NRC Research Press

ARTICLE

Hiding in plain sight: experimental evidence for birds as selective agents for host mimicry in mistletoes[1]

M.E. Cook, A. Leigh, and D.M. Watson

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/nonspecialist). 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.

Key words: mistletoe, mimicry, defoliation, visual search pattern.

Résumé : Plusieurs espèces de guis australiens sont cryptiques, ressemblant étroitement à leur hôte quant au feuillage et à l'apparence générale. Les oiseaux qui dispersent les graines ont été proposés comme agents de sélection au regard de la ressemblance à l'hôte, le gui cryptique n'étant localisé que grâce à une recherche minutieuse à l'intérieur des canopées, quel que soit le statut d'infection, ce qui accroît les populations de gui en augmentant la fréquence de dispersion des graines vers des hôtes non infectés, bien que cette idée n'ait pas été encore testée. Les auteurs ont mesuré la fréquentation par les oiseaux de gui en fruits ($n = 20$) sur deux jours consécutifs, la défoliation manuelle du gui ayant lieu avant le début de l'observation du deuxième jour, afin de déterminer l'effet de l'apparence visuelle du gui sur les oiseaux susceptibles de disperser les graines, anticipant que la défoliation réduise le nombre de visites. Les visites aux plants de guis ont été comparées entre les jours d'observation et la guilde alimentaire (spécialiste/non-spécialiste du gui). Les plants de guis intacts étaient visités plus fréquemment que les plants défoliés et les guildes alimentaires différaient quant à leurs habitudes de visite. Ce travail démontre que l'acuité visuelle des agents de dispersion des graines permet de distinguer de subtiles différences dans les phénotypes du gui chez les hôtes infectés, ce qui est cohérent avec l'hypothèse voulant que les plants de guis qui ressemblent le plus à leurs hôtes soient plus difficiles à percevoir de loin et que leurs graines soient donc plus susceptibles d'être dispersées chez les hôtes non infectés. [Traduit par la Rédaction]

Mots-clés : gui, mimétisme, défoliation, modèle de recherche visuelle.

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

---

Received 18 December 2019. Accepted 10 March 2020.

M.E. Cook and A. Leigh. University of Technology Sydney, School of Life Sciences, P.O. Box 123 Broadway, NSW 2007, Australia.
D.M. Watson. Institute for Land, Water and Society, Charles Sturt University, Albury–Wodonga Campus, P.O. Box 789, Albury, NSW 2640 Australia.

Corresponding author: M.E. Cook (email: melinda.cook01@gmail.com).

[1] This Article is one of a selection of papers published in the special issue from the IUFRO World Congress, Curitiba, Brazil 2019 Symposium on Mistletoes.

Botany **00**: 1–7 (0000) dx.doi.org/10.1139/cjb-2019-0209

reporting higher leaf concentrations of nitrogen in mimetic mistletoes on nitrogen fixing hosts (Scalon and Wright 2015) is consistent with this idea (Barlow and Wiens 1977; Ehleringer et al. 1986; 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 (hereinafter 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 nonmimetic mistletoe–host pairs. According to Calder's hypothesis (Calder 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 nonvisual 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 nonspecialist) 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.

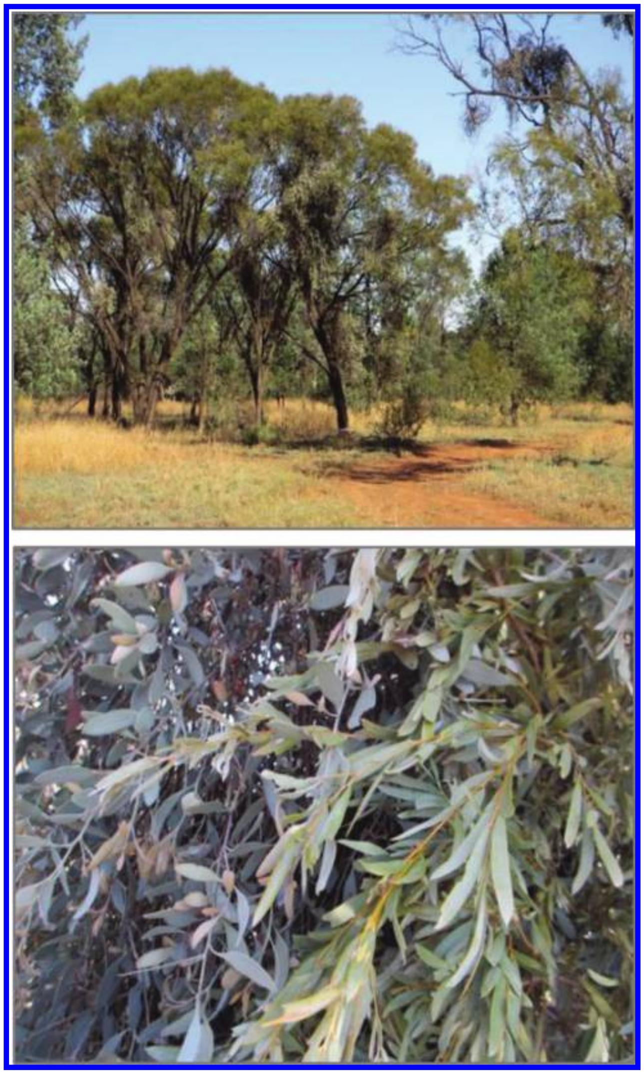
Materials and methods

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*, 2016*b*, 2016*c*). During the study period, Griffith received 116.2 mm of rainfall (Bureau of Meteorology 2016*d*, 2016*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 (Fig. 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,

Fig. 1. Top: Grey mistletoe (*Amyema quandang*) hosted by yarran (*Acacia homalophylla*) in Binya State Forest, New South Wales. Bottom: Grey mistletoe (*Amyema quandang*) foliage on the left and yarran (*Acacia homalophylla*) foliage on the right. [Colour online.]



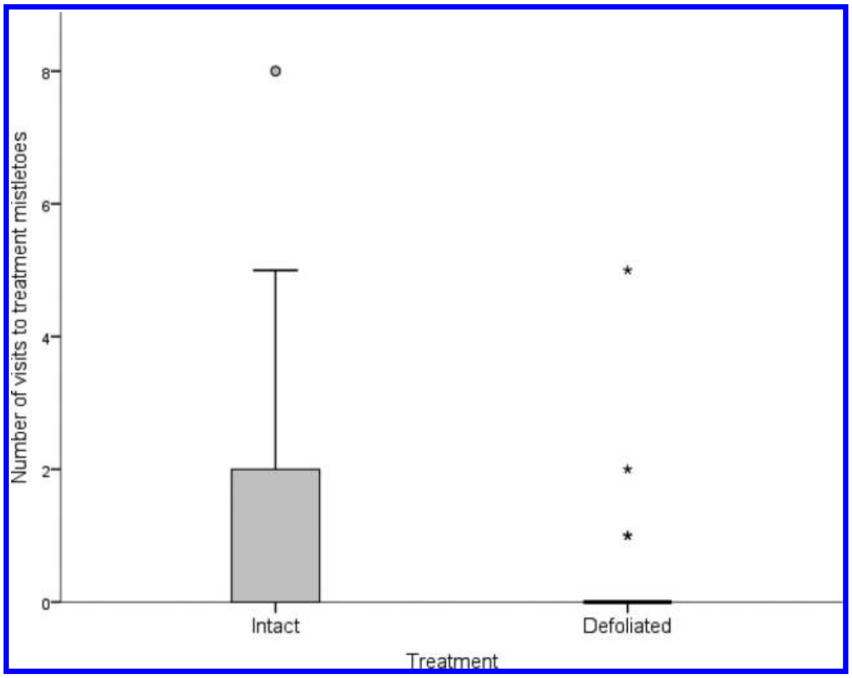
but peak fruiting occurs in the Austral spring and summer (Barea and Watson 2007). Both pollen and seeds are bird-dispersed, the former primarily by honeyeaters (Meliphagidae), the latter primarily by two mistletoe specialist frugivores: mistletoebird (*Dicaeum hirundinaceum*, Dicaeidae) and painted 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).

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 0700 h (AEST)] 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 ≥90% of the mistletoe foliage using secateurs to remove individual leaves (Fig. 2) but being careful to retain all fruit (both ripe and unripe).

Fig. 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, ≥90% of the foliage was removed, leaving fruits intact on the plant (B). Mistletoe is circled. [Colour online.]

Fig. 3. Total number of visits to experimental treatment mistletoes: intact mistletoes compared with 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 the standard error. Circles indicate outliers; stars indicate extreme outliers.



Experimental observations began no later than 0730 h (AEST) and continued for 3–4 h, then recommenced in the afternoon for a further 1–3 h, ending by 1830 h. Variation in observation length depended on rain, and averaged 5 h 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 binoculars (magnification, 8×; lens diameter, 42 mm).

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, because 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), and augmented by personal observation (see Cook 2017). The "mistletoe specialist" category composed 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, which do not regularly consume fruit.

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 nonhomogenous 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 v. 22, IBM Corp. 2013). We also tested whether the specialists responded differently from other visiting birds, using nonparametric, related samples tests. A two-way, unbalanced design ANOVA was used to compare the lengths of visits between specialists and nonspecialist birds.

Results

A total of 226 h 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 20 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 ($n = 20$, $z = -2.04$, $P = 0.03$) (Fig. 3), with more visits to the intact mistletoes.

Are specialists special? Visits by specialists vs. nonspecialists

Eight species of birds were observed visiting the experimental mistletoes over the 40 day period. Most visits to either intact or defoliated mistletoes were made by the specialist mistletoebird (*Dicaeum hirundiaceum*) (*n* = 13), followed by nonspecialists, including the yellow thornbill (*Acanthiza nana*) (*n* = 6), southern whiteface (*Aphelocephala leucopsis*) (*n* = 5), spiny-cheeked honeyeater (*Acanthagenys rufogularis*) (*n* = 4), and inland thornbill (*Acanthiza apicalis*) (*n* = 2), with the 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 ($n = 20$, $z = -1.43$, $P = 0.18$). Nonspecialists 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 nonspecialist birds ($F_{[1,29]} = 0.02$, $P = 0.89$).

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; Burns et al. 2011, 2015; Watson 2012), others may seek to visit the fruiting or flowering host tree (van Ommeren and Whitham 2002), whereas 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 Vander wall 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 with 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.

Acknowledgements

The field work for this research was conducted on the traditional lands of the Wiradjuri people. **Funding statement:** This work was funded by a Stuart Leslie Bird Research Award from Birdlife Australia; this research was conducted as part of a UTS MSc program (Australian Government Research Training Scheme). The fieldwork was conducted under UTS ACEC 2013-745, NPWS Scientific License SL101337 and Forestry Corporation: Forest Permit – Research.

References

Amsberry, L.K., and Steffen, J.E. 2008. Do contrastingly colored unripe fruits of the neotropical tree *Ardisia nigropunctata* attract avian seed dispersers? Biotropica, **40**: 575–580. doi:10.1111/j.1744-7429.2008.00421.x.

Atsatt, P.R. 1983. Mistletoe leaf shape: a host morphogen hypothesis. *In* The Biology of Mistletoes. *Edited by* D.M. Calder and P. Bernhardt. Academic Press Australia, NSW, Australia. pp. 259–275.

Aukema, J.E., and Martínez del Rio, C. 2002*a*. Mistletoes as parasites and seed dispersing birds as disease vectors: current understanding, challenges and opportunities. *In* Seed dispersal and frugivory: ecology, evolution and conservation. *Edited by* D.J. Levey, W.R. Silva, and M. Galetti. CAB International, Wallingford, Oxon, UK. pp. 99–110.

Aukema, J.E., and Martínez del Rio, C. 2002*b*. Where does a fruit-eating bird deposit mistletoe seeds? Seed deposition patterns and an experiment. Ecology, **83**(12): 3489–3496. doi:10.1890/0012-9658(2002)083[3489:WDAFEB]2.0.CO;2.

Bannister, P. 1989. Nitrogen concentration and mimicry in some New Zealand mistletoes. Oecologia, **79**: 128–132. doi:10.1007/BF00378249. PMID:28312822.

Barea, L.P. 2008. Interactions between frugivores and their resources: case studies with the Painted Honeyeater *Grantiella picta*. Ph.D. dissertation, Charles Sturt University, NSW, Australia.

Barea, L.P., and Watson, D.M. 2007. Temporal variation in food resources determines onset of breeding in an Australian mistletoe specialist. Emu, **107**: 203–209. doi:10.1071/MU07003.

Barker, R.D., and Vestjens, W.J.M. 1990. The food of Australian birds: 2. Passerines. CSIRO Australia, ACT, Australia.

Barlow, B., and Wiens, D. 1977. Host-parasite resemblance in Australian mistletoes: the case for cryptic mimicry. Evolution, **31**: 69–84. doi:10.1111/j.1558-5646.1977.tb00983.x. PMID:28567737.

Blick, R.A.J., Burns, K.C., and Moles, A.T. 2012. Predicting network topology of mistletoe–host interactions: do mistletoes really mimic their hosts? Oikos, **121**: 761–771. doi:10.1111/j.1600-0706.2011.19854.x.

Bureau of Meteorology, Australian Government. 2016*a*. Climate Data Online, monthly rainfall: Griffith Airport. Available from http://www.bom.gov.au/jsp/ncc/cdio/weatherData/av?p_nccObsCode=139&p_display_type=dataFile&p_startYear=&p_c=&p_stn_num=075041 [accessed 29 October 2016].

Bureau of Meteorology, Australian Government. 2016*b*. Climate Data Online, monthly mean maximum temperatures: Griffith Airport. Available from http://www.bom.gov.au/jsp/ncc/cdio/weatherData/av?p_nccObsCode=36&p_display_type=dataFile&p_startYear=&p_c=&p_stn_num=075041 [accessed 29 October 2016].

Bureau of Meteorology, Australian Government. 2016*c*. Climate Data Online, monthly mean minimum temperatures: Griffith Airport. Available from http://www.bom.gov.au/jsp/ncc/cdio/weatherData/av?p_nccObsCode=38&p_display_type=dataFile&p_startYear=&p_c=&p_stn_num=075041 [accessed 29 October 2016].

Bureau of Meteorology, Australian Government. 2016*d*. Climate Data Online, 2015 daily rainfall: Griffith Airport. Available from http://www.bom.gov.au/jsp/ncc/cdio/weatherData/av?p_nccObsCode=136&p_display_type=dailyDataFile&p_startYear=2015&p_c=-1126258944&p_stn_num=075041 [accessed 18 June 2017].

Bureau of Meteorology, Australian Government. 2016*e*. Climate Data Online, 2016 daily rainfall: Griffith Airport. Available from http://www.bom.gov.au/jsp/ncc/cdio/weatherData/av?p_nccObsCode=136&p_display_type=dailyDataFile&p_startYear=2016&p_c=-1126258944&p_stn_num=075041 [accessed 9 June 2017].

Burns, A.E., Cunningham, S.A., and Watson, D.M. 2011. Arthropod assemblages in tree canopies: a comparison of orders on box mistletoe (*Amyema miquelli*) and its host eucalypts. Aust. J. Entomol. **50**: 221–230. doi:10.1111/j.1440-6055.2011.00811.x.

Burns, A.E., Taylor, G.S., Watson, D.M., and Cunningham, S.A. 2015. Diversity and host specificity of Psylloidea (Hemiptera) inhabiting box mistletoe, *Amyema miquelli* (Loranthaceae) and three of its host *Eucalyptus* species. Aust. Entomol. **54**(3): 306–314. doi:10.1111/aen.12123.

Calder, D.M. 1983. Mistletoes in focus: an introduction. *In* The biology of mistletoes. *Edited by* D.M. Calder and P. Bernhardt. Academic Press Australia, NSW, Australia. pp. 1–18.

Canyon, D.V., and Hill, C.J. 1997. Mistletoe host-resemblance: a study of herbivory, nitrogen and moisture in two Australian mistletoes and their host trees. Aust. J. Ecol. **22**: 395–403. doi:10.1111/j.1442-9993.1997.tb00689.x.

Cook, M.E. 2017. Spatial memory, search images and environmental cues: how do frugivores find ripe mistletoe fruits? Master's thesis, University of Technology Sydney, Australia.

Cooney, S.J.N., Watson, D.M., and Young, J. 2006. Mistletoe nesting in Australian birds: A review. Emu, **106**: 1–12.

Ehleringer, J.R., Ullmann, I., Lange, O.L., Farquhar, G.D., Cowan, I.R., Schulze, E.-D., and Ziegler, H. 1986. Mistletoes: a hypothesis concerning morphological and chemical avoidance of herbivory. Oecologia, **70**: 234–237. doi:10.1007/BF00379245. PMID:28311663.

Hall, P.J., Badenoch-Jones, J., Parker, C.W., Letham, D.S., and Barlow, B.A. 1987. Identification and quantification of cytokinins in the xylem sap of mistletoes and their hosts in relation to leaf mimicry. Aust. J. Plant Physiol. **14**: 429–438. doi:10.1071/PP9870429.

IBM Corp. 2013. [Released.] IBM SPSS statistics for Windows, Version 22.0. IBM Corp, Armonk, New York.

Martínez del Rio, C., Silva, A., Medel, R., and Hourdequin, M. 1996. Seed dispersers as disease vectors: bird transmission of mistletoe seeds to plant hosts. Ecology, **77**(3): 912–921. doi:10.2307/2265511.

Rawsthorne, J., Watson, D.M., and Roshier, D.A. 2011. Implications of movement patterns of a dietary generalist for mistletoe seed dispersal. Austral Ecol. **36**: 650–655. doi:10.1111/j.1442-9993.2010.02200.x.

Reid, N. 1989. Dispersal of mistletoes by honeyeaters and flowerpeckers: components of seed dispersal quality. Ecology, **70**(1): 137–145. doi:10.2307/1938420.

Reid, N. 1990. Mutualistic interdependence between mistletoes (*Amyema quandang*), and Spiny-cheeked Honeyeaters and Mistletoebirds in an arid woodland. Aust. J. Ecol. **15**: 175–190. doi:10.1111/j.1442-9993.1990.tb01526.x.

Saleh, N., and Chittka, L. 2007. Traplining in bumblebees (*Bombus impatiens*): a foraging strategy's ontogeny and the importance of spatial reference memory in short-range foraging. Oecologia, **151**: 719–730. doi:10.1007/s00442-006-0607-9. PMID:17136553.

Scalon, M.C., and Wright, I.J. 2015. A global analysis of water and nitrogen relationships between mistletoes and their hosts: broad-scale tests of old and enduring hypotheses. Funct. Ecol. **29**: 1114–1124. doi:10.1111/1365-2435.12418.

Turner, R.J. 1991. Mistletoe in eucalypt forest–a resource for birds. Aust. For. **54**: 226–235. doi:10.1080/00049158.1991.10674582.

van Lent, J., Hernández-Barrios, J.C., Anten, N.P.R., and Martínez-Ramos, M. 2014. Defoliation effects on seed dispersal and seedling recruitment in a tropical rain forest understorey palm. J. Ecol. **102**: 709–720. doi:10.1111/1365-2745.12216.

van Ommeren, R.J., and Whitham, T.G. 2002. Changes in interactions between juniper and mistletoe mediated by shared avian frugivores: parasitism to potential mutualism. Oecologia, **130**: 281–288. doi:10.1007/s004420100792. PMID:28547152.

Vander Wall, S.B., and Beck, M.J. 2012. A comparison of frugivory and scatter-hoarding seed-dispersal syndromes. Bot. Rev. **78**: 10–31. doi:10.1007/s12229-011-9093-9.

Watson, D.M. 2012. The relative contribution of specialists and generalists to mistletoe dispersal: insights from a Neotropical forest. Biotropica, **45**: 195–202. doi:10.1111/j.1744-7429.2012.00905.x.

Watson, D.M. 2019. Mistletoes of southern Australia. 2nd ed. CSIRO Publishing, Melbourne, Australia.

Watson, D.M., and Rawsthorne, J. 2013. Mistletoe specialist frugivores: latterday 'Johnny Appleseeds' or self-serving market gardeners? Oecologia, **172**: 925–932. doi:10.1007/s00442-013-2693-9. PMID:23797409.