosed fly includes a wide variety of plant families including geranium, irises, violets and orchids. Although unrelated, all these guild members are morphologically similar having long, straight floral tubes or spurs, brightly colored flowers that open during the day, and no scent. Steve Johnson

Guild mimicry has been reported in the southern Australian genera *Diuris* and *Thelymitra* . Image on Left: *Diuris orientis* and right: *Thelymitra erosa*.

Disa draconis and its pollinator the mega-nosed fly or "Pinocchio fly" (*Moegistorhynchus longirostris*).

and Kim Steiner studied *Disa draconis* and found that, unlike the others in the guild, *draconis* has no nectar. The fly is deceived into visiting and pollinating the orchid because of its resemblance to other rewarding flowers in the guild. This false advertising is all that is necessary for the reproductive success. Such extreme specialization comes at a cost. The mega-nosed fly is threatened by the loss of wetland breeding habitat and by the loss of other insects they parasitize during their larval stage. Already, some flowers in the long-nosed guild produce no seeds because their exclusive pollinator is locally extinct.

Guild mimicry has been reported in the southern Australian genera *Diuris* and *Thelymitra* which resemble legumes and buzz-pollinated lilioids or dicots respectively. In the South African genus *Disa*, several species form parts of guilds pollinated by butterflies or long-proboscid flies. Guild members converge in flowering time, spur or flower-tube length, and flower color.

Peter Bernhardt and Pamela Burns-Balogh found that *Thelymitra nuda*, another nectarless orchid, mimics a guild of petaloid monocots in the family Anthericaceae. The orchid has the same blue-to-mauve tepals as the model species but has bushy, hairy lobes in the center of the flower mimicking pollen and stamen whereas the models have stamens. The deceiving orchid is pollinated by the same pollen-collecting bees which are fooled into thinking that the tricky orchid has pollen.

In addition, *Diuris maculata*, another nectarless orchid, is thought to be a Batesian guild mimic of similarly-colored flowers of "egg and bacon" peas in the various genera of *Mirbelieae* and *Bossiaeae*.

The similarity of the orchid to the models is striking in near-ultraviolet light visible to their shared bee pollinators, two species of Tricholette bees and one species of Leioproctus bees.

Generalized Food Deception or Non-Model Mimicry

Often, deceptive orchids do not resemble a particular nectariferous plant, but generally look like flowers that might have nectar on tap. Orchids, which practice this type of deception, often invest in a very showy floral display, often producing up to 30% more flowers per inflorescence to increase the chance of being noticed by a pollinator. The Western Australian *Elythranthera emarginata* (pink enamel orchid) has big, shiny, colorful, easy-to-locate flowers, a "flashy come-on," as Alcock states, that advertises nectar but is all show.

There appears to be a continuum between generalized food deception and a true resemblance to a particular flower. Johnson states that if an orchid does not evolve with a stable group of species, as might happen in repeated ice ages, it would be better to look like a nectar flower so you can exploit a number of "magnet" species. As he says, "The latter scenario seems more likely in the European flora, which is characterized by floral assemblages which are unlikely to have remained stable in the face of postglacial and anthropogenic changes." A mimic that is an exact match to a model may not have had time to evolve.

Anacamptis papilionacea and *Ant. boryi* show more generalized mimicry and can exploit a number of similarly-colored species. For example, *Ant. papilionacea* blooms alongside a variety of nectariferous species (*Salvia fruticosa, Asphodelus microcarpus, Bellevalia flexuosa*) and benefits by having a higher fruit set when alongside these rewarding flowers.

Orchis mascula uses generalized food deception exploiting the innate foraging behavior of insects. The orchid has a generalized resemblance to rewarding plants without specifically mimicking any one of them. Recently emerged naïve bees or insects on exploratory flights will visit it. The bumblebee queens can be deceived for a short period which coincides with the blooming of the flowers. The other pollinators, *Psithyrus* females, emerge later and visit places with abundant food flowers. In the process, they visit the orchid which blooms nearby, mainly the lower flowers which open first, since the insect learns not to visit the other flowers on the stalk. The attraction is based on visual and olfactory cues.

The Western Australian *Elythranthera emarginata* has big, shiny, colorful, easy-to-locate flowers, a "flashy come-on,"

Anacamptis papilionacea shows more generalized mimicry and can exploit a number of similarly-colored species.

In Eastern Australia, *Caladenia congesta* (the Black-Tongued Spider Orchid) mimics a lot of Australian plants which have black porous anthers that require rapid shaking to dislodge the pollen. The *congesta* lip has a large mass of black calli which project out. The orchid mimics these buzz-pollinated plants to lure the bees which fruitlessly attempt to shake the non-existent pollen from the lip.

Having several color morphs seems to increase pollinator success with general food deception orchids. Sometimes, the pollinator learns to avoid the mimic with time. In these cases, having another color morph slows learning. *Dactylorhiza sambucina* is exclusively pollinated by inexperienced bumblebee queens when they are still exploring their foraging territory. After a week or so, the queens establish nests and the number of visits to the nectarless orchid rapidly declines. While the queen is learning, she may learn to avoid the yellow morph of the orchid, but she will visit the purple morph until she learns that this, too, is unrewarding. *Anacamptis morio* and *Orchis mascula* also have similar color morphs ranging from purple through pink to white.

Cleistesiopsis divaricata also exhibits color variety. This nonrewarding orchid operates as a bee-food flower mimic exploiting naïve bees. *Divaricata* has polymorphism with flowers ranging from pale pink to deep rose and with different contrasting strips or mottled lip patterns. It is thought that this, too, is to prevent bees from learning to avoid flowers before trying out several. The orchid also has varied sepal configurations which might also slow down avoidance learning.

Imitating Fungus-Infected Foliage

Cypripedium fargesii, a critically-endangered species endemic to southwestern China, uses another deception to attract its flat-footed fly pollinators. Each short flowering stem bears rows of black spots on the upper surfaces, and the stem terminates in one small dark-red to dull-yellow flower with a faint unpleasant odor of rotting leaves. The orchid leaves mimic fungus-infected plant tissue and attracts fly pollinators that feed on exudates of plants infected with Cladosporium mold. When Cladosporium infects leaves and fruits, it produces black mold spots. The black spots on *C. fargesii*, along with the rotting leaf smell, fools these flies into thinking they are going to get a rotting leaf meal. Instead, they get nothing but a chance to pollinate this orchid.

According to Marc Hachadourian of the Bronx Botanical Gardens, it has been hypothesized that the jewel orchids with veins, like *Anoectochilus* and *Macodes* hiding as they do among the rotting leaf litter, may also mimic fungal hyphae. No published studies confirm this.

Brood Site Imitation: Come Lay Your Eggs on Me

Deception does not always involve the false promise of food or sex. Sometimes, orchids promise insects that they are a wonderful and appropriate place for them to lay their eggs—brood site imitation. The victims of this type of deceit are mostly Diptera (flies) and occasionally Coleoptera (beetles). Many fly larvae do not move very far to find a food source, so the female fly tries to make sure that her larvae will have a good place to develop. This deceit occurs in many highly-evolved plant families including Aristolochiceae, Asclepiadaceae, Araceae, Burmanniaceae, Hydnoraceae, Rafflesiaceae, Taccaceae, and, of course, Orchidaceae. Although the syndrome is absent from Europe, it is most common in the tropics (although examples do exist in temperate species.) Flowers tend to imitate desirable egg-laying sites such as carrion (sapromyophily), dung (copromyophily), mushrooms, or the fruiting body of fungus (mycetophily). Johannes Stokl and associates state, "With approximately 11% of orchid genera using brood-site mimicry, this is one of the most widespread deceptive mechanisms in the Orchidaceae."

Some of these flowers have traps to force the pollinator to linger a while, improving pollination chances. These orchids are often not passive and manipulate their pollinators into exactly the right place and position to receive or deposit pollinia. These involve one-way bristles, transparent windows, a one-way passage pouch or a mobile lip trap. Orchid genera that coerce insects with these tricks and traps include *Pterostylis, Paphiopedilum Bulbophyllum, Cirrhopetalum, Megaclinium, Anguloa, Masdevallia,* and *Pleurothallis*. Some have mobile filiform appendages (tails) which often produce scent or some are full of spots or hairs. Some like *Bulbophyllum medusae* use long moving parts to attract attention. Some orchids display the "fungus-gnat syndrome." Fungus gnats like to lay their eggs on fungus and are attracted to anything mushroom-like. S. de Vogel, in 1978, collected examples of fungus-mimicry in *Masdevallia* where the lip of the flower even had a horseshoe shape and radiating gill-like ridges on the side that faced downward just like a mushroom. In another example, the Australian genus *Corybas* has dark-colored flower heads borne near the ground level, mimicking the fruiting bodies of basidiomycetes (mushrooms). In a similar way, many of the South American genus *Dracula* have a mushroom smell and a fungus-shaped lip. The Japanese *Cypripedium debile* and *Cyp. fasciculatum,* native to coniferous forests of North America, bear modified flowers that droop near the ground and have a pouched lip whose entrance bears resemblance to small mushrooms. It emits a strong mushroom odor. Of course, this is just a trick. There is nothing at all mushroom-like for the larvae to eat on these flowers, and their offspring will sadly perish. However, the orchid stands a reasonable chance of getting pollinated, the point of this exercise.

Syrphid flies or hoverflies like to lay their eggs on plants that are infested with aphids. The adults feed on nectar or pollen, but the larvae feed on aphids and their honeydew excretions. *Epipactis veratrifolia* misleads female hoverflies by bearing structures that look and smell like aphids. On the epichile of the lip, there are small, orange, drop-like lumps like honeydew. On the hypochile are a number of black warty bubbles that look very aphid-like. The flowers produce the same volatile compounds as are found in the alarm pheromone of some aphid species. The aphids not only produce this compound when under attack, but they also produce a little of it all the time. It then is a reliable way of locating an aphid colony. The scent induces oviposition (egg-laying) in females of hoverflies like *Esisyrphus balteatus. Epipactis. veratrifolia* produces a scent that is similar to that of a number of aphid species. This generalized mimicry makes sense since its five pollinating hoverfly species feed on a number of different aphid species.

Dracula saulii has a mushroom smell and a fungus-shaped lip exhibiting the "fungus-gnat syndrome."

Several genera coerce insects with tricks and traps incluing *Anguloa* and *Pterostylis*. On left: *Anguloa virginalis* and on right: *Pterostylis scabrida*

Epipactis veratrifolia shows just how complicated deception can get. The flowers present a real nectar reward in addition to the deceptive impression of an aphid reward. Small amounts of nectar are presented freely on the lip. Males may try to defend the territory around the orchids and try to copulate with females approaching the flower. They may contribute to pollination as nectar feeders. The females hover, land on the lip, may lick the nectar, and lay an egg on the lip or other parts of the flower. They may pollinate the flower while licking and laying. Is this really a deceptive orchid? It does present a small amount of actual nectar reward, but it is, on the other hand, advertising a different reward from that which is actually provided, which is indeed deception.

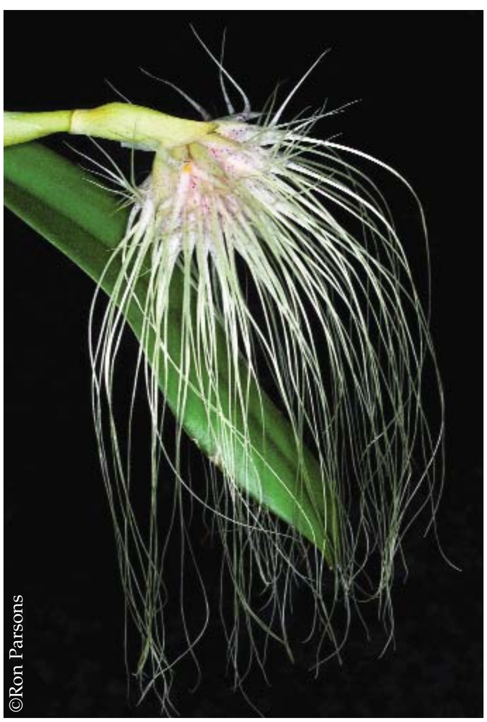
The large Asian genus *Paphiopedilum* attracts hoverflies to lay eggs on the staminode with its own version of aphid mimicry. John T. Atwood, in 1985, studied the syrphid fly *Dideopsis aegrata,* a regular pollinator of *Paphiopedilum rothschildianum* on Mt. Kinabalu. The flower emits a peppery smell and mimics brood sites of the female flies with the staminode and glandular hairs looking like an aphid colony. Aphids are usually found on nectariferous plants in the same habitat. Atwood found as many as 76 eggs on one staminode. It is thought that the egg-laying behavior is stimulated by lots of promising smells and structures—lines, spots, warts, textures, and contrasting colors. The fly falls in the pouch of the orchid and takes about a minute to climb out, pollinating the orchid after laying its eggs.

In *Paphiopedilum villosum*, color contrast is the long-distance lure with hoverflies attracted by the bright yellow staminode. The odor has been described as faintly like urine, which mimics the body fluids rich in salt that hoverflies like. Close-range attraction is thought to be the glittering staminode which suggests honeydew. There is a slippery wart in the center which throws the fly into the pouch. When the hoverfly climbs out, pollinia is attached to the thorax.

In the subtribe Pleurothallidinae, flies are often attracted by the smell of decay in sapromyiophilous orchids such as many species of *Pleurothallis, Masdevallia*, and *Bulbophyylum*. The rotten smell resembles their egg-laying site although, in others, it resembles a food source. Vogel suggested that, in many pleurothallidines, the flies are guided by osmophores on long appendages or flowers with smells like semen in *Myoxanthus reymondii*, musk in *Masdevallia caudata*, trimethylamine in *Diodonopsis erinacea*, or rancid butter in *Specklinia fuegi*. Bulbophyllums often have a nasty smell like decaying flesh, fungus, dirty diaper, or cat urine. To us, these are stinky, funny-looking, odd flowers. To the flies, they must seem beautiful and desirable places to entrust their offspring. For flies, it seems that bad smells are good things.

Prey Imitation or Food for Your Larvae

Close to the subject of brood site deception is prey imitation. An example of this is provided by the flowers of the rewardless orchid, *Dendrobium sinense*, a species endemic to the Chinese Island Hainan. Its sole pollinator is the hornet *Vespa bicolor.* The hornet likes to feed its larvae honeybees, and the orchid mimics the alarm pheromone of honeybees in order to attract prey-hunting hornets for pollination. The flower is white



Bulbophyllum medusae uses long moving parts to attract attention.

Corybas fordhamii has dark-colored flower heads borne near ground level, mimicking the fruiting bodies of mushrooms.

Paphiopedilum rothschildianum emits a peppery smell and mimics brood sites of the female flies with the staminode and glandular hairs looking like an aphid colony.

with a red center. Attracted by the distress call of the honeybees, the hornet pounces on the red center of the flower just as though it were attacking prey. Removal or deposition of pollinia occurred in 5 out of 30 visits. The orchid has adapted to the height and width of the pollinator to maximize pollination success.

In another study, flowers of *Epipactis helleborine*, pollinated by a wasp, emitted green-leaf volatiles (GLV) to attract foraging social wasps. This chemical is released by plant tissue that has been damaged by herbivorous insects like the caterpillar *Pieris brassicae*, a common prey item for wasps. The wasp visits the orchid to get the caterpillar but is just being tricked by false advertising and gets nothing. The orchid gets pollinated.

Pseudoantagonism or Get Out of My Space

Oncidiums are sometimes pollinated by territorial *Centris* bees which patrol the areas around their females by chasing away other bees; they deceive the bees by looking like intruding bees. The bees sit on high observing the surrounding area, and the oncidium flowers, dancing in the breeze are attacked as though they were intruding males. In the course of the attack, the bees touch the viscidia and pick up pollinia on their foreheads. It is thought that the outstretched petals with colored bars acts as a flight-pattern guide for maximum pollinia distribution. The territorial behavior is so strong that captured bees will return to defend the same territory after release. This attack on flower after flower is called "pseudoantagonism" although Dressler thought it should be called "pseudotrespassing." Examples of flowers involved in this deception are *Oncidium hyphaematicum*, *Oncidium planilabre*, *Trichocentrum lacerum*, and *Tolumnia bahamensis.*

Shelter from the Storm

Unlike females who sleep in the nest, males of many bee species sleep in nest holes when they have a chance to, in the open, or under the protection of a flower. Godfrey, in 1931, found that the Mediterranean genus *Serapias* offer such shelter to bees. Bees were observed entering *Srps. cordigera* and found sleeping in flowers of *Srps. vomeracea*. Pollination occurs in the afternoon when the males move from flower to flower searching for a sleeping hole. The sun in the morning warms these flowers to 3° F above ambient temperature. The orchid mimics the normal sleeping holes of the bees.

The genus *Serapias* seem very attractive to bees with six bees found in one plant, one bee to a flower. Only some of the plants were attractive to the insects although nobody knows why these were more desirable as a sleeping place. On one plant over 20 bees were pushing and shoving to find the best places. Females just used the plants in the afternoon to bask in the sun as they have their own nests.

As Kean Claesssens and Jacques Kleynen state, "Serapias apparently exploit their searching behavior by imitating a hole. The side lobes of the lip are quite dark, contributing to the creation of a dark, imitation hole. The setting sun makes the lip lighten, increasing flower conspicuousness." The flower has a tunnel-like appearance. Many different size insects can be accommodated in this deep tunnel, positioned in just the right way for pollinia to be attached to the forehead. Since bees probably obtain real shelter from the orchid, the characteristic as "deceptive" is open to debate. The plant is not a nest hole, just imitating one, but some claim if it is functioning as one, it is not REAL deception. This is yet another example of the complexity of the subject.

Why Did Deception Evolve?

There are many unsolved questions about why deception evolved in orchids preferentially and what advantages it may hold for the orchid. Deceptive orchids often show a markedly lower fruit set than rewarding species, only 2% in cypripediums, for example, during a 10-year study. Fruit set in other deceptive orchids is often very low, in the 17-20% range, so it would seem to be a disadvantage to rely on deception as a strategy. Many theories have been advanced for the evolution of deception. Schiestl includes the cost of nectar, low density, pollinia, pollinia loss, pollinia removal, and isolation, all of which need more tests and empirical proof. The theory that seems to have the most support at the present time is that deception promotes outcrossing, which is good for fitness and survival of the species.

Disappointed, frustrated pollinators tend to leave deceptive orchids more quickly, tend not to pollinate other orchids on the inflorescence and fly further away before their next copulation attempt. For example, in the sexually-deceptive *Caladenia tentaculata*, pollinators leave a patch after pseudocopulation and 87% of pollination events are outcrossing. Mean distance of pollen flow is 15.2 meters (45 feet) and maximum pollen flow is 58 meters (175 feet), much further than the nearest neighboring plant. In *Drakaea glyptodon*, pollinators fly as far as 132 meters (396 feet) after a pseudocopulation attempt. Insects that receive rewards in orchids tend to stay longer, visit more flowers on an inflorescence, and generally stick around in the neighborhood that has proven rewarding. Many studies, particularly in sexually-deceptive orchid systems, indicate that deception promotes beneficial outcrossing. Low fruit set does not necessarily indicate sexual failure but a trade-off that benefits the orchid by promoting sexual variety through outcrossing.

In addition, in the case of sexual deception, a whole new niche of pollinators becomes available, a group of sexually-aroused insect males. This new pool of pollinators increases the number of insect visitors available for pollination. However, Floria Schiestl adds, "Our understanding of the ultimate causes of deception in orchids remains very incomplete, and we need more studies addressing the link between deception and out-

Pollination of *Drakaea glyptodon*, step 1.

Pollination of *Drakaea glyptodon, step 2.*

Pollination of *Drakaea glyptodon*, step 3.

breeding, offspring quality, lifetime reproductive success, and the usage of pollinator niches."

It is thought that deception reduces geitonogamous pollination (pollination of more than one flower on the same inflorescence). Geitonogamy may reduce female fitness by producing inbred seeds that develop more slowly or abort in the early stages of development. It may also mean that less pollen is available for export to other flowers. Since orchids rely on pollinia, fertilization is highly efficient, and all of a flower's pollen may be transferred at once. This makes the impact of geitonogamy more severe. For orchids that produce thousands of seeds per capsule, the production of a few, high quality fruits and the maximization of pollen export may increase lifetime reproductive success more than a lot of poor quality capsules.

Although sexual deceptive is clearly a derived trait, food deception (or at least nectarless flowers) may be an ancestral trait in orchids, suggested by the nectarless flowers of primitive orchid genera such as *Apostasia* and *Neuwiedia*. Schiestl suggests that, in genera like *Disa* and *Anacamptis*, nectar evolved secondarily from food deception.

It is amazing to realize the number of cheating and lying orchids. Whether by pretending to be a food source, a willing and eager female, an invading male, or a friendly motel, orchids have made their living by the success of their swindle, and successful they have been. By raising mendacity to a high art, orchids have managed to survive in difficult times and difficult places. Our hats off to these lying, cheating, sexy survivors.✾

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About the Author

Carol Siegel, a retired English teacher and medical office manager, has been president and newsletter editor of the Greater Las Vegas Orchid Society for several years. She has spoken on 'The Sex Life of Orchids' at societies, museums, and universities around the country and has written articles on Nevada's native orchids in addition to many for the Orchid Digest. Carol leads groups of Clark County school children on tours of the Springs Preserve, a museum and nature center complex.

Carol Siegel
E-mail: growlove@cox.net