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Costs of deception and learned resistance in deceptive interactions

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The costs that species suffer when deceived are expected to drive learned resistance, although this relationship has seldom been studied experimentally. Flowers that elicit mating behaviour from male insects by mimicking conspecific females provide an ideal system for such investigation. Here, we explore interactions between a sexually deceptive daisy with multiple floral forms that vary in deceptiveness, and the male flies that pollinate it. We show that male pollinators are negatively impacted by the interaction, suffering potential mating costs in terms of their ability and time taken to locate genuine females within deceptive inflorescences. The severity of these costs is determined by the amount of mating behaviour elicited by deceptive inflorescences. However, inexperienced male flies exhibit the ability to learn to discriminate the most deceptive inflorescences as female mimics and subsequently reduce the amount of mating behaviour they exhibit on them with increased exposure. Experienced males, which interact with sexually deceptive forms naturally, exhibit similar patterns of reduced mating behaviour on deceptive inflorescences in multiple populations, indicating that pollinator learning is widespread. As sexually deceptive plants are typically dependent on the elicitation of mating behaviour from male pollinators for pollination, this may result in antagonistic coevolution within these systems.

1. Introduction

Resistance to being deceived is an important mechanism structuring deceptive interactions [1,2]. Within a mating context, this often involves the evolution of female resistance to exploitative or deceptive male traits [3]. This resistance can be driven by the costs that females suffer when deceived, such as reduced foraging efficiency when responding to deceptive male traits resembling food items [4]. As resistance to traits that exploit responses in a different context (sensory traps) typically involves interactions between females and their male suitors, most studies have focused only on animals [3,5]. Flowering plants, however, may have much to contribute, as floral mimicry and the deception of pollinators are widespread [6]. Flowers, for example, may mimic food items (pollen or nectar), oviposition substrates or even potential mates [7]. Mimicry of mating partners, termed sexual deception, entails specialized flowers that mimic the visual [8] and olfactory [9] mating cues of female insects in order to elicit mating behaviour from males that act as pollinators. Successful deception of male pollinators results in increased levels of outcrossing and pollen export for the plants [10,11]. However, very little is known about how this relationship impacts deceived pollinators and the potential costs they may suffer.

Recent reviews have suggested that any costs suffered by deceived males may be negligible, although they acknowledge that experimental evidence is required [12,13]. One of the few studies investigating the negative effects of sexual deception on a pollinating species proposed that the interaction might reduce fitness of the mimicked female insects as they receive less attention from male suitors when in the presence of deceptive flowers [14]. A follow-up study also showed that male pollinators in the field were less likely to find female insect dummies in closer proximity to deceptive flowers [15]. These results, together with a study reporting sperm wastage of male pollinators that attempt to copulate with sexually deceptive flowers [16], suggest that males may suffer considerable costs when deceived. Despite this, studies quantifying the actual costs suffered by male pollinators are

lacking. This is surprising, as several field studies report that male pollinators reduce the amount of mating behaviour they exhibit on sexually deceptive orchids with exposure [14–17]. This strongly suggests that pollinators can learn to resist deceptive flowers, which is most likely to occur if the costs involved are substantial. The extent and nature of costs suffered by deceived males, as well as their influence on pollinator learning in deceptive pollination systems, remain unknown.

Males of the pollinating bee fly, *Megapalpus capensis* Wiedemann, are attracted to and attempt to mate with fly-mimicking ray floret spots of the sexually deceptive African daisy, *Gorteria diffusa* Thund [11]. *Gorteria diffusa* comprises multiple floral forms that vary in their level of deceptiveness and some forms (Spring) have been reported to elicit mating behaviour from male pollinators at much higher frequencies than the sexually deceptive orchids on which most research in this field has been conducted [11,18]. It is also a relatively common plant in the landscape and can grow in dense aggregations, which may pose significant costs to deceived males in terms of reduced mating success. Using this study system, we investigated the impact of sexual deception on male bee fly pollinators. Specifically, we aimed to determine: (i) whether deceived males suffer any costs and how these costs are influenced by floral deceptiveness and prior experience, (ii) whether inexperienced males can learn to reduce mating behaviour on deceptive inflorescences with repeated exposure, and (iii) whether mating responses to deceptive inflorescences by experienced males in natural populations match predictions of learning based on our repeated exposure experiments.

2. Material and methods

(a) Study system

Gorteria diffusa comprises 14 geographically distinct floral forms within Namaqualand in South Africa [19]. These include feeding forms that induce only feeding behaviour in male and female flies, inspection forms that elicit inspection behaviour predominantly from mate-seeking males, and sexually deceptive forms that elicit mating behaviour exclusively from males [11]. Males and females forage for nectar and pollen on all floral forms. The ray floret spots of the sexually deceptive forms possess specialized papillate structures [20] and well-defined UV highlights that probably mimic mate recognition cues to which male flies are strongly attracted [8]. Mating in *M. capensis* often takes place on open daisy inflorescences wherein females sit and feed. Males exhibit mate-searching behaviour by moving repeatedly among inflorescences [11], landing on other flies and fly-mimicking spots alike.

(b) Costs to deceived males and the influence of deceptiveness and prior experience

We investigated male behaviour on *G. diffusa* forms differing in deceptiveness, including two feeding (Soeb, $n = 14$; Garies, $n = 16$), two inspection (Cal, $n = 15$; Okiep, $n = 15$) and two sexually deceptive forms (Nieuw, $n = 14$; Spring, $n = 15$ —floral forms described in [19]). These six forms represent the continuum of mating responses exhibited by male flies on *G. diffusa* [11]. We caught wild *M. capensis* males near the town of Kamieskroon (S 30, 12, 20.6; E 17, 56, 12.1) and used them in experiments on the same day. The inspection form Cal grows naturally in this area and is visited by *M. capensis* flies. The other floral forms investigated do not occur in this area and flies thus have no prior experience with their morphologies.

For each floral form, we created arrays of 20 fresh inflorescences spaced 6 cm apart. Before releasing individual male flies into 1 m³ gauze pollinator cages containing one of these arrays, we attached a dead *M. capensis* female (killed by exposure to -18°C for 30 min) on a non-spotted ray floret adjacent to a spotted ray floret within a single inflorescence on each array, selecting females of similar size for the various arrays. We recorded male behaviour on inflorescences as feeding or mating behaviour (*inspecting* = quick landings on ray floret spots, *changing* = flitting between different spots in an inflorescence, *hopping* = repeatedly hopping on a spot and arching abdomen downwards and *turning* = rotating on a spot) and calculated the percentage of total behaviour that involved mating behaviour for each experimental male. This served as an estimate of the level of deceptiveness of each floral form.

We allowed males a maximum of 20 min to locate the female and exhibit mating behaviour towards her. If they landed on the same inflorescence as the dead female without discovering her, we scored it as a missed mating opportunity. If males found the female, we recorded the time taken and scored it as a successful mating opportunity. We conservatively scored males that failed to find females as taking 20 min. We only used males on a particular floral form once and exposed them to the different forms in a random order. Since flies were used in multiple experiments, we employed generalized estimating equations (GEEs) to analyse our data as this controls for non-independence of multiple observations from each male. We used male identity as our repeated subject variable and the sequence of exposure of each male to the various floral forms as our within-subject variable to control for the potential influence of male experience across experiments. We selected an exchangeable correlation structure that assumes equal correlations within each male. To model the influence of mating behaviour towards *G. diffusa* on the success of males at locating females, we used the percentage mating behaviour exhibited by each male on *G. diffusa*'s deceptive spots as our covariate predictor for all analyses.

Firstly, we coded data as successful/unsuccessful and used a binomial distribution with a logit link function to model the probability of finding the female. We then calculated how much experimental time remained after each male found the female as $T = T_{\text{total}} - T_{\text{to locate female}}$ (zero time remaining for males that failed to find the female). This served as a quantitative measure of the efficiency of males at locating females that we analysed with a negative binomial distribution and log link function. Lastly, we modelled the number of missed mating opportunities that males experienced with a Poisson distribution and a log link function. We ran these models on the full dataset, as well as on a dataset that excluded male flies tested on arrays of the Cal form, because prior experience with this form may potentially influence the males' ability to locate females.

To compare the success of males at finding females on the different floral forms, we used a Cox proportional hazard model to produce hazard functions (which model the probability of males finding the females) for each floral form separately. We used the time males required to find the female as the time variable and the floral form it was tested on as the categorical covariate. All experiments were conducted in Kamieskroon during August and September 2011 on warm sunny days when flies are most active. During August 2009, we ran a smaller mating cost experiment with male flies using the same protocol described previously on two sexually deceptive floral forms (Nieuw and Spring, $n = 5$). Arrays in these experiments contained 12 fresh inflorescences and one live feeding female fly.

(c) Male learning in response to deception

To determine whether male flies possess the necessary learning capabilities to alleviate the costs of being deceived, we caught inexperienced males unfamiliar with sexually deceptive *G. diffusa*

Table 1. Results from GEE analyses modelling the effect of male mating behaviour directed towards *G. diffusa* spots on males' ability to find true females within inflorescences. Italics highlight significance values of $p < 0.05$. QICC, quasi-likelihood under independence model criterion; B , unstandardized regression coefficients.

response	including local Cal floral form						excluding local Cal floral form					
	N	QICC	B	s.e.	Wald	p -value	N	QICC	B	s.e.	Wald	p -value
probability of finding female	89	111.84	-0.02	0.01	3.47	0.06	74	86.59	-0.02	0.01	3.71	0.05
time remaining	89	695.48	-0.02	0.01	4.99	0.03	74	580.01	-0.03	0.01	6.60	0.01
missed mating opportunities ^a	63	81.54	0.02	<0.01	25.39	<0.001	49	63.74	0.02	<0.01	22.49	<0.001

^aSample sizes reduced as only males that landed on inflorescences containing dead females were used.

at two sites (Kamieskroon, $n = 10$; Englishman's Grave, $n = 9$, S 32 04 00.0, E 19 07 37.9). To test their putative learning abilities, we exposed these males repeatedly to arrays of 20 fresh inflorescences of the Spring form of *G. diffusa*, as this form elicits the strongest mating response from male flies [11] and is thus most likely to induce learning. Our protocol consisted of releasing inexperienced males into a pollinator cage containing a floral array and recording their behaviour as feeding or mating for 10 min (first exposure). We left males in the cage for an additional 10 min to ensure that they familiarized themselves with the deceptive spots and to allow any putative learning to take place. Males were then caught and rested for 10 min to reduce the potential of fatigue and lack of sexual motivation affecting subsequent behaviour. We then released the males back onto an array and recorded their behaviour for another 10 min (second exposure). We analysed differences in the percentage of mating behaviour between these two exposures with Wilcoxon Matched Pairs Tests. Experiments were conducted in Kamieskroon in 2010 and the Biedouw Valley (Englishman's Grave males) in 2011 during August and September on warm sunny days.

(d) Patterns of learning from natural populations

Flies in our experimental learning set-up may have displayed reduced mating behaviour as a result of fatigue or reduced sexual motivation because of repeated experimentation. To exclude this possibility and to explore the generality of the learning response, we also determined the intensity of mating responses to *G. diffusa* spots in male flies from multiple populations that differed in their prior experience of sexually deceptive forms of *G. diffusa*. Males belonged to two categories: those from areas where sexually deceptive *G. diffusa* is absent (inexperienced) and those from areas where it is present (experienced). We reasoned that mating responses of inexperienced flies should match first exposure males from our repeated exposure experiments and mating responses of experienced males should match second exposure males, if reduced mating activity after repeated exposure occurs through learning. Inexperienced males included males caught in the KK2 ($n = 10$, S 30, 12, 33.3; E 18, 2, 58.4) and ARA ($n = 10$, S 30, 05, 40.0; E 17, 54, 27.5) populations, as well as first exposure males from our repeated exposure experiments (KK1 and EG populations). Experienced males were caught in the SCH ($n = 16$, S 29 39 14.5; E 17 53 20.9) and CAM ($n = 15$, S 31 22 46.8; E 19 5 38.1) populations, and included second exposure males from our repeated exposure experiments (KK1 and EG). Males from each population were exposed to floral arrays of the Spring form as described in our learning experiments for 10 min. For each male, we recorded the percentage of mating behaviour they exhibited in response to the deceptive spots of the Spring floral form. We analysed inexperienced and experienced datasets

separately, as the males from our repeated exposure experiments were treated as both inexperienced (first exposure) and experienced (second exposure), and thus not independent.

We analysed male mating behaviour with nested ANOVAs, specifying the source of males used (repeated exposure males versus wild caught males) and population nested within source as predictor variables to test specifically for differences between repeated exposure males and males from the field, and for differences between populations from the same source. We also ran a nested ANOVA with only the wild caught males using experience level (experienced versus inexperienced) and population nested within experience level as predictors to determine whether mating responses from natural populations where sexually deceptive *G. diffusa* grows differ from populations where it is absent. During all of our experiments, inflorescences in arrays were replaced as necessary. Statistical analyses were performed in the SPSS 20 statistical package (SPSS Inc., Chicago, USA) and residual versus predicted value plots were inspected to control for potential overdispersion.

3. Results

(a) Costs to deceived males and the influence of deceptiveness and prior experience

We used 41 male flies in 89 experimental trials across six floral forms of *G. diffusa* varying in their deceptiveness. Our GEE results revealed that the amount of mating behaviour males exhibit on deceptive spots (i.e. the strength of deception) significantly affects their potential mating success. When analysing the full dataset that includes males tested on the locally occurring Cal floral form with which they have prior experience, both the amount of time taken to find females and the number of missed mating opportunities they experienced were negatively affected by the percentage of mating behaviour exhibited on deceptive spots (table 1). When excluding flies tested on this familiar form, however, the probability of finding the female was also significantly affected. The models excluding these flies also revealed better fit to our data (expressed as the corrected quasi-likelihood under independence model criterion—QICC) and were more significant overall, suggesting that males tested on the local Cal form did not closely match the patterns of males tested on the other unfamiliar floral forms.

This was confirmed by the hazard plots, which revealed that males had the greatest probability of finding females on arrays of the Cal form, despite the fact that both the Soeb and Garies forms were considerably less deceptive (figure 1).

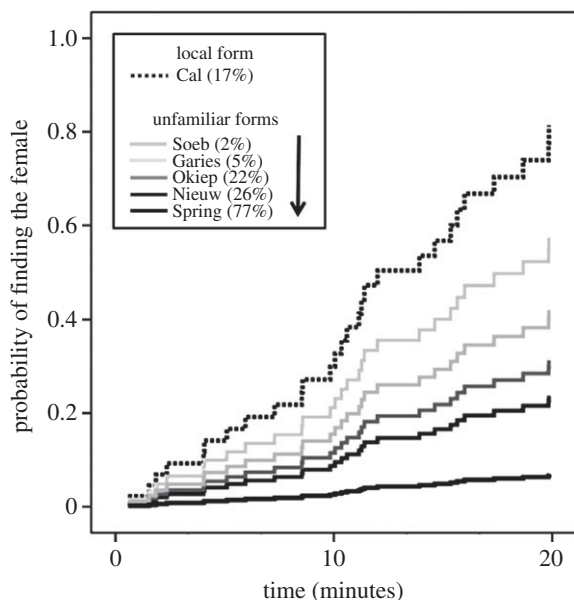


Figure 1. Cox proportional hazard plot illustrating the probability of males finding the female on arrays of the floral forms investigated. Males exhibited the highest probability on the locally occurring Cal form, suggesting that prior experience may enhance their ability to locate females. The other unfamiliar forms indicate a clear decrease in probability, with an increase in mating behaviour exhibited on deceptive spots (downward arrow in legend). The means of mating behaviour exhibited by males on each form are indicated in parentheses. Males had the lowest probability of finding females on the most deceptive Spring form.

Discounting the local Cal form, males tested on unfamiliar forms showed a clear trend of decreasing probability of finding the female on forms that elicit more mating behaviour, with males exhibiting the lowest probabilities on the most deceptive Spring form. This form had the lowest proportion of males finding the female (Spring = 0.07, range of proportions across floral forms: 0.07–0.4) and induced the greatest number of missed mating opportunities (mean \pm s.d.: Spring = 3.33 ± 3.14 , range of means across forms: 0–3.33). Costs suffered by males in our 2009 experiment using live females were qualitatively similar, indicating that our results were not affected by the use of dead females.

(b) Male learning in response to deception

Our repeated exposure experiments revealed that male flies from both the Kamieskroon (Wilcoxon Matched Pairs Test: $Z = 2.701$, $n = 10$, $p = 0.007$) and Englishman's Grave ($Z = 2.521$, $n = 9$, $p = 0.012$) sites exhibited significantly less mating behaviour towards the fly-mimicking spots of the deceptive Spring form during their second exposure (figure 2). Males from Kamieskroon also showed significantly less mating behaviour in all the mating categories we observed except hopping (inspecting; $Z = 1.992$, $n = 10$, $p = 0.047$; changing $Z = 1.992$, $n = 10$, $p = 0.047$ and turning $Z = 2.547$, $n = 10$, $p = 0.011$). Males from Englishman's Grave did so for changing ($Z = 2.023$, $n = 9$, $p = 0.043$), although they exhibited near significant reductions in inspecting ($Z = 1.83$, $n = 9$, $p < 0.07$) and turning behaviours ($Z = 1.83$, $n = 9$, $p < 0.07$).

(c) Patterns of learning from natural populations

Results from our nested ANOVA analyses investigating differences between repeated exposure males and wild caught males

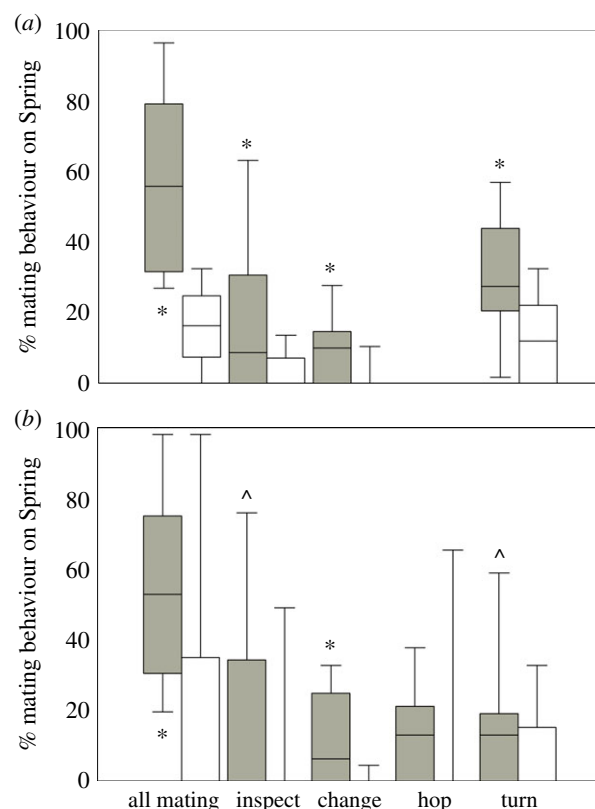


Figure 2. Boxplots showing the median and 95th and 5th percentiles for the mating behaviour as a percentage of total behaviour exhibited by inexperienced males from (a) Kamieskroon ($n = 10$) and (b) Englishman's Grave ($n = 9$) during their first (filled bars) and second (unfilled bars) exposures to the sexually deceptive Spring floral form. Asterisks (*) indicate significant differences between exposures at $p < 0.05$ and symbol hats (^) near significant difference at $p < 0.07$.

revealed no effect of source ($F_{1,35} = 1.918$, $p = 0.175$) or population nested within source ($F_{2,35} = 0.763$, $p = 0.474$) on the mating responses of inexperienced males (figure 3). Similarly, there were no effects of source ($F_{1,46} = 0.019$, $p = 0.890$) or population nested within source ($F_{2,46} = 0.501$, $p = 0.609$) for experienced males. This indicates that our experimental results are similar to patterns from natural populations and that the reduction in mating behaviour that we observed in experimental males was not driven by fatigue or lack of sexual motivation owing to repeated exposure, as wild caught males are unlikely to be affected by these factors. Analyses using only wild caught males revealed that experience level (experienced versus inexperienced) was highly significant in determining their mating responses towards deceptive inflorescences ($F_{1,47} = 82.594$, $p < 0.0001$). Population nested within experience level, however, was not a significant predictor ($F_{2,47} = 1.712$, $p = 0.192$), indicating that responses are comparable among experienced/inexperienced populations. These results confirm that reduced mating behaviour towards deceptive inflorescences occurs through exposure to sexually deceptive *G. diffusa*, and suggests that pollinator learning may be widespread.

4. Discussion

We show that male pollinators deceived by *G. diffusa*'s fly-mimicking spots suffer potential mating costs. The severity of these costs is determined by the amount of mating behaviour they exhibit on deceptive spots (the extent to which they are

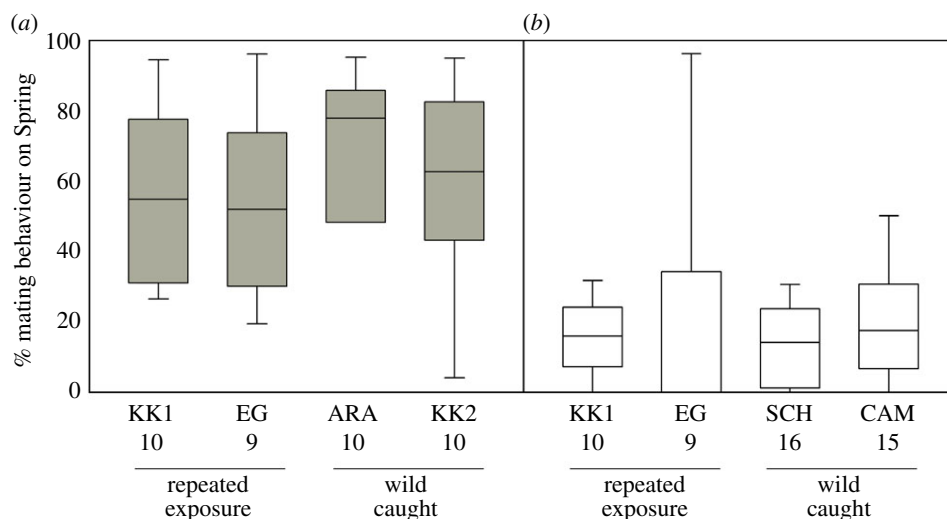


Figure 3. Boxplots of the percentage of mating behaviour exhibited by males from different populations on arrays of the most deceptive Spring form. Inexperienced males (filled bars) (a) are from sites where no sexually deceptive *G. diffusa* grows, while experienced males (unfilled bars) (b) are from sites where it does occur. Datasets for inexperienced and experienced flies were analysed separately with nested ANOVAs, which indicated the lack of differentiation between the mating responses of repeated exposure males and wild caught males, revealing the generality of our repeated exposure results. Population names and the sample size of males tested in each are indicated.

deceived). Prior experience with deceptive forms, however, may help alleviate these costs as males had the greatest probability of finding females on their familiar local floral form. This is potentially driven by learned behaviour, entailing a reduction in the amount of mating behaviour they exhibit on deceptive floral spots. Our repeated exposure experiments confirmed this hypothesis by revealing that naive males learn to reduce their mating behaviour on the deceptive spots of the most deceptive Spring form with experience. Results from wild caught males corroborate this finding, as males from populations where sexually deceptive *G. diffusa* grow naturally exhibit comparable levels of mating behaviour on the Spring form as experimental males during their second exposure. This pattern implies that reduced mating responses on deceptive spots are the result of exposure to sexually deceptive *G. diffusa*, and not experimental protocol or population differences such as variation in *M. capensis* densities or sex ratios.

Field studies on sexually deceptive European *Ophrys* orchids have also documented that Hymenopteran male pollinators quickly learn to avoid deceptive flowers [17]. Males in these systems seem to learn to identify individual flowers, but not the signals involved in deception, as mating behaviour remains high when exposed to new flowers [17]. Male pollinators of sexually deceptive orchids in Australia, however, reduce their mating behaviour with exposure, even if this is to new flowers [14,16]. In our study, experienced male flies from multiple populations where sexually deceptive *G. diffusa* grows exhibited reduced mating behaviour compared with inexperienced males, even when tested on new inflorescences within a new locality. This suggests that reductions in male mating behaviour are not due to learned avoidance of localities or individual inflorescences, but perhaps rather due to an ability to recognize and resist the deceptive signals of *G. diffusa*.

Such learned resistance can have detrimental effects on the reproductive fitness of sexually deceptive floral forms that rely on male mating behaviour [11], which may suggest that inexperienced males are the primary pollinators of these forms. However, it is not known how long learned resistance is retained in *M. capensis* as we used all of our males in experiments on the same day that we caught them. It may thus also

be possible that experienced males lose their learned resistance to deceptive spots over time, thereby remaining effective pollinators throughout their lifetime. A recent capture–mark–recapture study on the pollinators of an Australian sexually deceptive orchid revealed that male wasps are unlikely to retain learning past 24 h [21]. This may be of great importance in the maintenance of sexual deception, as avoiding sexually deceptive flowers after visitation coupled with the dissipation of such learned avoidance will increase outcrossing rates without reducing the available pollinator pool at a site.

The reasons why pollinators exhibit such learning behaviour on sexually deceptive flowers in the first place are still poorly understood [13]. It may be that the occurrence of learning depends on the actual costs suffered when males are deceived. The males in our study that exhibited learned avoidance were either from sites containing sexually deceptive *G. diffusa*, or inexperienced males repeatedly exposed to the most deceptive Spring form. Learning behaviour might thus represent an evolved response to being deceived. Another likely possibility is that mating-related learning behaviour originated in male–female interactions in order to avoid wasting time and energy on unsuccessful mating attempts. Males from different insect orders have been found to reduce mating behaviour in response to heterospecific or unresponsive conspecific females with experience [22,23], illustrating the prevalence of learned avoidance among insects. It also suggests that the behaviour might be pre-adaptive and not limited to species involved in antagonistic or deceptive interactions. If this ability evolved in male–female interactions, experience with sexually deceptive flowers may still modify and shape the observed rates of learning in insects as variation in the capacity to learn is heritable [24].

Heritable learning ability implies that antagonistic co-evolution may potentially operate in these systems. Within *G. diffusa* [11] and sexually deceptive orchids [16], the floral forms/species that elicit the most intense mating behaviour from male pollinators enjoy the highest reproductive success. Unless they rely solely on newly emerged inexperienced males for pollination, learned avoidance could place them

under selection to increase their deceptiveness and/or deter learning. Male pollinators, for their part, suffer reproductive costs when they are deceived and may therefore experience selection for increased learning capacity. Learning, however, can also largely be influenced by the ratio of models (female insects) to mimics (deceptive flowers). This factor has been demonstrated to be important, both experimentally [25] and theoretically [26], for pollinator learning in food deceptive species. Whatever the ultimate causes of learning, we illustrate that pollinators suffer potentially severe costs when deceived and that they can learn to discriminate mimics with increased exposure. These results have important implications for evolutionary interactions in all deceptive systems as they show that responses to exploitation depend on

various factors, including the severity and frequency of the costs suffered as well as potential preadaptations. Future studies may help elucidate an intriguing role for antagonistic coevolution within sexual deception by investigating model to mimic ratios and comparing the learning abilities of deceived individuals from across species' ranges.

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References

- Darst CR, Cummings ME. 2006 Predator learning favours mimicry of a less-toxic model in poison frogs. *Nature* **440**, 208–211. (doi:10.1038/nature04297)
- Cheney KL. 2008 The role of avoidance learning in an aggressive mimicry system. *Behav. Ecol.* **19**, 583–588. (doi:10.1093/beheco/arm001)
- Holland B, Rice WR. 1998 Perspective: chase-away sexual selection: antagonistic seduction versus resistance. *Evolution* **52**, 1–7. (doi:10.2307/2410914)
- García CM, Lemus YS. 2012 Foraging costs drive female resistance to a sensory trap. *Proc. R. Soc. B* **279**, 2261–2268. (doi:10.1098/rspb.2011.2611)
- Christy JH. 1995 Mimicry, mate choice, and the sensory trap hypothesis. *Am. Nat.* **146**, 171–181. (doi:10.1086/285793)
- Roy BA, Widmer A. 1999 Floral mimicry: a fascinating yet poorly understood phenomenon. *Trends Plant Sci.* **4**, 325–330. (doi:10.1016/S1360-1385(99)01445-4)
- Dafni A. 1984 Mimicry and deception in pollination. *Annu. Rev. Ecol. Syst.* **15**, 259–278. (doi:10.1146/annurev.es.15.110184.001355)
- De Jager ML, Ellis AG. 2012 Gender-specific preferences for floral traits. *Funct. Ecol.* **26**, 1197–1204. (doi:10.1111/j.1365-2435.2012.02028.x)
- Schiestl FP, Peakall R, Mant JG, Ibarra F, Schulz C, Franke S, Francke W. 2003 The chemistry of sexual deception in an orchid-wasp pollination system. *Science* **302**, 437–438. (doi:10.1126/science.1087835)
- Peakall R, Beattie AJ. 1996 Ecological and genetic consequences of pollination by sexual deception in the orchid *Caladenia tentaculata*. *Evolution* **50**, 2207–2220. (doi:10.2307/2410692)
- Ellis AG, Johnson SD. 2010 Floral mimicry enhances pollen export: the evolution of pollination by sexual deceit outside of the Orchidaceae. *Am. Nat.* **176**, E143–E151. (doi:10.1086/656487)
- Schiestl FP. 2005 On the success of a swindle: pollination by deception in orchids. *Naturwissenschaften* **92**, 255–264. (doi:10.1007/s00114-005-0636-y)
- Gaskell AC. 2011 Orchid pollination by sexual deception: pollinator perspectives. *Biol. Rev.* **86**, 33–75. (doi:10.1111/j.1469-185X.2010.00134.x)
- Wong BBM, Schiestl FP. 2002 How an orchid harms its pollinator. *Proc. R. Soc. Lond. B* **269**, 1529–1532. (doi:10.1098/rspb.2002.2052)
- Wong BBM, Salzmann C, Schiestl FP. 2004 Pollinator attractiveness increases with distance from flowering orchids. *Proc. R. Soc. Lond. B* **271**, S212–S214. (doi:10.1098/rsbl.2003.0149)
- Gaskell AC, Winnick CG, Herberstein ME. 2008 Orchid sexual deceit provokes ejaculation. *Am. Nat.* **171**, E206–E212. (doi:10.1086/587532)
- Ayasse M, Schiestl FP, Paulus HF, Löfstedt C, Hansson B, Ibarra F, Francke W. 2000 Evolution of reproductive strategies in the sexually deceptive Orchid *Ophrys sphegodes*: how does flower-specific variation of odor signals influence reproductive success? *Evolution* **54**, 1995–2006. (doi:10.1554/0014-3820(2000)054[1995:EORSIT]2.0.CO;2)
- De Jager ML, Ellis AG. 2013 The influence of pollinator phylogeography and mate preference on floral divergence within a sexually deceptive daisy. *Evolution* **67**, 1706–1714. (doi:10.1111/evo.12070)
- Ellis AG, Johnson SD. 2009 The evolution of floral variation without pollinator shifts in *Gorteria diffusa* (Asteraceae). *Am. J. Bot.* **96**, 793–801. (doi:10.3732/ajb.0800222)
- Thomas MM, Rudall PJ, Ellis AG, Savolainen V, Glover BJ. 2009 Development of a complex floral trait: the pollinator-attracting petal spots of the beetle daisy, *Gorteria diffusa* (Asteraceae). *Am. J. Bot.* **96**, 2184–2196. (doi:10.3732/ajb.0900079)
- Whitehead MR, Peakall R. 2013 Short-term but not long-term patch avoidance in an orchid-pollinating solitary wasp. *Behav. Ecol.* **24**, 162–168. (doi:10.1093/beheco/ars149)
- Wcislo WT. 1987 The role of learning in the mating biology of a sweat bee *Lasioglossum zephyrum* (Hymenoptera: Halictidae). *Behav. Ecol. Sociobiol.* **20**, 179–185. (doi:10.1007/BF00299731)
- Dukas R. 2004 Male fruit flies learn to avoid interspecific courtship. *Behav. Ecol.* **15**, 695–698. (doi:10.1093/beheco/arh068)
- Dukas R. 2008 Evolutionary biology of insect learning. *Annu. Rev. Entomol.* **53**, 145–160. (doi:10.1146/annurev.ento.53.103106.093343)
- Anderson B, Johnson SD. 2006 The effects of floral mimics and models on each others' fitness. *Proc. R. Soc. B* **273**, 969–974. (doi:10.1098/rspb.2005.3401)
- Ferdy J, Gouyon P, Moret J, Godelle B. 1998 Pollinator behavior and deceptive pollination: learning process and floral evolution. *Am. Nat.* **152**, 696–705. (doi:10.1086/286200)