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Do bird species richness and community structure vary with mistletoe flowering and fruiting in Western Australia?

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Running Head: Mistletoe fruit affects bird community structure

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Abstract

Worldwide, mistletoes act as a keystone resource, providing food (nectar, fruit and foliage) and structural (nesting sites) resources to hundreds of fauna species. In Australia, loranthaceous mistletoes depend on birds for pollination and dispersal, and provide important nectar and fruit resources to a large number of nectarivorous and frugivorous bird species. We investigated whether bird species richness and community structure varies with flowering and fruiting of two common mistletoe species (family Loranthaceae, *Amyema preissii* and *Am. miquelii*) through monthly surveys for one year at five sites in south–west Western Australia. Flowering and fruiting periods were distinct and differed both amongst sites and between mistletoe species. Nectar and ripe fruit were available for up to 5 and 6–7 months (*Am. miquelii* and *Am. preissii* respectively) at individual sites, but were available every month of the year across all sites. The presence of fruiting, but not flowering, mistletoe was associated with changes in bird community structure. Mistletoebirds (*Dicaeum hirundinaceum*) were significantly more likely to be recorded during months when ripe mistletoe fruit was present and the overall bird species richness was higher for these survey months. Mistletoes provide important resources, but further investigation is required to assess keystone species status in south-west WA.

Introduction

Mistletoes are a polyphyletic group of shrubby, aerial hemiparasitic flowering plants with over 1,500 species found over a wide range of habitats and across all continents with the exception of Antarctica (Kuijt 1969; Calder 1983; Watson 2001). A diversity of ‘showy’ mistletoes (family Loranthaceae) is native to Australia, with 75 species currently recognised (Barlow 1984; Barlow 1992; Watson 2011). Watson *et al.* (2001) first proposed that mistletoes act as a keystone resource (*sensu* Power *et al.* 1996) in forests and woodlands worldwide, due to the pervasive effects they have on these habitats through the provision of nutritional and nesting resources (confirmed by Watson and Herring 2012). Peres (2000) identified four criteria used to define a keystone plant: reliability and abundance of resources, degree of consumer specificity and temporal redundancy. Kotliar (2000) further proposed that keystone species should perform functions not otherwise carried out. In this study, we address whether two species of loranthaceous mistletoes in south-west Western Australia (WA) meet the keystone criteria established by these authors.

In Australia, mistletoe nectars and fruits are consumed by at least 50 bird species, including several honeyeater species (Keast 1958; Reid 1987; Turner 1991; Brown *et al.* 1997). In addition to providing a nutritious food source, many mistletoe species also display extended flowering and fruiting phenologies which minimise competition with other plant species, but is also important for sustaining populations of their avian pollinators and dispersers. Australian mistletoes continually draw upon their host’s water and nutrient resources and consequently are able to flower and set fruit during dry seasons when little other nectar or fruit is available in the landscape (Paton and Ford 1977; Reid 1986; Watson 2001). In addition to flowering and fruiting at different times to most other plants, discontinuous ripening (both within a species and amongst species within communities) extends flowering and fruiting periods (Reid 1986; Hawksworth and Wiens 1996; Watson 2001). For example, most temperate southern Australian mistletoes flower during summer, contrasting with largely spring and autumn flowering for the majority of ornithophilous plant species present in these areas (Reid 1986; Watson 2011). In more arid areas, where mistletoes are a critical food source to nectarivorous species, some mistletoe species flower during winter, others during summer, while other species exhibit all year round flowering (Reid 1986; Watson 2011). Mistletoes also provide the most reliable (and sometimes the only) source of fruit for their avian dispersers. Further, their semi-succulent leaves have a high concentration of nutrients and are consumed by herbivores (Watson 2001). Their dense, multibranched structure means that many mistletoe species offer important nest and foraging sites for animals in an otherwise open canopy (see review by Watson 2001). In Australia, bird species from more than 60 families (across 16 orders) and several mammalian families nest in mistletoe, and 66% (of 330 species) of Australian arboreal nesting bird species have been recorded using mistletoes as nest sites (Cooney *et al.* 2006). Many insectivorous species (e.g.

thornbills, whistlers) also use mistletoe clumps as a foraging substrate, as mistletoe often has abundant and distinctive insect assemblages (Turner 1991; Watson 2001; Start 2011; Watson 2011); however Burns *et al.* (2011) found no difference in insect assemblages. Mistletoes therefore reliably provide important food and shelter resources for hundreds of fauna species, providing resources and ecosystem services out of proportion to their abundance and contribution to biomass (Davidson *et al.* 1989; Watson 2001; Watson 2002; Mathiasen *et al.* 2008; Watson and Herring 2012).

Loranthaceous mistletoes provide birds with important nectar and fruit resources (Kuijt 1969; Calder 1983; Davidar 1985; Reid 1986; Ladley *et al.* 1997; Robertson *et al.* 1999). With two exceptions, the root-parasitic Western Australian Christmas tree, *Nuytsia floribunda*, and *Atkinsonia ligustrina* (Hawkeswood 1981; Watson 2011), all Australian loranthaceous mistletoes are pollinated by birds. These mistletoes tend to display brightly-coloured, odourless flowers, with abundant, sugar-rich nectar (up to 60% total sugar content, primarily glucose and fructose sugars, Reid 1986; Stiles and Freeman 1993; Baker *et al.* 1998), characteristics typically associated with ornithophilous pollination. Although they are not dependent on mistletoe nectar as a primary food source, a wide range of bird species pollinate these mistletoes, including several species of honeyeaters (Reid 1986; Watson 2001; Watson 2011). The degree of consumer specificity between mistletoes and their pollinators has led several authors to suggest that long term negative consequences for both interacting organisms and perhaps indeed the entire ecosystem may ensue if this balance were disrupted (Reid *et al.* 1995; Watson 2001).

Birds are also responsible for seed dispersal for nearly all Australian loranthaceous mistletoes (with the exception of *N. floribunda*, which is wind dispersed (Watson 2011)). Mature mistletoe fruits are often brightly coloured, fairly large and sweet and act as a food source for obligate and opportunistic bird species worldwide (see review by Watson 2001). The composition of the fleshy fruit pulp surrounded by a layer of viscin varies among species, but most mistletoe fruits contain a high proportion of carbohydrates, lipids and protein (López de Buen and Ornelas 2001; Watson 2001; Barea 2008).

In addition to supporting generalist feeders, Australian mistletoes also support two mistletoe fruit specialists. The Mistletoebird, *Dicaeum hirundinaceum*, is found throughout mainland Australia (Keast 1958; Blakers *et al.* 1984) and is locally nomadic, its presence corresponding with the availability of fruiting mistletoe (Rawsthorne *et al.* 2012). The rare Painted Honeyeater, *Grantiella picta*, found across the eastern inland side of the continent (Reid 1986), is considered the original (Australian) 'mistletoe bird' as the Mistletoebird did not colonise Australia until possibly as recently as the Holocene (~12,000 YBP, Reid 1991). The diversification and radiation of mistletoes across

Australia has therefore depended upon species such as the Painted Honeyeater and its ancestors (Watson 2011).

Despite their importance as a food resource, there have been few studies examining how mistletoe may influence changes in Australian bird communities (see studies by Turner 1991; Watson 2002; Watson *et al.* 2011; Watson and Herring 2012). Additionally, we have extremely limited information on mistletoe fruiting and flowering phenology in south–west WA. The aim of this study was to investigate if bird species richness and community structure varies with flowering and fruiting of two Loranthaceae mistletoe species common in south–west WA, the wire leaf mistletoe (*Amyema preissii*) and box mistletoe (*Am. miquelii*). This study examined how flowering and fruiting phenology compared with year–round bird community surveys. We predicted that: 1) there would be a greater number of bird species present (i.e. greater species richness) at our study sites when mistletoe flowers or fruit were available, and 2) bird community structure at our study sites would reflect variability in available resources, and 3) Mistletoebirds would only be present in an area when ripe mistletoe fruit was available. We then discuss the findings of this study in relation to the keystone criteria identified by Peres (2000) and Kotliar (2000).

Methods

Study sites

The study was conducted at five sites (100 x 200 m) in south–west WA where mistletoe was extremely abundant, from February 2010 to January 2011 (Table 1). Two sites contained *Am. preissii* parasitising *Acacia* spp. hosts, whilst three contained *Am. miquelii* parasitising *Eucalyptus* and *Corymbia* hosts. All sites were dominated by mistletoe with few other sources of fruit or nectar present (Table 1), with the exception of Araluen. Araluen is surrounded by a dense urban matrix, including flowering and fruiting plants in extensive adjacent gardens; and while Forrestfield was also surrounded by suburban matrix, the area is more rural with larger property sizes and more native vegetation (Table 1). One of the sites (York 2) contained both species of mistletoe, however *Am. preissii* was present in extremely low densities on 2 individual trees only. In south–west WA, flowering and fruiting records suggested that both mistletoe species have narrow flowering and fruiting periods (A.N. Start, pers. comm.). Flowering (January to March) and fruiting (April to July) periods of *Am. preissii* differ from those of *Am. miquelii* in south-west WA, which has flowering records from March to April and fruiting records from June, November and December (A.N. Start, pers. comm.).

South–west WA experiences hot summers and cool wet winters. York (in the highly fragmented agricultural wheatbelt of WA) is situated further inland than the other sites, and experiences a more extreme temperature range and lower rainfall compared to the other sites (Table 1).

Fruit and flower phenology

The flowering and fruiting phenologies of *Am. preissii* and *Am. miquelii* were measured by counts of flowers (categorised as ‘bud’, ‘open’ or ‘senescent’) and fruit (‘immature’, ‘unripe’, ‘ripe’ or ‘bare’) at approximately 5 week intervals. At each site, 30 cm sections of tagged branches (measured proximally from the tip of the branch) of up to 21 randomly–selected mistletoe plants were monitored for each survey period, as per Barea and Watson (2007). These branches ranged in height from 0.5–15m high. Each tagged branch was monitored every 5 weeks, with counts made of flowers (buds through senescence) and fruit (unripe through to stalks where fruit had been removed (‘bare’)). As the total number of flowers and fruits varied between branches, an index of relative fruit and flower abundance was calculated (expressed as the proportion of fruit and flowers per 30 cm of branch, summing to 1) which were averaged across all mistletoe plants for each site/host. Mistletoes surveyed included *Am. preissii* parasitising *Acacia baileyana* (n=21), *Ac. podalyriifolia* (n=21) and *Ac. acuminata* (n=21), and *Am. miquelii* parasitising *Eucalyptus accedens* (n=14) and *Corymbia calophylla* (n=16, n=18; Table 1).

Bird species

Monthly surveys of bird species presence/absence at each site were carried out using a standardised search method (Watson 2003). We did not attempt to estimate bird species abundance due to different detectabilities of species. At least three 20–minute surveys were conducted back–to–back, with the stopping rule (after three surveys being reached) that the number of species seen in a single sampling period of 20 minutes was less than or equal to the number of species seen in two previous subsequent sampling periods (Watson 2003; Watson 2004b). Surveys commenced within 90 minutes after sunrise (0503 to 0718).

Statistical analysis

Differences in fruiting and flowering periods were compared among sites (and host species in the case of Araluen) and month by two–way ANOVA, with *Tukey–Kramer post hoc* tests for unequal sample sizes as required. Proportions of ripe fruit and open flowers were arcsine squareroot transformed prior to analysis to meet requirements of parametric statistics.

1) *Bird species richness* (total number of bird species recorded) was compared among sites and for months when flowers or fruit were present (‘open’ and ‘ripe’) or absent (‘bud’, ‘senescent’ and

‘immature’, ‘unripe’, ‘bare’) by two-way ANOVA, with *Tukey–Kramer post hoc* tests for unequal sample sizes as required.

2) *Bird community structure*: Bird data, classified as presence (1) or absence (0) for each bird species for each monthly survey, were analysed by multidimensional scaling (MDS) in the program PAST 2.08b (Hammer *et al.* 2001). Bird community structure was then compared via two-way analysis of similarity (ANOSIM, Bray–Curtis similarity matrices; PAST 2.08b), using site (1-5) and either flowering (comparing months with or without ‘open’ flowers) or fruiting (comparing months with or without ‘ripe’ fruit available) as independent factors. The ANOSIM test statistic (R) contrasts the differences among groups with variation within groups, a large positive R (up to 1) signifying dissimilarity between groups; significance is calculated via permutation (Clarke 1993). Similarity Percentage (SIMPER) was then used to assess which individual species were primarily responsible for observed differences (Clarke 1993) and then subsequently for feeding guilds (frugivore, nectarivore, insectivore, granivore and omnivore, see Electronic Appendix 1).

3) *Presence/absence of bird species*: To examine the relationship of bird species and mistletoe flower presence, contingency tables were constructed for each month of the presence/absence of individual bird species compared to the presence/absence of mistletoe flowers or fruit. These contingency tables were analysed for significance via Fisher’s exact probability using STATISTICA (StatSoft Inc 2007), followed by a Bonferroni correction.

Statistical significance was set to $\alpha < 0.05$. Results are presented as mean \pm S.D.

Results

41 bird species were recorded over 53 surveys at the five sites, including 2 frugivorous (Mistletoebird and Silvereeye) and 6 nectarivorous species (Brown, New Holland, Singing and White-cheeked honeyeaters, Red Wattlebird and Western Spinebill, Electronic Appendix 1).

Presence of mistletoe flowers: Flowers (and therefore nectar) of both mistletoe species were available for 2 to 3 months at each site, spanning the Australian summer and autumn months (from December to February; *Am. preissii*, Fig. 1a, c, e; from December to May; *Am. miquelii*, Fig. 1b, d, f), with peak abundances occurring at different times at each site (Fig. 1). A significant site by month interaction ($F_{48,1014}=59.66$, $P < 0.001$) showed that flowering periods differed among sites and between mistletoe species. We note, however, that differences between hosts at the same site did not affect flowering or fruiting phenology (*Am. preissii* was monitored on hosts *Ac. baileyana* and *Ac. podalyriifolia* at Araluen, see Figs. 1c, e).

1) *Bird species richness*: There were no significant differences in bird species richness (i.e. number of species recorded) between months when mistletoe was flowering or not (flowers present: 11.1 ± 4.1 , $n=13$ monthly surveys; flowers absent: 9.8 ± 4.0 bird species, $n=40$ surveys; $F_{1,43} < 0.01$, $P=0.975$), or differences among sites ($F_{4,43}=0.57$, $P=0.686$). However, a significant interaction term (site by presence of flowers: $F_{4,43}=6.49$, $P < 0.001$, Fig. 2a), showed that Araluen had significantly higher bird species richness compared to all other sites (with the exception of York 1) when flowers were not present (outside the summer months, *Tukey-Kramer post hoc* tests). There were also no significant differences in bird species richness when the presence of nectarivorous species only ($n=6$ species) was compared for months when mistletoe was flowering vs months when flowers were absent (flowers present: 1.9 ± 1.8 , $n=13$ monthly surveys; flowers absent: 1.7 ± 1.3 bird species, $n=40$ surveys; $F_{1,43}=1.11$, $P=0.297$). There was a significant difference among sites ($F_{4,43}=20.71$, $P < 0.001$), and a significant interaction term (site by presence of flowers: $F_{4,43}=2.80$, $P=0.037$, Fig. 2b) demonstrated that even when flowers were not present, Araluen had significantly more nectarivorous species compared to all other sites (with the exception of York 2, *Tukey-Kramer post hoc* tests).

2) *Bird community structure*: Bird community structure also varied among sites (two-way ANOSIM; site: $R=0.75$, $P < 0.001$), but the presence of flowering mistletoe (comparing months with or without 'open' flowers) did not have a significant effect on bird community structure (flowering: $R=0.08$, $P=0.208$).

3) *Presence/absence of bird species*: The Grey Butcherbird (*Cracticus torquatus*) was the only bird species that was more likely to be recorded during months when mistletoe was flowering (Fisher's exact test: $P=0.042$), while the Western Gerygone was less likely to be recorded during these months ($P=0.042$). However, as these differences were not significant after Bonferroni correction, these results will not be discussed further. During surveys, four nectarivorous honeyeater species (Brown, New Holland, Singing, and White-cheeked honeyeaters) were directly observed feeding on flowers of both mistletoe species.

Presence of ripe mistletoe fruit: Ripe fruit appeared some 2–7 months after flowering, and was available for 2 to 5 months, with peak abundances occurring in winter (June and August: *Am. preissii*, Fig. 1a, c, e) and spring/summer (November and January: *Am. miquelii*, Fig. 1b, d, f). A significant interaction term (site by month: $F_{48,1014}=26.66$, $P < 0.001$) demonstrated that fruiting periods differed among sites and between mistletoe species.

1) *Bird species richness*: There were significantly more bird species present (i.e. greater species richness) when surveys were carried out when ripe mistletoe fruit was present (fruit present: 12.06 ± 4.27 , $n=16$ monthly surveys; fruit absent: 9.24 ± 3.65 , $n=37$ surveys; $F_{1,43}=7.94$, $P=0.007$). There was also a significant difference among sites ($F_{4,43}=13.60$, $P < 0.001$) and a significant

interaction term (site by month: $F_{4,43}=3.77$, $P=0.010$; Figure 2c) with the two sites surrounded by urban matrix showing significantly higher (Araluen) or lower (Forrestfield) bird species richness (Fig. 2c).

2) *Bird community structure*: Bird community structure was significantly different for months when ripe mistletoe fruit was present, compared with months when fruit was absent or unripe (two-way ANOSIM; fruiting: $R=0.28$, $P=0.002$), with significant differences also present among sites (site: $R=0.88$, $P<0.001$). The Mistletoebird made the greatest contribution of all species ($n=41$) to the distinction between bird community structure for fruiting and non-fruiting months (6.3%, SIMPER). When analysed for the five feeding guilds (SIMPER, standardised by the number of species within each guild), the two frugivore species contributed an average of 32.7% to the distinction, compared with 25.2% for six nectarivore species, 17.6% for five omnivorous species, 14.9% for seven granivore species and 9.6% for 21 insectivore species.

3) *Presence/absence of bird species*: The Mistletoebird was the only species that was significantly more likely to be recorded during months when ripe mistletoe fruit was present (Fisher's exact test: $P<0.001$, significant after Bonferroni correction), although Mistletoebirds were also recorded at three sites (York 1, Paruna, York 2) during months when no ripe mistletoe fruits were recorded (2, 1 and 5 months for these sites, respectively). The Mistletoebird and a parrot, the Australian Ringneck, *Barnardius zonarius*, were the only bird species directly observed consuming mistletoe fruit during our surveys (the Australian Ringneck feeding on *Am. preissii*; Mistletoebirds feeding on both mistletoe species). Mistletoebirds were frequently observed probing the green unripe fruits of *Am. miquelii* and pale pink fruits of *Am. preissii* and then either rejecting (*Am. miquelii* and *Am. preissii*) or occasionally ingesting the unripe fruit (*Am. preissii* only). Many other species were observed perching within mistletoe clumps, including the Yellow-rumped Thornbill, Red-capped Robin, Rufous Whistler, Grey Fantail, Varied Sittella, Weebill, Striated Pardalote, Western Spinebill and Silvereye.

Discussion

In this study, we recorded 1) greater bird species richness and 2) altered bird community structure in the presence of fruiting mistletoe, with 3) a higher chance of sighting Mistletoebirds for months when ripe fruit was present. Can mistletoes in south-west WA therefore be described as a keystone resource? We discuss the findings of this study and literature records in relation to the keystone criterion identified in the introduction.

Reliability of mistletoe resources: The wire leaf mistletoe *Am. preissii* and box mistletoe *Am. miquelii* are important resources for bird communities in south–west WA due to the wide distribution of these plants as well as their extended flowering and fruiting times. *Am. preissii* and *Am. miquelii* each had flowers or fruit available for half the year (*Am. preissii* 6–7 months and *Am. miquelii* 5 months) and across sites timing of flowering and fruiting was offset so that resources were available over all months of the year. We predicted that there would be a greater number of bird species present at our study sites when mistletoe flowers or fruit were available, and that bird community structure would reflect available resources. The presence of ripe mistletoe fruit was correlated with significantly higher bird species richness and altered community structure. Importantly, the patterns of fruit presence did not coincide across our field sites (maximum 100 km apart), and yet the presence of bird species was associated with site–specific timing of fruit presence. Therefore, while we are not able to entirely discount ecosystem–wide effects such as bird detectability (Field *et al.* 2002), spring and winter migration (see review on partial migration by Chan 2001) and rainfall driven surges attracting locally nomadic species (as well as promoting mistletoe recruiting and fruiting, Reid 1987; Yan and Reid 1995), the findings of the present study are consistent with those of previous studies that have positively linked increased species richness to mistletoe density (Turner 1991; Bennetts *et al.* 1996), and manipulative studies comparing the avifauna of two adjacent woodland remnants where one site had been manually cleared of mistletoe (Watson 2002; Watson and Herring 2012). Reid (1986) reported that mistletoe is one of the few reliable sources of fruit in eucalypt forests of south–eastern Australia, and while we only recorded fruiting phenology over one year, anecdotal observations (K. Napier, pers. obs.) suggest that mistletoe fruit is predictably available at each site from year to year, and is therefore extremely reliable. Mistletoes in south-west WA appear to fulfil the criterion of resource reliability, as they appear to be predictably available every year to sustain consumers such as the Mistletoebird.

Abundance of mistletoe: Crude measures of mistletoe abundance at each site in the present study indicated that mistletoe is super–abundant in the 2 ha search areas at each, but resource patch density (sensu Peres 2000) was not measured in the present study. With this caveat, mistletoe appears to be super–abundant at the sites presented in this study, typical of fragmented landscapes in south–western WA, and fulfilling the criterion of high abundance (sensu Peres 2000). However, the attribute of resource abundance as a criterion for keystone species status is seen as secondary to the redundancy, reliability and specificity of a given resource (Peres 2000).

Degree of consumer specificity: Resources may range from being extremely generalised, if they are consumed by at least half of the species in a bird community, to extremely specialised, if they are consumed by 5% or less of the species (Peres 2000). Mistletoes promote biodiversity by providing plentiful resources such as nutrient–rich fruit, nectar and leaf litter, as well as sheltered nesting sites

and foliar arthropods (Watson 2001; Cooney *et al.* 2006; Watson *et al.* 2011). While the influence of these resources on the structure of the avian community can be difficult to elucidate (Watson *et al.* 2011), a number of studies have documented the link between the presence of aerial mistletoes and greater avian species richness (e.g. Turner 1991; Bennetts *et al.* 1996; Watson 2002; Watson and Herring 2012). The present study clearly indicates temporal effects in bird species presence correlated with the availability of ripe mistletoe fruit. We had predicted that frugivorous birds would be more likely to be present when ripe mistletoe fruit was available. Not surprisingly, presence of the only mistletoe fruit specialist found in WA, the Mistletoebird, was associated with the presence of fruiting mistletoe, and Mistletoebirds were observed feeding on both species of mistletoe fruit. Australian Ringneck parrots are opportunistic feeders (Higgins 1999) and were observed ingesting *Am. preissii* fruits and have been previously recorded (Forde 1986) feeding on the fruits of *Am. quandang* and *Lysiana exocarpi* (both species are found in WA, but are generally restricted to the southern edge of the Great Victoria Desert and the Nullarbor Plain; Western Australian Herbarium 1998-; Watson 2011). Several other bird species (nectarivorous, granivorous and insectivorous) that are known to regularly consume or opportunistically supplement their diets with mistletoe fruit, including the Singing Honeyeater, Red Wattlebird, Silveryeye, and Yellow-rumped Thornbill (see Reid 1986 and references therein), were recorded in the present study, although none were sighted feeding on the fruit. Although these individual species did not show significant patterns in presence/absence on their own, the overall pattern was a significant increase in species richness and changes in the structure of the bird community for months with mistletoe fruit present compared with months when fruit was absent.

Many nectarivorous, as well as insectivorous and generalist species feed on the nectar of Australian mistletoes (see Watson 2001). In the present study, although four nectarivorous honeyeater species were observed feeding on the nectar of both mistletoe species, we did not find that the presence of these species at our study sites was linked with the presence of mistletoe flowers. Many insectivorous species were also observed perching in mistletoe clumps, which may reflect enhanced foraging opportunities presented by the abundance of insects associated with mistletoes (Turner 1991; Burns *et al.* 2011; Watson 2011; Watson *et al.* 2011).

Findings from the literature therefore suggest support for the criterion of consumer specificity proposed by Peres (2000), although in the present study, only the presence of a single species (the Mistletoebird) was positively correlated with fruiting mistletoe; mistletoe, in this study, would therefore be classified as an extremely specialised resource, and fails to meet this criterion as it is not consumed by a large proportion of the bird assemblage with which they coexist (i.e. extremely generalised resource). This criterion requires further investigation.

Temporal redundancy of mistletoe: Under the keystone criterion of temporal redundancy density (sensu Peres 2000), a resource may be considered entirely indispensable if it is available during periods of overall resource scarcity. Mistletoes in the fragmented landscapes assessed in this study may then be considered a ‘low redundancy’ resource as they were often the only source of fleshy fruit and nectar available (with the exception of Araluen, where blackberry *Rubus* sp. was present, see Table 1), and would therefore be considered entirely indispensable. Temporal and spatial fluctuations within and among habitats due to both individual movements and population processes occur in most bird communities (Malizia 2001). The distribution and abundance of food resources, in particular, influences the movements of many birds (Levey 1988). The foraging efficiency of nectarivores and frugivores is also affected by the temporal pattern of flower and fruit availability: if nectar and fruits are temporally and spatially predictable, animals may retain this information and visit plants with available resources without random, undirected searching (Wright 2005). Unlike *Am. quandang* (surveyed at Middleback Station, South Australia, Reid 1990), which exhibits continuous ripe fruit production due to an overlap in successive annual fruit crops, the fruiting and flowering within *Am. preissii* and *Am. miquelii* at each site was fairly distinct. However, across all five sites examined in the present study, nectar and/or ripe fruit was available for every month of the year due to staggered flowering and fruiting of these two species, as well as geographic variation in timing. While the study by Reid (1990) showed that *Am. quandang* was able to sustain permanent populations of Mistletoebirds due to the continuous fruit availability, it appears that the distinct, but staggered fruiting phenology of *Am. preissii* and *Am. miquelii* in south–west WA (and South Australia, Yan 1993) supports more locally–nomadic movements of Mistletoebirds. We note that Mistletoebirds were present at three sites during months when no ripe mistletoe fruits were recorded, and that this may be attributed to slight differences in fruiting and flowering phenology that were not captured by our survey methods (e.g. ripe fruit present on mistletoe plants that were not monitored during surveys), or Mistletoebirds feeding on the unripe fruits of *Am. preissii*. With the caveat that fruiting and flowering phenology was recorded for only one year, mistletoe appears to be a temporally reliable source of fruit and nectar (see also Yan 1993). Through the provision of fruit and nectar resources, these mistletoes act to sustain nomadic populations of Mistletoebirds and assist to sustain permanent populations of nectarivorous birds in the local area throughout the year.

Resources (functions) not otherwise present: About 18 million ha or 86.5% of the agricultural region of Western Australia has been cleared, and in the wheatbelt, the percentage is estimated to be 93% (DEP 1997). For example, 22 districts in the wheatbelt have less than 10% native vegetation cover (Shepherd *et al.* 2001), and the few patches of remaining native vegetation exist in fragmented and isolated patches. Similar environmental disturbances have occurred in agricultural landscapes across Australia. The quality of food resources in these fragmented landscapes is an important consideration

in terms of sustenance for fauna species. For example, Norton *et al.* (1995) predicted that in extremely fragmented habitats (such as the heavily cleared wheatbelt area), mistletoes would eventually become extinct due to regional declines in key avian pollinators and dispersers (Saunders 1993), as has been recorded in the wheatbelt area north of the town of Kellerberrin (Norton *et al.* 1995). Loranthaceous mistletoes naturally have a patchy distribution across the landscape, due to both the patterns of bird dispersal (Reid and Lange 1988; Reid *et al.* 1995) and narrow microsite tolerances coupled with host specificity (Knutson 1983; Yan and Reid 1995). The distribution of Australian mistletoes in fragmented habitats is likely dependent on mistletoe distribution prior to fragmentation and the impact of fragmentation on the avian pollinators and dispersers (Norton *et al.* 1995). Mistletoes have become more abundant in fragmented habitats in southeast Australia (Reid *et al.* 1994; Watson 2001), and tend to be either super-abundant or absent in fragmented areas of southwest WA (Norton *et al.* 1995). The presence of these plants (and the resources they provide) in fragmented, otherwise resource-poor habitats, may therefore counteract the detrimental effects caused by habitat fragmentation (Kelly *et al.* 2000; Watson 2002) and may further support their recognition as important bird resources. Mistletoes therefore play a unique role in the fragmented landscapes examined in the present study in their provision of vital food resources to Mistletoebirds.

Our findings of increased species richness and changes in the structure of the bird community demonstrate that *Am. preissii* and *Am. miquelii* may provide important food and shelter resources for bird species in fragmented south-west Western Australian woodlands. However, while mistletoes produce highly reliable, low redundancy fruit resources that play a unique role in fragmented landscapes in south-west WA, we failed to find evidence that mistletoe nectar and fruit are consumed by a wide range of bird species. Instead, the only bird species reliant on these food resources is the specialist Mistletoebird. The potential for the keystone status of mistletoes in south-west WA requires further investigation, with comprehensive experimental ‘mistletoe removal’ tests such as those performed by Watson (2002) and Watson and Herring (2012) recommended.

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Figure legends:

Fig. 1: Flowering and fruiting phenology of the mistletoes *Amyema preissii* (left hand panel) and *Amyema miquelii* (right hand panel) from February 2010 to January 2011. *Am. preissii*: two locations on 3 host species; York 1: *Acacia acuminata* (a) n=21; Araluen: *Ac. baileyana* (c) n=21, *Ac. podalyrifolia* (e) n=21. *Am. miquelii*: three locations on 2 host species; Paruna: *Eucalyptus accedens* (b) n=14; Forrestfield: *Corymbia calophylla* (d) n=16; York 2: *C. calophylla* (e) n=18. Values are expressed as the average proportion of flowers and fruits per 30cm of branch. Lines denote flowers, solids denote fruits. Course lines denote flowers in 'bud', crossed lines denote 'open' and fine lines denote 'senescent'. Light grey denotes 'immature' fruits, grey denote 'unripe', black denote 'ripe' and white denote 'bare'. Arrows indicate peak abundances of flowers (grey) and fruit (black).

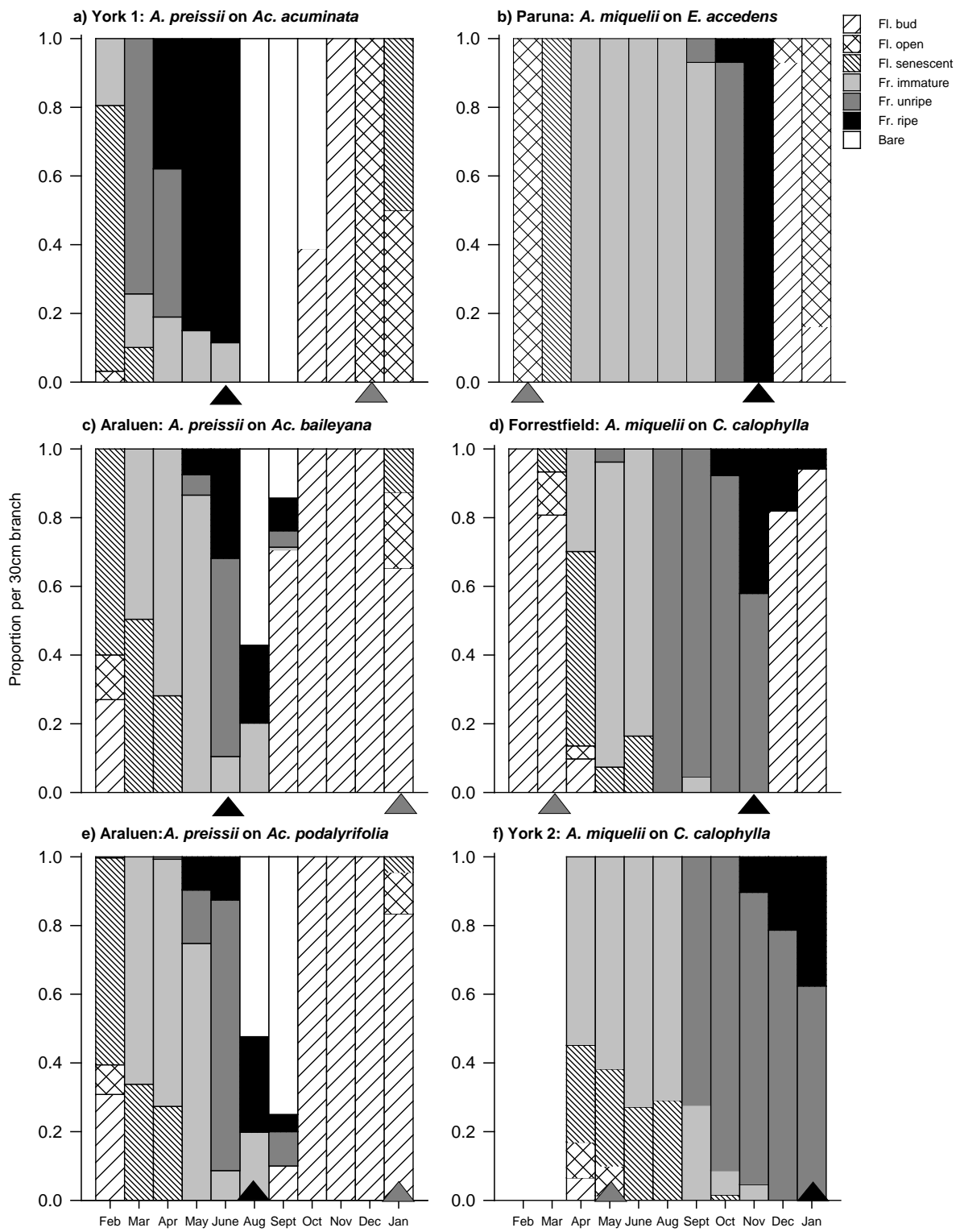
Fig. 2. The number of bird species recorded at each site in the presence (1) or absence (0) of open flowers (a) and ripe fruit (c), and the number of nectarivorous bird species recorded at each site in the presence (1) and absence (0) of open flowers (b). Numbers of surveys/months contributing to each data point for absent and present, respectively, are shown in parentheses. Values are expressed as means \pm SEM.

Table 1. The characteristics of the five sites surveyed in south-west Western Australia.

The range of all mistletoe plant heights are presented underneath species names, with heights of tagged mistletoe plants underlined. Dates exclude the month of July for all sites. Rainfall range is shown for ‘winter’ (May to September inclusive). Weather data obtained for 1981-2010 (Bureau of Meteorology 2011) from the nearest meteorological station to the study areas: Araluen and Forrestfield – Gosnells City (32°02’S, 115°58’E); Paruna – Pearce RAAF (31°40’S, 116°1’E); York 1 and York 2 – York (31°53’S, 116°46’E).

Site		Total time recorded: dates	Mistletoe species	Host species	Site description	Vegetation	Days with Temp. max. >35°C, min <2°C; Avg. annual rainfall (winter rainfall range)
1 ‘Araluen’	Araluen Country Club, Roleystone, WA (32°08’S, 116°05’E)	11 months: Feb 2010 – Jan 2011	<i>Amyema preissii</i> , <u>0.5</u> – 2m	<i>Acacia baileyana</i> <i>Ac. podalyriifolia</i> (non WA natives)	A heavily watered suburban garden with both non-native and native plants present	<i>Nerium oleander</i> , <i>Corymbia calophylla</i> , <i>Eucalyptus wandoo</i> , <i>E. forestiana</i> , as well as various <i>Eucalyptus</i> , <i>Grevillea</i> and <i>Callistemon</i> species and one species of <i>Rubus</i> also present	35, 1 day 795 mm (83 – 165 mm)
2 ‘York 1’	Private farming property, York, WA (31°51’S, 116°44’E)	11 months: Feb 2010 – Jan 2011	<i>Am. preissii</i> <u>0.5 – 2</u> – 5m	<i>Ac. acuminata</i>	A fragmented, semi arid <i>Acacia</i> woodland subject to grazing	Dominated by <i>Ac. acuminata</i>	45, 47 days 401 mm (44 – 71 mm)
3 ‘Paruna’	Paruna Sanctuary, Avon Valley, WA (31°41’S, 116°7’E)	11 months: Feb 2010 – Jan 2011	<i>Am. miquelii</i> <u>10 – 15</u> – 25m	<i>E. accedens</i> <i>E. wandoo</i> <i>C. calophylla</i>	Australian Wildlife Conservancy, pristine warm temperate Eucalypt woodland	<i>E. accedens</i> and <i>E. wandoo</i> , with scattered <i>C. calophylla</i>	31, 3 days 669 mm (70 – 133 mm)
4 ‘Forrestfield’	Forrestfield, WA (32°0’S, 116°1’E)	11 months: Feb 2010 – Jan 2011	<i>Am. miquelii</i> <u>2 – 4</u> – 20m	<i>C. calophylla</i> <i>E. wandoo</i>	Roadside suburban reserve in a fragmented low Eucalypt woodland	Dominated by <i>C. calophylla</i> with scattered <i>E. wandoo</i> , with <i>Hovea pungens</i> , <i>Goodenia fasciculata</i> and <i>Banksia</i> spp present	35, 1 day 795 mm (83 – 165 mm)
5 ‘York 2’	Private farming property, York, WA (31°50’S, 116°44’E)	9 months: April 2010 – Jan 2011	<i>Am. miquelii</i> <u>2 – 4</u> – 20m	<i>C. calophylla</i> <i>E. wandoo</i>	A fragmented, semi-arid <i>Eucalyptus</i> woodland, subject to grazing	Dominated by <i>C. calophylla</i> and <i>E. wandoo</i> . <i>Gastrolobium</i> and <i>Banksia</i> spp. also present, as well as <i>Ac. acuminata</i> (parasitised with	45, 47 days 401 mm (44 – 71 mm)

very low densities of *Am. preissii*).



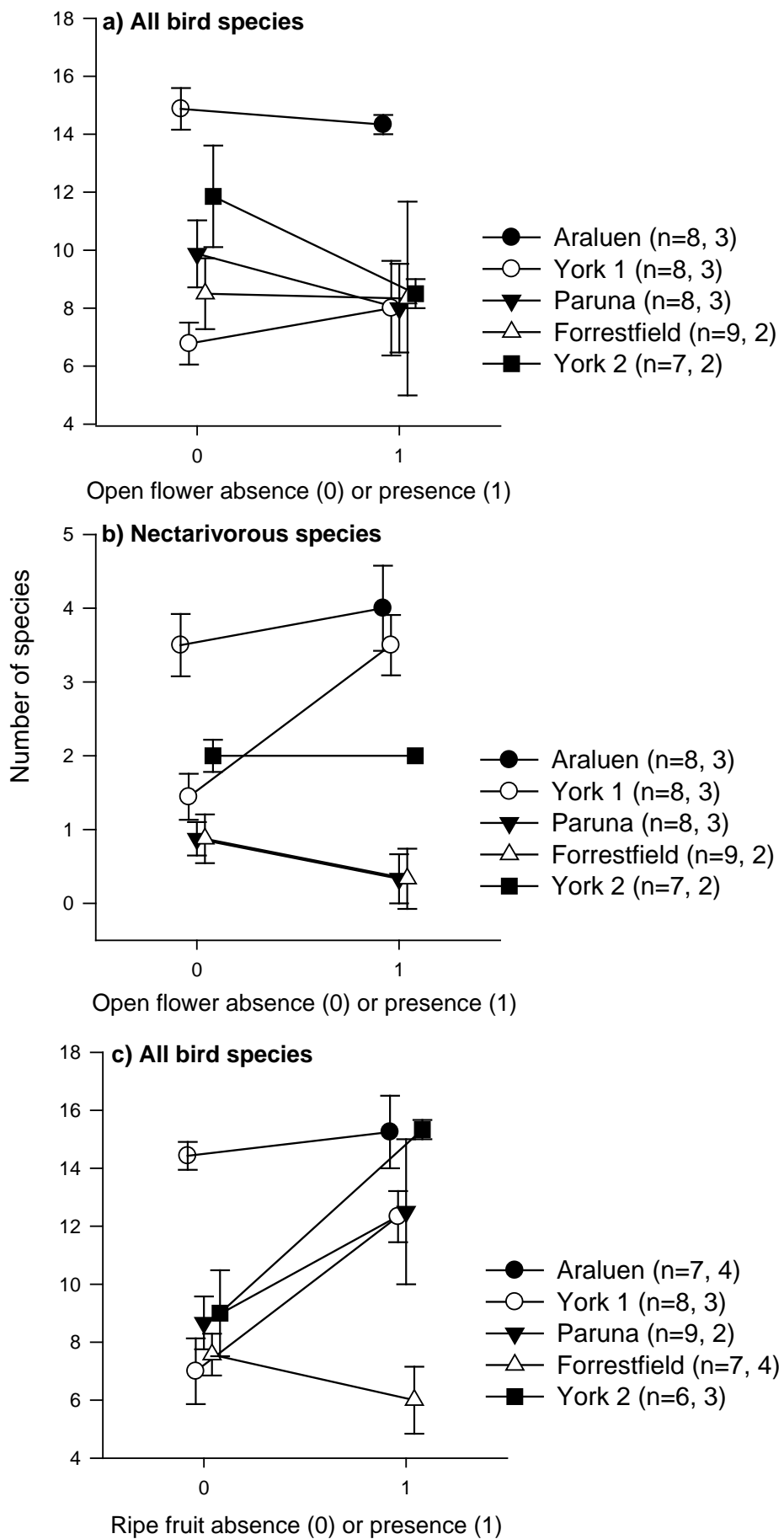


Fig 2

Electronic Appendix 1: Bird species recorded in 53 surveys over 5 sites in south-west Western Australia from February 2010 to January 2011.

Surveys were conducted approximately every 5 weeks from February 2010 to January 2011 (11 surveys in total for Araluen, York 1, Paruna and Forrestfield; 9 surveys in total for York 2 from April 2010 to January 2011). The total number of observations was n= 511. F refers to frugivore, I (insectivore), N (nectarivore), G (granivore), and O (omnivore). Nomenclature follows Christidis and Boles (2008).

Scientific name:	Common name:	Mistletoe present at site: Feeding guild:	Number of surveys present				
			<i>Amyema preissii</i>		<i>Amyema miquelii</i>		
			Araluen	York 1	Paruna	Forrestfield	York 2
Columbidae							
<i>Phaps chalcoptera</i>	Common Bronzewing	G	11	2			
<i>Ocyphaps lophotes</i>	Crested Pigeon	G	1				
Cacatuidae							
<i>Calyptorhynchus banksii</i>	Red-tailed Black-Cockatoo	G	1			3	
<i>Calyptorhynchus latirostris</i>	Carnaby's Black-Cockatoo	G			3		
<i>Eolophus roseicapillus</i>	Galah	G	7	1	3		5
Psittacidae							
<i>Barnardius zonarius</i>	Australian Ringneck	G	11	7	9	11	8
<i>Purpureicephalus spurius</i>	Red-capped Parrot	G	3		6		
Cuculidae							
<i>Cacomantis pallidus</i>	Palid Cuckoo	I					1
<i>Cacomantis flabelliformis</i>	Fan-tailed Cuckoo	I				1	
Climacteridae							
<i>Climacteris rufa</i>	Rufous Treecreeper	I			8		
Maluridae							
<i>Malurus splendens</i>	Splendid Fairy-wren	I	8		1		2
Acanthizidae							
<i>Smicromis brevirostris</i>	Weebill	I			11	7	2
<i>Gerygone fusca</i>	Western Gerygone	I	10	5	8	7	
<i>Acanthiza chrysorrhoa</i>	Yellow-rumped Thornbill	I	11	9			2
<i>Acanthiza apicalis</i>	Inland Thornbill	I	7				
Pardalotidae							
<i>Pardalotus striatus</i>	Striated Pardalote	I	8		9	7	
Meliphagidae							
<i>Acanthorhynchus superciliosus</i>	Western Spinebill	N	6				6
<i>Lichenostomus virescens</i>	Singing Honeyeater	N		4		9	
<i>Anthochaera carunculata</i>	Red Wattlebird	N	11		1	2	
<i>Lichmera indistincta</i>	Brown Honeyeater	N	4	4	7	8	8
<i>Phylidonyris novaehollandiae</i>	New Holland Honeyeater	N	11			1	
<i>Phylidonyris niger</i>	White-cheeked Honeyeater	N	8				5
Pomatostomidae							
<i>Pomatostomus superciliosus</i>	White-browed Babbler	O		4			
Neosittidae							
<i>Daphoenositta chrysoptera</i>	Varied Sittella	I					4
Campephagidae							
<i>Coracina novaehollandiae</i>	Black-faced Cuckoo-shrike	I			1	2	1
Pachycephalidae							
<i>Pachycephala rufiventris</i>	Rufous Whistler	I	3	3	2	3	3
<i>Colluricincla harmonica</i>	Grey Shrike-thrush	O		4	6		1
Artamidae							
<i>Artamus cinereus</i>	Black-faced Woodswallow	I					2
<i>Cracticus torquatus</i>	Grey Butcherbird	O	2	2			
<i>Cracticus tibicen</i>	Australian Magpie	I	10	3			2
<i>Strepera versicolor</i>	Grey Currawong	O			2		
Rhipiduridae							

<i>Rhipidura albiscapa</i>	Grey Fantail	I	5	9	9		3
<i>Rhipidura leucophrys</i>	Willie Wagtail	I		8			9
Corvidae							
<i>Corvus coronoides</i>	Australian Raven	O	6	4	7	1	4
Monarchidae							
<i>Grallina cyanoleuca</i>	Magpie-lark	I	2				
Petroicidae							
<i>Petroica boodang</i>	Scarlet Robin	I	3	2			
<i>Petroica goodenovii</i>	Red-capped Robin	I		9			5
Timaliidae							
<i>Zosterops lateralis</i>	Silvereye	F	5	1		5	5
Hirundinidae							
<i>Petrochelidon nigricans</i>	Tree Martin	I			2		5
Nectariniidae							
<i>Dicaeum hirundinaceum</i>	Mistletoebird	F	4	7	3	4	8
Motacillidae							
<i>Anthus novaeseelandiae</i>	Australasian Pipit	I					1

Christidis, L., and Boles, W. E. (2008). 'Systematics and taxonomy of Australian birds.' (CSIRO Publishing: Melbourne.)