IDEAS & PERSPECTIVES

Are some species 'robust' to exploitation? Explaining persistence in deceptive relationships

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Abstract

Animals and plants trick others in an extraordinary diversity of ways to gain fitness benefits. Mimicry and deception can, for example, lure prey, reduce the costs of parental care or aid in pollination–in ways that impose fitness costs on the exploited party. The evolutionary maintenance of such asymmetric relationships often relies on these costs being mitigated through counter-adaptations, low encounter rates, or indirect fitness benefits. However, these mechanisms do not always explain the evolutionary persistence of some classic deceptive interactions.

Sexually deceptive pollination (in which plants trick male pollinators into mating with their flowers) has evolved multiple times independently, mainly in the southern hemisphere and especially in Australasia and Central and South America. This trickery imposes considerable costs on the males: they miss out on mating opportunities, and in some cases, waste their limited sperm on the flower. These relationships appear stable, yet in some cases there is little evidence suggesting that their persistence relies on counter-adaptations, low encounter rates, or indirect fitness benefits. So, how might these relationships persist?

Here, we introduce and explore an additional hypothesis from systems biology: that some species are robust to exploitation. Robustness arises from a species' innate traits and means they are robust against costs of exploitation. This allows species to persist where a population without those traits would not, making them ideal candidates for exploitation. We propose that this mechanism may help inform new research approaches and provide insight into how exploited species might persist.

Keywords Sexual deception · Antagonistic coevolution · Persistence

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Introduction

A species' evolutionary trajectory can change due to interactions with other species. Coevolution, or reciprocal change between species (Bronstein 2001; Price 2003; Soler 2013; Hui et al. 2015), can drive selection for traits that maintain or increase an individual's fitness (Brockhurst and Koskella 2013; Hembry et al. 2014). Coevolution involves a range of interactions, including mutualisms. However, exploitative relationships, where exploiters secure fitness benefits (e.g. food or improved reproduction) at the cost of the other party, are also a common outcome of coevolution (Mokkonen and Lindstedt 2016).

The evolutionary maintenance of mutualistic relationships is relatively straightforward – if both parties benefit, there is strong selection for mutualisms or factors that reinforce mutualisms (Bronstein 2009, 2015). Indeed, the most compelling evidence for coevolution or co-speciation arises from research on mutualistic relationships (Vienne et al. 2013). Contrarily, the relationships that impose fitness costs on only one partner are harder to explain (Kokko and Brooks 2003). Theory predicts that, if costs are sufficient, deceptive relationships should break down, due to the extinction, decline, or evolved resistance of the exploited partner (Gibson et al. 2010; Ricklefs 2010; Hesse and Buckling 2016; Vitale and Best 2019). Extant deceptive relationships may well be a temporary snapshot in evolutionary time. However, exploitative relationships can persist in nature, due to a fascinating variety of mechanisms.

Orchids provide an overlooked opportunity for studying exploitation and mechanisms of persistence. Although many orchids do offer pollinators a reward such as nectar, rewardlessness and deception are very common (Shrestha et al. 2020). Deceptive orchids exploit their pollinators' foraging and reproductive behaviours: they do not offer any reward, and can even harm their pollinator (Wong and Schiestl 2002; Brunton Martin et al. 2020). Sexual deception can be an extreme form of pollination, in which flowers lure a male pollinator with duplicitous sex signals. Fooled males mate with the flower and unintentionally collect or deliver pollinia (Schiestl 2005). In some cases, males will ejaculate and waste sperm on the orchid (Blanco and Barboza 2005; Gaskett et al. 2008; Brunton Martin et al. 2020). As well as missed mating opportunities, new data shows that sperm wastage is costly (Wong and Schiestl 2002; de Jager and Ellis 2014), as males can become sperm depleted, at least temporarily (Brunton Martin et al. 2020). Despite these costs, sexual deception persists and is reasonably common: 20% of deceptive genera present sexual deception (Jersáková et al. 2006). Although recent work challenges the long-held idea that one-third of orchids are deceptive, rewardlessness, and therefore sexual deception, are probably relatively common in the family Orchidaceae (Shrestha et al. 2020), despite the known costs to pollinators.

Here, we explore how relationships persist when there are high costs, focusing on deceptive orchids. We assess the evidence for low encounter rates, indirect benefits, or coevolutionary arms-races. In addition, we use an extreme example of sexual deception that triggers pollinator ejaculation to propose an additional hypothesis that applies an idea from the field of systems biology, (Kitano 2004; Whitacre 2012)robustness, that could help explain the persistence of such deceptive relationships. We propose that future work exploring persistence might test for these traits in other exploitative interactions.

Existing hypotheses for the maintenance of exploitation

Exploitation occurs across an extensive range of ecological interactions and taxa, and costs vary. For instance, deception can result in death for the exploited party: to hunt spiders, assassin bugs imitate the vibrations of trapped insects (Wignall and Taylor 2011); praying mantises mimic flowers to lure pollinators as prey (O'Hanlon et al. 2014). Exploited individuals may also lose young - brood-parasitic cuckoos have eggs and chicks that mimic those of their hosts, and parasitic chicks will often kill their nest-mates (Feeney et al. 2014) – or lose the potential to have offspring: sexually deceptive orchids use mimicry and signal biases to fool male insects into mating with, and pollinating their flowers (Gaskett 2011; Gaskett et al. 2017), sometimes eliciting ejaculation. On the other hand, costs of exploitation may be negligible, as when quorum sensing bacteria signal others to produce 'common goods' without producing it themselves (Diggle et al. 2007; Czárán and Hoekstra 2009; Katzianer et al. 2015).

When there are costs, exploitative relationships might be maintained via antagonistic coevolution, or an arms-race, as occurs between cuckoos and their hosts (Feeney 2017). In other taxa, the maintenance of exploitative interactions is via indirect fitness benefits accruing to the exploited partner, for instance in praying mantids where sexual cannibalism also enhances paternity (Barry et al. 2008; Sardell et al. 2012). Finally, low incidence or encounter rates can mean exploitation imposes only weak selection on the exploited partner (Kokko

Table 1 Summary of studies that have investigated evidence for negative frequency dependent selection in deceptive orchid genera

Deception	Species	Polymorphism	Finding	Conclusion	Study
Food deceptive	*Dactylorhiza sambucina*	Colour	Male and female reproductive success of plants declined with frequency of colour morph in the population.	Advantage for rare colour morph.	Gigord et al. 2001
			No correlation between male and female reproductive success and colour morph frequency. Red morphs received more second visits, yellow more first visits. Pollinia removal and fruit set increased with frequency of yellow morph.	No advantage for rare colour morph.	Pellegrino et al. 2005
			The more dominant colour morph (yellow) had the most pollinia export and deposition.	No advantage for rare colour morph.	Groiß et al. 2017
Sexually deceptive	*Lepanthes rupestris*	Colour	Reproductive success did not differ between colour morphs.	No advantage for rare colour morph.	Tremblay and Ackerman 2007
	Cypripedium calceolus	Scent	Rarer scent morphs did not significantly differ in probability of fruit set.	No advantage for rare scent morph.	Braunschmid and Dötterl 2020

and Rankin 2006; Kokko et al. 2008). This is often suggested as an explanation for why pollinators do not learn to avoid rewardless or deceptive orchids (Pérez-Hérnandes et al. 2011). Alternatively, low encounter rates might also be maintained by negative frequency-dependent selection, which may arise from pollinator learning or avoidance (Schiestl 2005). Here, we briefly discuss each of these mechanisms in the context of orchid deception:

Low encounter rates and frequency dependent selection

One of the most intuitive mechanisms for the persistence of costly relationships is simply the idea that low encounter rates allow populations to persist because incidences of exploitation or conflict are very rare (Kokko and Rankin 2006; Kokko et al. 2008). The less an exploited group encounters the exploiter, the less of an impact that exploiter has on the population – reducing the chance for learning or counteradaptation and allowing the deceptive relationship to persist. In deceptive orchids, low encounter rates may be a product of deceptive orchid density and pollinator learning resulting in negative frequency-dependent selection. However, few studies test the presence of negative-frequency dependent selection, and there is mixed evidence of any benefit of being rare (Table 1). In one food deceptive orchid, *Dactylorhiza sambucina*, rare colour morphs had a reproductive advantage (Gigord et al. 2001) demonstrating evidence for negative-frequency dependent selection – but this is the only known example, and has not yet been successfully replicated in the same species Pellegrino et al. 2005; Groiß et al. 2017; reviewed in Sapir et al. 2021). In several other studies, this was also not the case either in terms of colour polymorphisms (Tremblay and Ackerman 2007; reviewed in Juillet and Scopece 2010); or scent polymorphisms (Braunschmid and Dötterl 2020).

In sexually deceptive orchids, low encounter rates could arise because pollinators quickly learn to avoid deceptive orchids, a mechanism that may even be accelerated when orchids are highly abundant. For example, a few studies suggest short-term pollinator avoidance in response to sexual deception (Wong and Schiestl 2002; Schiestl 2005; Paulus 2006; Jersáková et al. 2006; Whitehead and Peakall 2013; Weinstein et al. 2016). However, avoidance of orchids may not necessarily be a learned behaviour in response to orchids. If we consider the pre-existing behaviour of these sexually deceptive orchids' pollinators (which are typically solitary parasitoid wasps or bees; Gaskett 2011), a male wasp may typically avoid a site where he has mated previously to reduce the chance of remating with the same female. The typical mating system of solitary parasitoid wasps involves females releasing sex pheromones to attract a male and mating just once during her lifetime (monandry). Males of these species are therefore under intense scramble competition to find and mate with a signalling female, but they will mate with several females in their life (polygyny; Quicke 2014). Thus, there is likely to be strong selection on males to avoid responding to mated females, depending on their learning rate. When a solitary male parasitoid has found and mated with a virgin female, he usually will not return to that site – even if a new virgin female is placed there (Goh and Morse 2010; Quicke 2014). Although, in some sexually deceptive systems experienced males can learn to recognise that deceptive flowers are mimics, reducing their mating behaviour (de Jager and Ellis 2014). Interestingly, male bees deceived by *Ophrys* orchids can learn to avoid the scent of one flower, but variation in scent means that the male will go back to different flowers on the same or different plants (Ayasse et al. 2007). In other rewardless systems (e.g. food deception), pollinators will learn to avoid

all plants in a dense patch of deceivers, but they are less likely to avoid a deceptive orchid when among similar, rewarding plants (Johnson et al. 2003) – thus, low density allows for the persistence of the relationship.

Indirect fitness benefits

Exploitation can persist when indirect fitness benefits compensate for the costs to the exploited party (Sardell et al. 2012; Dimitriu et al. 2016). For example, indirect benefits are obtained by cannibalised male praying mantids, because although sexual cannibalism kills males, it provides them with paternity benefits. Cannibalistic females substantially improve their body condition by consuming males before, during or immediately after mating (Barry et al. 2008). Becoming lunch, of course, comes at a cost to the courting male. Nevertheless, males indirectly benefit through increased fertilisation success and improved offspring survival (Welke and Schneider 2012), although not at all if they are eaten before mating.

No studies have found that deceptive orchids offer any indirect benefits to any pollinators. One (very tenuous) possibility is that pollinators could benefit from brief periods of shelter in sexually deceptive orchids with trap mechanisms, e.g. *Pterostylis*. Hence, it is unlikely that sexual deception persists due to this mechanism – there are certainly no rewards they offer that would outweigh the costs of reproductive loss.

Coevolutionary arms-race

Another potential mechanism for the maintenance of sexual deception is through a coevolutionary arms-race. Under this mechanism, deception by orchids could select for pollinator traits that improve the exploited species' fitness, e.g., increased ability to differentiate between orchids and real females. In turn, these defences select for counter-adaptations in the deceiver, e.g., more accurate mimicry. Cuckoo brood parasites and their hosts are a classic example of an arms-race. Exploitation selects for host recognition of parasitic eggs and mobbing of parasites (Kilner and Langmore 2011; Feeney et al. 2014). In turn, this selects for cuckoo cryptic plumage and behaviour, and eggs and chicks with features that match those of their hosts (Marchetti 2000; Spottiswoode and Stevens 2011; Feeney 2017).

Resistance or tolerance can be key mechanisms reducing costs of arms-races (Svensson and Råberg 2010). In brood parasitism, resistance minimises the number of exploitations, e.g. hosts that mob and deter cuckoos. Resistance can drive deceptive relationships to extinction (Vienne et al. 2013), whereas tolerance reduces the fitness impact of exploitation. For instance, Eurasian magpie (*Pica pica*) tolerate brood parasitism by rearing their young alongside cuckoo chicks, and increasing their own clutch size (Soler et al. 2001). Tolerance may not result in an arms-race because it does not inhibit exploiter fitness (Svensson and Råberg 2010; Fornoni 2011). Importantly, a coevolutionary arms-race is unlikely to allow maintenance of deception as it often results in the exploited species becoming extinct or escaping exploitation (some theoretical models suggest prolonged coexistence; Huang et al. 2017; Hui et al. 2018; Schenk et al. 2020).

Does sexual deception co-evolve?

Although there are few studies of coevolution between sexually deceptive orchids and their pollinators, it is widely accepted that orchid species adapt to their pollinator preferences (box 1). Floral scent mimicry has received the most research attention and it is clear that sexual deception relies primarily on orchids' precise chemical mimicry of the species-specific sex pheromones of the female of the pollinating species (Bohman et al. 2016; Peakall et al. 2020; Hayashi et al. 2021), particularly for long-range attraction. Pollinators can also exert selection on orchid colour and morphology: sexually deceptive orchids that adapt to match the morphologies of their pollinators can achieve more efficient pollination (Newman et al. 2015).

While there are no explicitly documented cases of coevolution between sexually deceptive orchids and their pollinators, it is clear that deceptive orchids can evolve in response to their pollinators and are labile in terms of their morphology, scent, and colour. Do their pollinators coevolve in response to these changes? Coevolution is documented between rewarding flowers and their pollinators (Ricklefs 2010; Bili et al. 2016; Vamosi et al. 2006; Arditti et al. 2012) and between rewarding orchids and their pollinators (Boberg et al. 2014; Anderson and Johnson 2007). However, there is presently no evidence that pollinators evolve in response to deceptive pollination. Furthermore, phylogenies suggest that coevolution is unlikely because of the different branch lengths (time since splitting) of pollinator and orchid groups (Mant et al. 2002). Regardless, there are very few explorations of how coevolution may function in deceptive plant-pollinator relationships (Wong and Schiestl 2002). In order to best explore this possibility, it is vital that the fitness costs of sexual deception are established.

Box 1: Evidence for pollinator selection on orchid traits

Deceived orchid pollinators can exert selection on both orchid morphology and scent. For instance, Peakall et al. (2010) found that changes in the floral scent of Australian sexually deceptive *Chiloglottis* orchids attracts new pollinator species, leading to floral isolation and speciation. Similarly, morphological manipulation of *Chiloglottis* species shows that pollinators reduce copulation duration (and therefore pollen transfer) when pollinating flowers with abnormal callus-tip distances or shortened labella (de Jager and Peakall 2016, 2019).

In european *Ophrys* orchids, pollinators are less effective at pollinating when they interact with flowers that have altered lips (the third petal of the orchid that serves as a landing platform for pollinators) and therefore inadequate gripping points on the flower (Rakosy et al. 2017).

Sexually deceptive orchids may also be under selection to be highly detectable for pollinators (Rakosy et al. 2012; Kelly and Gaskett 2014; Gaskett et al. 2017) or have colours that match those of female pollinators (Gaskett and Herberstein 2009).

Are costs of sexual deception sufficient for coevolution?

The costs sexually deceptive orchids impose on their pollinators, particularly in terms of sperm wastage, have only recently been explored or discovered (Blanco and Barboza 2005; Brunton Martin et al. 2020; Cohen et al. 2021). If orchid interference is a substantial cost

to pollinators, we might expect coevolutionary responses in the pollinator's reproductive behaviour or anatomy– such as an arms' race like that observed between cuckoos and their hosts.

Sexual deception can affect male pollinators by causing missed mating opportunities with real females and wasted ejaculate Wong et al. 2004; de Jager and Ellis 2014; Wong and Schiestl 2002; Brunton Martin et al. 2020). Females of the pollinator species are also likely to suffer costs. They must compete with orchids for mates in both space and time because their mating season coincides with orchid flowering season, and the orchids only occur where wasp populations are present (Gaskett and Herberstein 2006; Brunton-Martin et al. 2021).

Sperm production can be energetically costly: male cockroaches, *Nauphoeta cinerea*, demonstrate a nutrient trade-off between sperm production and pre-copulatory attractiveness (Bunning et al. 2015); male and female seed beetles, *Callosobruchus maculatus*, invest equally reproductive effort, losing body mass – and males who mate more than once show reduced ejaculate size (Savalli and Fox 1999; Wagner and Bakare 2017). In flour beetles, *Tribolium castaneum*, males with higher mating success have longer sperm, which was shown to be costly to produce as protein-restricted males had shorter, less successful sperm (Godwin et al. 2017). This was also found in *Drosophila melanogaster*: long sperm males had lower mating success, suggesting a trade-off between pre-copulatory sexual selection and post-copulatory advantages of long sperm (Zajitschek et al. 2019). Parasitoid wasps, who are the primary pollinators of sexually deceptive orchids (Gaskett 2011) often have limited sperm production in their lifetime (Boivin et al. 2005; Damiens and Boivin 2006; Boulton et al. 2015). Parasitoid females generally cannot detect whether males have sperm, so if they mate with a sperm-depleted male, they may never receive a full complement of sperm, or remain pseudo-virgin for their lifetime (Abe 2019). If males do replenish sperm, they typically produce fewer spermatozoa at a lower rate and with a higher proportion of infertile sperm with every mating event (Wedell et al. 2002; Pizzari et al. 2008; Vega-Trejo et al. 2019). To date, there is only one study estimating sperm production in an orchid pollinator: males of *Lissopimpla excelsa* were found to at least become temporarily sperm depleted (Brunton Martin et al. 2020). The procedural challenges of detecting spermatophores on orchids (Bressac et al. 2008) may have led to an underestimation of how common ejaculation is. However, recent work is discovering the presence of spermatophores in other deceptive interactions: Cohen et al. (2021) recently reported that beetle sperm was found on the labellum of the sexually deceptive orchid, *Disa forficaria*, and Blanco and Barboza (2005) report a putative spermatophore on flowers of the sexually deceptive orchid, *Lepanthes glicensteinii*. Building on this, it would be interesting to determine pollinator sperm capacity (and whether sperm deposits are present) in other sexually deceptive systems. If ejaculation on orchids is common, then this cost may be sufficient to alter pollinators' fitness, even if temporary (see Brunton-Martin et al. 2021b); if not, the interaction's costs may well be negligible.

At present, there are just a few tantalising suggestions that these types of costs could be sufficient to drive change in a sexually deceived pollinator species. One study has suggested that the presence of sexually deceptive orchids interrupt the normal mating behaviour of pollinators, and in response, selection may act on females' learned avoidance of deceptive orchids, to improve their chances of reproduction (Wong et al. 2004). We note, however, that this might occur because female parasitoids perceive a high density of females, and are

avoiding competition for hosts (Mathiron et al. 2019). Another study, comparing male pollinators of a single species from sites with and without natural populations of orchids, found that males in sympatry with sexually deceptive orchids had smaller ejaculates but a similar sperm volume (Brunton Martin et al. 2020). This change might be a counteradaptation in response to sperm loss, but confirming this will rely on establishing both proximate and ultimate costs (see De Mazancourt et al. 2005). This change in sperm allocation behaviour might be a strategic response to the perception of abundant females (and orchids) in the males' habitat (Parker and Pizzari 2010), or lower quality females (i.e. orchids; Reinhold et al. 2002). For both early studies, it is unclear whether these behavioural changes arise through plasticity or counter-adaptation. It would be interesting to determine whether there are any morphological changes in deceived populations of pollinators. For instance, since pheromone mimicry is the main source of attraction in orchids (Ayasse et al. 2011; Bohman et al. 2019), future research might focus on differences in the chemosensory structures of pollinators. These might indicate counteradaptations that would allow pollinators to better distinguish orchids from real females and allow assessment of whether this correlates with reduced encounter rates.

Case study: *Cryptostylis* orchids

The Australasian sexually deceptive *Cryptostylis* orchids are exceptional deceivers, exploiting males of the solitary parasitoid wasp species *Lissopimpla excelsa* (Family: Ichneumonidae, subfamily: Pimplinae, Fig. 1). These orchids frequently trick males into mating with, and ejaculating on, the flower during pollination (Gaskett et al. 2008; Brunton Martin et al. 2020). Parasitoid species can become permanently or temporarily sperm depleted after several mating events with females (Olsson et al. 1997; Boivin et al. 2005; Damiens and Boivin 2006; de Jager and Ellis 2014; Boulton et al. 2015), and male *L. excelsa* may become

Fig. 1 In pursuit of pollination, a *Cryptostylis subulata* orchid tricks its ichneumonid wasp pollinator, *Lissopimpla excelsa*, into ejaculating and wasting his sperm. Sperm loss and missed mating opportunities could impose great costs on deceived pollinators' populations – how does this relationship persist? Image courtesy of C. Young

at least temporarily sperm depleted (Brunton Martin et al. 2020) when mating with orchids. *Cryptostylis* orchids may therefore interfere in pollinator reproduction by imposing sperm limitation on females. This could be by depleting males of sperm or preventing males from encountering real females. Despite this, orchids achieve exceptionally high pollination rates for sexually deceptive orchids (*Cryptostylis*: 70% (Gaskett 2011; Schiestl et al. 2004) compared to an average of 13–39% for sexually deceptive orchids in Australia (Brundrett 2019) excluding *Cryptostlyis* orchids).

Applying existing hypotheses to *Cryptostylis-Lissopimpla*

Low encounter rates may maintain the interaction between *Cryptostylis* and its sperm-depleted pollinator - individual-based modelling of a haplodiploid pollinator population indicates that the less males search and find deceptive orchids, the higher the pollinator population's persistence (see: Brunton-Martin et al. 2021b). However, this mechanism does not fully explain the persistence and success of this relationship: *Cryptostylis*' high pollination rates suggest frequent interactions with the pollinator, counter to what we might expect if encounter rates were low. Regardless of the mechanism behind this phenomenon, it is crucial to assess the lifetime fitness costs imposed on pollinators, and pollinator population sizes in areas with orchids, to determine the true impact of deceptive orchids and whether their success is simply owed to pollinator abundance. Indirect fitness benefits are unlikely, as deceptive orchids never offer rewards to their pollinators – although this has not been explicitly tested for *Cryptostlyis* orchids. The costs of sperm limitation may be sufficient to promote an arms-race between orchid and pollinator, but this has not yet been explicitly tested.

## Haplodiploidy and persistence

The three mechanisms – low encounter rates, indirect fitness benefits and counteradaptations – do not seem to have sufficient evidence to support the idea that they, alone, might explain the persistence of the interaction between *Cryptostylis* orchids and their pollinator. Indirect fitness benefits are unlikely, the evidence for low encounter rates is meagre (Table 1); and the presence of an arms-race has not yet been thoroughly explored. Indeed, many gaps remain in our understanding of this system – and each of these three hypotheses warrant explicit testing in the context of sexual deception. However, we propose the application of another hypothesis (robustness) derived from work in systems biology. This hypothesis does not preclude or require the other three mechanisms, but is simply another way in which we might understand exploited species' persistence.

Sexually deceptive orchids are almost exclusively pollinated by solitary hymenopterans (Gaskett et al. 2008), but sexual deception with sperm wastage in beetles and fungus gnats has recently been reported (Phillips et al. 2014; Cohen et al. 2021). All Hymenoptera (wasps, bees and ants) are haplodiploid and have one ancient, arrhenotokous origin (Normark 2006), that pre-dates the evolution of sexual deception. Sexual deception likely arose between 16.1 and 4.6 MYA (corresponding with divergence of the genus, *Ophrys* (Breitkopf et al. 2015), whereas haplodiploid Ichneumonidae arose ~ 228MYA ((Peters et al. 2017). Diploidy has never evolved in the hymenopterans, and the most prevalent form of haplodiploidy in the

Hymenoptera is arrhenotokous haplodiploidy, where diploid females arise from fertilised eggs, and haploid males from unfertilised eggs (Heimpel & de Boer, 2008).

The preponderance of haplodiploid pollinators for deceptive orchids is striking when comparing the relative proportions of haplodiploid and diploid pollinators across different orchid pollination strategies (Fig. 2). Using the Atlas of Orchid Pollination (Van der Cingel 2001) for an overview of pollinators and pollination strategies, we found an association between sex-determination systems in pollinators and orchid pollination strategy. Rewarding orchid species and food deceptive orchid pollinators are approximately equally split between diploids and haplodiploids, whereas sexually deceptive orchid species have 90% haplodiploid pollinators (Fig. 2). Orchids with other deceptive pollination systems such as brood site deception and sensory traps are also predominantly pollinated by non-haplodiploid pollinators. We note that the deception of hymenopteran pollinators (an entirely haplodiploid order) appears to be the ancestral state in at least the subtribe Orchidinae (which includes the large European sexually deceptive genus *Ophrys*; Inda et al. 2012), and we predict it may be ancestral for the sister tribe Diurideae from the same subfamily (Orchidoideae), which includes all 9 of the Australian hymenopteran-pollinated sexually deceptive genera. Yet, the discovery of other sexually deceived orchid pollinators (e.g. beetles and fungus gnats; (Reiter et al. 2019; Cohen et al. 2021; Hayashi et al. 2021) that are not

Fig. 2 Relative proportions of haplodiploid and not haplodiploid pollinators across different known pollination strategies for 755 species of Orchidaceae (excluding autogamous orchids; data from Van der Cingel 2001). Pollinators included Hymenoptera (haplodiploid), and Diptera, Coleoptera, Lepidoptera and birds (all not haplodiploid). Pollinator type (haplodiploid or not) appears to relate to pollination strategy. Pollination strategies that were not rewarding, but otherwise unclear were described as 'sensory traps'
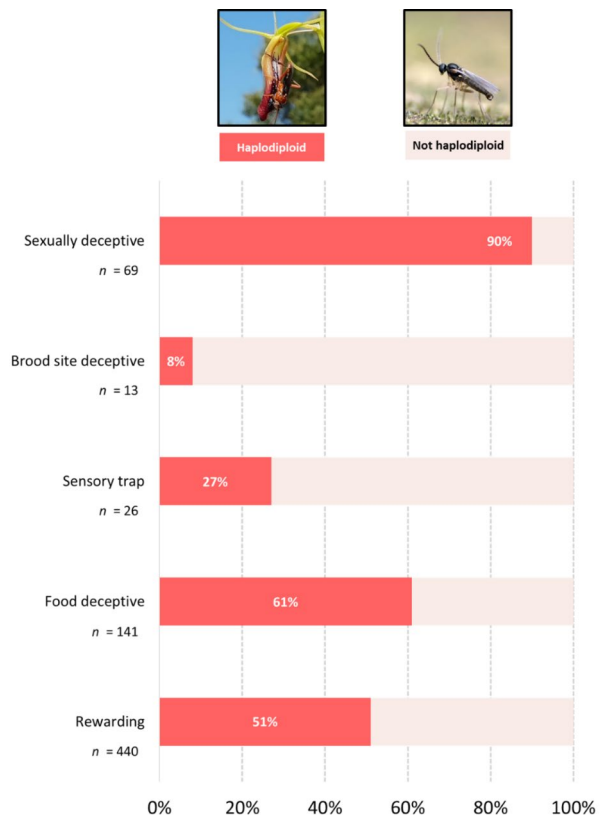
haplodiploid. Hence, more work identifying the pollinators of sexually deceptive orchids will be useful to confirm whether haplodiploid pollinators are, indeed, as common as they seem, and thus if haplodiploidy is a critical factor in the evolutionary maintenance of sexual deception.

However, in the context of *Cryptostylis* orchids, haplodiploidy may ensure their pollinators are robust to potential costs of sperm limitation elicited by sexual deception. Haplodiploid females can reproduce without sperm (albeit, all their offspring are male; Godfray 1990) and can facultatively adjust the sex ratio of their offspring when they do (Burton-Chellew et al. 2008; Booksmythe et al. 2017). Therefore, female mating failure due to sperm loss or missed mating opportunities could drive an increase in sons from generation to generation, causing a male-biased sex ratio. In turn, this male-biased sex ratio would reduce the costs of deception to the pollinator population and benefit the orchids. There would be new, naïve males for orchids to exploit, but also enough males in the population to keep some females fertilised and producing daughters. In this way, the population might persist over time. This contrasts with sexually deceptive orchids that target a diploid pollinator species, which cannot reproduce without matings and sperm.

Using mathematical modelling, we tested whether haplodiploidy renders pollinators robust to sexual deception (Brunton-Martin et al. 2021a). We found that haplodiploidy does indeed act as a mitigating mechanism: deceived haplodiploid populations are better able to withstand costs associated with sexual deception (in terms of persistence and maintaining fitness) than an otherwise identical diploid population. Their persistence partially resulted from the haplodiploid pollinator population reaching a stable, male-biased sex ratio. Using surveys of museum and citizen science records, we were able to test this aspect of the model: finding that pollinator populations that live in sympatry with *Cryptostylis* orchids were more male-biased than populations that do not live with *Cryptostylis* orchids (Brunton-Martin et al. 2021b). Future work should also establish the sex-ratio of pollinator populations in the field.

In this way, haplodiploidy allows pollinators to be robust against sexual deception, and can be readily exploited with a lower risk of extinction. We propose that this phenomenon may exist in other exploitative systems: a life-history trait may influence whether a given species or group is prone to exploitation, henceforth, we refer to this new hypothesis as 'robustness' (and traits that confer 'robustness' as 'robust traits').

Robustness as hypothesis

Defining robustness

The idea of robustness has been explored in systems biology. Specifically, this is where biological systems are hypothesised to have an intrinsic ability to maintain functions when exposed to perturbations (Kitano 2004; Whitacre 2012). In the context of sexual deception, we propose that this intrinsic ability arises from a trait that exists prior to the exploitative relationship. The definition of robustness is perhaps better understood by contrasting it with the existing concepts of resistance and tolerance (Fig. 3; Svensson and Råberg 2010). Robustness, like tolerance, is distinct from resistance in that it neither acts to lower exploiter fitness, nor does it reduce the direct costs of exploitation. However, robustness is distinct
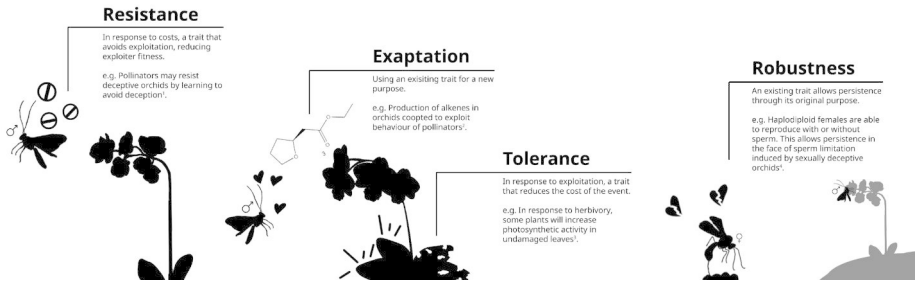
Fig. 3 Contrasting different mechanisms for persistance: resistance, exaptation, tolerance against 'robustness'. Citations: Resistance – [1]de Jager and Ellis 2014; Exaptation [2]Schiestl and Cozzolino 2008, chemical compound example from Bohman et al. 2019; Tolerance –[3]Tiffin 2000; Robustness – [4](Kitano 2004; Whitacre 2012)

from both strategies because it does not arise as a defensive strategy in response to an antagonist. Instead, rather than evolving as a defence strategy, robust traits are pre-existing in the deceived species (Vitale and Best 2019).

Pre-existing traits are observed in another similar evolutionary scenario: exaptation (i.e. co-opting an existing trait for a new defence function; Fig. 3, Gould and Vrba 1982). Unlike an exaptation, however, a robust trait is still utilised for its original function, but also simultaneously improves a populations' persistence in the face of exploitation.

We propose that robustness does not exclude the evolution of adaptations and counter-adaptations, but may weaken the costs that drive them. Robust traits may operate in concert with one of the other hypotheses for the maintenance of deceptive systems, low encounter rates, but seems unlikely to be compatible with the indirect benefits hypothesis, because robustness does not involve any benefit to the exploited species.

Testing for robust traits

Testing for the presence of robust traits in an exploitative relationship is difficult, as it will vary from trait to trait. We propose that the framework used in the *Cryptostylis* case-study may prove useful when exploring this phenomenon. Firstly, mathematical modelling and simulations are a useful tool for capturing traits that might impact persistence (Kitano 2002; Daniels et al. 2008; Whitacre 2012). For instance, modelling the exploited population with and without the proposed trait will produce testable outcomes. While robust traits are fixed in the species, theoretical modelling that removes the trait and holds all else equal allows for clarity on how, exactly, a trait might influence persistence. For a trait to be robust, we would expect the exploited population with the trait to have better persistence and fitness than the same (theoretical) population without the trait.

Then, quantitative research to assess whether the predicted outcomes indeed occur in nature, and perhaps comparisons with sister species that do and do not have a fixed robust trait. Furthermore, meta-analyses that utilise existing knowledge and explore the preponderance of putative robust traits in antagonistic relationships (parasitism or predation, for example) and the impact on exploiters (in terms of mortality rates, infection rates or reproduction rates) might reveal the importance of robustness as a mechanism.

Towards a general mechanism

This concept of robustness could be useful for exploring persistence of an exploited species in other systems and may be particularly useful in exceptional instances of extreme exploitation. Intriguingly, one other orchid that triggers pollinator ejaculation may have a different robust trait preventing pollinator extinction. *Lepanthes* orchids provoke ejaculation, but their pollinator is diploid fungus gnats (Diptera; Blanco and Barboza 2005), and fungus gnats may well be a much more common sexually deceived pollinator than currently documented (Reiter et al. 2020; Hayashi et al. 2021). However, fungus gnats can also have a male biased sex ratio, not via an internal mechanism like haplodiploid insects, instead fungus gnat sex ratios become more male-biased at cool temperatures (Nigro et al. 2007; Pandey and Tripathi 2008; Farsani et al. 2013). *Lepanthes* orchids bloom in colder weather (April – June) and grow in cold climates, and so fungus gnat populations might well have a male-biased sex ratio. This may confer robustness to these pollinators but remains to be tested empirically. Robustness may also be conveyed, for instance, via differences in developmental modes of cuckoo hosts (altricial, or early development state at birth, versus precocial, or late development state at birth) may play an important role in understanding the long-term stability of obligate interspecific brood parasitism (Yom-Tov and Geffen 2006). Three of the four orders of species that exhibit obligate interspecific brood parasitism (Cuculiformes, Piciformes, and Passeriformes) are altricial, while only one order (Anseriformes) is precocial. There is a greater duration of parental care in altricial species that might allow parasitised individuals time to reduce the costs of deception (Sheriff et al. 2018), and yet the appearance of altricial young may allow parasitic chicks to remain inconspicuous for longer (Scheiber et al. 2017). Additionally, because precocial species have longer incubation times and invest more in eggs, the cost of rejecting an egg may be greater for them, whereas an altricial species may reject an egg and re-lay (Augustine et al. 2019) with lower costs. Better understanding these types of relationships are important, particularly when we consider that these systems are often species-specific and thus fragile to climate change and other anthropogenic effects.

Robustness, combined with the mechanisms mentioned previously for the maintenance of costly relationships, is hopefully a useful avenue of research in behavioural and evolutionary ecology. This mechanism may help shape our understanding of the coexistence of exploitative species and their hosts.

Declarations

Conflict of interest The authors have no conflicts of interest to declare.

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