

0 **The restricted seed rain of a mistletoe specialist** 535 **John Rawsthorne, David M. Watson and David A. Roshier** 55

J. Rawsthorne, D. M. Watson (dwatson@csu.edu.au) and D. A. Roshier, Inst. for Land, Water and Society, Charles Sturt Univ., PO Box 789, Albury, NSW 2640, Australia. DAR also at: Centre for Integrative Ecology, School of Life and Environmental Sciences, Deakin Univ., Waurn Ponds Campus, Geelong, VIC 3217, Australia.

10 Specialist frugivores are the dominant consumers of mistletoe fruit in many regions and have been shown to intensify 65
infections of host plants as a result of their rapid gut passage rates and dependence on existing infections. The role of spe-
cialist frugivores in long distance dispersal of mistletoe and establishment of new infections is unclear, and has not been
15 explicitly evaluated previously. Here we critically examine the premise that specialists are the dominant dispersers by exam-
ining the role of an Australian mistletoe specialist (mistletoebird *Dicaeum hirundinaceum* Dicaeidae) in dispersing mistletoe
(*Amyema preissii* Santalales: Loranthaceae) seeds beyond infected host stands. We use two primary lines of evidence –
20 presence of birds using remote call recorders, and presence of dispersed seeds via surveys for defecated seeds on host
branches. The observed and inferred movements of the mistletoebird were wholly restricted to habitat patches containing
mistletoe, and this bird was not observed to transport seeds to nearby uninfected host stands within the study system.
While mistletoe specialists may provide much of the within-stand dispersal service for mistletoes, this serves only to
25 aggregate and intensify existing infections. We suggest that long distance dispersal of mistletoe seeds beyond existing hosts
and infection centres is not performed by these dietary specialists, these services more likely to be provided by generalist
frugivores and other occasional mistletoe fruit consumers. 75

25 Specialised frugivores, particularly birds, bats and primates, have long been regarded as high quality dispersers for many
fruiting plants (McKey 1975, Howe and Estabrook 1977). Frugivorous birds are the primary vector for seed dispersal
30 of most mistletoes, via defecation or regurgitation of seeds onto small branches of suitable plant hosts (Calder 1983,
Reid 1986), and mistletoes have attracted an unprecedented suite of specialised fruit consumers (Reid 1991, Watson
2004). Indeed, the dispersal of mistletoe seed is regularly invoked as an exemplar of the apparently tight, mutually
35 beneficial relationships between plants and specialised frugivores (Howe and Estabrook 1977, Carlo and Aukema
2005, Bronstein et al. 2007). Nonetheless, dietary generalists that consume mistletoe fruit as part of a broader diet are
40 known to act as regular seed dispersers (Godschalk 1985, Reid 1989, Murphy et al. 1993) and dispersal by wind,
epizoochory on birds and endozoochory by mammals also occur in limited contexts (Calder 1983, Reid 1986, Amico
and Aizen 2000).
45 The specific dispersal requirements of mistletoes have encouraged reciprocal adaptation of mistletoes and birds,
and specialised mistletoe frugivores have evolved independently in eight avian lineages including non-passerines
(Lybiidae of Africa), sub-oscine passerines (Cotingidae, Tityridae and Tyrannidae of Central and South America)
50 and oscine passerines (Dicaeidae of India, south-east Asia and Australia; Ptilonotidae of North and Central America,
Meliphagidae in Australia; Fringillidae (Euphoniinae) in Central and South America) (Reid 1991, Restrepo et al. 80
2002, Watson 2004). Mistletoe specialists typically are brightly coloured and highly mobile, with small bodies, rela-
tively large gapes and modified guts to allow for rapid pas-
sage of fruits (Richardson and Wooller 1988, Watson 2004) and are considered to have amongst the most highly spe- 85
cialised diets of all frugivorous birds (Restrepo et al. 2002). The repeated evolution of mistletoe specialists with extreme
dietary specialisation and similar physical characteristics worldwide suggests a central role of these specialists in the
ecology and diversification of mistletoes (Restrepo et al. 2002). 90
Through a combination of their foraging and seed dis-
posal behaviours, social interactions and nest-site placement,
mistletoe specialists can cause aggregation in mistletoe infec-
tions at a range of scales (Overton 1994, Martínez del Rio
95 et al. 1995, Aukema and Martínez del Rio 2002a, b, Ward
and Paton 2007). By contrast, little is known about dispersal
beyond existing infections and it is unclear whether these
services are performed by mistletoe specialists or by dietary
generalist frugivores that consume mistletoe fruits as part
100 of a broader diet (Carlo and Aukema 2005, Rawsthorne
et al. 2011).
As part of a broader research programme on mistletoe
dispersal, we asked the question: does a mistletoe special-
ist disperse mistletoe seeds to hosts beyond existing areas
105 of mistletoe infection? We addressed this by recording

0 mistletoebird *Dicaeum hirundinaceum*: Dicaeidae occur- 61
rence in infected and mistletoe-free areas in a floristically 62
simple host/mistletoe system, using a series of remote call 63
recorders to detect presences and estimate absences. We also 64
65 recorded the positions and qualities of defecated mistletoe
7 seeds relative to existing mistletoe infections in the same
8 system, as a direct indicator of seed dispersal in host stands
9 with and without mistletoe. By comparing bird occurrence
10 and positions of dispersed seeds with the pattern of estab-
11 lished mistletoe infection, we evaluated both qualitative
12 and quantitative aspects of mistletoe seed dispersal by a mis-
13 tletoe specialist.

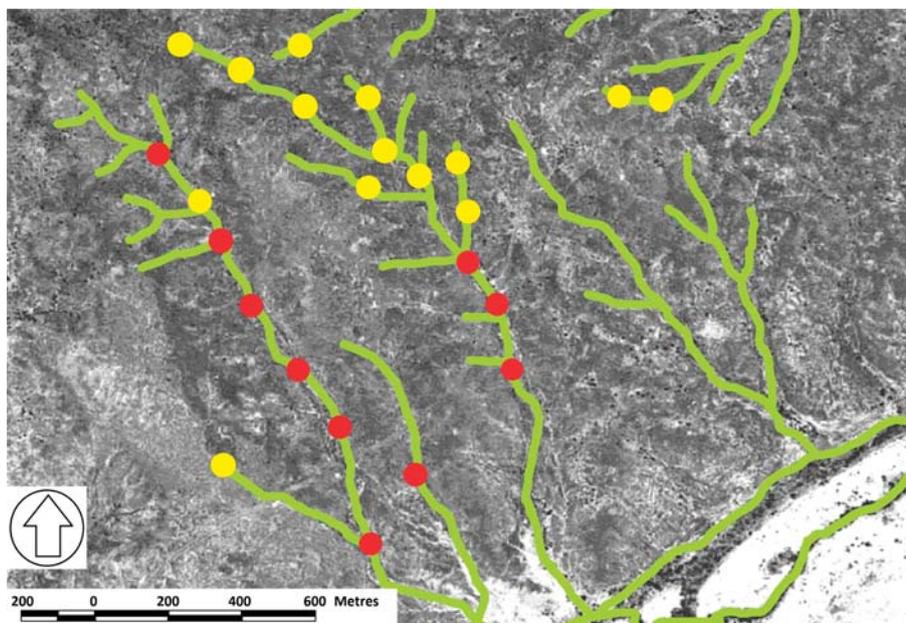
15 Methods

16 The study was conducted near Mount Wood homestead 66
(29°29'0"S, 142°14'28"E) in Sturt National Park within 67
the arid rangelands of inland Australia, during an extended 68
drought in the austral autumn and winter of 2006, with a 69
20 repeat sampling in the winter of 2010. The region experi-
ences hot summers and mild winters, with January average
21 maximum temperature of 36°C and July average minimum
22 temperature of 5°C. The study site was intersected by
23 several ephemeral creek lines draining otherwise treeless
24 stony desert (Fig. 1), with drainage lines vegetated by xero-
phytic shrubs including *Acacia tetragonophylla* (dead finish),
25 *A. cana* (cabbage tree wattle), *A. calcicola* (northern mulga)
and the root parasite *Santalum leptocladum* (northern sand-
26 wood). *Amyema preissii* (wire-leaved mistletoe) was the
30 dominant aerial parasite species, principally infecting *Acacia*
tetragonophylla. Other mistletoes present at low densities
at the study site included *Amyema maidenii* (pale-leaved mis-
31 tletoe), *A. miraculosa* (fleshy mistletoe) and *Lysiana exocarpi*

(harlequin mistletoe), although *A. preissii* was the only mis- 61
tletoe providing a significant fruit resource during the study 62
period. The study area was chosen specifically because of its 63
structural and floristic simplicity and the ease of accessi- 64
65 bility to individual mistletoes and host branches on relatively
small host shrubs.

The mistletoe species present in the site are all dispersed 66
via endozoochory by birds (Liddy 1983, Reid 1986, 67
Watson 2011). Known mistletoe seed dispersers that 68
70 have been recorded within 2 km of the study region are
the mistletoebird, spiny-cheeked honeyeater *Acanthagenys*
rufogularis, yellow-throated miner *Manorina flavigula*,
singing honeyeater *Lichenostomus virescens*, pied honeyeater
Certhionyx variegatus and olive-backed oriole *Oriolus*
sagittatus (Liddy 1983, Reid 1986, Watson 2004, Watson 75
and Rawsthorne unpubl.). Of these species, the mistletoe-
bird is a mistletoe specialist with anatomical adaptations
for a diet that consists mainly of mistletoe fruit (Richardson
and Wooller 1988, Reid 1991, Barea and Herrera 2009), 80
while the remainder are generalist foragers that take mis-
tletoe fruits as part of a broader diet (Higgins et al. 2001,
Watson 2011).

Mistletoebirds give regular calls, and their vocalizations 81
are sufficiently distinctive that their presence can readily 82
be detected by auditory cues alone. Remote call record- 83
ers (Faunatech Wildlife Technical Consultants, Bairnsdale, 84
VIC) were deployed in 28 positions within *Acacia* stands,
including areas with and without mistletoe infection (Fig. 1)
to detect presences of bird species at each location. Record- 85
ers were separated from each other by at least 150 m, to 86
ensure the same bird call was not recorded on more than 87
one recorder simultaneously. Call recorders operated on 88
pre-programmed duty cycles for 15-min periods in early 89
morning, mid morning and late afternoon between March 90
91 and April 2010.



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Figure 1. Aerial image of study site near Mount Wood in Sturt National Park, northwest NSW, Australia. Green lines indicate occurrences of woody vegetation along ephemeral drainage lines; apart from the green lines, the landscape was stony downs free of woody vegetation; red dots indicate remote call recorder locations with mistletoe infection; yellow dots indicate remote call recorder locations where hosts were mistletoe-free. Further sample points were to the northeast of the image. Seed searches were conducted at a subset of remote call recorder locations.

0 and July 2006 to record bird calls on magnetic tapes. These
times were chosen to avoid the windiest periods of day
where recordings were unusable, while still targeting peaks
in bird activity. The choice of length of recording period
was a trade-off between detecting birds that called infrequently
5 and recording multiple individuals within a single
session – a 15 min period gave a reasonable balance between
these competing aims. Recordings were transcribed by one
of us (JR) by listening to the tapes and noting species calling
during each 15 min recording period to determine presence
10 or absence. On several occasions, we were within view of
stands containing call recorders, enabling independent
validation of their efficacy. In all cases when mistletoebirds
or honeyeaters were seen within the stands, contact calls or
full songs could clearly be discerned from the recordings.

15 The presence of dispersed mistletoe seeds can be accurately
determined via careful searches of host branches (Aukema and
Martinez del Rio 2002b) and the disperser can often be
directly identified by the context and characteristics of the
defecated seeds (Reid 1989, Amico et al. 2011),
20 and so we searched for seeds as a direct indicator of seed
dispersal in the study system. In July 2006 after several
months of mistletoe fruiting we conducted systematic 1-h
fixed effort searches for defecated mistletoe seeds on branches
of potential host plants at each of 17 locations within and
25 beyond existing mistletoe infection areas in the study
system. Of the 17 surveyed locations within stands of *Acacia*
spp., 10 had established mistletoe infections and 7 were
completely free of mistletoes. Seed searches of 11 mistletoe-free
sites in the same area were also undertaken in July 2010,
30 again after a prolonged period of mistletoe fruiting within
the study system. Search locations corresponded to a subset
of remote call recorder positions (Fig. 1), thus were approximately
200 m apart. A blind control test was performed to determine
the rate of false negatives in the search. A colleague placed
35 one seed on a host at one of the mistletoe-free survey
locations, and one of us (JR) conducted a 1-h search. This
was performed three times and in each case the seed was
found within the search period, indicating that the search
process was effective at finding even small numbers of
40 dispersed seeds. We determined whether mistletoebird or a
generalist forager had dispersed each seed discovered in the



[AQ2] Figure 2. *Amyema preissii* seeds defecated by mistletoebird on an
acacia branch. Seeds defecated by mistletoebird are typically
arranged in a viscin-coated string of several seeds, which causes
60 the string to adhere to the branch where the seeds can germinate.

seed survey by applying the specific criteria of Reid (1989).
Thus the presence of a zigzag viscid thread along the perch or
the arrangement of up to four seeds in a string was assumed
to indicate that the seed was defecated by mistletoebird,
65 while the presence of macroscopic exoskeleton fragments
or non mistletoe seeds and fruit remains, or the haphazard
aggregation of seeds in clumps was taken to indicate that
seeds had been dispersed by a spiny cheeked honeyeater or
another generalist forager.

70 The results of the two different sampling methods (remote
call recorders and seed searches) and multiple sampling
events were combined within a single probability framework
to provide an indication of the statistical likelihood of the
prima facie conclusions that might be reached based
75 on the observations. For the 2006 remote call recorder and
seed search datasets, data was collected in both areas with
mistletoe infection and in adjacent mistletoe-free areas, while
the 2010 seed search data herein relates only to the mistletoe-
free areas. The data from areas with mistletoe infection
80 are used to provide estimates of detectability of mistletoe
dispersers in an area that they are known to visit, and in
which they are known to disperse seeds, for the two survey
methods. These estimates of detectability were then used to
calculate the likelihood of the results of observations in the
85 mistletoe-free areas, for different assumed underlying levels
of seed dispersal to those sites. We articulate, for the first
time, quantitative limits on the implied level of seed dispersal
to mistletoe-free areas provided by a mistletoe specialist.

Results

90 A total of 369 15-min remote call recordings was made,
although 88 of these periods were discarded due to high wind
rendering call identification impossible. Of the remaining
281 recording periods, 103 were in areas with mistletoe
95 infection and 178 were in mistletoe-free areas. Mistletoebird
was recorded in eight periods, each time within areas of
mistletoe infection. Singing honeyeater was recorded six
times (four times in mistletoe-free areas, and twice in
100 infected areas), yellow-throated miner was recorded twice
in mistletoe-free areas, while spiny-cheeked and pied honey-
eaters and orioles were not recorded by this method.

105 Each of the ten seed searches conducted in 2006 in areas
with established mistletoes had mistletoe seeds present on
host branches, with the number of defecated seeds found
within the 1h search period ranging from 5 to 119 seeds
(46 ± 40 seeds; mean \pm SD). There were no defecated
110 mistletoe seeds found in any of the 7 mistletoe-free sites
surveyed in 2006 or in any of the 11 mistletoe-free sites
surveyed in 2010. All mistletoe seeds found during these
searches (and all incidentally observed seeds) were deposited
singly or in short strings of up to four seeds. In many cases
115 a zigzag viscid thread was observed where the seed was
attached to the host branch, indicating defecation by
mistletoebird (Reid 1989). No exoskeletons or other items
indicating defecation by honeyeaters or other dietary
generalists were observed with defecated mistletoe seeds,
and no clumps of seeds or strings longer than 4 seeds were
120 observed. Thus, all dispersed seeds found in the seed
survey or otherwise can be assigned to mistletoebirds.

0 **Likelihood analysis**

Our results show that every seed search and every remote call recording (RCR) survey in mistletoe-free areas failed to find evidence of seed dispersal by mistletoebird. We can ask two questions to quantify the significance of these results: 1) if the rate of seed dispersal to mistletoe-free sites is, say 20%, what is the chance that an individual site survey would produce a negative result? 2) if the rate of seed dispersal to mistletoe-free sites is, say 20%, what is the chance that all 178 RCR and 18 seed search surveys in mistletoe-free sites would produce negative results?

To answer the first question, we need to consider both the chance that seed dispersal to a site has occurred (this is arbitrarily 20% in our question above) and the chance that this seed dispersal was detected using our survey methods (i.e. detectability rate). Assume detectability of seeds on branches and detectability of birds by remote call recorder per unit time do not vary between infected and mistletoe-free sites.

Define: S = underlying rate of seed dispersal to individual mistletoe-free survey sites. This is the hypothetical situation to be examined, and we have nominated a rate of 20%. d_{RCR} = probability of detection of mistletoebird in a site with fruiting mistletoe, using the remote call recorder survey technique. This can be estimated using our results as $d_{RCR} = 8/103 \approx 8\%$, i.e. the probability of detecting a mistletoebird using an RCR in a site with fruiting mistletoe where it is known to visit is estimated to be 8%. d_{SEARCH} = probability of detection of mistletoebird in a site with fruiting mistletoe, using the seed search survey technique. This can be estimated from our results as $d_{SEARCH} = 10/10 \approx 100\%$, i.e. the probability of inferring the presence of a mistletoebird via seed search in a site where it is known to visit is estimated to be 100%. $P(x | y)$ = probability that x occurs given that y applies. nil_{RCR} = no seed dispersal activity detected in a single remote call recording period at a single mistletoe-free site. nil_{SEARCH} = no seed dispersal activity detected in a single seed search at a single mistletoe-free site. nil_{ALL} = no seed dispersal activity detected in a single seed search in any of 178 RCR sessions and 18 seed searches in mistletoe-free sites.

Using this notation, we see that:

$$P(nil_{SEARCH} | S) = (1 - S \times d_{SEARCH}) = 1 - S$$

$$P(nil_{RCR} | S) = (1 - S \times d_{RCR}) = 1 - 0.08S$$

So the probability that a seed search in a mistletoe-free site found no seeds, if the underlying rate of dispersal was $S = 20\%$, is 80%. Similarly the probability of a single remote call recording session in a mistletoe-free area not detecting mistletoebird, for $S = 20\%$, is 98.4%.

To answer the second question, we can combine the probabilities of nil findings in all mistletoe-free sites and surveys for a given underlying rate of seed dispersal S . Assuming that the result of each survey site, method and period is independent of each other survey result, the results can be combined in a single framework as follows:

$$P(nil_{ALL} | S) = (1 - S \times d_{SEARCH})^{18} \times (1 - S \times d_{RCR})^{178}$$

Thus, for $S = 20\%$, $P(nil_{ALL} | S = 20\%) = (1 - 0.08 \times 20\%)^{178} \times (1 - 20\%)^{18} = 0.001$. We can conclude that if

the underlying rate of mistletoebird-mediated seed rain in a given mistletoe-free site is 20%, the chance of finding no evidence of seed dispersal by mistletoebird across our 178 RCR surveys and 18 seed searches in mistletoe-free sites is 0.1% (i.e. very low). Conversely, given our survey effort and results in mistletoe free areas, the likelihood that the rate of seed rain to mistletoe-free areas is not as high as 20% is $1 - 0.1\% = 99.9\%$; i.e. we can confidently assert that the rate of seed dispersal by mistletoebird to a given mistletoe-free survey site is lower than 20%.

By repeating the above analysis at different underlying rates of seed rain S , we can be about 96% sure that the seed rain rate in a given mistletoe-free survey site is not as high as 10%, and about 81% sure that the seed rain rate is not as high as 5%. We can only be 56% sure, based on our survey effort, that the rate of seed rain is not as high as 2.5%. Adopting a likelihood threshold of 80%, we can exclude rates of seed rain by mistletoebird in mistletoe-free areas any higher than 5%, but we cannot safely draw conclusions about lower rates of seed rain in mistletoe-free areas without unacceptably increasing the chance of a type II error.

Discussion

The mistletoebird was regularly observed dispersing mistletoe seeds during the study period, although recorded seed dispersal was, in the specific context of our study, restricted wholly to areas with existing mistletoe infection. Foraging and defecation observations (including defecations by mist-netted birds; Rawsthorne unpubl.) and the characteristics of defecated seeds on branches all supported this finding. Spiny-cheeked and singing honeyeaters had previously been observed consuming mistletoe fruits in the study system but, despite extended periods of fieldwork during the study period including mist-netting, radio-tracking and targeted observations at fruiting mistletoes, we did not observe mistletoe fruit consumption or defecation in the region during the study period by any species apart from the mistletoebird (Rawsthorne 2007), and no deposited seeds showed any characteristic that indicated dispersal by any bird other than the mistletoebird.

With only the mistletoebird recorded dispersing mistletoe seeds during the study period, the study gave a rare insight into the pattern of seed rain derived solely via a mistletoe specialist, with no contribution from generalist foragers. We observed a highly contagious pattern of dispersed seeds to sites with existing mistletoe infection, consistent with previously observed clumped distributions of mistletoe infections at both host and stand scale (Godschalk 1985, Martinez del Rio et al. 1996, Aukema and Martinez del Rio 2002a, Ward and Paton 2007). More importantly, we found no evidence of dispersal of seeds to mistletoe-free areas in the study system, and we were able to infer via likelihood analysis that the rate of seed rain in individual mistletoe-free sites is probably $< 5\%$; i.e. mistletoe-free sites adjacent to mistletoe infection rarely receive dispersed seeds via mistletoebirds. It is possible that there was some low level of seed dispersal to mistletoe-free host patches as mistletoebirds moved between areas of mistletoe infection, but neither our formal methods nor our extensive informal observations detected any evidence of this.

0	Rather than an aberrant result, the finding that mistletoebirds are restricted primarily to existing areas of infection is consistent with information about other mistletoe specialist frugivores. We note the contextual limitation of our study, and the potential for different densities of fruit to result in different seed dispersal patterns (Carlo and Morales 2008). However research on painted honeyeaters <i>Grantiella picta</i> demonstrated that birds selected areas with high mistletoe densities for feeding and nest location, only undertaking long-distance movements once mistletoe fruit became unavailable (Barea and Herrera 2009, Watson 2011). Likewise, phainopepla <i>Phainopepla nitens</i> establish small tightly defended territories around aggregations of fruiting mistletoe plants in winter, coinciding with a period when their digestive tract becomes dramatically shorter as they become completely frugivorous (Walsberg 1975). We suggest this pattern of restriction to areas of resource concentration is common among mistletoe specialists, and the contagious pattern of seed dispersal (Aukema and Martinez del Rio 2002b, Carlo and Aukema 2005) is the norm.	61
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	Long distance dispersal	
25	Little is known of dispersal of mistletoe seeds beyond existing patches of infection. While the mistletoebird may be ineffective in dispersing seeds to uninfected host stands, that does not mean that the mistletoebird does not transport seeds relatively long distances from one infection centre to the next. It is quite possible, and perhaps likely in some contexts, that mistletoe specialists regularly transport mistletoe seeds via endozoochory between infection centres that are widely separated in space. There are several consequences of such dispersal. First, by transporting propagules between infections, mistletoe specialists may promote genetic diversity in mistletoe populations, an important benefit for parasitic plants that are in constant coevolutionary arms races with their hosts (Yan 1990, Rödl and Ward 2002). Second, by foraging on fruits of more than one species and transporting seeds between infection patches, mistletoe specialists may promote co-occurrence of multiple mistletoe species within stands, and epiparasitism for species pairs sharing fruiting seasons (Watson 2011). Reid (1986) noted the overlapping phenologies of different mistletoes in arid Australian systems, and the potential for otherwise depauperate regions to provide year-round fruit and nectar resources when multiple mistletoe species are present – the mistletoebird may promote this phenomenon by promoting co-occurrence of multiple mistletoe species. Both the birds and the parasite benefit from this effect.	85
30		90
35		95
40		100
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50	Comparisons with other specialist frugivores	
55	While it may be tempting to generalise the qualitative findings reported herein to all specialist frugivores, there are some crucial differences between mistletoe specialists and other specialist frugivores. Foremost, mistletoe specialists have particularly narrow dietary breadth relative to other specialist frugivores. In an arid Australian system the mistletoebird was shown to draw 85% of its diet from fruits of two species of mistletoe (Reid 1990), while in an arid North American system phainopeplas <i>Phainopepla nitens</i> feed primarily on fruits of a single mistletoe species during winter (Walsberg 1975). In contrast to the mistletoe specialists, other exemplar specialist frugivores have much broader fruit diets: resplendent quetzals <i>Pharomachrus mocinno</i> have been found to feed on a minimum of 12–18 species of fruits at most times of year (Wheelwright 1983); five Brazilian cotingas were shown to feed on fruits of between 10 and 45 species (Pizo et al. 2002) (the sixth cotinga in that study, the only mistletoe consumer of the six, had a narrower dietary breadth of eight fruits); while nocturnal, echo-locating, colonial oilbirds <i>Steatornis caripensis</i> consumed fruits from over 30 species from three main families in a Venezuelan study system (Bosque et al. 1995). Perhaps the only frugivore with a similar degree of dietary specialisation to the mistletoe specialists is the vulturine parrot <i>Psittrichas fulgidus</i> of New Guinea, which feeds exclusively on fruits of several species of strangler figs (Mack 1999). Interestingly, these figs are hemiepiphytic, have specific seed placement requirements on host branches, and resist consumption by non-specialist birds, all characteristics shared with mistletoes.	110
60		115
		121
	References	
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	Amico, G. and Aizen, M. A. 2000. Mistletoe seed dispersal by a marsupial. – <i>Nature</i> 408: 929–930.	
	Amico, G., Rodriguez-Cabal, M. A. and Aizen, M. A. 2011. Geographic variation in fruit colour is associated with contrasting seed disperser assemblages in a south-Andean mistletoe. – <i>Ecography</i> 34: 318–326.	
	Aukema, J. E. and Martinez del Rio, C. 2002a. Variation in mistletoe seed deposition: effects of intra- and interspecific host characteristics. – <i>Ecography</i> 25: 139–144.	
	Aukema, J. E. and Martinez del Rio, C. 2002b. Where does a fruit-eating bird deposit mistletoe seeds? Seed deposition patterns and an experiment. – <i>Ecology</i> 83: 3489–3496.	

- 0 Barea, L. P. and Herrera, M. L. G. 2009. Sources of protein in two semi-arid zone mistletoe specialists: insights from stable isotopes. – *Austral Ecol.* 34: 821–828.
- Bosque, C., Ramirez, R. and Rodriguez, D. 1995. The diet of the oilbird in Venezuela. – *Ornitol. Neotrop.* 6: 67–80.
- 5 Bronstein, J. L., Izhaki, I., Nathan, R., Tewksbury, J., Spiegel, O. and Lotan, A. 2007. Fleshy-fruited plants and frugivores in desert ecosystems. – In: Dennis, A. J., Schupp, E. W., Green, R. J. and Westcott, D. W. (eds), *Seed dispersal: theory and its application in a changing world*. CAB International, pp. 148–177.
- 10 Calder, M. 1983. Mistletoes in focus. – In: Calder, M. and Bernhardt, P. (eds), *The biology of mistletoes*. Academic Press, pp. 1–18.
- Carlo, T. A. and Aukema, J. E. 2005. Female-directed dispersal and facilitation between a tropical mistletoe and a dioecious host. – *Ecology* 86: 3245–3251.
- 15 Carlo, T. A. and Morales, J. M. 2008. Inequalities in fruit-removal and seed dispersal: consequences of bird behaviour, neighbourhood density and landscape aggregation. – *J. Ecol.* 96: 609–618.
- Godschalk, S. K. B. 1985. Feeding behaviour of avian dispersers of mistletoe fruit in the Loskop Dam Nature Reserve, South Africa. – *S. Afr. J. Zool.* 20: 136–146.
- 20 Higgins, P. J., Peter, J. M. and Steele, W. K. 2001. *Handbook of Australian, New Zealand and Antarctic birds. Volume 5: tyrant-flycatchers to chats*. – Oxford Univ. Press.
- Howe, H. F. and Primack, R. B. 1975. Differential seed dispersal by birds of the tree *Casearia nitida* (Flacourtiaceae). – *Biotropica* 7: 278–283.
- Howe, H. F. and Estabrook, G. F. 1977. On intraspecific competition for avian dispersers in tropical trees. – *Am. Nat.* 111: 817–832.
- Liddy, J. 1983. Dispersal of Australian mistletoes: the Cowiebank study. – In: Calder, M. and Bernhardt, P. (eds), *The biology of mistletoes*. Academic Press, pp. 101–116.
- 30 Mack, A. L. 1999. The Pesquet's or vulturine parrot – a species in need of study. *Psittascene* 11: 2–3.
- Martínez del Río, C., Hourdequin, M., Silva, A. and Medel, R. 1995. The influence of cactus size and previous infection on bird deposition of mistletoe seeds. – *Aust. J. Ecol.* 20: 571–576.
- 35 Martínez del Río, C., Silva, A., Medel, R. and Hourdequin, M. 1996. Seed dispersers as disease vectors: bird transmission of mistletoe seeds to plant hosts. – *Ecology* 77: 912–921.
- McKey, D. 1975. The ecology of coevolved seed dispersal systems. – In: Gilbert, L. E. and Raven, P. H. (eds), *Coevolution of animals and plants*. Univ. of Texas Press, pp. 159–191.
- 40 Murphy, S. R., Reid, N., Yan, Z. G. and Venable, W. N. 1993. Differential passage time of mistletoe fruits through the gut of honeyeaters and flowerpeckers – effects on seedling establishment. – *Oecologia* 93: 171–176.
- 45 Overton, J. M. 1994. Dispersal and infection in mistletoe meta-populations. – *J. Ecol.* 82: 711–723.
- Pizo, M. A., Silva, W. R., Galetti, M. and Laps, R. 2002. Frugivory in cotingas of the Atlantic Forest of southeast Brazil. – *Ararajuba* 10: 177–185.
- Rawsthorne, J. 2007. Constraints on the dispersal of parasitic plants: the role of frugivorous birds. – PhD thesis, Charles Sturt Univ., Thurgoona, Australia.
- 65 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.
- Reid, N. 1986. Pollination and seed dispersal of mistletoes (Loranthaceae) by birds in southern Australia. – In: Ford, H. A. and Paton, D. C. (eds), *The dynamic partnership: birds and plants in southern Australia*. Government Printer, SA, pp. 64–84.
- Reid, N. 1989. Dispersal of mistletoes by honeyeaters and flowerpeckers – components of seed dispersal quality. – *Ecology* 70: 137–145.
- 75 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.
- Reid, N. 1991. Coevolution of mistletoes and frugivorous birds. – *Aust. J. Ecol.* 16: 457–469.
- Restrepo, C., Sargent, S., Levey, D. J. and Watson, D. M. 2002. The role of vertebrates in the diversification of new world mistletoes. – In: Levey, D. J., Silva, W. R. and Galetti, M. (eds), *Seed dispersal and frugivory: ecology, evolution and conservation*. CAB International, pp. 83–98.
- 85 Richardson, K. C. and Wooller, R. D. 1988. The alimentary-tract of a specialist frugivore, the mistletoebird, *Dicaeum hirundinaceum*, in relation to its diet. – *Aust. J. Zool.* 36: 373–382.
- Rödl, T. and Ward, D. 2002. Host recognition in a desert mistletoe: early stages of development are influenced by substrate and host origin. – *Funct. Ecol.* 16: 128–134.
- 90 Walsberg, G. E. 1975. Digestive adaptations of *Phainopepla nitens* associated with the eating of mistletoe berries. – *Condor* 77: 169–174.
- Ward, M. J. and Paton, D. C. 2007. Predicting mistletoe seed shadow and patterns of seed rain from movements of the mistletoebird, *Dicaeum hirundinaceum*. – *Austral Ecol.* 32: 113–121.
- 95 Watson, D. M. 2004. Mistletoe – a unique constituent of canopies worldwide. – In: Loman, M. and Rinker, B. (eds), *Forest canopies*, 2nd ed. (fully revised). Academic Press, pp. 212–223.
- 100 Watson, D. M. 2011. *Mistletoes of southern Australia*. – CSIRO Publishing.
- Wheelwright, N. 1983. Fruits and the ecology of resplendent quetzals. – *Auk* 100: 286–301.
- Yan, Z. 1990. Host specificity of *Lysiana exocarpi* subsp., *exocarpi* and other mistletoes in southern South Australia. – *Aust. J. Bot.* 38: 475–486.
- 105
- 110
- 115
- 121