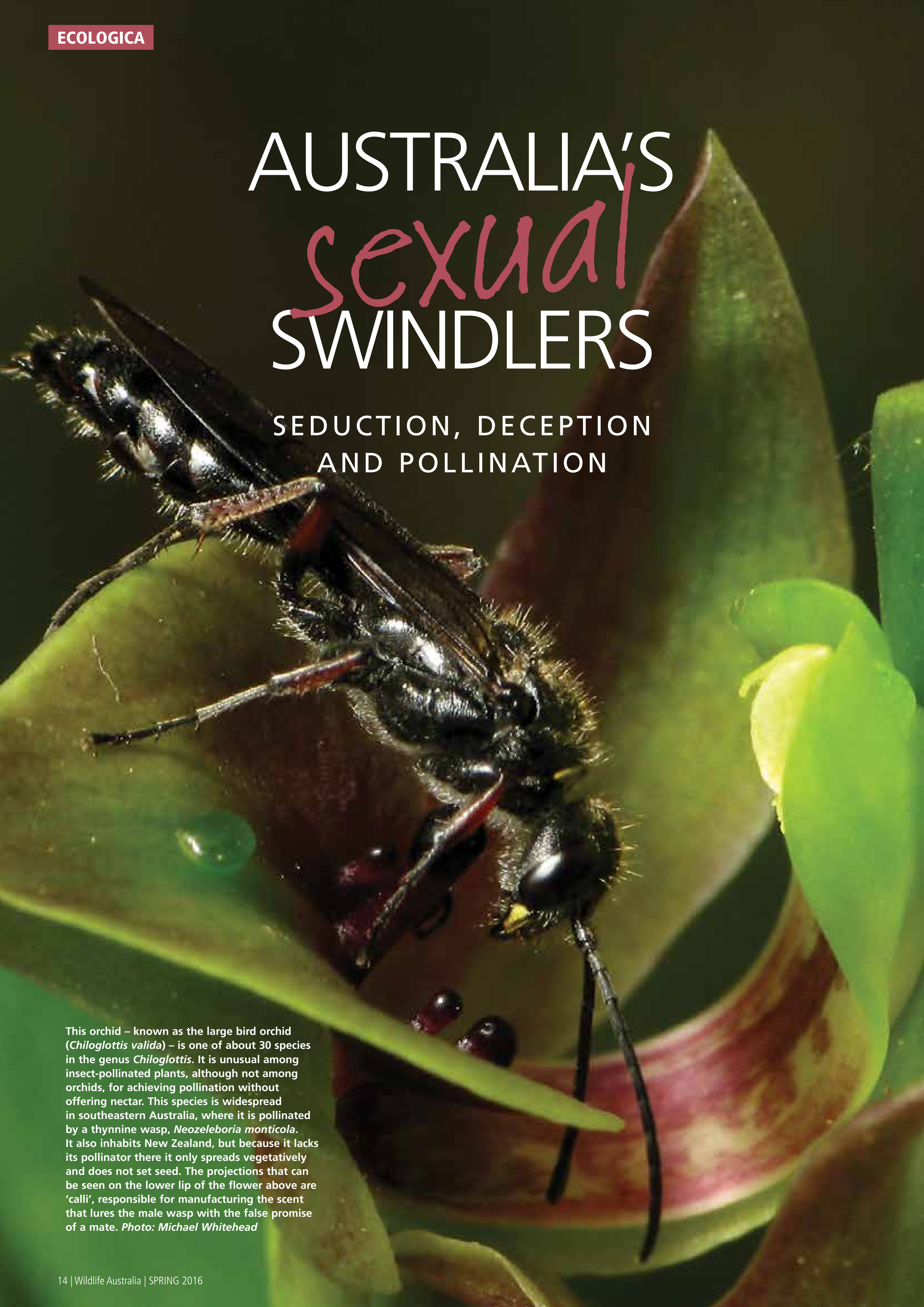

AUSTRALIA'S *sexual* SWINDLERS

SEDUCTION, DECEPTION AND POLLINATION

This orchid – known as the large bird orchid (*Chiloglottis valida*) – is one of about 30 species in the genus *Chiloglottis*. It is unusual among insect-pollinated plants, although not among orchids, for achieving pollination without offering nectar. This species is widespread in southeastern Australia, where it is pollinated by a thynnine wasp, *Neozeleboria monticola*. It also inhabits New Zealand, but because it lacks its pollinator there it only spreads vegetatively and does not set seed. The projections that can be seen on the lower lip of the flower above are 'calli', responsible for manufacturing the scent that lures the male wasp with the false promise of a mate. *Photo: Michael Whitehead*

Hundreds of Australian orchids lure their pollinators with a false promise of sex. Botanist **Michael Whitehead** explains how they get away with it and why it's so successful.

Bird orchids are not much to look at. They huddle modestly on the forest floor among bracken, snowgrass and rotting logs, each twin-leafed plant holding aloft a lone flower. It is spring in the Blue Mountains. The understory thrums with newly emerged insects, as flowers vie for their attention with billboards of saturated colour and alluring perfumes promising sweet nectar. The diminutive bird orchid flowers, dressed in subdued shades of green and burgundy, are easy to overlook. But they beckon one animal with an irresistible power.

Zipping about among the insect hordes are the slender flower wasps. As they fly in characteristic swinging arcs, they sample the air's odour plumes, hunting for a specific scent. Occasionally, one alights on a bird orchid. It spins frantically, searching, then probes with its abdomen and clutches at projections on the orchid's lower petal. When lined up, it bumps the orchid's sex organs and is promptly loaded with a bright yellow package of pollen.

In this encounter the orchid and wasp each sought a mate. When the wasp leaves bearing pollen, the orchid is on its way to achieving pollination, but the wasp has been duped and wins nothing – no mate, and not even a sip of nectar.

As in fully one third of all orchids, the bird orchids are tricksters in not providing a nectar reward to their pollinators. Instead, they achieve pollination by sexual deception, luring male flower wasps by mimicking the sex pheromone of receptive females.

This seems an unlikely scenario. What are the odds of an orchid's floral scent evolving to precisely match the compound emitted by receptive female wasps? It also seems precarious. Each wasp species typically emits unique sex pheromones, so the mimicry locks an orchid into relying on a single pollinator species. If the wasp learns to avoid the orchid's scent, or if it goes extinct, the orchid is probably doomed.

But far from being an evolutionary quirk, sexually deceptive pollination has evolved numerous times in orchids, including a remarkable six times (at least) in Australia. Scattered across the country are hundreds of sexually deceptive species. Among them are spider orchids, elbow orchids, hammer orchids, dragon orchids, duck orchids, hare orchids, beard orchids and greenhoods. With more than half the world's reported cases, Australia is a hotspot for sexually deceptive pollination.

I have spent several years investigating sexual deception to better understand how it works and why it succeeds. It is a compelling example of the power of evolution, and an opportunity to study the interface between plant evolution and insect behaviour and cognition – flowers as the product of a pollinator's internal world.

For my PhD I studied two bird orchids. The large (or common) bird orchid (*Chiloglottis valida*) is widespread in moist gullies and on sheltered slopes in the central and southern ranges of southeastern Australia. *Chiloglottis* aff. *jeanesii* (undescribed but closely related to the mountain bird orchid, *Chiloglottis jeanesii*) is known from two locations nested within the range of *Chiloglottis valida*. The two species often grow intermingled, they are difficult to tell apart, and both flower at the same time of the year.

Solving the puzzle

Charles Darwin was mystified by orchids that did not offer nectar. In his 1862 book which launched the foundations of pollination biology with the convoluted title *On the Various Contrivances by Which British and Foreign Orchids Are Fertilised by Insects, and on the Good Effects of Intercrossing*, he explained how orchid flowers could be shaped by natural selection through cross-fertilisation by insects. But, he wondered, how do the orchids offering no reward persuade insects to keep pollinating them? And why do the flowers of genus *Ophrys* resemble insects, as reflected in their popular names – the bee orchid (*Ophrys apifera*) and the fly orchid (*Ophrys insectifera*)? He dismissed one current hypothesis that they were intended to deter insects. In a footnote he mentioned observations by a Mr Price of frequent attacks by a bee on the bee orchid, and added, 'What this … means I cannot conjecture'.

An Australian naturalist was among the first to answer Darwin's puzzles about orchids. In 1927 Edith Coleman, a school teacher in Blackburn, Victoria, turned her talent for observations of the natural world to a peculiar native orchid. Resembling flesh more than flower, the tongue orchids (genus *Cryptostylis*) had caught her attention for their allure to *Lissopimpla excelsa*, now known as the orchid dupe wasp. She discerned that the male wasps were 'answering to an irresistible sex-instinct', and found ejaculate on the flowers. By an experiment through a window she showed that a scent barely detectable to humans seemed to 'lure the insects to the flowers from quite a distance'.

Targeted marketing

In an impressive display of targeted marketing, the two bird orchids I studied have each 'tuned in' to a different flower wasp through subtle variations of a chemical lure. *Chiloglottis valida* emits a molecule dubbed 'chiloglottone 1' that attracts one flower wasp, *Neozeleboria monticola*, while *Chiloglottis* aff. *jeanesii* emits 'chiloglottone 3', which attracts an undescribed species in the same genus. The discovery of the structure of chiloglottones by researchers at the Australian National University has created the exciting potential to experimentally probe the evolutionary causes and consequences of sexual deception. By lacing pin heads with each of the molecules, and allowing wasps of each species to choose between them, I was able to prove that each chiloglottone entices only a single species. There was no cross-attraction.

The use of a signature sex pheromone ensures that an orchid doesn't waste pollen on the wrong wasp, and keeps the two bird orchid species from hybridising with each other. Through artificial hand-crosses I showed that the two species were capable of producing hybrid offspring, even though this does not occur in nature. The reproductive gulf between these two species due to the slightly different scents they produce implies that selective pollinator attraction can drive the creation of new species.

This could help explain why Australia is home to so many sexually deceptive orchid species, for we are rich in potential orchid pollinators. Most of our sexually deceptive orchids, including the bird orchids, attract wasps from the Thynnidae family. A recent study in a small patch of bush near Margaret River in Western Australia uncovered a staggering 28 thynnine wasp species, most previously unknown to science. With each of these species most likely having their own private sex pheromone, there is a kaleidoscope of chemical communication channels for different orchids to exploit.

The hapless wasps

Very little is known about thynnine wasps. The females are wingless and live most of their adult lives underground, where

Chiloglottis valida* (left) and *Chiloglottis aff. jeanesii* (right) are the two sexually deceptive bird orchids studied by the author. With only minor differences in appearance, they are very difficult to tell apart. Despite being capable of cross-breeding, their gene pools are isolated from each other because they attract different pollinating wasps. *Photos: Michael Whitehead

The discovery of the chemical structure of the sex pheromones emitted by female wasps of the genus *Neozeleboria* has paved the way for some exciting experiments with the pollinators of bird orchids. The author tested the learning ability of *Neozeleboria cryptoides* wasps by enticing them to a dressmaker's pin spiked with synthetic sex pheromone (left), trapping them and attaching a 0.5 millimetre microdot label (right) for identification. The wasps showed limited ability to learn from their failure to find a mate on the pinhead, and returned to it the following day. *Photos: Michael Whitehead*

they are thought to lay their eggs in the larvae of wood- or soil-dwelling ants or beetles. When ready to mate, they emerge, climb to the top of a shrub or blade of grass, and 'call' for a male by emitting the pheromone. The fast-flying males race to respond, for the first to arrive gets to scoop up the female and carry her away. Mating occurs on the wing, and in true dinner-and-date style, the couple stops for a feed at a nectar flower before the male drops his mate back at ground level.

A tryst with a deceptive orchid offers a duped wasp nothing. Even worse, it may deprive him of mating opportunities if he is diverted from a female wasp or cannot find one among the false advertisements. There are even documented cases of male wasps dropping females in preference for an orchid.

The orchids' success depends on the male wasps failing to learn from their first experience of being duped. To test this, I needed a way to identify individual wasps in the field. The smallest radio-transmitters are too big for these wasps, so I used 'microdots', tiny discs with miniature serial numbers used to label car parts to trace thefts. By luring wasps to a synthetic pheromone bait, capturing them with a net, marking them with a microdot, then releasing them and measuring their return, I was able to test the learning ability of *Neozeleboria cryptoides*, which pollinates the broadlip bird orchid (*Chiloglottis trapeziformis*). I found that wasp visits to the synthetic pheromone declined rapidly after just one minute and remained low all that day. But many of the same wasps returned to the synthetic bait the next day, ready to be duped all over again, implying that if they did learn at all – suggested by the initial avoidance – they had forgotten it within a day.

A winning strategy

Pollinators of honest plants (those that offer nectar for pollination services) frequently move between flowers on the same plant or neighbouring plants. Called 'optimal foraging', it makes economic sense for a pollinator to exhaust the nectar supplies in a patch before putting energy into finding a new buffet. But it can lead to inbreeding problems for plants. Neighbours are usually close relatives, so short pollen movements are likely to result in less fit, inbred offspring. This is a high risk for bird orchids, for they form colonies of clones by budding off from underground tubers. The seeds produced by genetically identical parents germinate and grow less than half as well as those from unrelated parents.

That is why the short memory of flower wasps is helpful for bird orchids. Directly after being fooled, the wasp not only leaves the offending orchid but then actively avoids it, moving pollen beyond the colony boundary. In a genetic study, I found that bird orchids were sired by fathers a median 14 metres away

Sexually deceptive orchids are much more common in Australia than once thought. Twenty years ago, it was thought there were about 70 such species. The most recent tally is more than 300. They are richest in southwest Western Australia – the carousel spider orchid (*Caladenia arenicola*, left) is one of dozens of sexually deceptive species there. They are also rich in southeastern Australia, where this mantis orchid (*Caladenia tentaculata*, right) is quite common. *Photos: Michael Whitehead*

Australia abounds in sexually deceptive orchids and even more so in thynnine wasp species that can potentially be fooled into pollinating them. Here are three examples from Western Australia. Left: wasps (*Zaspilothynnus nigripes*) tussle over the Carbunup king spider orchid (*Caladenia procera*), a critically endangered species. Centre: *Zaspilothynnus nigripes* is also the pollinator for a related species, the king spider orchid (*Caladenia pectinata*). Right: the hammer orchid (*Drakaea glyptodon*) is pollinated by *Zaspilothynnus trilobatus*. Photos: Michael Whitehead*

(a substantial distance for a plant just 10 centimetres tall), and some were separated by more than 100 metres.

Writers have often portrayed orchids as plants of agency and intelligence. Through their astounding manipulation of pollinator behaviour, the sexually deceptive species certainly live up to this reputation. Edith Coleman wrote in the *Victorian Naturalist* that the orchids she studied had 'a Machiavellian cunning almost beyond belief'. The exploitation of wasps' mating behaviour solves a problem all plants face: how to not only attract a pollinator but persuade it to leave quickly. In so doing they maximise the distance their pollen travels and thereby the quality of their offspring. By duping one species into servicing them exclusively, they avoid pollen waste. And by deceiving rather than rewarding their pollinators they avoid the costs of nectar production and most of the advertising costs as well.

A tryst with a deceptive orchid offers a duped wasp nothing.

Even though we have learned much about the natural history of sexual deception, the reason for it evolving at least six times in Australian orchids remains a mystery. Work at the cutting edge of genetics by Rod Peakall and his team at the Australian National University may soon provide some answers. They suspect that an ancestor of the tribe left a genetic legacy, such as a duplicated gene, which codes for a chemical at the base of the manufacturing pathway for floral scents. This may have provided the grist for the evolutionary mill to repeatedly generate new molecules for sexually deceptive pollination. ■

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