

SENDING PRIVATE MESSAGES: FLORAL ULTRAVIOLET SIGNALS ARE ASSOCIATED WITH POLLINATION SYNDROMES IN *ERICA*

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Abstract—The presence of ultraviolet (UV, wavelengths between 300-400 nm) reflectance in insect-pollinated flowers has been linked to pollination efficiency and pollination shifts, but little is known about its prevalence and function in other pollination systems and African species. We chose the genus *Erica* for studying the prevalence of UV because of its extreme radiation (c. 680 species) in the Cape, South Africa, with a diversity of pollination syndromes. This study quantified the prevalence and brightness of UV reflectance for five *Erica* pollination syndromes and tested pollinator preferences for UV reflectance in the two groups with the highest prevalence: sunbirds and long-proboscid flies. Our results show that UV colouration is absent or rare in *Erica* species pollinated by unclassified insects, rodents or wind. About 17 % of bird-pollinated species reflected UV but choice experiments revealed that free-ranging sunbirds showed no preference for UV signals. All sampled long-proboscid fly-pollinated species reflected UV and its experimental removal decreased seed set drastically, suggesting that long-proboscid flies in the Cape strongly prefer or depend on UV and thereby contributed to selecting for the evolution of this signal.

Keywords—Flower colour, Fynbos, Long-proboscid fly, Nectariniidae, UV, Vision ecology

INTRODUCTION

Colour is one of the most important flower advertisements for pollinators. Consequently, pollinators have contributed greatly to the large diversity of flower colours in angiosperms, which evoke specific behavioural responses in different flower visitors due to the differences in their colour vision systems and neural processing (Junker et al. 2013). Although many pollinators are able to see ultra-violet reflectance (UV, wavelengths between 300-400 nm; Shrestha et al. 2016), it has only been studied for a few species in the Cape Floristic Region (e.g., Peter et al. 2004; Peter & Johnson 2008; Welsford & Johnson 2012). Plants in the Cape might benefit from using UV reflectance to be more conspicuous to their preferred pollinators (Chen et al. 2020). On the other hand, UV absorbing compounds protect plants against damage through UV-B radiation, thus UV reflecting flowers are left vulnerable (Llorens et al.

2015) and this signal should only evolve if increased pollination services offset the fitness costs incurred.

The mega-diverse genus *Erica* (c. 680 species in the Cape, South Africa) is highly suitable for studying this because of its diversity of flower colours and pollinators (Rebelo et al. 1985). The species can be grouped into five pollination syndromes: insect-, bird-, long-proboscid fly- (LPF), rodent- and wind-pollinated (Rebelo et al. 1985; Turner et al. 2011; Lombardi et al. 2017). Since these species share an evolutionary history, a comparison of the prevalence of UV reflectance between pollination syndromes could indicate the role of pollinators in selecting for UV signals. Differences in colour vision and behavioural responses between the pollinators might have selected for different signals amongst the pollination syndromes and thereby contributed to reproductive isolation and species divergence (e.g. Streisfeld et al. 2013).

There has been little research on the pollination of specific *Erica* species grouped into the insect-pollinated syndrome, thus there might be a variety of functional groups pollinating them (van der Niet 2021). However, there seems to be a large number of bee-pollinated species (personal observation; Bouman et al. 2017). Hymenopterans in general are able to perceive UV but mostly have lower discrimination abilities in the UV area of the spectrum (Peitsch et al. 1992). Thus, we expect little UV reflection for species with this pollination syndrome.

LPF-pollinated *Erica* flowers can be distinguished based on their long ampullaceous corollas with narrow openings and spreading lobes and therefore are the most discrete functional group within the insect-pollinated species (Rebelo et al. 1985; Lombardi et al. 2021; Newman & Johnson 2021). There are no studies on UV vision in LPFs, specifically, but other flies have been recorded to see UV (Troje 1993). Fly-pollinated flowers have been shown to differ significantly in their colouration from bee-pollinated flowers (Shrestha et al. 2019) but different species of flower-visiting flies also differ greatly in colour preferences amongst each other (Lunau 2014), thus making it difficult to predict the prevalence of UV in LPF-pollinated flowers.

It has been shown that African nectarivorous birds (sunbirds and sugarbirds, Nectariniidae and Promeropidae, respectively) have genes for the receptors that enable them to perceive UV reflectance (Ödeen & Håstad 2010). Their behavioural response to UV, however, has not been tested yet. Bird-pollinated *Erica* species can be recognised by their long corollas, absence of floral scent and large nectar volume (van der Niet et al. 2014). Many bird-pollinated flowers around the world are red, which has been attributed to this colour being less conspicuous to bees that lack a photoreceptor for long wavelengths (Rodríguez-Gironés & Santamaría 2004). By being less conspicuous to bees, bird-pollinated flowers can avoid being visited by these less efficient pollinators or nectar robbers (de Camargo et al. 2019). Due to bees having less discrimination ability in the UV range, bird-pollinated species may also make use of short-wavelength cues to attract their pollinators and to be less conspicuous to bees (Lunau et al. 2011; Shrestha et al. 2013).

Thus, we expect a higher prevalence of UV for bird-pollinated species than for bee-pollinated species.

Rodents possess photoreceptors that are sensitive to UV light (Jacobs et al. 1991), but since the rodents pollinating *Erica* species are nocturnal (Turner et al. 2011; Lombardi et al. 2017) we do not expect them to be attracted by visual cues. Thus, we do not predict rodent-pollinated *Erica* species to reflect UV. Wind-pollinated species, too, are not expected to experience any selection for UV reflectance.

This study aims to (a) quantify the prevalence and brightness of UV reflectance in *Erica* across different pollination syndromes, and (b) test pollinator preference in the groups with the highest prevalence since this may have been the mechanism that selected for the signal. We expect higher prevalence of UV reflectance in flowers pollinated by UV perceiving animals. Additionally, if certain pollinators have driven the evolution of UV signals, we expect them to show a preference for UV colouration.

MATERIALS AND METHODS

UV PREVALENCE ACROSS POLLINATION SYNDROMES

To quantify the prevalence of UV reflectance, flower reflectance was measured in 125 *Erica* species collected in the Cape Floristic Region, South Africa (Tab. S1, Tab. S2). For each species, the reflectance of three to five flowers was measured using a spectrophotometer (Jazz model with PX-2 Pulsed Xenon light source, Ocean Optics, Dunedin, FL) and then averaged. For the species with two-coloured flowers, both colours were measured separately and for 11 of the species, different colour morphotypes were measured. For each reflectance spectrum, the lowest reflectance value was added to the reflectance at all wavelengths to correct negative values in the spectra, whereafter the spectra were smoothed (smoothing parameter = 0.2), averaged and analysed using the R package pavo (Maia et al. 2013). The contribution of UV (300–400 nm) to total brightness (the sum of all reflectance values between 300–700 nm) was recorded as a percentage of the total reflectance between 300–700 nm. Additionally, it was recorded to which pollination syndrome the species belongs (bird, LPF, unclassified insect, wind, rodent; Rebelo et al.

1985; Turner et al. 2011; Lombardi et al. 2017). Variation in UV reflectance between pollination syndromes was analysed using a generalised linear model with quasipoisson error structure followed by a Tukey post-hoc test to identify the differences between the groups.

UV PREFERENCE IN SUNBIRDS

To test if sunbirds exhibit a preference for flowers which reflect UV, choice experiments were conducted with free-ranging sunbirds and model flowers. Each model inflorescence consisted of a wooden stick to which five 1.5 ml Eppendorf tubes (model flowers, opening width 9.8 mm, length 38.9 mm) were attached at the upper end approximately 1 m above the ground to imitate an inflorescence. For UV-reflecting model flowers, the Eppendorf tubes were covered with white UV-reflecting bleached printing paper and transparent tape (Sellotape). For non-UV-reflecting model flowers the Eppendorf tubes were additionally painted with a white non-UV-reflecting paint (Tipp-Ex) on top of the paper before covering them in transparent tape. Comparing the colours through bird vision models indicated that birds should easily be able to discriminate between them (6.8 JND, Fig. S1). The model flowers were filled with 50 μ l of 10% (weight/weight) sucrose solution and set up among natural fynbos vegetation at the Cape of Good Hope section of Table Mountain National Park (34.266° S, 18.463° E). Four pairs of UV-reflecting and non-UV reflecting inflorescences (50 cm apart) were set up at least 2 m apart.

Subsequently, visits by unmarked, free-ranging sunbirds were recorded through focal observations for 37 hours spread over six days. Consecutive visits to different inflorescences by the same individual were classified as one foraging bout. After each foraging bout, the sugar water was refilled in visited flowers. To reduce the effect of inflorescence location and social learning on birds' foraging choices (Jackson & Nicolson 1998; Kaczorowski et al. 2014), the inflorescences were switched around every hour. A two-sided t-test was used to compare the number of visits to UV reflecting and non-UV reflecting flowers.

UV LEARNING IN SUNBIRDS

Sunbirds have been shown to learn from colour cues to increase their foraging success (Whitfield et

al. 2014) and thus, even if they do not exhibit a preference for UV-reflecting flowers, their ability to see UV and use this flower signal as a cue can be demonstrated with learning experiments. A learning experiment was set up at the same study site but in a different season and with differently coloured model flowers to ensure the experiments did not influence each other. We used model inflorescences that were constructed with three 0.5 ml Eppendorf tubes (opening width 6.8 mm, length 30.0 mm) attached. Model flowers were painted with pink UV-reflective paint (UV Purple Fish Vision Paint, Reel Wings Decoy) and a UV-transparent polish (UV Fish Vision Gloss Coating, Reel Wings Decoy) for UV-reflecting model flowers or a UV-absorbent polish (Dulux Woodgard Timbavarnish clear) for non-UV-reflecting model flowers. The reflectance spectra of these two treatments were very similar except for the difference in the UV range (6.77 JND, Fig. S2). The UV reflective model flowers were filled with 20 μ l of 15 % (weight/weight) sucrose solution and non-UV flowers remained empty. Each model inflorescence with UV reflection was set up 50 cm apart from another one without UV reflection.

Subsequently, sunbird visits were recorded through focal observations for 18 hours spread over three days. After each visit the sugar water was refilled. To avoid any bias for positions, every 30 minutes the flowers were switched around. Visits within the same foraging bout were averaged and a linear model was fitted to explore the relationship between the proportion of rewarding choices (= UV-reflective flowers) per foraging bout and elapsed time, since we expected the birds to increasingly visit rewarding flowers over time if they were learning.

UV PREFERENCE IN LONG-PROBOSCID FLIES

It has been shown that LPFs have colour preferences when visiting flowers (Valentin et al. 2006; Whitehead et al. 2019). To test if LPFs in the Cape exhibit a preference for flowers that reflect UV, the seed set of flowers with UV, without UV and a scent control were compared. A population of *E. aristata*, which reflects UV and is pollinated by LPFs (Lombardi et al. 2021), occurring at Vogelgat Nature Reserve (34.391°S, 19.315°E) was used. For each treatment we randomly chose 15 plants that were about 1m apart from the next treated plant and had at least two unvisited flowers (Geerts &

Pauw 2011). For the treatment with UV reflection, the flowers were left unmanipulated. For the treatment without UV, the flowers were painted with sunscreen (Island Tribe SPF 50 Gel) to remove UV reflectance from their corolla sides and lobes without changing the rest of the reflectance spectrum (Fig. S3). Modelling of fly vision shows that those two treatments are visually distinguishable to flies (Troje 1993; Fig. S4). It has been shown in other systems that treatment with sunscreen itself does not deter pollinators (Johnson & Andersson 2003). Additionally, we do not expect scent to affect the pollinators, since LPF-pollinated flowers rarely produce scent (Goldblatt & Manning 2000). Nevertheless, as a scent control we applied sunscreen only to the pedicels and bracts, so that the flowers remained UV-reflective and any changes in seed set would be due to altered scent. The three treatments were applied on separate plants to avoid pollinators choosing flowers based on their proximity to flowers with a different treatment. After flowering, the fruits were collected, and seed set was determined by extracting the seeds from the fruits and counting them under a dissection microscope. Seed set from the same plant was averaged and a generalised linear model with quasipoisson error structure was fitted to test for a difference in the average

number of seeds in relation to treatment followed by a Kruskal-Wallis post-hoc test to identify the differences between the groups.

RESULTS

UV PREVALENCE ACROSS POLLINATION SYNDROMES

To classify UV and non-UV reflecting species, a cut-off of 10 % contribution of UV to the total brightness was chosen based on the grouping in Fig. 1. The overall prevalence of UV in the sampled *Erica* species according to this measure was 12.3 % with an average reflection maximum in the UV range of 6.0 %. For bird-pollinated species, the prevalence of UV was 16.9 % with an average reflection maximum in the UV range, for only the flowers with UV, of 12.1%. A 100 % of the LPF-pollinated species reflected UV (Fig. 2) with an average reflection maximum in the UV range of 41.6%, while only 1.4 % of unclassified insect-pollinated *Erica* reflected UV. We detected no UV reflection in wind- or rodent-pollinated species (Fig. 1). The LPF-pollinated *Erica* species reflect significantly more UV than all other pollination syndromes and bird-pollinated *Erica* species reflect significantly more UV than unclassified insect-pollinated species (Tab. S3, Tab. S4).

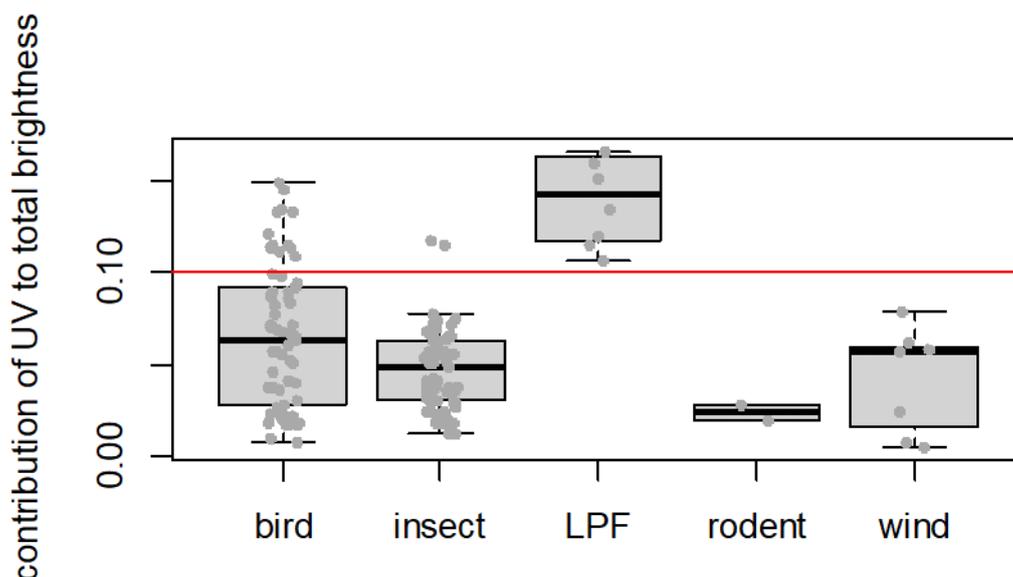


Figure 1. Contribution of UV reflectance (300-400 nm) to total brightness for *Erica* species in relation to their pollination syndrome (centre line, median; box limits, upper and lower quartiles; whiskers, 1.5x interquartile range), red line indicating UV reflectance for samples above 0.1. Number of species: bird = 61, insect = 69, LPF = 8, rodent = 2, wind = 7.



Figure 2. Long-proboscid fly-pollinated species *Erica ampullacea*, *Erica aristata* and *Erica fastigiata coventryi* (left to right) with ultraviolet reflectance (violet areas). Photos taken by S McCarren with a UV-sensitive camera.

UV PREFERENCE IN SUNBIRDS

Sunbirds showed no preference for flowers with or without UV reflectance ($P = 0.939$, $t = 0.08$, $df = 170$). A total of 171 visits to the model flowers during 74 separate feeding bouts were recorded, of which all, but one, were by malachite sunbirds *Nectarinia famosa*. Although none of the previously colour-ringed sunbirds visited the model flowers, male malachite sunbirds were moulting into their breeding plumage and exhibited unique moult patterns. A camera trap was set up by a feeder at the study site. From the pictures, the moult patterns were compared and at least ten different individual males could be identified. This way of identifying individuals is not possible for females, however at one point three female individuals were observed at the same time. Thus, the visitations recorded were from at least 13 different individuals.

UV LEARNING IN SUNBIRDS

When presented with different rewards, sunbirds initially did not discriminate between UV and non-UV flowers, but with proceeding time their preference for the rewarding colour increased (Estimate = 0.02, $SE < 0.01$, $F = 14.02$, $P < 0.001$, Fig. 3). A total of 587 visits to the model flowers during 201 separate feeding bouts were recorded, of which 45 were by southern double-collared sunbirds *Cinnyris chalybeus* and 156 were by orange-breasted sunbirds *Anthobaphes violacea*. Although only one of the previously colour-ringed sunbirds visited the model flowers, at least 9 different individuals could be identified based on their species, sex, age and number in a group.

UV PREFERENCE IN LONG-PROBOSCID FLIES

There were significant differences between the treatments (Table S5). After experimentally removing UV reflection from the corollas in *Erica aristata* flowers (Fig. S3, Fig. S4), the treated plants without UV showed lower seed set than the flowers with UV and the scent control (Table S6, Fig. 4). There was no difference between the scent control and the unmanipulated flowers with UV (Table S6, Fig. 4). Looking at LPF-pollinated *Erica* flowers with a UV-sensitive camera, it is noticeable that the corolla tube and lobes reflect UV strongly, but the centre around the corolla opening absorbs UV (Fig. 2).

DISCUSSION

Our results show that UV colouration only plays a minor role for bird pollination of *Erica* but seems highly important for the evolution of the mutualism between LPFs in the Cape and the specialised *Erica* species they pollinate.

As expected, we found no UV reflection in the rodent- or wind-pollinated species. There was little UV reflection in the unclassified insect-pollinated, which might be due to lower discrimination abilities in hymenopterans (Peitsch et al. 1992). However, more ecological studies are necessary to identify the specific pollinators. The recorded UV reflection for the unclassified insect-pollinated species can be solely attributed to two species: *E. haematocodon* and *E. denticulata*. The pollinator of *E.*

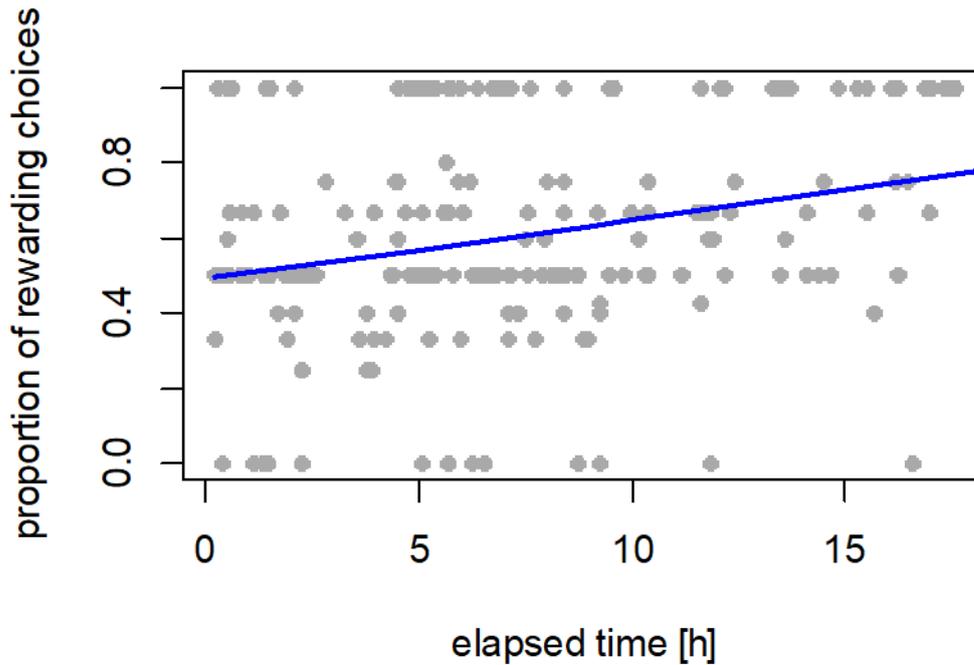


Figure 3. Proportion of rewarding choices (= UV-reflective flowers) made by sunbirds in response to elapsed time in hours, CI in light blue. Observations were conducted over three days (Day 1: 0- 2.5 hours, Day 2: 2.5-11 hours, Day 3: 11-16 hours).

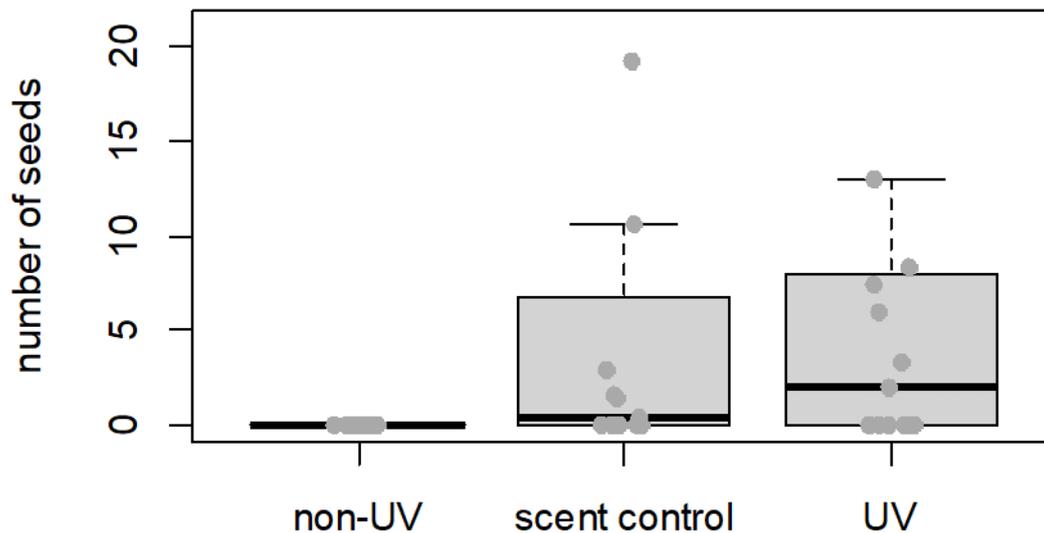


Figure 4. Average number of seeds per plant in *Erica aristata* without UV reflection, with UV-reflection and scent control (centre line, median; box limits, upper and lower quartiles; whiskers, 1.5x interquartile range), $N = 15$.

haematocodon has not been studied yet, but it has red flowers which is unusual for small-flowered *Erica* species (Rebello & Siegfried 1985). If it is pollinated by a hymenopteran, reflecting both red and UV light could increase the pollinator's ability to detect the flowers (Chen et al. 2020). *Erica denticulata*, on the other hand, is moth-pollinated (Rebello et al. 1985). Moths are able to see UV

(Karalius & Būda 2007) and use UV bullseye patterns for foraging (Hirota et al. 2019). In the moth-pollinated form of *E. plukenetii*, however, no UV was detected (van der Niet et al. 2014). Thus, further studies are necessary to understand the prevalence of UV patterns in moth-pollinated plants.

Some of the bird-pollinated species reflect UV but sunbirds do not show an innate preference for UV reflecting flowers and only learn to prefer them when the rewards differ. This suggests that UV plays only a small role for bird pollination in *Erica*. Sunbirds might primarily use their UV vision to perceive UV signals in plumage (Shawkey et al. 2017) for sexual selection. Its role for bird pollination seems to be no bigger than for other floral colours (Kevan et al. 2001) but it might make it easier for sunbirds to discriminate between co-occurring species and therefore reinforce the pollinator's floral constancy (Lunau et al. 2011; Papiorek et al. 2016) and contribute to creating the geographic mosaic of flower colours in bird-pollinated *Erica* species (Coetzee A et al. 2021). Additionally, some bird-pollinated *Erica* species might have evolved UV reflectance as a mechanism to avoid being conspicuous to less effective pollinators and nectar robbers which might have lower discrimination abilities in the UV range (Lunau et al. 2011; Shrestha et al. 2013).

All LPF-pollinated species we tested reflect UV at high intensities, which suggests that it is important for their pollination. Additionally, Newman & Johnson (2021) found that *E. irrorata* and *E. junonia* which are both pollinated by LPFs also reflect UV. This is supported by the fact that untreated *Erica aristata* flowers were significantly more likely to produce seed than non-UV flowers. Colour preferences do not necessarily translate into observable fitness differences in *Erica* species (Heystek et al. 2014). Thus, the LPFs that pollinate these species seem to have an exceptional preference for UV. The absence of a difference between the scent control and the untreated flowers indicates that LPFs do not discriminate between flowers based on scent differences caused by the application of sunscreen.

The presence of a UV pattern on the LPF-pollinated *Erica* flowers with UV reflectance on the corolla tube and lobes and absorbance around the corolla opening suggests that UV might serve to establish a nectar guide. Floral UV patterns with central absorbance (UV bullseye) are common in nature (e.g., Koski & Ashman 2016; Moyers et al. 2017; Hirota et al. 2019; Klomberg et al. 2019) and can increase flower conspicuousness (Koski and Ashman 2014). It has been shown that the removal of nectar guides in LPF-pollinated flowers

dramatically reduces the likelihood of proboscis insertion and consequently decreases plant fitness (Hansen et al. 2012). Thus, the experimental removal of UV reflection in *Erica aristata* might cause blurring of the UV bullseye and thereby prevent LPFs from inserting their long proboscis.

All sampled LPF-pollinated *Erica* species are light pink with darker nectar guides, which aligns with the LPF pollination guild described for the Cape (Manning and Goldblatt 1997). Flowers of the other genera in this guild also appear to reflect UV (e.g., *Adenandra villosa*, *Brachysiphon acutus*, *Gladiolus carneus*, *Pelargonium cuculatum*, *Tritonia cooperi quadrialata*; McCarren S unpublished data) which indicates that LPFs in the Cape generally have a preference for UV.

There appear to have been several independent origins of UV reflectance in the genus *Erica* based on the current phylogeny (e.g. *E. viscaria*, *E. ampullacea*, *E. blenna*, *E. fastigiata*, *E. glandulosa* and *E. haematocodon* reflect UV and are on separate branches according to Pirie et al. 2016), however phylogenetic relationships were not included in this study, since not all the sampled species have been included in the phylogeny yet.

Our results found an association between UV reflectance and pollination syndromes, as well as between UV reflectance and pollinator behaviour. This, together with the patterns of phylogenetic independence of UV reflectance and pollination syndromes in *Erica*, suggests that UV reflectance may have contributed to driving shifts in pollination systems. Changes in UV reflection have also been associated with pollinator shifts in other genera (Martínez-Harms et al. 2020). However, more research is necessary to identify the changes in pigmentation that cause UV-reflection in some *Erica* species and to understand the visual system of LPFs.

APPENDICES

Additional supporting information may be found in the online version of this article:

Table S1. *Erica* species sampled with UV reflectance.

Table S2. Locations at which *Erica* species were sampled.

Table S3. UV in relation to pollination syndrome. Output from generalised linear model.

Table S4. UV in relation to pollination syndrome. Output from Tukey post-hoc test.

Table S5. Average number of seeds per treatment. Output from generalised linear model.

Table S6. Average number of seeds per treatment. Output from Kruskal-Wallis post-hoc test.

Figure S1. Spectral reflectance of A) White non-UV model flower and B) White UV model flower.

Figure S2. Spectral reflectance of A) Pink non-UV model flower and B) Pink UV model flower.

Figure S3. Spectral reflectance of A) *E. aristata* after treatment with sunscreen and B) untreated *E. aristata* flowers.

Figure S4. Treated and untreated flowers of *E. aristata* are different according to the Troje fly colour model.

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AUTHOR CONTRIBUTION

The idea for this study originally came from AC. Data collection and statistical analyses were performed by SM, guided by AC and JJM. The manuscript was prepared by SM, JJM and AC.

Conflicts of interest: The authors declare that they have no conflict of interest.

Ethics approval: The research was approved by the University of Cape Town's Science Faculty Animal Ethics Committee (permit number: 2018/v12/AC). All applicable institutional and national guidelines for the care and use of animals were followed. All necessary permits for access to the sites, collection of plant material, capturing and ringing of birds were acquired from Cape Nature and South African National Parks (SANPARKS).

Availability of data: The datasets used and analysed during the current study are available from the corresponding author on reasonable request.

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