1 RESEARCH ARTICLE

2 **Title**

3 # Mimicking orchids lure bees from afar with exaggerated ultraviolet

4 # signals

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Conflict of interest

43 Authors declare no competing interests.

Author contributions

45 DS, SC, MG, KL, AGD conceived the ideas and designed methodology; DS, MB, AG collected the data;

46 LG, DS, AG, SC, AGD analysed the data; DS, MG, KL, SC led the writing of the manuscript. All authors

47 contributed critically to the drafts and gave final approval for publication.

Data availability statement

49 Data needed to evaluate the conclusions in the paper are presented in the Supplementary Information.

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Abstract

1. Flowers have many sensory traits to appeal to pollinators, including ultraviolet (UV) absorbing markings, which are well known for attracting bees at close proximity (e.g. < 1 m). While striking UV signals have been thought to attract pollinators also at greater distances of meters, how the signals impact the plant pollination success over distance remains unknown. Here we report the case of the Australian orchid *Diuris brumalis,* a non-rewarding species, pollinated by bees via mimicry of rewarding pea plant *Daviesia decurrens*. When distant from the pea plant, *Diuris brumalis* was hypothesized to enhance pollinator attraction by exaggerately mimicking the floral ultraviolet (UV) reflecting patterns of its model.

2. By experimentally modulating floral UV reflectance with a UV screening solution, we quantified the orchid pollination success at variable distance from the model plants.

3. We demonstrate that the deceptive orchid *Diuris brumalis* attracts bee pollinators by emphasizing the visual stimuli, which mimic the floral UV signalling of the rewarding model *D. decurrens*. Moreover, the exaggerated UV reflectance of *D. brumalis* flowers impacted pollinators' visitation at an optimal distance from *D. decurrens*, and the effect decreased when orchids were too close or too far away from the model.

4. Our findings show that salient UV flower signalling plays a functional role in visual floral mimicry, likely exploiting perceptual gaps in bee neural coding, and mediates the plant pollination success at much greater spatial scales than previously expected.

Keywords: ecological interactions, flower attraction, bee sensory ecology, visual food deception, orchid floral mimicry, pollination success, salient stimuli, ultraviolet reflectance

1. Introduction

The art of deception, involving a range of strategies individuals adopt to change the perception and behaviour of others, is commonly practiced by many organisms across the animal and plant kingdoms. Mimicry, a form of deception, allows individuals to conceal their identity and avoid recognition by (more or less) closely imitating the behaviour or resembling the appearance of their models (Dawkins & Krebs, 1979). One of the most remarkable examples of these deceptive adaptations is the duping of pollinating animals by plant mimics. Amongst the 32 families of deceptive plants (Renner, 2006), orchids are undoubtedly the master tricksters. With an estimate of about one-third of all species lacking floral reward to pollinators (Dafni, 1984; Ackerman, 1986a; Jersáková et a.l, 2006), orchids deceive by luring food-seeking

85 animals by fine-tuned mimicry (i.e. Batesian floral mimicry) or general, even inaccurate, resemblance of

86 rewarding flowers (e.g. generalized food deception; Shretha et al., 2020). Surprisingly, how plants succeed

87 in their deception despite widespread imperfect mimicry remains poorly understood (Roy & Widmer, 1999;

88 Schiestl, 2005; Vereecken & Schiestl, 2008). In animals, the success of imperfect mimicry has been

89 explained by high-salience traits, which overshadow other 'less important' traits (Cuthill, 2014; Kazemi et

90 al., 2014) by being highly discriminable from the background (Frieman & Reilly, 2015). Although high-

91 salience signals such as attention-grabbing colours and visual patterns occur as frequently in animals

92 (Kazemi et al., 2014) as in plants (Peter & Johnson, 2008; Jersáková et al., 2012; Peter & Johnson, 2013),

93 their role in explaining imperfect mimicry in plants has received comparatively less attention (Vereecken &

94 Schiestl, 2008). In this study, we examined the role salient ultraviolet (UV) signalling plays in the imperfect

95 floral mimicry of a rewardless orchid that falsely advertises a reward to attract bees when afar from model

96 plants.

97 Flowering plants and pollinating insects interact through a wide range of sensory modalities which affect

98 both the pollinator's foraging behaviour and the plant's reproductive success (Leonard et al., 2011a;

99 Glover, 2011). Pollinating insects, in particular bees, make their foraging decisions most effectively by

100 combining visual, olfactory and somatosensory floral signals (Leonard at al., 2011a; Kulahci et al., 2008),

101 yet their innate preference for conspicuous floral displays makes colour and contrasting visual patterns the

102 primary means by which plants first attract them (Naug & Arathi, 2007; van der Kooi et al., 2019). Bees,

103 the main flower visitors, have phylogenetically conserved trichromatic vision (Briscoe & Chittka, 2001)

104 which can be conveniently modelled with maximum sensitivity UV (approx. 340 nm), Blue (435 nm) and

105 Green (560 nm) photoreceptors (Chittka & Kevan, 2005). Plants produce striking floral markings and

106 patterns by absorbing and reflecting UV light (Briscoe & Chittka, 2001; Dinkel & Lunau, 2001; Lunau et al.,

107 2006; Papiorek et al., 2016; Lunau et al., 2021). Interestingly, it is the UV reflectance display rather than

108 UV pattern (absorbance and reflectance) that increases insect visitation (Johnson & Andersson, 2002;

109 Klomberg et al., 2019). The high chromatic contrast that such UV signals can generate is thought to

110 enhance colour salience in an opponent colour system (Lunau et al., 2006; Papiorek et al., 2016; Chittka

111 et al., 2001); however, such chromatic contrast is assumed to work only at relatively short distances of

112 about few centimetres (e.g. UV absorbing "floral guides"; Giurfa et al., 1996; Garcia et al., 2001; Horth et

113 al., 2014; Orbán & Plowright, 2014). This is because bees typically only use the long wavelength green

114 input channel of their visual system to enable fast achromatic processing and detection of small target

115 signals (Klomberg et al., 2019), although some psychophysics shows that alternative chromatic channels

116 may in some cases also be important for bee detection and recognition (Zhang et al., 1995; Morawetz et

117 al., 2013; Dyer et al., 2019). That UV reflectance can also attract pollinator insects from further afield has

118 been posited for decades (Daumer, 1956; Daumer, 1958; Burr et al., 1995; Koski & Ashman, 2014) but

119 remains unverified.

120 Salient UV signals against the background may be particularly relevant for increasing long distance

121 attractiveness in plants that employ flower mimicry (Dyer, 1996). One such plant is the Australian donkey

122 orchid *Diuris brumalis* whose outer petals appear yellow to human vision, and also reflect large amounts of

123 UV that would be conspicuous to the visual system of bees (Burr et al., 1995). *Diuris brumalis* is a food-

124 deceptive species which secures pollination by resembling the co-occurring rewarding pea plant *Daviesia*

125 *decurrens* (Scaccabarozzi et al., 2018). The mimicry signals consist of both colour reflectance and inner

126 flower shape, as the outer petals diverge from the pea flower shape (Scaccabarozzi et al., 2018). In

127 addition, the size of the orchid flower is about three times bigger than the pea flower (Fig. 1 a). Whilst the

128 mimicry in size and shape is imperfect, the orchid coloration, with the average colour loci corresponding to

129 the UV region, is perceptually similar to the pea model in colour space; such overlap (< 0.06 colour

130 hexagon units) makes the two species not readily distinguishable in the eyes of their bee pollinator,

131 *Trichocolletes* spp. (Hymenoptera: Collectidae, Fig 1a; Scaccabarozzi et al., 2018). Food-deceptive

132 orchids are known for gaining their pollination success not only by resembling a specific rewarding model

133 flower (Scaccabarozzi et al., 2018; Schaefer & Ruxton, 2009; Dyer et al., 2012), but also exaggerating their

134 floral signals that advertise the false reward and thus increase pollinator responses (Ackerman, 1996b).

135 We hypothesized that the two UV reflecting outer petals of *Diuris* function as exaggerated version (for UV

136 reflectance display) of the floral signal display *Trichocolletes* bees normally encounter in the rewarding

137 *Daviesia* peas. We expected that modulating the *Diuris* exaggerated UV signals over a spatial scale does

138 affect pollination success when orchids are relatively distant from their model food plants because

139 pollinators are more likely to mistake the orchid for the rewarding model when afar. Here we report that the

140 orchid not only uses exaggerated UV reflectance to falsely advertise a potential reward to attract bees from

141 afar, but the ruse works most effectively at an optimal distance of several meters revealing the functional

142 role of salient visual stimuli when mimicry is imperfect.

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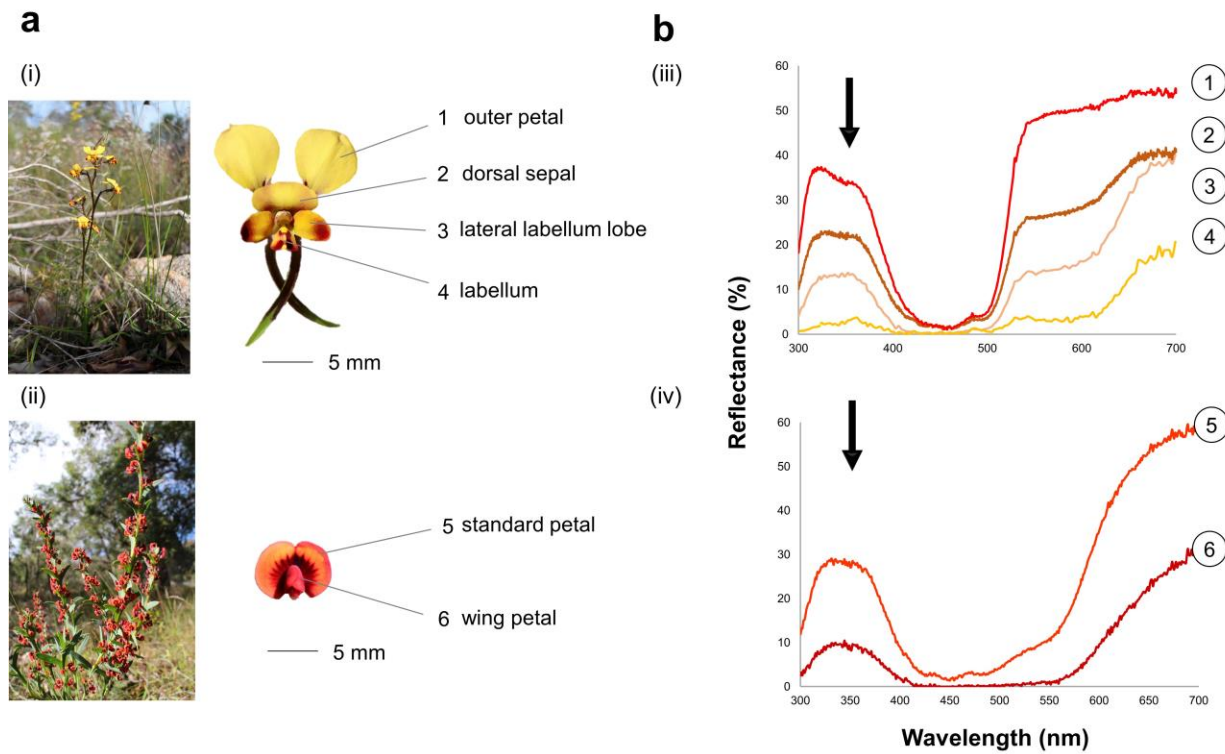
2. Materials and Methods

144

145 **Study system.** Endemic to Western Australia, the orchid *Diuris brumalis* produces yellow–brown

146 nectarless flowers between July and August and is pollinated via mimicry of rewarding pea plants

147 (*Daviesia* spp.) by *Trichocolletes* (Colletideae) native bees (Scaccabarozzi et al., 2018). *Trichocolletes* is a

148 genus of solitary bees that are specialist and speed (visits last less than two seconds) feeder on pea

149 flowers and displaying a distinctive and identical behaviour on both orchids and peas, confirming that it is

150 successfully deceived. The orchid mimics the papilionaceous flower typical of the pea model and while the

151 visible spectrum differs between the mimic and model flower, they are likely to look similar through a bee

152 visual model (Scaccabarozzi et al., 2018). However, the orchid flower diverges from the pea flower

153 structure for exhibiting two prominent outer petals.

154 We carried out our study in *Diuris brumalis* populations spread along the Darling Range in Western

155 Australia during 2018, 2019 and 2020 (Table S1). *In situ* studies and experimental setting were preferred

156   as the orchids are protected by national regulation and their withdrawl is only allowed for few biological

157   material.

158

159   **Floral morphology and colour properties.** To test the hypothesis that the two outer petals of *Diuris* may

160   function as an exaggerated version of *Daviesia* floral signals, we determined whether the orchid outer

161   petals had the highest UV reflectance, so amplifying the UV reflectance of the pea model. Firstly, we

162   determined whether the outer petals were the component of the *Diuris* flower with the highest UV spectral

163   reflectance. We obtained UV measurements for each floral component (n = 6 flowers) for both species

164   using a Cary 4000 UV-Vis spectrophotometer (Agilent Technologies, CA) and calculating the average

165   spectral reflectance for each floral part.

166   Secondly, we measured the size of the flower components of the flower in 10 plants of both *Diuris* and

167   *Daviesia* (Fig. S1; Data source S1). We obtained for both species a UV salient signal ratio according to cut

168   value of Australian flowers following Dyer (1996) (see Data source S1). Flower components' area were

169   estimated as follows: as flowers of *Diuris* and *Daviesia* show minimal concavity or convexity, the area of

170   the outer and central component of *Diuris* were estimated by approximating the components to the closest

171   geometric figures, the ellipse (orange) and the circle (green), respectively (Fig. S1). *Daviesia* standard

172   petals' area was approximated to an ellipse, to which was subtracted a secondary minor ellipse

173   circumscribing the wing and keel petals (Fig. S1; Data source S1).

174   To quantify the contrast of the respective flower signals we used the bee visual parameters according to

175   Chittka and Kevan (2005) and neural coding that enable converting visual signals sensed by each receptor

176   channel into Excitation values between 0 and 1.0. The visual system was adapted to foliage background

177   with a biologically relevant neural resting Excitation value of 0.5 and a contrast of zero (Chittka et al., 1994;

178   Spaethe et al., 2001). This model enables the calculation of absolute contrast values ranging from 0 to 0.5

179   (maximum contrast) for any stimulus that is different to the background as perceived by the visual system

180   of bees (Table 1).

181   False colour photography in 'bee view' format was used to reveal the overall colour pattern perceived by

182   bees of *Diuris* and *Daviesia* flowers (Fig. 2 a, Fig. 2b; see Methods S3 in Supporting Information).

183   Spectrometer measuremens of flower components of *Diuris* and *Daviesia* were converted according to the

184   established bee visual model (Chittka, 1992). Location of colour loci was calculated as from mean of

185   reflectance for floral parts of *Diuris brumalis,* and *Daviesia decurrens* (Fig. 2 c).

186   **Model-mimic distance experiment.** To test whether *Diuris* pollination success varies depending on the

187   distance to the model pea plants, in 2019 we first quantified distance between an individual orchid and all

188   the surrounding pea models within a quadrat of 30 x 30 m centred on a single orchid plant (N = 122

189   orchids across 5 populations; Fig. S2) for all orchid plants per population. As a result, all quadrats were

190   overalapped within the same population, but not among populations (as distance between population was

191   greater than 500 m). To quantify pollination attraction, we recorded the number of pollinaria removed by

192   pollinators in all orchids per population, counting the number of flowers in both orchids and pea plants

193   (pollinia removed in orchids were counted by visually observing the lack of pollinia at the top of the

194   column). We analysed the distance data by using a Generalized Mixed Effect Model (GLMM) with Poisson

195   distribution. The response variable in the model was the number of pollinaria removed and the fixed effects

196   were the distance from the pea model and the number of orchid flowers. Population was treated as

197   random factor, since it was found to be significant in influencing the number of pollinaria removed. The

198   model was evaluated for its dispersion parameter and residuals were evaluated for the assumption of

199   overdispersion and homoschedasticity.

200   **Ultraviolet manipulations experiments.** Subsequent manipulation experiments were carried out in field

201   in 2019 and 2020 by screening the UV properties of the two *Diuris* outer petals with an UV filter solution

202   (see Johnson & Andersson, 2002; Peter & Johnson, 2013), which effectively eliminates UV reflectance

203   whilst transmitting all wavelengths above 400 nm (Fig. 2 a, Fig. 2 b i.e., UV filter). To confirm that treated

204   *Diuris* outer petals did not excite the UV bee photoreceptor as untreated petals and *Daviesia* petals did, we

205   analised the spectral reflectance measurements for the different floral component using the model of bee

206 vision including treated petals (Chittka, 1992; Table 1). False colour photography in 'bee view' format was

207 applied on *Diuris* flower with treated outer petals to show the overall colour pattern (Fig. 2 b).

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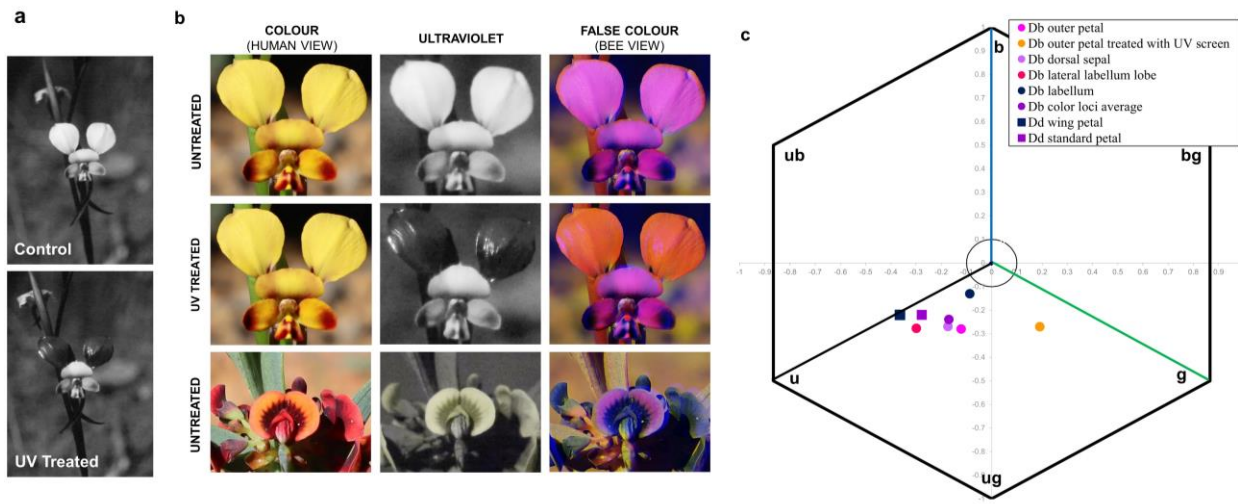
Fig. 2. Colour patterns perceived by bees in treated and untreated *Diuris* flowers and untreated

Daviesia. (**a**) *Diuris* flower photographed in UV before (control, C) and after applying the UV absorbant

filter on the outer petals (UV treated, T). (**b**) False colour photography in 'bee view' reveals the overall

colour pattern perceived by bees in treated (i.e., application of the UV filter solution) and untreated outer

petals of *Diuris* flower and untreated *Daviesia* flower. The UV filter is effectively a long pass filter

transmitting all wavelengths above 400 nm, free of fragrance, oil, PABA, alcohol, parabens and

preservatives (Kinesys, Canada). Importantly, the UV images of treated outer petals show very similar

reflectance properties to the background and stem foliage reflectance, confirming that the experimental

manipulation knocked out UV signalling with respect to background colouration. (**c**) Location of colour loci

was calculated as from mean of reflectance for floral parts of *Diuris brumalis* (Db), and *Daviesia decurrens*

(Dd). The calculations were made using the Hexagon colour model of bee vision (Chittka, 1992). This

model represents the internal perception of flower colours by bee pollinators, and resultant sectors [u

(ultraviolet); ub (ultraviolet-blue); b (blue) bg (blue-green); g (green); ug (ultraviolet-green)] show how bees

likely interpret spectral signals].

In the first field manipulation experiment (in 2019), we tested the hypothesis that UV reflectance enhances

orchid pollination success (pollen removal) only when orchids are out of patch of model pea plants. We

quantified the number of pollinaria removed from *Diuris* flowers by free-foraging bees when the mimicking

orchid occurred inside [IN] and outside [OUT] the 30 x 30 m patch of model plants (within a maximum

227   distance of 10 meters from the patch; Fig. 3a). The patch size encompassed most orchid plants belonging

228   to an individual population according to former studies on pollination success of *Diuris* at this location

229   (Scaccabarozzi et al., 2018). Over a 4-day period, all orchids in both [IN] and [OUT] groups (N = 400

230   across 5 populations, Table S1) were treated with the UV filter. Within each group, a randomly selected

231   half of the orchids was sprayed on the front and back of the two outer petals (treatment, T) and the other

232   half of the orchids at the base of the corolla (control, C). Number of flowers was standardised in each

233   group by removing exceeding flowers. The filter was applied before the daily peak of bee activity and left

234   for 3 hours (correspoding to the filter persistence on petals) from 11.00 am to 1.00 pm and the number of

235   pollinia removed from the orchids within each group was recorded during the subsequent two-hour period

236   (1.00 to 3.00 pm). Prior to the filter application, the treated and untreated plants were numbered and

237   tagged. We also recorded the number of pollinia already removed per flower / per plant to make sure of the

238   net counting of pollinia. When revisiting the plants for scoring pollinia, we checked the plants in the same

239   order followed prior to the treatement. Statistics were based on comparisons of removed pollinia between

240   experimental groups (UV-treated petals) and control groups (UV-untreated petals).

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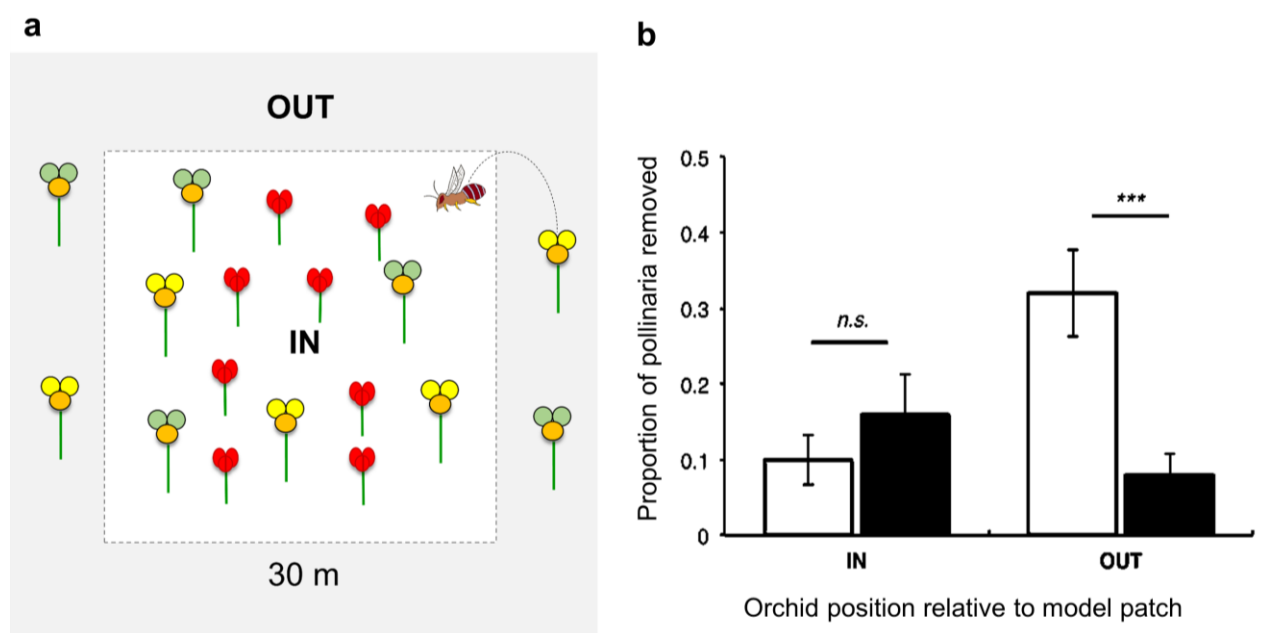
243   **Fig. 3. Effect of distance from model plants on *Diuris* pollination success.** (**a**) *Diuris* orchids (yellow

244   [untreated] and green [UV treated] flowers) inside [IN] and outside [OUT] a 30 x 30 m patch with *Daviesia*

245   pea (red flowers). (**b**) Mean proportion of pollinaria bees removed from treated (black bars; T) and

246   untreated *Diuris* flowers (white bars; C) relative to the orchid's distance ([IN] and [OUT]) from the model

247   pea. Each experimental group consists of N = 100 orchids. Error bars are 95% confidence intervals; *n.s.*

248 no significant difference among experimental groups; ***significant difference at Bonferroni corrected α =

249 0.0125.

250 In the second field manipulation experiment (in 2020), we tested the hypothesis that by displaying an

251 exaggerated version of *Daviesia*'s attractive UV reflectance, *Diuris* benefits from pollinators that mistake it

252 for the rewarding model from afar. We quantified pollinaria removal within 63 orchid groups randomly

253 selected across three large orchid populations (Table S1, Populations 1, 2,3). Each orchid group consisted

254 of two orchid clumps, each containing between 2 and 12 plants. Each orchid clump was selected to be at

255 approximately the same distance from a model pea plant (from 0 to 15 m) at a variable angle from the pea

256 plant (Fig. 4a).
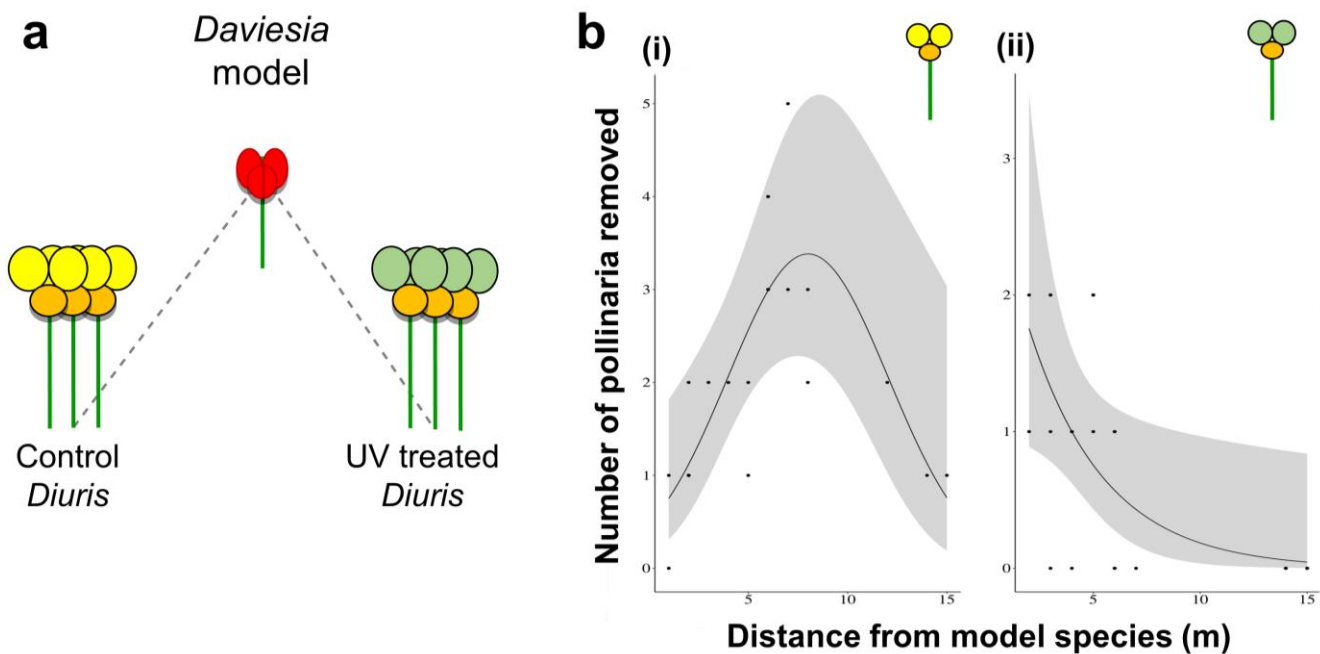
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258 **Fig. 4. Effect of *Diuris* UV reflectance on the orchid's pollination success relative to mimic-model**

259 **distance.** (**a**) Experimental set up treated, untreated orchid groups and pea plants, (**b**) Pollinaria removal

260 was quantified in 195 orchids (N = 476 orchid flowers). Pollination success of control *Diuris* relative to

261 distance from *Daviesia* (i) was best described by an inverted parabolic function peaking at ~8 m distance

262 from model pea ($\chi2$=9.87, p < 0.05 for the squared and linear term respectively) (N=238 flowers, n =43

263 pollinia removed). Pollination success of UV treated orchids (ii) exhibited an exponential decrease with

264 distance from model pea plants ($\chi2$=10.26, p < 0.001); (N=238 orchid flowers, n =17 pollinia removed).

265 Refer to Data source S7 for full data.

266   Within each orchid group, *Diuris* floral display (i.e., number of flowers in each clump) was standardized by

267   removing excess flowers. Within each group, the UV filter solution was sprayed on the outer petals of one

268   clump (treatment, T) and at the base of the corolla on the other clump (control, C) as in the previous

269   experiment (same treatment and plant visitation timing). Prior to the UV filter application, the treated and

270   untreated plants were numbered, tagged and the number of pollinia removed per flower / per plant was

271   recorded. Pea plant flowers range was uniform among plants at the time of experiment. The number of

272   pollinaria removed from the UV treated and control orchids within each group was recorded as a function

273   of of the orchid's distance to the pea plant and was modelled by a Poisson GLMM (appropriate for count

274   data) with a fixed effect for treatment.

275

276   **3. Results**

277

278   *Outer petals in the mimic orchid display an exaggerated UV signal of model plants*

279

280   Spectral reflectance and morphological measurements of flowers components confirmed that *Diuris*

281   functioned as an exaggerated version of the floral signals bees normally encounter in the rewarding

282   *Daviesia* peas. The outer petals proved to be both the largest component of the orchid flower and the area

283   with the highest UV reflectance (Fig. 1b; Fig S1, Data source S1). *Diuris* flowers produced an overall

284   higher UV salient signal ratio (ratio=0.84) comparing to *Daviesia* flowers (ratio=0.69; Data source S1)

285   representing a 22% increase of surface area reflecting UV signal (Data source S1). The strength of the UV

286   signalling in *Diuris* had a contrast value of 0.34 which is 26% greater than the UV channel contrast value of

287   0.27 in *Daviesia* standard petals (Table 1). False colour photography in 'bee view' revealed the similarity of

288   the overall colour pattern perceived by bees of *Diuris* and *Daviesia* flowers (Fig. 2 b).

289   According to the colour model, petals of *Diuris* and petals of *Daviesia* are located in the bee perceived "ug"

290   (UV-green) and "u" (ultraviolet) sectors of the Hexagon colour space related to the excitation of bee

291   photoreceptors and subsequent bee neural coding of information (Fig. 2 c; Table 1) (Chittka, 1992; Chittka

292   et al., 1994).

293

294

295 *Orchid pollination success relate to mimic-model distance*

296

297 Mimic-model distance on large scale revealed that the number of pollinaria removed from the orchid

298 flowers decreased significantly with distance between orchid and pea (Fig. S2). Specifically, pollination

299 success decreased significantly with the square of orchids' distance from the pea model (χ^2=17.09, p <

300 0.001) and was compromised when the distance between orchid and pea was greater than 15 m (χ^2=9.49,

301 p = 0.002).

302

303 *The exaggerated UV signal enhances the orchid success relative to model plants*

304

305 Field manipulation experiments showed that the exaggerated UV signal of *Diuris* outer petals enhances

306 the orchid's pollination success. The UV filter treatment had no attracting or repelling effect on the

307 pollinators (see Methods S1 in Supporting Information).

308 Treated petals of *Diuris brumalis* are located in the bee perceived "g" (green) Hexagon sector and did not

309 excite bee UV photoreceptors (Fig. 2 c; Table 1). Secondly, the colour model confirmed that excitation of

310 Green receptor, which is known to be important for how bees efficiently find flowers (Giurfa et al., 1996;

311 Skorupski & Chittka, 2010; Garcia et al., 2021), was not affected by UV filter treatment (Table 1).   False

312 colour photography in 'bee view' confirmed that the UV filter knocked out UV signalling with respect to

313 background colouration (Fig. 2 b).

314 In the first field manipulation experiment, we quantified the number of pollinaria removed from treated and

315 control *Diuris* flowers by free-foraging bees when the mimicking orchid co-occurred with the model pea

316 within a 30 x 30-m patch per orchid population [IN] and when the mimics occurred outside the patch of

317 model plants [OUT] (Fig. 3a). The application of the UV filter on the two outer petals resulted in a

318 significant effect on the number of pollinaria removed by bees from the orchid flowers (χ^2=19.81, p <

319 0.001). There was no difference in the pollination success of *Diuris* whose outer petals had been treated

320 with the UV filter [IN-T] compared to untreated control orchids [IN-C] inside the patchs of model plants (Fig.

321 3b). Outside the patchs of model plants, however, orchids with UV-filter treatment [OUT-T] experienced

322 significantly lower pollinaria removal than control ones [OUT-C] (Fig. 3b).

323   In the second field manipulation experiment, we found that pollination success of control *Diuris* increased

324   with distance by peaking at ~8 m away from the model peas before declining and becoming ineffectual at

325   distances greater that 15 m (Fig. 4bi). We detected no effect of UV reflectance on *Diuris* pollination

326   success when the orchids were closer than a few meters to their model pea plants (Fig. 4bi, Fig. 4bii).

327

4. Discussion

329   Our results establish that *Diuris* orchids mimic and exaggerate *Daviesia*'s attractive floral signals in terms

330   of UV reflectance, display, and contrast as perceived by bee pollinators. Flowers that reflect greater than

331   10% UV radiation, like *Diuris* and *Daviesia*, are shown to have evolved this salient trait to improve

332   communication with bees since most organic background material like leaf foliage has very low UV

333   reflectance (Dyer, 1993; Chittka et al., 1994; Spaethe et al., 2001; van der Kooi et al., 2019).

334   By masking the UV reflectance in half of the orchids inside the *Daviesia*'s patch, the treatment effectively

335   made those *Diuris* displaying the exaggerated UV signal a rarer phenotype, which would be predicted to

336   enjoy greater pollination success by negative frequency-dependent selection (Schiestl, 2005; Schiestl &

337   Johnson, 2013). Instead, there was no difference in the pollination success of *Diuris* whose outer petals

338   had been UV screened [IN-T] compared to untreated control orchids [IN-C] inside the *Daviesia*'s patch

339   (Fig. 3b). At closer range, within pea patch, bees apparently recognise plants by spotting other visual traits

340   as the shape of *Diuris* two outer petals. For example, a colour trait may become less effective in ensuring

341   successful mimicry when other secondary traits such as size and shape of the flowers can be better

342   discriminated (Gigord et al., 2002; Johnson et al., 2006). Outside the model patch, however, orchids with

343   UV-filter treatment [OUT-T] experienced substantially lower pollinaria removal than control ones [OUT-C]

344   (Fig. 3b), due to a lack of the salient signal which is associated to the model trait. Thus, the exaggerated

345   UV signal produced by *Diuris* outer petals only increased the orchid's pollination success when the mimic

346   was further away from its models' patch. Our findings demonstrate that salient floral UV reflectance plays

347   a critical role in ensuring *Diuris* pollination success and explain why the exaggerated UV signal is

348   strategically relevant in floral mimicry when the model is not very close to the mimic. According to previous

349   theories predicting the effectiveness of the mimic's floral stimuli to decline with distance from its model

350   (Johnson & Schiestl, 2016; Duffy & Johnson, 2017), we also found that the number of pollinaria removed

351 from the orchid flowers decreased significantly with distance between orchid and pea (Fig. S2). However,

352 the strength and direction of this effect may vary across different spatial scales and conclusions about the

353 importance of floral stimuli will depend on the scales at which studies are undertaken. For example, by

354 examining the mimic-model effect at considerably smaller spatial scales than usually investigated (i.e.,

355 tens to hundreds of meters) (Duffy & Johnson, 2017; Johnson et al., 2003; Peter & Johnson, 2008), our

356 results show that the exaggerated UV reflectance of *Diuris* outer petals function to enhance pollination at

357 an optimal model-mimic range of ~8 m. *Diuri*s outer petals might promote pollinator deception via bee

358 cognitive misclassification (Dyer et al, 2012; Johnson & Schiestl, 2016), displaying colour frequencies

359 below the optimal range of colour disciminations in hymenopteran (i.e. 400-500 nm) (Peitsch et al., 1992),

360 especially for free-flying honeybees (von Helversen, 1972; Rohde et al., 2013).

361 But why might the observed distance range from model species be optimal? To understand this question,

362 we must delve into both the neurophysiology and physiology of how bee pollinators perceive their world.

363 When a bee receives sweet tasting nectar reward from a rewarding plant like *Daviesia decurrens,* this

364 promotes a sustained positive neural response via the ventral unpaired median (VUM) neurons that permit

365 an association between flower and reward with a sustained spiking response of about 15s (Hammer, 1993;

366 Perry, 2013), and can enable simple associative learning of colour information (Dyer & Chittka, 2004;

367 Giurfa, 2004). It is also known that precise colour memory in both bees and humans requires simultaneous

368 viewing conditions that decay in less than a second once a target model is no longer in view (Uchikawa &

369 Ikeda, 1981; Dyer & Neumeyer, 2005); therefore, being close to a model species might allow a bee to

370 identify potential differences that unmask the deception (von Helversen, 1972). Given that bees may fly up

371 to about 7 m in a second (Spaethe et al., 2001; Srinivasan & Lehrer, 1985), we hypothesize the 8 m

372 distance we observed for optimal pollination success is beyond the theoretical upper limit where precise

373 colour vision operates; at such distances, the bee has to recall from memory what it thought was rewarding

374 and tends to prefer a slightly more salient comparative stimulus, an effect related to peak shift

375 discrimination (Lynn et al., 2005; Leonard et al., 2011b; Martínez-Harms et al., 2014). The fast visits of

376 *Trichocolletes* bees on both model and mimic flowers (Scaccabarozzi et al., 2018), suggest that *Diuris*

377 benefits from foraging speed behaviour that unfavours the accuracy of bee choices (Chittka et al., 2003).

378 Thus, we propose that orchids like *Diuris* master deception by employing both exaggerated signalling and

379 by exploiting the perceptual gaps in pollinators' visual processing.

380   Our results also highlight that we gain a very different understanding of the relative role of floral signals if

381   we work at one scale over another and consider the dynamics of pollinator perception. For example, orchid

382   pollination success was greatest when the mimics where further away from their models (e.g. ouside the

383   patch), but within a maximum distance of 10 meters from the model patch. Because the pollination

384   success of deceptive species can be subject to both competition and facilitation effects depending on the

385   density of rewarding (Julliet et al., 2007) and conspecific plants (Duffy & Stout, 2011) the competition

386   orchids experienced within the patch of floriferous pea plants would have been at its strongest (Fig. 3b).

387   However when we accounted for both floral density of conspecific and model plants along a continuous

388   and wider spatial scale (Fig. S2), the pollination success pronouncedly declined at distances greater than

389   15 m from model plants. At such distances, the orchids no longer had to contend with the peas for

390   pollinators' attention but the beneficial effect of facilitation between the the plant species also

391   disapperared. Therefore, the importance of exaggerated UV reflectance in attracting pollinators from a

392   range of several meters can be missed and/or mistakenly dismissed if not measured at the scale at which

393   it has its strongest ecologically-relevant effect. Such a long-range signal might not be suspected

394   considering the typical acuity range of bee chromatic vision for stationary stimuli within the confined space

395   of a Y-maze (Giurfa et al., 1996). Overall, our results demonstrate that the functional role of UV reflectance

396   signalling is contingent on the relative distance between deceptive and rewarding species and their

397   pollinators; the distance described here operates at spatial scales of meters, which are much greater than

398   previously described for floral colours. The terminal position of the outer petals on a long stemmed plant

399   (Fig. 1a) likely promotes (wind) movement of this exaggerated UV signal that can be even better perceived

400   from afar by foraging bees (Stojecev et al, 2011; Brock et al., 2016) by acting as a 'flag signal'.

401   Contributing to a range of floral displays aimed at pollinator senses, UV reflectance acts as an important

402   visual cue in many flowering plant species (Johnson & Andrersson, 2002; Klomberg et al., 2019). The high

403   UV reflectance of *Diuris* outer petals enables bees to find these relatively scarce flowers from a distance of

404   meters. Selection may favour deceptive floral displays capable of longer range UV signalling that help

405   pollinators such as solitary bees to locate flowers in habitats where the distribution of rewarding model

406   flowers is patchy, explaining why relatively large, salient UV signals with high background contrast have

407   evolved in the mimic (Rohde et al., 2013). By revealing that floral salient UV displays are efficiently used

408   by bees not only at the very close ranges already well-documented, but also from further afield (see also

409   Supporting information, Methods S2), we may explain how plant deception succeeds despite imperfect

410   floral mimicry. This finding invite us to extend our understanding of the adaptive significance of UV

411   reflectance and salient signalling that plants display in an captivating phenomenon such as the floral

412   mimicry and more general in nature.

413

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607 **Tables**

608

609 **Table 1.** Average of excitation values (± SD: standard deviation) of bee photoreceptors (UV, blue,

610 green) according to Chittka[46,47] and relative corrected values for *Diuris* and *Daviesia* flower

611 components as shown in Fig. 1, including *Diuris* outer petals treated by UV filter. Excitation values

612 range between 0 and 1.0 where a value of 0.5 represents no excitation of the sensory neural

613 channel, and so absolute maximum excitation contrast is 0.5 for each respective channel.

614

Flower components		E(uv)±SD	E(uv)-0.5	E(b)±SD	E(b)-0.5	E(g)±SD	E(g)-0.5
1	*Diuris brumalis* outer petal	0.84±0.03	0.34	0.49±0.07	0.01	0.70±0.03	0.20
	Diuris brumalis outer petal treated with UV filter	0.48±0.03	0.02	0.32±0.07	0.18	0.70±0.03	0.20
2	*Diuris brumalis* dorsal sepal	0.77±0.09	0.27	0.40±0.09	0.10	0.57±0.07	0.07
3	*Diuris brumalis* lateral labellum lobe	0.64±0.17	0.14	0.20±0.11	0.30	0.42±0.17	0.08
4	*Diuris brumalis* labellum	0.25±0.17	0.25	0.07±0.07	0.43	0.15±0.03	0.35
5	*Daviesia decurrens* standard petal	0.77±0.02	0.27	0.39±0.09	0.11	0.45±0.06	0.05
6	*Daviesia decurrens* wing petal	0.56±0.10	0.06	0.13±0.05	0.37	0.14±0.06	0.36

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