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Implications of movement patterns of a dietary generalist for mistletoe seed dispersal

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Abstract Mistletoes are dispersed primarily by frugivorous birds and have highly aggregated distributions at multiple scales. Mistletoe specialist frugivores have been found to intensify infections within infected hosts and stands, and this is considered the most likely mechanism underlying clumped mistletoe distributions at these scales. How these patchy infections first develop and whether seed dispersers also contribute to aggregated mistletoe distributions at landscape and regional scales have not been evaluated. Here we predict the mistletoe seed shadow of a dietary generalist (spiny-cheeked honeyeater *Acanthagenys rufogularis* Aves: Meliphagidae), by combining our observations of movements via radio telemetry with previous data on gut passage times to estimate seed dispersal curves for individual birds. There was considerable variation in movements and inferred seed dispersal between individuals, with non-breeding birds predicted to regularly transport *Amyema quandang* (Santalales: Loranthaceae) seeds up to 700 m; well beyond the boundaries of an existing mistletoe infection. As the first work to consider explicitly the distance component of mistletoe seed dispersal by dietary generalists, this study poses further questions about the relative seed dispersal roles of dietary generalists and mistletoe specialists. Moreover, our findings highlight considerable intraspecific variation in movement and foraging behaviour, suggesting gender and reproductive status of birds should be considered explicitly when quantifying seed dispersal services.

Key words: Acanthagenys, frugivore, honeyeater, mistletoe specialist, seed dispersal curve, seed shadow.

INTRODUCTION

Parasitic plants such as mistletoes are dependent on their hosts for part or all of their nutrition; their distributional range effectively constrained by occurrence of suitable host plants. Rather than being uniformly distributed within host populations, however, mistletoe distributions are highly aggregated and large areas of seemingly suitable habitat are mistletoe free (Watson 2009).

There are at least two plausible explanations for the realized distribution of mistletoe being less than the range of hosts. First, hosts may not be suitable – variations in host or site attributes, including nutrient and water availability (Watson 2009), host resistance to infection (Medel 2000) and indirect effects, such as frequency of fire (Jurskis *et al.* 2005) and density of herbivores (Norton *et al.* 1997), may limit the likelihood of mistletoe establishment or survival to maturity on some hosts or in particular areas, some or all of the time. Second, vector behaviour may limit mistletoe distributions – seed dispersers may not visit all areas of the landscape, or may not disperse mistletoe seeds while visiting, thereby limiting the realized distribution of mistletoe. It is the second of these possibilities, disperser limitation, which is the focus of this contribution.

The primary mechanism for seed dispersal of mistletoes in most systems is endozoochory by frugivorous birds (Reid 1991; Restrepo *et al.* 2002). Both mistletoe specialists, with specific behavioural and anatomical adaptations to mistletoe fruit consumption (e.g. *Phainopepla nitens* in North America, Walsberg 1975; *Dicaeum* spp. in southern Asia, Davidar 1983) and dietary generalists (e.g. *Sylvia atricapilla* in Europe, Snow & Snow 1988; *Philepitta castanea* in Madagascar, Rakotomanana 1998), may be effective seed dispersers (Godschalk 1983; Reid 1989; Carlo & Aukema 2005). While mistletoe specialists have evolved independently in seven lineages worldwide, including Dicaeidae, Ptilogonatidae, Fringillinae and Tyrannidae (Reid 1991; Restrepo *et al.* 2002; Watson 2004), there are ecosystems where generalists perform all seed dispersal duties (e.g. Europe, Snow & Snow 1988), and specialists and generalists often coexist (Reid 1989; Murphy *et al.* 1993; Carlo & Aukema 2005).

While frugivore behaviours that lead to contagious dispersal and aggregation of mistletoes within hosts and stands have been well studied (e.g. Reid 1989; Overton 1994; Martínez del Rio *et al.* 1995; Aukema & Martínez del Rio 2002a,b), little is known about

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how infections arise initially or how mistletoe is dispersed to distant stands (Restrepo *et al.* 2002). Are the same vectors involved and, if so, what behaviours underlie long-distance dispersal of seeds to vacant patches? Some mistletoes, notably the dwarf mistletoes (Arceuthobium: Viscaceae), achieve long-distance dispersal via seeds adhering to feathers and fur (Ostry & Nicholls 1979), but epizoochory is rare in other host/mistletoe systems (Watson 2001). In Australia, Keast (1958) presumed that the mistletoebird (*Dicaeum hirundinaceum*) is a long-distance disperser of mistletoe seed. However, rapid gut-passage time (average 14 min., Murphy *et al.* 1993) and a specialized diet predicated on the presence of mistletoe (Reid 1986) suggest this is unlikely. In South Africa, Godschalk (1983) discounted mistletoe specialists as long-distance dispersers and speculated that a dietary generalist bird, *Colius indicus*, was the main long-distance disperser of mistletoe seeds, while Carlo and Aukema (2005) suggested that generalist frugivores were the more likely vectors for new infections. Despite frequent supposition, however, the importance of dietary generalists as long-distance mistletoe dispersers has not been studied explicitly and their contribution to mistletoe distribution at multiple scales remains unknown.

As part of a broader research programme on mistletoe dispersal, we asked the question: do dietary generalists regularly disperse seeds beyond existing infections, thereby potentially establishing new infections? We measured the movements of individual dietary generalists (spiny-cheeked honeyeater *Acanthagenys rufogularis*; Meliphagidae) with radiotelemetry and combined resultant movement data with existing gut passage data (Murphy *et al.* 1993) to calculate seed dispersal curves. The predicted range of dispersed seeds suggests that dietary generalists regularly transport seeds beyond mistletoe infections, and indicates that they may make a disproportionate contribution to longer-distance dispersal and establishment of new mistletoe infections.

METHODS

Study sites and mistletoe species

The study was conducted in an agricultural landscape near Forbes in central NSW, Australia (33°40′S, 147°40′E) in the austral spring of 2006. Although Forbes has an annual average rainfall of 520 mm, fieldwork was conducted during a severe and prolonged drought, with no rain in the preceding 6 weeks and below-average rainfall for each of the preceding 6 years (Commonwealth Bureau of Meteorology, Melbourne). The site was a roadside stand (18.8 ha) of open *Acacia pendula* woodland uniformly infected with *Amyema quandang* (Santalales: Loranthaceae) (approximately 900 mistletoes per hectare; Rawsthorne 2007). It was a distinct patch of acacia woodland within a fragmented roadside network incorporating *Eucalyptus* spp., *Callitris endlicheri* and *Casuarina cristata*. Apart from roadside woodlands, most land in this region was cleared for production agriculture, although some nearby ridges contained woodland remnants (Rawsthorne 2007).

Amyema quandang was the only mistletoe detected within 1 km of the site, and represented the only fruit source of any kind located in or near the site during the study period (Rawsthorne 2007). This mistletoe parasitizes a variety of acacia hosts throughout temperate and arid south-eastern Australia (Reid 1986; Watson 2011) and it provides a gradually ripening year-round supply of 7–13 mm diameter fruits (Reid 1990), each containing a single seed 4–8 mm in diameter. Ripe *A. quandang* fruits were available in the study site for at least 2 months prior to radio tracking and were available throughout the study period.

Mistletoe dispersers

The seeds from all Australian mistletoes (apart from the aberrant *Nuytsia floribunda*) are bird-dispersed, predominantly by endozoochory. Dispersers are primarily from the families Meliphagidae, Dicaeidae and Oriolidae (Watson 2004), although many other birds consume mistletoe fruits and further effective dispersers may be identified (Reid 1986). In this study we focussed on one known disperser, the spiny-cheeked honeyeater, which was common in the site and regularly observed consuming mistletoe fruits and defecating intact seeds during the study period. This species has a varied diet including insects and other arthropods, fruit and nectar, and inhabits a range of habitats across arid and semi-arid Australia (Higgins *et al.* 2001). Mistletoe fruit is a seasonally important food source for this species (Keast 1968) and, although these birds have no specific anatomical adaptations to fruit consumption (Barea 2008), spiny-cheeked honeyeaters disperse viable mistletoe seeds via gut passage (Reid 1990; Murphy *et al.* 1993). In addition to spiny-cheeked honeyeaters, four other potential dispersers were present: two mistletoe specialists (painted honeyeater *Grantiella picta* and mistletoebird *Dicaeum hirundinaceum*; Richardson & Wooller 1988; Reid 1991; Barea & Herrera 2009); and two other dietary generalists (singing honeyeater *Lichenostomus virescens*, striped honeyeater *Plectorhyncha lanceolata*) that take mistletoe fruits as part of a broader diet (Barea 2008).

Movements of a dietary generalist – radiotelemetry

To determine the frequency, path-length and overall extent of spiny-cheeked honeyeater movements in the study system, eight birds were captured in mist nets and fitted with radio transmitters (Holohil LB-2N) and unique colour combinations of leg bands. Individual birds weighed at least 45 g, so the 0.38 g transmitters were about 0.8% of bird mass, well below the threshold of weight considered to affect bird movements (Cochran 1980). Transmitters were secured using a

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cotton leg harness and were glued to the harness knot with two-part epoxy (after Rappole & Tipton 1991).

Although this species does not exhibit sexual dimorphism, during banding and transmitter attachment, we noted that one bird of each of two territorial breeding pairs had a heavily vascularized brood patch and incubated, while the other bird of the pair had no brood patch and never incubated. Female-only incubation has been recorded in other meliphagids (Higgins *et al.* 2001), so this is not unexpected. We assigned all incubating birds or birds with well-vascularized brood patches to be female, and any birds that were obvious breeding partners of females so identified to be male.

Each bird was tracked after release for a minimum of 8 h in sessions of 1 h or more between 26 October and 3 November 2006, including at least 1 h during early morning, midday and late afternoon to incorporate diel variation in movements. During tracking periods, positional fixes were taken at least every 5 min and all movements to new trees within each 5-min period were recorded to generate complete movement paths. Positions of birds were determined by direct observation, recorded as the location of the trunk of the perch tree using a handheld GPS (Garmin-72) with a positional accuracy of at least 5 m. Where visual detection was not immediately possible, triangulation using hand-held 2- or 3-element Yagi antennae was used to narrow down the possible positions, which were then confirmed visually. Movement paths were mapped using the Animal Movement extension in ArcView (Hooge *et al.* 1999), and then overlaid on SPOT-5 satellite imagery (scene 383417, 21 January 2005). Rather than estimating home range size or other movement metrics, the objective of radiotelemetry was to identify heterogeneity in spatial occurrence and habitat use of the honeyeaters with respect to mistletoe occurrence. The extent of mistletoe occurrence within the study area was established by inspecting all host plants within the area, extending more than 2 km past the limits of the patch along each road, and all paddock trees in the surrounding cleared land were checked individually.

To estimate the range of movements for individual birds, minimum convex polygons were determined for each bird using the Animal Movement extension in ArcView (Hooge *et al.* 1999). The movement ranges in this study were determined using all radio-tracked positions for each bird, rather than just data points which can be considered independent from each other, and so were the largest possible minimum convex polygons for a given set of movement paths.

Estimation of seed dispersal curves

To infer the spatial distribution of mistletoe seeds dispersed by radio-tracked birds, a seed dispersal curve was estimated for each individual bird by combining gut passage time and bird movement data (after Murray 1988). Each resulting curve is a frequency distribution of predicted displacement of seeds from a typical point of origin in the form of a frequency histogram with seed displacement from origin on the *x*-axis (Murray 1988; Ward & Paton 2007). A distribution of bird displacement from the origin for each elapsed minute up to 90 min was estimated from movement data for each individual bird. This was achieved by determining a bird's displacement from a starting position within a movement path for each subsequent minute of that movement path, and then aggregating these data across many such 'initial' locations for each bird (after Murray 1988). A frequency distribution of gut passage times was determined by fitting a log-normal distribution to 435 observed gut passage times of *A. quandang* seeds in spiny-cheeked honeyeaters collected in a previous study (Murphy *et al.* 1993; Rawsthorne *et al.* 2009; Fig. 1). These two data sources were combined for each bird by randomly selecting an elapsed time from the gut passage time lognormal distribution and a movement distance from the empirical distribution of movements appropriate to that elapsed time. For each bird 1000 iterations were aggregated to predict a frequency distribution of potential displacements of seeds from a typical point of origin, that is, an estimated seed dispersal curve. This approach assumes that bird movements and defecations are independent of each other. We did not allow for any bias in the estimated seed shadow because of interdependence between gut passage and movement (e.g. a tendency for defecation prior to long flights).

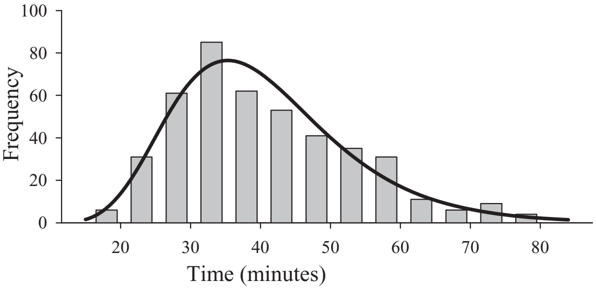

Fig. 1. Distribution of gut passage times in minutes for *Amyema quandang* mistletoe seeds consumed by spiny-cheeked honeyeater *Acanthagenys rufogularis*. Vertical bars are counts of 435 observed gut passage times from a previous study (Murphy *et al.* 1993) grouped into 5-min intervals; the curve is a smoothed frequency distribution fitted using a log-normal distribution parameterized using the observed data ($\mu = 3.658$, $\sigma = 0.3065$; $\chi^2 = 13.4$, $P > 0.25$) using the method described by Rawsthorne *et al.* (2009).

RESULTS

The eight tracked spiny-cheeked honeyeaters consisted of two incubating pairs (pair one: male BW, female RR, and pair two: male BB, female WW), one female with a vascularized brood patch but no nest or obvious partner (bird OW), and three other birds without obvious partners (birds RW, BR and OO). Individual birds were tracked for between 475 and 696 min (average 533 min) over periods of between three and eight consecutive days, with between three and eight movement paths per bird and movement path durations averaging 87 min. In total, 49 movement paths were recorded, spanning 4262 min of observation.

From systematic checking of all host plants (both in roadside stands and scattered paddock trees), the

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extent of mistletoe occurrence was established within the study area (Fig. 2). The infection patch extended about 1 km further north, and there was a mistletoe-free buffer of at least 1 km in all directions beyond this infected patch.

Movement paths (Fig. 2) and extent of movement determined by minimum convex polygon (Fig. 3) varied greatly between individuals. Some birds (e.g. bird BB) were restricted to small exclusive breeding territories wholly within the area of mistletoe infection, while others (e.g. bird BR) moved regularly from the mistletoe infected area to uninfected areas, where they were observed feeding on nectar and sallying for insects. All radio-tracked birds were observed feeding on mistletoe fruits.

Seed dispersal curves for the eight individuals (Fig. 3) varied between highly leptokurtic distributions (e.g. bird BB) and platykurtic distributions without a pronounced peak at the mean and a wide range of likely dispersal distances (e.g. bird BR). The mean inferred seed dispersal distance for individuals varied from 26 m to 377 m. The inferred probability of a seed being deposited within 50 m of source varied from 9% to 74% for different individuals. This difference between individuals was also evident in the longer-distance dispersal potential, with the inferred probability of dispersal of a seed beyond 200 m varying between individuals from 0% to 76%. The inferred probability of dispersal of a seed beyond 500 m was 0% for five individuals, but was as high as 42% for bird OO.

DISCUSSION

Our seed shadow results indicate that spiny-cheeked honeyeaters are capable of regularly transporting mistletoe seeds beyond existing mistletoe infections. The transit times between infected and mistletoe-free foraging areas were much shorter than the average gut passage time (approximately 40 min; Murphy *et al.* 1993), and our results predict that some individuals will regularly disperse mistletoe seeds up to 700 m, well beyond the boundaries of existing mistletoe infections.

Recorded movements and inferred seed dispersal distances varied considerably between individual birds. Rather than an idiosyncratic finding or an artefact of our methodology, this variation is consistent with previous work on the same plant–animal interactions, studied elsewhere. Reid (1984) conducted comprehensive research on spiny-cheeked honeyeaters in an *Acacia*/*Amyema quandang* system near Whyalla in South Australia, where individually marked birds maintained and defended exclusive territories ranging from 1 to 5 ha. During a severe drought, territories broke down and some individuals undertook movements to areas up to 4 km away (Reid 1984). While neither our data nor Reid's provide a large enough sample size to draw statistical conclusions, the finding that non-territorial birds have fundamentally different movement patterns (and hence seed dispersal patterns) to birds in fixed breeding territories is consistent between the two studies, and suggests that a consideration of life history stage and potential impacts on seed

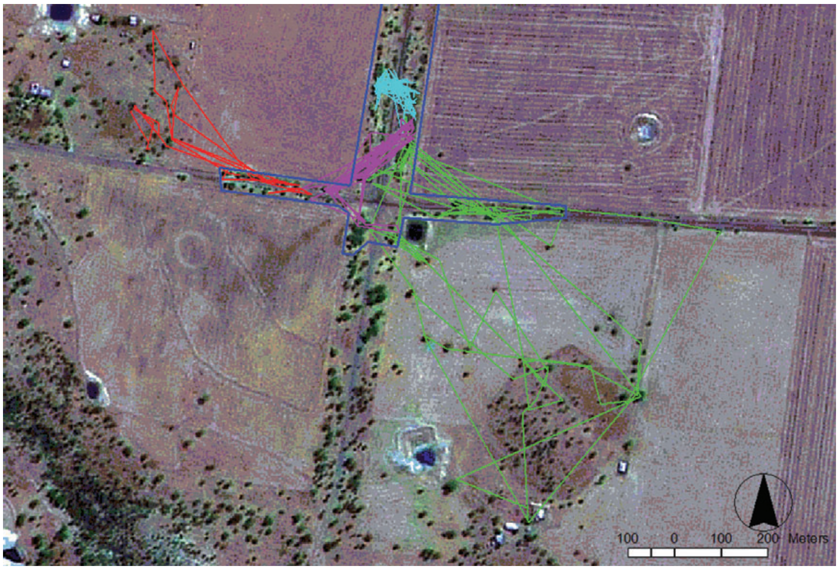

Fig. 2. Movement paths of four individual spiny-cheeked honeyeaters *Acanthagenys rufogularis* relative to a patch of acacia woodland infected with mistletoe near Forbes, south-eastern Australia. Paths shown are for bird BB (light blue lines, the male of a breeding pair); bird RR (purple lines, the female of a second breeding pair); bird BR (green lines, a non-breeding bird); and bird RW (red lines, a female with brood patch but no obvious partner, nest or young). The dark blue line indicates the southern extent of *A. quandang* infection on acacia hosts; the infection patch extended about 1 km further north, and there was a mistletoe-free buffer of at least 1 km in all directions beyond this infected patch.

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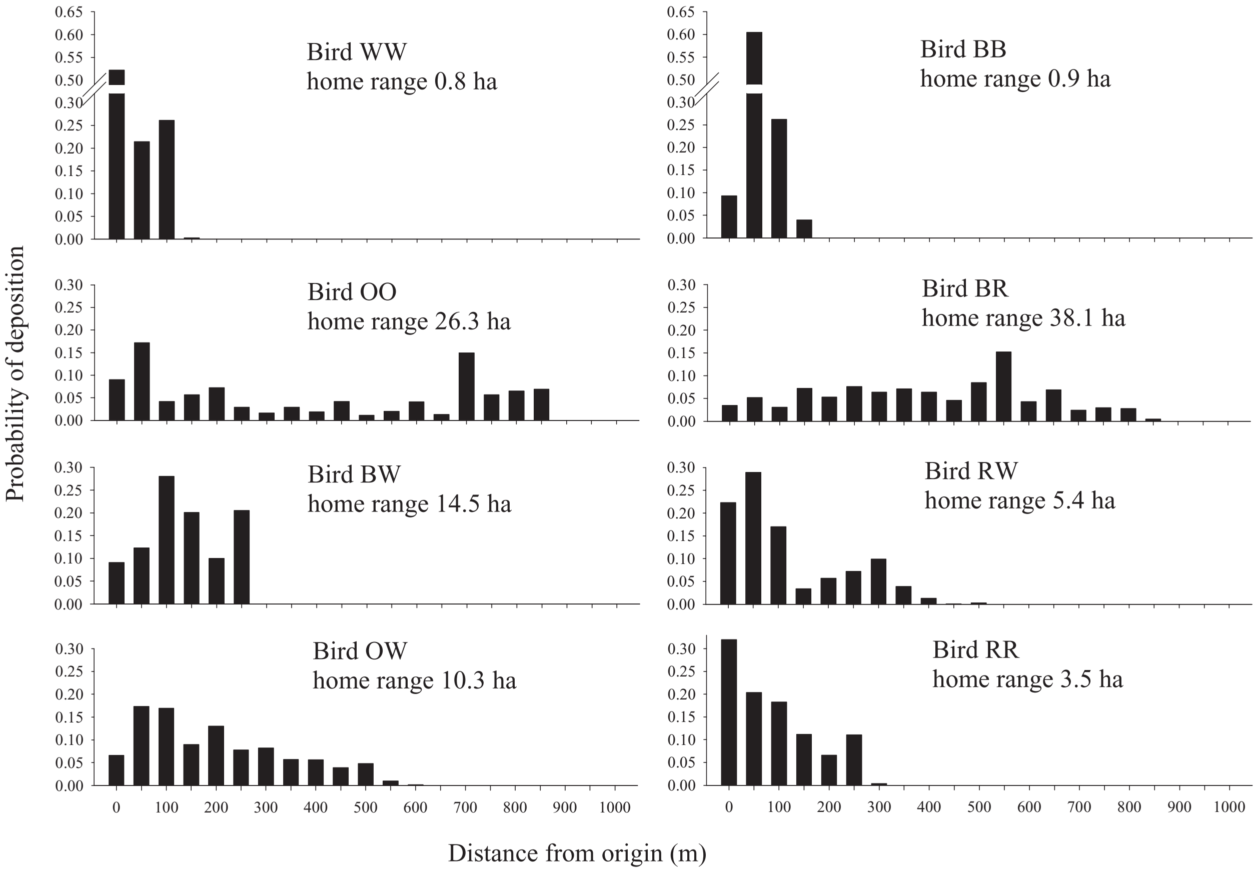

Fig. 3. Seed dispersal curves for eight individual spiny-cheeked honeyeaters *Acanthagenys rufogularis* showing the inferred probability of seed deposition at various distances from source. These curves were derived for each bird by combining the probability distributions for bird displacements from a generalized point of origin over time (drawn from radio telemetry data; Fig. 2) and a log-normal distribution of *Amyema quandang* mistletoe seed gut passage times determined based on data collected in a previous study (Murphy *et al.* 1993; Fig. 1). Also shown on labels are home range sizes for each bird, determined as the minimum convex polygon of all radio-tracked positions.

shadow may be relevant in studies of frugivory. Likewise, the marked differences in home range size between males and females for pairs in fixed territories merit further study. While researchers studying insectivorous birds have noted consistent differences in the foraging behaviours and diets of males and females (e.g. *Setophaga ruticilla*; Holmes *et al.* 1978), sex-based differences among frugivores have rarely been noted (but see Wheelwright 1983), and may provide another component of variation in seed dispersal.

While it may be intuitively apparent that dietary generalists – by the nature of their varied diet and hence movements which are less dependent on mistletoe – may transport mistletoe seeds beyond infections, this has not been measured previously, and opinions regarding the relative roles of generalists and specialists have differed among ornithologists. While our data do not compare specialists and generalists, previous work in a temperate Australian system (Ward & Paton 2007) showed that a mistletoe specialist (mistletoebird) had shorter inferred dispersal distances (15% of seeds transported beyond 200 m, 3% of seeds beyond 500 m) and a seed rain which was strongly associated with existing mistletoe occurrence. A direct comparison between movements of a specialist and a generalist at a single time and place may be definitive, but the comparison between our results and those of Ward and Paton supports the hypothesis of Godschalk (1983) and Carlo and Aukema (2005), that generalists are the more likely and effective long-distance dispersers of mistletoes.

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