



Conspicuous, green flowers are an honest signal of nectar rewards in a bird-pollinated tree (*Fuchsia excorticata*, Onagraceae)

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Abstract

Bird-pollinated flowers typically appear ‘red’. *Fuchsia excorticata* (Onagraceae), a gynodioecious tree species endemic to New Zealand, is a notable exception. It produces ‘green’, cauliflorous flowers at early stages in flower ontogeny, when pistils are receptive. Flowers later turn ‘red’ as they lose their receptivity. We conducted field observations and spectrographic analyses to test whether: (1) receptive, green-phase flowers are actually more conspicuous to avian pollinators against their natural backgrounds than unreceptive, red-phase flowers, (2) green-phase flowers produce more nectar, and (3) relationships between flower conspicuousness and nectar production are similar in females and hermaphrodites. Results showed that the reflectance properties of green-phase flowers sharply contrast ‘orange’ tree bark, their natural visual background, rendering them more conspicuous to the avian eye than red-phase flowers. Green-phase flowers also produced more nectar than red-phase flowers as an honest signal of rewards. Similar results were observed in both female and hermaphrodite plants. Overall results provide an unusual example of reversed flower-background colour contrasts, with ‘reddish’ hues being incorporated into the visual backgrounds of floral displays rather than being associated with the flowers themselves. They also illustrate that flower conspicuousness can serve as an honest signal of nectar rewards to pollinators.

Keywords Colour · Hue · Gender dimorphism · New Zealand · Pollination syndrome

Introduction

Flowers come in an enormous diversity of colours, due to an assortment of factors including herbivores and abiotic conditions (Tenhumberg et al. 2022). Some of this diversity can also be attributed to selection by different pollinators, which vary in their capacity to detect different colours (see Bischoff et al. 2013; Lord et al. 2013; Essenberg 2021). For example, the long wavelength retinal cone possessed by most birds detects photons between 500 and 650 nm, which roughly corresponds with wavelengths that humans perceive as ‘red’. The flowers of many bird-pollinated plants therefore reflect light that appears ‘red’ to human eyes (Rodríguez-Gironés and Santamaría 2004; Cronk and Ojeda 2008; Schiestl and Johnson 2013; Shrestha et al. 2013).

An object’s conspicuousness is determined by factors other than its colour per se. Conspicuousness is determined by the spectral contrast between an object and its visual background (see Ford et al. 1979; Burns and Dalen 2002; Schmidt et al. 2004), which is mediated by pollinator sensory capacity, cognition, memory, and learning. Flowers and fruits are more conspicuous when the dissimilarity between their reflective properties and that of their visual background increases (Stournaras and Schaefer 2017; Lim and Burns 2022). Ambient light can also affect conspicuousness, increasing in brighter light. Although known to be important, factors other than colour (e.g. orientation) can determine a flower’s attractiveness to pollinators. Pollinators often visit flowers for energetic rewards, e.g. nectar (Burdon et al. 2020; Brzosko and Mirski 2021). So many pollinators quickly learn to discriminate among flowers that differ in reward levels, often using floral traits other than their colour or conspicuousness (Essenberg 2021; Ito et al. 2021).

Tree fuchsia (*Fuchsia excorticata*, Onagraceae, J.R.Forst. et G.Forst., L.f.) is a well-studied tree species from New Zealand (see Van Etten et al. 2018 and refs within). It is one of only a handful of native trees that is deciduous, losing

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its leaves in autumn and replacing them with new leaves in spring (McGlone et al. 2004). Most trees begin to reproduce in late winter when trees are leafless, by producing large, tubular flowers on pedicles that are attached directly to tree trunks (i.e. cauliflory). Perhaps the most distinctive aspect of the appearance of *F. excorticata* is its flaky bark, which has a distinctive ‘orange’ hue to human observers.

Although they are visited by a variety of native birds (Burns 2013; Biddick and Burns 2018), detailed study across New Zealand has shown that honeyeaters (tūī, *Prosthemadera novaeseelandiae*, and korimako, *Anthornis melanura*) are their primary, legitimate pollinators (Delph and Lively 1985; Castro and Robertson 1997; Robertson et al. 2008). In areas without substantial populations of honeyeaters, *F. excorticata* is often pollen limited and regularly experiences reproductive failure (Robertson et al. 2008), leading to widespread conservation concern (Iles and Kelly 2014).

Pioneering work on its pollination biology showed that it is gynodioecious (Delph and Lively 1985, 1989), with populations comprised of more hermaphrodite than female trees (Robertson et al. 2011). Flowers change markedly in colour during their ontogeny. Younger flowers are ‘green’ in appearance with faint ‘purple’ streaking, whereas older flowers are ‘red’ in appearance. Younger, ‘green’ flowers produce more nectar and are visited more frequently by birds than older ‘red’ flowers (Delph and Lively 1989). Flower fertility also varies through ontogeny, with receptivity declining with flower age, regardless of whether they have been pollinated (Delph and Lively 1989). This results in an apparently anomalous circumstance where the colour ‘red’ is associated with an unrewarding and unreceptive flower phase. Delph and Lively (1989) hypothesise that the red pigmentation of older flowers acts as a deterrent, directing pollinators away from unreceptive flowers, in contrast to previous work on other species indicating that red flower pigmentation serves as an attractant to bird pollinators (see Johnson 2022).

Building upon previous study, we collected several types of field data to better understand the unusual floral morphology of *F. excorticata*. We measured nectar production, in addition to flower colours and their associated bark backgrounds to test whether: (1) receptive, green-phase flowers are more conspicuous to the avian eye against bark backgrounds than red-phase flowers, (2) green-phase flowers produce more nectar, and (3) relationships between flower conspicuousness and nectar production are similar in females and hermaphrodites.

Methods

All data were collected over two flowering seasons (2019–2020) in a forest reserve on the North Island of New Zealand known as ‘Zealandia’, which lies close to the coast

(41°18.3' S, 174°44.8' E) and experiences a mild, temperate climate (see Burns 2013). The dominant vegetation in the reserve is broadleaf-conifer forest composed of evergreen trees, tree ferns, shrubs, and lianas (see Lim and Burns 2022, 2023).

To test whether green-phase flowers are more conspicuous than red-phase flowers, and whether levels of flower conspicuousness differ between hermaphrodite and female flowers, we measured the spectral contrasts between flowers and their visual backgrounds (i.e. tree bark), utilising simple colour pattern measures related to spectral sensitivities of birds (Vorobyev and Osorio 1998; Endler and Mielke 2005). In the Austral spring (August–December) of 2019, we caged three sets of three flowers on each of five hermaphrodite and female *F. excorticata* trees (total $n=90$) with pollination bags (PBS International, United Kingdom) after they opened. Three days after opening, one set of three flowers was randomly selected, removed from their parent tree and immediately transported into laboratory conditions for spectrographic analyses. The remaining sets of flowers were removed on days 6 and 9 following the ontogenetic stages of Delph and Lively (1985), i.e. ‘green-phase’, ‘transitional’, or ‘red-phase’. In addition to flower measurements, three bark samples immediately behind each flower cluster were collected to characterise spectral backgrounds at each time interval.

To quantify flower reflectance, we randomly selected a single lanceolate lobe extending from the hypanthium of each flower and measured its spectrum using a USB Ocean Optics 2000 spectroradiometer and Xenon Pulse X2 lamp Ocean Optics light source (OceanOptics, Florida, USA). The process was repeated on background samples of bark. We standardised and measured reflectance relative to a white reflectance standard (Ocean Optics WS-1, OceanOptics, Florida, USA) and a matt black paper card background (black standard). The distance between each object and the probe was fixed at 1 cm, with the angle of illumination and reflection fixed at 45°. All samples were measured against the same matt black paper card in the laboratory. Spectral properties were calculated using SpectraSuite software following Fadzly et al. (2009) (Ocean Optics, Florida, USA). The UVS visual system, based on the spectral sensitivities and receptor noise of the four cone types possessed by the blue tit (*Cyanistes caeruleus*), was used to analyse flower and bark hues as they would appear in tetrahedral colour space (Hart et al. 2000; Hart 2001; Hart and Vorobyev 2005). Typical avian pollinators of *F. excorticata* such as korimako and tūī belong to the order Passeriformes, which mostly utilise the UVS visual system (van Hazel et al. 2013). Relative output values of each of the four cones (u, s, m and l) were calculated in MATLAB (MatLab 2018) following Stoddard and Prum (2008). Relative output values of each of the four cones were then transformed into tetrahedral

colour space following Endler and Mielke (2005). Flower conspicuousness was quantified as the Euclidean distance between the flower and the background bark in tetrahedral colour space following Burns et al. (2009), where a large Euclidean distance reflects greater contrast between flower and background.

To test whether flower conspicuousness differed between hermaphrodite and female flowers, we conducted a linear mixed model. In this model, flower conspicuousness (i.e. the Euclidean distance between flowers and their natural backgrounds in tetrahedral colour space) was used as the dependent variable. Gender was included as a fixed effect with two levels (hermaphrodite and female). Flower ontogeny was included as a second fixed effect with three levels ('green-phase', 'transitional', or 'red-phase'), and parent tree was considered a random effect. Analyses were conducted using the *lmer4* package (Bates et al. 2015) in the R environment (R Core Team 2018). Dependent variables in all tests were logarithm-transformed prior to analyses to conform to assumptions.

Previous work documented that green-phase flowers produce more nectar than red-phase flowers (Delph and Lively 1989). To determine whether nectar production differs between genders and if it covaries with flower size, 4–7 (median = 5) flowers on each of 10 hermaphrodite and female trees were caged with pollination bags in 2019 (PBS International, United Kingdom, total $n = 110$). This was repeated in 2020 for 10 flowers on each of five hermaphrodite and female trees (total $n = 100$). Trees selected for measurement were located at least 20 m apart and one metre away from marked trails. Nectar was completely removed from each flower once a day for 3 consecutive days between 9.00 am and 11.30 am in the morning after flower dehiscence, using a combination of 1 μ l and 5 μ l microcapillary tubes (Drummond Scientific, USA) and 0.5 mm glass capillary tubes (Advanced Instruments, USA). We quantified flower size as the product of the length and width of each flower tube. We then conducted a linear model with nectar production as the dependent variable, gender as a fixed factor with two levels (i.e. females and hermaphrodites) and flower size as a covariate (Fig. 1).

Results

Flower conspicuousness varied through ontogeny and differed between female and hermaphrodite flowers (Fig. 2). Linear model analyses revealed a significant effect of ontogeny on flower conspicuousness ($F = 102.08$, $p < 0.001$), indicating that younger flowers were more conspicuous than older flowers. A significant effect of gender was also observed ($F = 6.12$, $p = 0.038$), indicating that hermaphrodites were more conspicuous than female flowers. No

interaction was observed between flower ontogeny and gender ($F = 2.13$, $p = 0.126$), indicating differences in conspicuousness between genders was consistent through flower ontogeny.

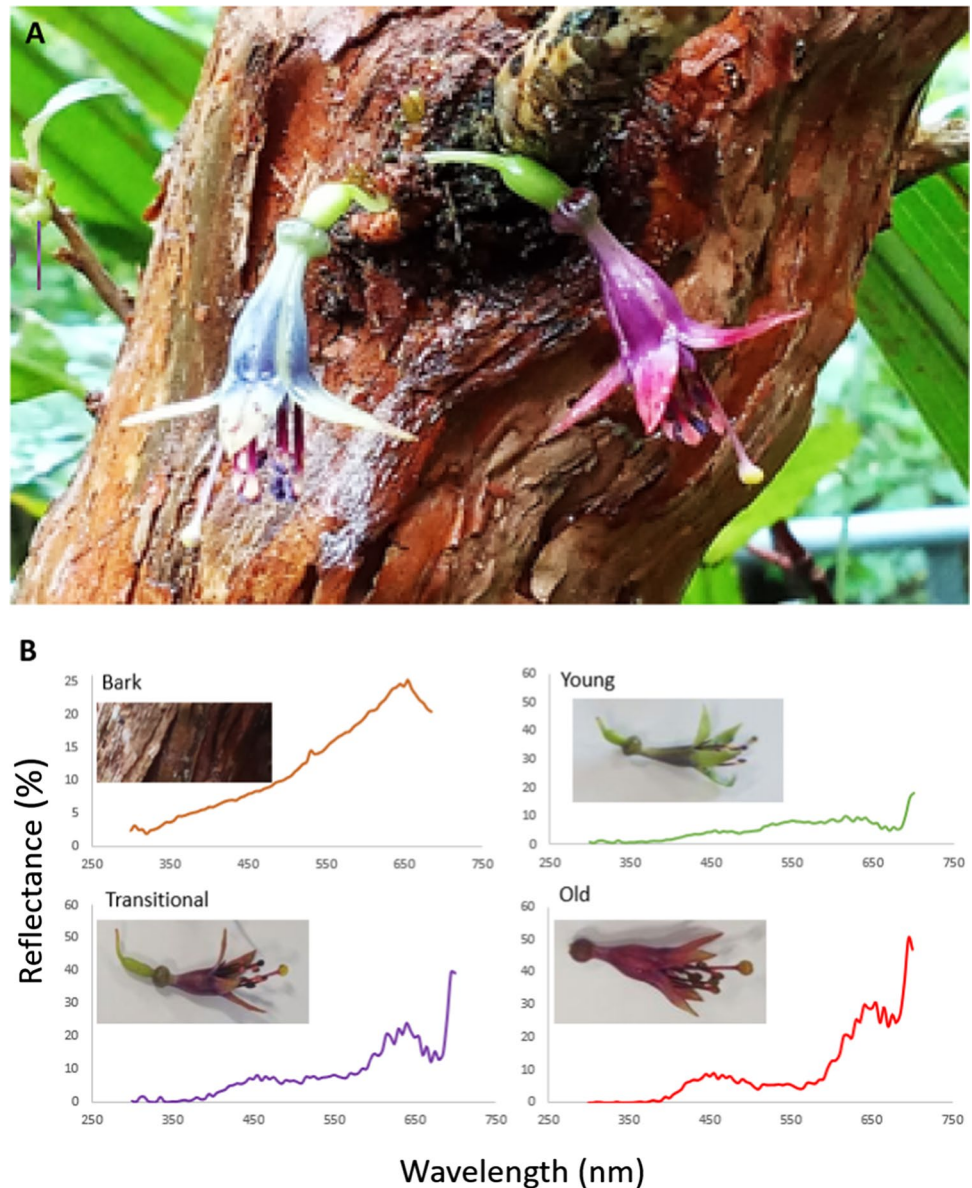
In addition to previous work indicating that nectar production differs between stages of flower ontogeny (Delph and Lively 1989), nectar production differed between genders (Fig. 3). Linear model analysis indicated that nectar production was positively related to flower size ($F = 307.37$, $p < 0.001$). Nectar production was also higher in hermaphrodite flowers ($F = 54.06$, $p < 0.001$). A significant interaction between flower size and gender on nectar production was also observed ($F = 4.66$, $p < 0.032$), indicating that nectar production was positively related to flower size in female flowers, but not hermaphrodites.

Discussion

Bird-pollinated flowers are often 'red' in appearance to human eyes (see de Camargo et al. 2019). Although bird pollinated throughout its range (Delph and Lively 1985; Robertson et al. 2008; Iles and Kelly 2014), *F. excorticata* produces 'green' flowers when receptive, which would seem to be inconsistent with the pollination syndrome hypothesis (Fenster et al. 2004; Ollerton et al. 2009; Chmel et al. 2021). However, an object's apparency results not only from its reflectance properties per se, but also from the contrast between its reflectance properties and that of its visual background (Burns and Dalen 2002; Schaefer et al. 2004). Rather than being produced against a background of 'green' leaves, the pedicles of most *F. excorticata* flowers attach directly to woody stems that are covered in flaky, 'orange' bark. Although the evolutionary origins of cauliflory are unknown, results from spectrographic analyses revealed that ontogenetic changes in flower colour from 'green' to 'red' promote a clear ontogenetic gradient in flower conspicuousness, similar to that observed in other families (e.g. Myrtaceae, Haemodoraceae, see also Weiss 1991, 1995; Ohashi et al. 2015). Younger, receptive, 'green' flowers sharply contrast 'orange' bark. As flowers age and become less receptive, they turn 'red', which makes them more difficult for birds to discern against 'orange' bark. Therefore, while inconsistent with the pollinator syndrome hypothesis per se (see Faegri and van der Pijl 1979), flower colours in *F. excorticata* are clearly linked to bird pollinators.

In a pioneering study, Delph and Lively (1989) found that nectar production varies throughout the life of *F. excorticata* flowers and covaries with ontogenetic changes in flower colour; green-phase flowers produce more nectar than red-phase flowers. Therefore, flower conspicuousness appears to be an honest signal of nectar rewards and birds visit green-phase flowers more frequently than red-phase flowers.

Fig. 1 **A** Young ('green') and old ('red') hermaphrodite flowers against the reddish-orange bark of the gynodioecious tree *Fuchsia excorticata*. **B** Average reflectance spectra of tree bark, young flowers, transitional flowers, and old flowers



Although uncommon, green receptive flowers are not restricted to *F. excorticata*. Other examples include *Melaleuca diosmifolia* (Myrtaceae) and *Combretum lanceolatum* (Combretaceae) (see also Wester et al. 2016). *Anigozanthus viridus* (Haemodoraceae) from Western Australia produces green flowers associated with red accessory structures, and the flowers of *A. preissii* change colour from green to red through time, in an apparently similar manner to *F. excorticata*.

Previous research has shown that a wide variety of floral traits, including scent (Burdon et al. 2020) and the size and shape of corollas (Essenberg 2021) can serve as honest signals of nectar rewards. However, dishonest signals are also common in nature, particularly in species that are less profitable (Ito et al. 2021). To promote foraging efficiency,

pollinators often learn to identify specific floral traits that honestly signal greater energetic rewards (Devegili and Farji-Brener 2021). However, in *F. excorticata* the honest signal of profitability appears to be how readily detectable flowers are to bird pollinators against their natural backgrounds. Previous work has documented similar relationships between flower conspicuousness in some, but not all, previously studied species (Stournaras and Schaefer 2017).

Spectrographic analyses showed that while both hermaphrodite and female flowers decline in conspicuousness throughout their ontogeny, green-phase, hermaphrodite flowers are more conspicuous than green-phase, female flowers. Our measurements of nectar production showed that hermaphrodites also produce more nectar than females. Therefore, in addition to directing pollinators to receptive,

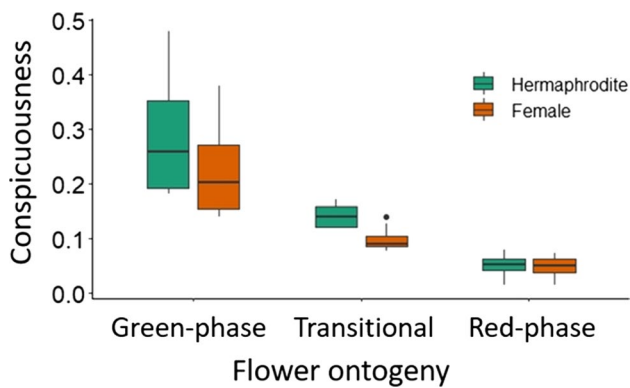


Fig. 2 Boxplots comparing the conspicuousness (Euclidian distances between flower and background colours in tetrahedral colour space) hermaphrodite and female flowers throughout Delph and Lively's (1985) three stages of flower ontogeny. Boxes encompass 75% of observations, the horizontal lines within boxes represent medians and vertical lines represent the range and points are outliers

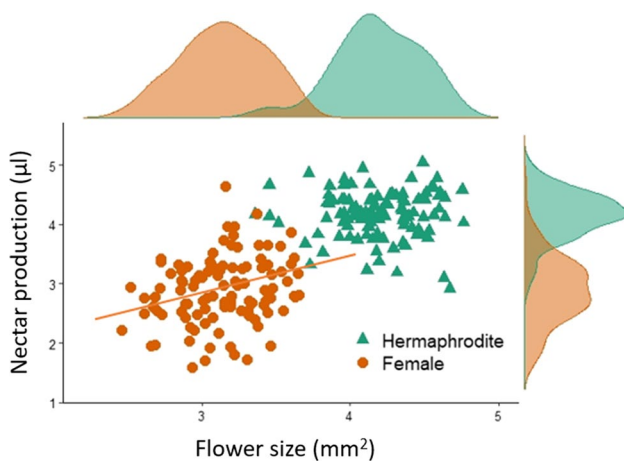


Fig. 3 Relationship between (log) nectar production and (log) flower size in hermaphrodite (green triangles) and female (orange circles) flowers of *Fuchsia excorticata*. Density plots illustrate frequency distributions of flower size and nectar production in both flower gender

green-phase flowers within flower displays, flower conspicuousness provides an honest signal of differences in nectar rewards between hermaphrodite and female trees.

To human eyes, green-phase flowers are more spectrally heterogeneous than transitional and red-phase flowers. While green-phase flowers appear to be mostly 'green', they also have small streaks of 'purple'. We did not attempt to delineate between these regions of flower lobes, and future work would benefit from considering apparently heterogeneous regions separately.

Differences in nectar rewards between genders may arise from differences in the advantages of multiple flower visits. Unlike females, which hypothetically just need to be

visited once for successful reproduction, hermaphrodites may benefit from multiple pollinator visits to facilitate male function (i.e. pollen transport). Previous research has documented widespread support for greater nectar production in hermaphrodite flowers (Essenberg 2021). Our measurements of nectar production also illustrated differences in the allometry of nectar production.

While nectar production was unrelated to flower size in hermaphrodites, a weak positive relationship was observed between nectar production and flower size in females. This result may arise from pollen limitation. If smaller female flowers have fewer ovules, they need less pollen for complete fertilisation. On the other hand, if larger female flowers have more ovules, they might not be completely fertilised after a single pollinator visit and may therefore benefit from producing more nectar to facilitate multiple pollinator visits.

Overall results provide an example of reversed flower-background colour contrasts in a bird-pollinated plant. Bird-pollinated plants typically produce 'red' flowers amongst 'green' foliage. However, in *F. excorticata*, red pigmentation is associated with the background of floral displays rather than the flowers themselves. Furthermore, results show that flower conspicuousness is an honest signal of nectar production, at two scales of resolution. While nectar production and flower conspicuousness are higher in hermaphrodites than in females, both genders show the same ontogenetic trends in signal honesty. Younger, green-phase flowers are more conspicuous and produce more nectar than older, red-phase flowers. Overall results from this study illustrate that bird-pollinated flowers need not be 'red' to signal effectively to avian pollinators.

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Authors' contributions KCB developed the idea for the paper. GL collected field data and conducted all analyses. Both KCB and GL wrote the manuscript together.

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Data availability All data will be made publicly available upon publication.

Declarations

Competing interests The authors declare no competing interests.

Ethical approval The authors declare that the study was conducted under the ethical guidelines of Victoria University of Wellington, Zealandia forest reserve and the government of New Zealand.

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