

Hiding in plain sight: experimental evidence for birds as selective agents for host mimicry in mistletoes

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Hiding in plain sight: experimental evidence for birds as selective agents for host mimicry in mistletoes

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Abstract

Many Australian mistletoe species are cryptic, closely resembling their host foliage and overall appearance. Seed-dispersing birds have been proposed as a selective agent for host resemblance, with cryptic mistletoes only located by thoroughly searching through canopies regardless of infection status, boosting mistletoe populations by increasing the frequency of seeds dispersed to uninfected hosts however, this idea is as yet untested. We measured bird visitation to fruiting mistletoes ($n = 20$) over two consecutive days, with manual defoliation of the mistletoe occurring before observation began on the second day to determine the effect of the visual appearance of the mistletoe on potential seed-dispersing birds, expecting defoliation to reduce the number of visits. Visits to the mistletoes were compared between days of observation and dietary guild (mistletoe specialist/non-specialist). Intact mistletoes were visited more than the defoliated mistletoes and the dietary guilds differed in their visitation patterns. This work demonstrates that the visual acuity of seed-dispersers can distinguish subtle differences in mistletoe phenotypes within infected hosts, consistent with the hypothesis that those mistletoes that more closely resemble their hosts are more difficult to perceive from afar and therefore more likely to have their seeds dispersed to uninfected hosts.

Keywords: Mistletoe, mimicry, defoliation, visual search pattern

Introduction

Many Australian mistletoes bear a striking resemblance to their principal host plants. While most pronounced in leaf size and shape, this resemblance extends to colour, branch morphology and overall appearance, with some mistletoes within host canopies only detectable to the human eye when flowering or fruiting (Barlow and Wiens 1977; Watson 2019). This pattern has long intrigued ecologists, but a mechanistic explanation has proven elusive. Most research has centred on herbivore deception (the nitrogen-limitation hypothesis of mistletoe mimicry, Barlow and Wiens 1977); recent work reporting higher leaf nitrogen concentration in mimetic mistletoes on nitrogen fixing hosts (Scalon and Wright 2015) is consistent with this idea (Barlow and Wiens 1977; Ehleringer et al. 1986 and Bannister 1989). However, while this hypothesis goes some way to explaining the nitrogen concentration of mimetic mistletoes it does not offer a satisfactory explanation for the phenomenon of mimetic mistletoes on non-nitrogen fixing hosts. Nor are the other proffered herbivore deception hypotheses able to account for the arthropod herbivores that prefer mistletoes (Canyon and Hill 1997; Blick et al. 2012), or the occurrence of host mimicry in systems without mammalian herbivores (e.g. New Zealand mistletoes and mangrove mistletoes).

The incidence of mistletoe host-mimicry extends beyond what would be expected from natural co-evolution in similar environments (Barlow and Wiens 1977) and is not fully supported by the host-morphogen hypothesis, which states that a mistletoe shares morphogens or cytokinins with its host and gradually (over many generations) becomes more visually/physically similar to a given host species (Atsatt 1983; Hall et al. 1987). However, an alternative hypothesis suggested by Calder (1983), has not yet been tested. Rather than hiding from natural enemies, Calder suggested that host mimicry may have evolved to promote dispersal to uninfected hosts. Mistletoe seed dispersal patterns suggest that birds return to

known infected trees (hereafter referred to as host trees) and spend time foraging amongst the mistletoes in the canopy, depositing seeds in previously infected hosts (Martínez del Rio et al. 1996; Aukema and Martínez del Rio, 2002*a*). These known host trees become infection centres for further dispersal and spread of mistletoe infections, a common pattern of mistletoe seed dispersal and distribution (Aukema and Martínez del Rio 2002*b*). However, much of this research has been conducted on non-mimetic mistletoe-host pairs. According to Calder's hypothesis (1983), those mistletoes that most closely resemble their favoured hosts would be difficult for their dispersers (predominantly birds) to discern within the canopy. Thus, rather than forming a mistletoe-specific search image and flying from mistletoe to mistletoe or infected tree to infected tree, fruit-eating birds would instead need to search host canopies carefully, prolonging the time spent in the canopy, and maximising the probability of seeds from previous meals being deposited. Importantly, this hypothesis predicts that frugivores will be unable to assess infection status from afar, thereby ensuring dispersal to uninfected hosts. Calder's hypothesis assumes that birds rely on visual cues to find mistletoes—an untested prediction that motivated this research. Here we used defoliation to increase mistletoe crypsis within host canopies and evaluate the effect on seed dispersal, estimated by comparing bird visitation (after Watson 2012). Few studies have used artificial manipulation of plants to test visual search image hypotheses (but see Amsberry and Steffen 2008). This study uses a novel technique to test the effects of visual disturbance (mistletoe with or without foliage) on foraging bird search patterns and the potential use of a mistletoe-based search image. Thus, if seed-dispersing birds are involved in driving selection for host mimicry in mistletoes, those birds would likely rely on visual cues to discern mistletoe plants within host canopies. We therefore would expect experimental manipulation of the mistletoe appearance (e.g. shape of the whole plant) to affect visitation, with rates decreasing following defoliation. Alternatively, if birds rely on another non-visual strategy, e.g. spatial memory of where fruiting mistletoes occur, we would expect no effect of treatment, with defoliated mistletoes visited at rates

comparable to rates for pre-treatment mistletoes with intact foliage. Birds that rely on the mistletoe differently (e.g. specialist versus non-specialist) may use different strategies to find the mistletoe and therefore we would expect the defoliation to produce different effects on the rates of visitation. Finally, if seed-dispersing birds rely on visual cues to find any kind of ripe fruit, we would expect visitation to increase after treatment, as defoliation should make the fruit more visible.

Materials and methods

Site and species description

This study was carried out in Binya State Forest, 20 km east of Griffith, 34°13'S, 140°16'E, Australia, with data collected in December 2015 and February 2016. Long-term average annual rainfall for Griffith is 396 mm; mean annual maximum temperatures are 24°C and minima average 10.0°C (Bureau of Meteorology 2016 *a, b, c*). During the study period, Griffith received 116.2 mm of rainfall (Bureau of Meteorology 2016 *d, e*). The predominant vegetation type in this region is semi-arid woodland, with the canopy at the study site composed primarily of White Cypress Pine (*Callitris glaucophylla*, Cupressaceae), Yarran (*Acacia homalophylla*, Fabaceae) and Belah (*Casuarina cristata*, Casuarinaceae), with sub-dominant stands of Buloke (*Allocasuarina luehmannii*, Casuarinaceae) and Poplar box (*Eucalyptus populneus*, Myrtaceae). The native vegetation was extensively cleared ~120 years ago, now persisting only in protected areas and small remnants on private land and along roadsides. The dominant land uses in the area are irrigated rice, viticulture and cattle grazing.

Grey Mistletoe (*Amyema quandang*, Loranthaceae) is the principal mistletoe in the area, growing almost exclusively on Yarran at the study site (Figure 1) to which it is weakly mimetic.

It is a woody, aerial hemi-parasite with chalky-grey foliage and cryptic greyish flower buds opening to reveal deep red coloured flowers inside the petals and pale yellow fleshy fruits (Watson 2019). As with many other mistletoes, Grey Mistletoe exhibits extended phenology, with flowers and fruit present in most months, but peak fruiting occurs in the Austral spring and summer (Barea and Watson 2007). Both pollen and seeds are bird-dispersed, the former primarily by honeyeaters (Meliphagidae), the latter primarily by two mistletoe specialist frugivores: Mistletoebird (*Dicaeum hirundinaceum*, Dicaeidae) and Painted Honeyeater (*Grantiella picta*, Meliphagidae) and two generalist frugivores: Spiny-cheeked Honeyeater (*Acanthagenys rufogularis*, Meliphagidae) and Singing Honeyeater, (*Lichenstomus virescens*, Meliphagidae); numerous other bird species opportunistically consume the fruits and occasionally disperse seeds (Barea 2008; Watson 2019).

>>>>>INSERT FIGURE 1 AROUND HERE<<<<<

Experimental procedure

A defoliation experiment was designed to investigate the foraging behaviour of mistletoe-eating frugivores and their potential use of a search image to locate mistletoe fruits in the woodland canopy. Twenty trees infected with mistletoe were randomly selected, with one individual mistletoe per host tree selected for manipulation. Experimental hosts were no less than 10 m apart and hosted between one and 23 other mistletoes. Observations of the selected mistletoe were made over two consecutive days, with defoliation occurring pre-dawn (completed by 7 am) on the second day. The selected mistletoes for Day 1 observations will henceforth be referred to as 'intact' mistletoes and Day 2 observations as 'defoliated'

mistletoes. Defoliation consisted of removing $\geq 90\%$ of the mistletoe foliage using secateurs to remove individual leaves (Figure 2) but being careful to retain all fruit (both ripe and unripe).

Experimental observations began no later than 7:30 am (AEST) and continued for 3–4 hours, then recommenced in the afternoon for a further 1–3 hours, ending by 6:30 pm. Variation in observation length depended on rain and averaged 5 hours across the 20 replicates. Birds and mistletoes were observed from a distance of approximately 15 m depending on the density of vegetation between the seated observer and the mistletoe under observation, using 8 x 42 binoculars.

A visit was recorded if the bird perched in the experimental mistletoe; birds confining their movements to host branches or flying through the mistletoe without landing were not counted as a visit. All visits were considered potential foraging episodes by the birds as many searched the fruits and foliage while they perched or hopped through the mistletoe. Each visiting bird species was identified and assigned to one of two dietary guilds based on their reliance on mistletoe fruits following dietary records in Barker and Vestjens (1990), diet and seed dispersal information in Rawsthorne et al. (2011), augmented by personal observation (see Cook 2017). The 'mistletoe specialist' category comprised solely of the Mistletoebird (Painted Honeyeaters were absent from this site during the study period); 'non-specialist' comprised the generalist frugivores and other opportunistic birds, that do not regularly consume fruit.

<Insert figure 2 here>

Data analysis

Each experimental mistletoe observed across two days (the day before and the day of defoliation) was counted as a replicate ($n = 20$). For analysis, the data were treated as related samples and were non-normally distributed with non-homogenous variance. Therefore, to test for differences in the number of bird visits to the treatment mistletoes before vs. after leaf removal, a Sign test was conducted using SPSS (IBM SPSS Statistics v22, 2013). We also tested if the specialists responded differently from other visiting birds, using non-parametric, related samples tests. A two-way, unbalanced design ANOVA was used to compare the lengths of visits between specialists and non-specialist birds.

Results

A total of 226 hours of observation was recorded across 20 replicate mistletoes, with 33 visits to experimental mistletoes recorded; 24 visits on day one (intact) and nine visits on day two (defoliated). Of the twenty mistletoes, seven were visited on day one and four on day two. Only four mistletoes were visited on both days. The number of visits to the mistletoes with and without leaves was significantly different ($n = 20$, $z = -2.04$, $P = 0.03$) (Figure 3), with more visits to the intact mistletoes.

Are specialists special? Visits by specialists vs. non-specialists

Eight species of birds were observed visiting the experimental mistletoes over the forty day period. Most visits to either intact or defoliated mistletoes were made by the specialist Mistletoebird (*Dicaeum hirundiaceum*) ($n = 13$), followed by non-specialists, including Yellow thornbill (*Acanthiza nana*) ($n = 6$), Southern Whiteface (*Aphelocephala leucopsis*) ($n = 5$), Spiny-cheeked Honeyeater (*Acanthagenys rufogularis*) ($n = 4$), Inland Thornbill (*Acanthiza apicalis*) ($n = 2$), with Eastern Yellow Robin (*Eopsaltria australis*), Red-capped Robin (*Petroica goodenovii*) and Singing Honeyeater (*Lichenstomus virescens*) each visiting on a single occasion. There was

no significant difference in the number of visits made by the specialist Mistletoebird to intact vs. defoliated mistletoes ($n = 20$, $z = -1.43$, $P = 0.18$). Non-specialists visited the intact mistletoes significantly more than the defoliated mistletoes ($n = 20$, $z = -2.06$, $P = 0.04$). There was no significant difference in the length of time spent visiting the treatment mistletoes by the specialist and non-specialist birds ($F(1, 29) = 0.02$, $P = 0.89$).

<Insert figure 3 here>

Discussion

The appearance of cryptic mistletoes has been hypothesised to change the foraging behaviour of seed dispersing birds, reducing the likelihood of search image formation and increasing potential seed dispersal to new hosts (Calder 1983; Watson 2019). This manipulative experiment set out to determine the influence of mistletoe appearance on the visitation of its avian seed dispersers. Our expectation was that birds using visual cues to discern the mistletoe within the woodland canopy would visit intact mistletoes significantly more frequently than the defoliated mistletoes. We found that the intact mistletoes received significantly more visits than the defoliated mistletoes. Thus, we suggest that the overall visual appearance of the mistletoe plants does have a direct influence on the foraging decisions of the seed-dispersing birds.

The visual appearance of a plant may signal its quality to potential visiting birds, with the implication that if the plants are unhealthy, the fruits on offer are also of poor quality (van Lent et al. 2014). As such, those potential visitors may view defoliated mistletoes not worthy of a meal. Alternatively, the lack of leaves may have disrupted the search image or association used by the birds to locate mistletoe, rendering it as unrecognisable, unknown and not worth

visiting. Importantly, fruits are not the only reason a bird might visit a mistletoe plant; insectivorous birds might visit to feed on arthropods in the canopy (Turner 1991; Watson 2012; Burns et al. 2011, 2015), others may seek to visit the fruiting or flowering host tree (van Ommersen and Whitham 2002), while others may seek out a sheltered nesting spot (Cooney et al. 2006). Our findings suggest that the foliage as well as the fruit was influential in attracting birds, indicating that other benefits of dense foliage, such as cover from predators while feeding, may influence the foragers. Factors such as the location of the mistletoe in the host tree, the abundance of mistletoes or the number and quality of fruits on offer may also play a role in influencing potential mistletoe visitors and should be considered in future experiments.

If foraging birds used an alternative strategy, we predicted that visitation would be equal across mistletoes before and after defoliation. While seven different species of non-specialist birds were observed visiting the mistletoes, they favoured intact mistletoes, unlike the specialist Mistletoebird, which demonstrated no visitation preference. For non-specialists, potentially in search of foods other than fruits, this visitation pattern suggests that they rely primarily on canopy density or other holistic visual cues when seeking mistletoe, with a defoliated or unhealthy looking plant signalling poor quality fruits and poor forage available to the birds (Amsberry and Steffen 2008).

Previous research by Reid (1989) has shown that in Australia the primary dispersers of mistletoe include the specialist Mistletoebird and the dietary generalist or non-specialist Spiny-cheeked Honeyeater. Such research has also demonstrated that while the specialist Mistletoebird successfully deposits viable mistletoe seeds in favourable growing positions or safe sites, those sites are usually in trees that already host mistletoe, thereby increasing the mistletoe load on the host tree and increasing the stress that confers (Reid 1989, 1990). The specialist Mistletoebird is almost entirely reliant on the fruits of the mistletoe (Reid 1989; Watson 2019) and we predicted that if they used a visual search image, they would visit the

defoliated mistletoes more as the fruits would be more exposed and visible. That visitation by the specialist Mistletoebirds did not differ significantly between intact and defoliated mistletoes suggests that they may not rely primarily on visual cues when seeking out mistletoe but on spatial memory or other search strategies (Cook 2017). Such strategies have been recorded for other specialist species, including seed hoarders (see Vanderwall and Beck 2012) and nectar feeders (e.g. traplining strategies e.g. Saleh and Chittka 2007). Unlike the Mistletoebird, the generalist Spiny-cheeked Honeyeater disperses viable mistletoe seeds further afield in suitable safe sites (Reid 1989; Rawsthorne et al. 2011). Being more likely to forage on mistletoe fruits opportunistically and dispersing the seeds further, generalists are primarily reliant on visual cues, rather than on loyalty to a particular patch of mistletoes (Watson 2012).

The searching strategies employed by visiting birds to find fruiting mistletoes over time may in turn influence the visual appearance of the mistletoe (Calder 1983). Seed-dispersing non-specialists (e.g. generalists) that seek mistletoe based on its visual appearance may drive increasingly tight resemblance between the host and parasite. By visiting many potential host trees in search of those hosting mistletoe, non-specialist (e.g. generalist and opportunist) birds may disperse seeds to those potential hosts as they search from tree to tree. As parasites, transmission to uninfected hosts is a critical determinant of mistletoe population viability (Watson and Rawsthorne 2013), so even a subtle increase in the number of seeds being transported to uninfected hosts will lead to dramatic differences in population-scale trajectories. Such dispersal patterns over time may induce the mistletoe to more closely resemble the common host in visual appearance such as foliage shape and colour as it promotes dispersal to suitable, new host trees. One method to estimate the potential of these seed dispersing non-specialists to drive host-mimicry is to compare the contribution of these dietary generalists to seed dispersal of host-mimicking and non-mimicking mistletoes across a broad geographical distribution. This comparison would reveal whether the generalists drive

directional selection of host-mimicking mistletoes mediated by a search image of the mistletoe, and inform a wider understanding of how birds locate particular resources with heterogeneous canopies.

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Figure 1. Top: Grey mistletoe (*Amyema quandang*) hosted by Yarran (*Acacia homalophylla*) in Binya State Forest, NSW. Bottom: Grey mistletoe (*Amyema quandang*) foliage on the left and Yarran (*Acacia homalophylla*) foliage on the right.

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Figure 2. Example before and after of the defoliation of Grey Mistletoe (*Amyema quandang*). Mistletoes were observed over two days for bird visits to the manipulated mistletoes. The first day the mistletoe was intact and un-manipulated (A); on the second day, before observations commenced, $\geq 90\%$ of the foliage was removed, leaving fruits intact on the plant (B). Mistletoe is circled.

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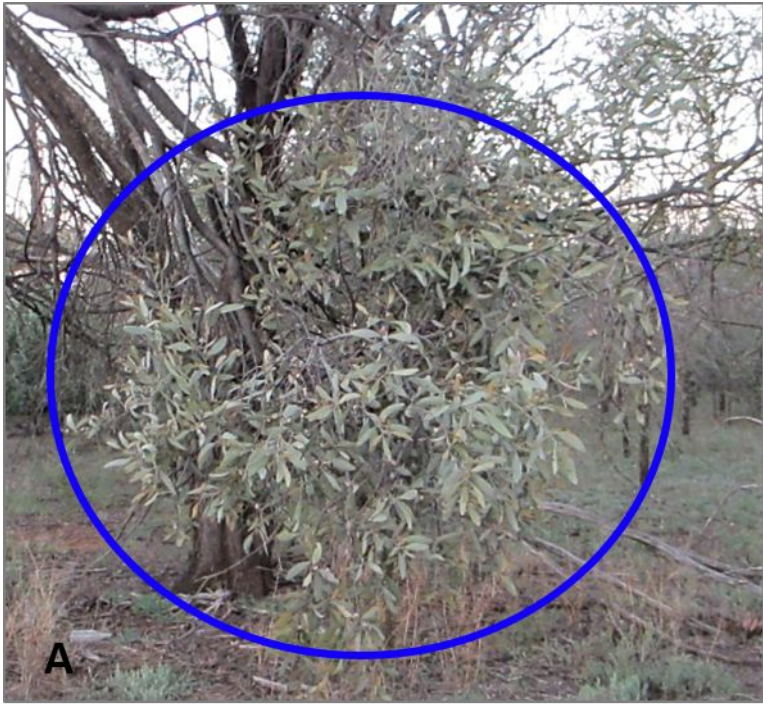


Figure 3. Total number of visits to experimental treatment mistletoes: intact mistletoes compared to the same mistletoes after being defoliated, leaving all the fruits but only 10% of the foliage on the plant ($n = 20$ replicates). Error bars represent standard error. Circles are outliers, stars are extreme outliers.

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