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The Relative Contribution of Specialists and Generalists to Mistletoe Dispersal: Insights from a Neotropical Rain Forest

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ABSTRACT

Mistletoes rely on birds for seed dispersal, but the presumed importance of mistletoe-specialist frugivores has not been critically examined nor compared with generalist frugivores and opportunistic foragers. The contribution of these three groups was compared directly by quantifying bird visitation to fruiting mistletoe plants (*Oryctanthus occidentalis*: Loranthaceae) at Barro Colorado Island, Panama, and by comparing these results with proportions calculated from other empirical studies of mistletoe visitation conducted elsewhere. After more than 100 h of timed watches, 23 bird species were recorded visiting eight heavily infected host trees (*Luehea seemannii:* Tiliaceae). Eight of these species visited mistletoe, of which five (all tyrannids) consumed mistletoe fruit. Although two mistletoe specialist frugivores (*Tyrannulus elatus* and *Zimmerius vilissimus*) removed most fruit (73%), more than a quarter was consumed by one generalist frugivore (*Mionectes oleagineus*) and two opportunists (*Myiozetetes cayanensis* and *Myiozetetes similis*). Post consumption behaviour varied: the specialists flew from mistletoe to mistletoe, the generalist rested in the subcanopy and understory, and the opportunists spent most time hawking insects and resting high in the canopy. Integrating these data with previous work, the dietary specialization, short gut passage rate and strict habitat preferences of mistletoe specialists suggests that their services relate primarily to intensification and contagious dispersal, while species with broader diets are more likely to visit uninfected trees and establish new infections. The presumed importance of mistletoe-specialist frugivores was not supported and mistletoes are considered to be comparable to many other bird-dispersed plants, relying on both specialist and generalist frugivores, while opportunists may be disproportionately important in long-distance dispersal.

Key words: Barro Colorado Island; frugivory and seed dispersal; Loranthaceae; *Mionectes oleagineus*; *Miozetetes*; *Tyrannulus elatus*; *Zimmerius vilissimus.*

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Many plants rely on animals as seed vectors, exhibiting various strategies to attract seed dispersers and encourage their movement to favorable germination sites away from the parent plant while minimizing losses from seed predators and other natural enemies. The relative contribution of seed dispersers to plant recruitment can be considered in terms of four factors—frequency of visitation, number of seeds dispersed, quality of seed treatment and quality of seed deposition—these interacting determinants collectively defining seed disperser effectiveness (Schupp 1993, Schupp *et al.* 2010). This unifying concept emphasizes between-disperser differences and, although more inclusive than previous frameworks for studying endozoochorous seed dispersal (Howe & Estabrook 1977, Wheelwright & Orians 1982), its application relies on an understanding of disperser movements (*e.g.*, Rawsthorne *et al.* 2011), the effects of seed treatment on germinability (*e.g.*, Martìnez del Rio & Restrepo 1993), the defining attributes of safe sites for seedling establishment (Aukema 2004) and post-consumption behaviour of dispersers (*e.g.*, Aukema & Martìnez del Rio 2004). Even when these parameters are known, variation in post-deposition factors—including seed predation, dormancy and secondary dispersal—affect seed fate and eventual plant recruitment (Forget *et al.* 2002) making the individual importance of a specific seed disperser to the recruitment of a specific plant difficult to isolate and quantify.

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Mistletoes are a diverse group of parasitic plants with a suite of life history characteristics that makes them useful models to study seed dispersal: their seeds lack a testa and remain viable for a matter of days, germination rates are high and independent of microclimate and safe sites for establishment are readily defined by host range (Sargent 2000, Aukema & Martìnez del Rio 2004). Unlike most parasitic plants that attach to host roots below ground, mistletoes form permanent connections to the branches of their host (Mathiasen *et al.* 2008), a habit that makes mistletoes more reliant on directed dispersal than any other group of plants (Restrepo *et al.* 2002, Aukema 2004). Birds are the principal seed dispersers for most mistletoes, induced to transport their sticky seeds by the surrounding parenchymatous pulp (Watson 2001). Most research on mistletoe seed dispersal has focused on mistletoe specialist frugivores, a group of birds from eight families (Lybiidae, Tyrannidae, Cotingidae, Tityridae, Meliphagidae, Ptilogonatidae, Dicaeidae, Fringillidae) that rely on mistletoe fruit as their principal food source (Davidar 1983, Godschalk 1985, Reid 1991, Watson 2001, Rawsthorne *et al.* 2011). In addition to behavioral and anatomical adaptations to their restricted diet, many of these species feed mistletoe fruit to their nestlings, making them some of the most specialized of all vertebrate frugivores (Snow 1981, Rawsthorne *et al.* 2012).

Although these dietary specialists may account for the majority of mistletoe fruits consumed, their presumed importance as principal seed dispersers warrants further scrutiny. In Europe, North Africa, Madagascar, New Zealand, most of North America and all oceanic islands, mistletoe specialist frugivores are absent —mistletoe seeds are dispersed primarily by birds with broad diets (Watson 2004, Mathiasen *et al.* 2008). Even in regions with mistletoe specialists, many other birds consume mistletoe fruit and disperse their seeds (Reid 1989, López de Buen & Ornelas 2001, Guerra & Marini 2002). Indeed, some of these non-specialists may be more effective in dispersing seeds beyond existing infections, their broader diet necessitating regular movement to stands and habitats without mistletoe and their longer gut passage rates allowing longer-distance dispersal (Godschalk 1985, Rawsthorne *et al.* 2011). So, if successful dispersal is considered in terms of moving seeds to uninfected hosts (as in other host–parasite systems; Boulinier *et al.* 2001), the services provided by specialists may actually be less effective than birds with greater dietary breadth (Rawsthorne *et al.* 2012).

Two landmark studies of mistletoe dispersal in the Neotropics compared proportions of fruit consumed by specialist and non-specialist birds visiting different mistletoe species and considered components of dispersal services provided (Restrepo 1987, Sargent 1994). By quantifying movement and perching preferences relative to suitable sites for mistletoe establishment (at branch and tree scales), post-consumption behavior of specialists was demonstrated to lead to aggregation within already infected hosts (Sargent 1994). These studies documented two different mistletoe-specialist frugivore systems, with Euphonias (*Euphonia* spp; Fringillidae) specializing on viscaceous mistletoes, and various flycatchers (Tyrannidae) specialising on loranthaceous mistletoes (Sargent 2000, Restrepo *et al.* 2002). This work also distinguished two classes of non-specialist fruit consumers: generalist frugivores that regularly take mistletoe fruit as part of a broader diet dominated by fruit (hereafter, generalists), and insectivorous, nectarivorous, granivorous or omnivorous species that occasionally consume fruit, including mistletoe fruit (opportunists). While numerous subsequent studies have measured visitation rates of birds to mistletoe in various regions, the relative amount of fruit consumed by generalists and opportunists has rarely been considered, post consumption behavior remains largely unknown, and any differences in associated dispersal quality from the plants perspective remain unclear.

To complement and contextualize previous species-specific studies in temperate and arid systems (Barea & Watson 2007, Rawsthorne *et al.* 2011, 2012), I conducted an observational study of the complete assemblage of species visiting fruiting mistletoe plants in a tropical system. I compare the contribution of specialist, generalist and opportunist mistletoe fruit consumers to seed dispersal by quantifying visitation frequency and feeding rate. Integrating these findings with a critical re-evaluation of previous research on bird-mistletoe interactions, I consider the seed dispersal effectiveness of these three groups and determine whether specialist frugivores necessarily represent the most effective mistletoe dispersers.

METHODS

Study area.—With representatives from five of the eight avian families containing mistletoe specialist frugivores, Neotropical forests are the ideal system to address these questions (Restrepo *et al.* 2002, Watson 2004). This study was undertaken at the Smithsonian Tropical Research Institute's field research station on Barro Colorado Island in the canal zone of central Panama. Observations were collected during a 4 mo period in 2006 (7 September–18 December inclusive), timed to coincide with peak mistletoe fruiting during the mid–late wet season (after Leck 1972). Barro Colorado Island is a 1562 ha fragment of humid lowland evergreen forest isolated in 1914 when the Chagres River was dammed during construction of the Panama Canal. The island has been the focus of comprehensive ornithological and botanical research, with a rich assemblage of frugivores recorded, including two mistletoe specialist tyrannids and three *Euphonia* species (Robinson 2001). Further information about the history and biota, vegetation and fauna of the island are summarized by Leigh *et al.* (1996); for further information about the avifauna and its long-term dynamics, see Karr (1982) and Robinson (2001).

Study species.—As with many lowland rain forests, mistletoes are a diverse but easily overlooked component of the canopy (Nadkarni & Matelson 1989, Arruda *et al.* 2009). Croat (1978) recorded seven species (Viscaceae and Loranthaceae) from Barro Colorado Island but, during 5 mo of fieldwork including 400 h of systematic bird surveys from trails, canopy access towers and the surrounding waters (see Watson 2010), the only mistletoes observed were *Oryctanthus occidentalis* (Loranthaceae). Leck (1972) suggested that this species was the most abundant mistletoe on the island, found on a wide range of canopy trees and occasionally epiparasitic on other mistletoe species (Kuijt 1964). *Oryctanthus occidentalis* has abundant cylindrical fruit (approximately 4 × 2 mm) borne throughout the year on 30 mm long spikes projecting from leaf axils (Croat 1978). As mistletoe plants were observed primarily infecting mature *Luehea seemannii* (Tiliaceae) trees, a comprehensive survey of all *L. seemannii* trees visible from the shore (approx. 65 km) was undertaken, and the eight most heavily infected trees were selected for further study (from 385 trees, 105 of which were infected). The primary reason for selecting these trees was ease of observation, and I recognize that fringing vegetation around a man-made lake is not representative of lowland Neotropical rain forests generally. Finally, despite the wide range of species hosting this mistletoe, restricting this study to a single host lacking flesh fruit minimizes variation in visitation related to host characteristics (after Lara *et al.* 2009) and decreases the likelihood of frugivores being attracted to host trees for resources other than mistletoe fruit (see Carlo & Aukema 2005).

Quantifying visitation.—Fruit removal is one of the main components of seed dispersal and, by compiling visitation frequencies, foraging bout durations and feeding rates, different species were compared directly in terms of the proportion of fruit consumed (after Howe & Primack 1975, Restrepo *et al.* 2002). 100.5 h of observations (partitioned into 201 30-min timed watches) were conducted at eight infected trees, including one large tree at the edge of the laboratory clearing containing approximately 72 visible mistletoe clumps and seven other trees in the fringing vegetation around the northern and eastern sides of the island each hosting at least 20 visible mistletoe clumps (range 20–57). These trees were a minimum of 600 m distance from one-another to maximize independence. Observations were carried out from an adjacent balcony for the tree in the laboratory clearing and from a small boat anchored within 10 m of the shore for the seven other trees, using both vocalizations and plumage (magnified with 10 × 40 binoculars) to confirm identities of visiting birds. 100 h was deemed a sufficient sample size to compare patterns of fruit consumption by different bird species, while still being a relatively modest survey effort to facilitate comparable studies of mistletoe visitation in other habitats/regions. Watches commenced no earlier than one hour after dawn and no later than one hour before dusk. The study period coincided with the wet season so occasional showers occurred during watches but data were not recorded during heavy rain. Ten additional watches were conducted at night to determine whether any nocturnal animals visited mistletoe plants, and several motion-triggered cameras with infra-red flashes were deployed on the balcony immediately facing the large host tree at the edge of the laboratory clearing.

During each 30-min watch, all species visiting the host tree were noted, as were visits to mistletoe clumps not associated with fruit consumption to identify potential agents of dispersal by epizoochory (mistletoe seeds have been recorded adhering to plumage and pelage of non-feeding visitors to fruiting clumps, see Punter & Gilbert 1989 and references therein). If mistletoe fruits were consumed, the following data were recorded: bird species, duration of foraging bout (including time spent actively foraging for fruit and moving from one mistletoe clump to another) and the number of individual mistletoe clumps visited before leaving the host tree. When an individual bird that was continuously feeding on mistletoe fruit remained clearly in view, the number of fruits being consumed and the overall duration of the feeding bout (in seconds) was noted and used to estimate feeding rate (mean number of fruits consumed per minute; after Restrepo 1987). Even with multiple trees widely distributed from one another, repeat visits by the same individual birds are likely, meaning some observations are not independent of one another (see Sargent 1994). Accordingly, quantitative comparisons of mean foraging bout durations, feeding rates and other statistical analyses are not warranted, these data better considered in qualitative terms by calculating overall proportions of fruit consumed by each species/group of species. Species were classified as mistletoe specialists, generalist frugivores or opportunists using previous dietary studies (summarized in Table 1) and proportions calculated as the product of mean feeding rate and the sum of all foraging bouts observed during the entire 100.5 h of formal observation.

TABLE 1. *Summary of the five species observed consuming mistletoe fruit during 201 30-min watches of eight heavily infected host trees on Barro Colorado Island, Panama. For foraging bouts per hour, number of clumps visited per foraging bout, foraging bout duration and feeding rate per minute, means and ranges are provided. Except for feeding rate per minute (for which sample sizes are given beside the main), sample sizes are the total number of foraging bouts recorded for each species. Foraging bouts per hour was calculated by doubling the number of foraging bouts recorded per 30 min watch and estimates frequency of visitation when present (*i.e., *not over the entire 100.5 h of formal observations). Body mass data from Dunning (1993); dietary information from Stiles & Skutch 1989, Westcott & Graham 2000, Dyrcz & Flinks 2003, Sargent 1994.*

	'Specialists'		'Generalist'	'Opportunists'	
Common name	Yellow-crowned Tyrannulet	Paltry Tyrannulet	Ochre-bellied Flycatcher	Rusty-margined Flycatcher	Social Flycatcher
Linnean name	*Tyrannulus elatus*	*Zimmerius vilissimus*	*Mionectes oleagineus*	*Myiozetetes cayanensis*	*Myiozetetes similis*
Body mass	7.8 g	9.7 g	12.1 g	25.9 g	28 g
Diet	Primarily mistletoe fruit, other small berries, insects	Primarily mistletoe fruit, other small berries, insects	Primarily fruit (small berries) and insects	Primarily insects; fruit, arillate seeds	Primarily insects, fruit, arillate seeds
No. foraging bouts	312	54	88	6	20
Foraging bouts per hour	7.5 (2–32)	3.3 (2–8)	7.7 (2–22)	2.5 (2–4)	3.8 (2–10)
Number of. clumps per foraging bout	2.6 (1–10)	2.6 (1–8)	2.7 (1–7)	1.6 (1–2)	3.2 (1–6)
Foraging bout duration (s)	61.5 (10–270)	66.6 (15–278)	89 (10–456)	53.3 (20–100)	102 (15–290)
Feed rate per minute	10.3 (16) (2–46)	9.4 (2) (7–12)	7.2 (12) (3–12)	8.6 (5) (3–19)	7.4 (4) (5–10)
Prop. fruit consumed	62%	11%	20.4%	1%	5.6%

To evaluate the generality of emergent findings, I conducted a thorough review of previous studies of bird-mistletoe interactions (published in English during the last 40 yr), focusing on studies of Loranthaceous species, but including selected studies of mistletoes in other families for comparison. Only those studies recording data for all species visiting fruiting mistletoes and based on a minimum of 50 h of observations were used to calculate proportions of fruits consumed. If feeding rates were not provided, consumption was estimated based on feeding bout duration, with birds classified as specialists, generalists or opportunists based on empirical data presented in the original study.

RESULTS

During 100.5 h of formal observation of eight *L. seemannii* trees, eight species of birds were recorded visiting mistletoe clumps, of which five species consumed fruit; two mistletoe specialists (Yellow-crowned Tyrannulet *Tyrannulus elatus*, Paltry Tyrannulet *Zimmerius vilissimus*); one generalist frugivore (Ochre-bellied Flycatcher *Mionectes oleagineus*); and two opportunists (Rusty-margined Flycatcher *Myiozetetes cayanensis* and Social Flycatcher *Myiozetetes similis*)—visitation data and sources of dietary information for these flycatchers (Tyrannidae) are summarized in Table 1 (names follow American Ornithologists' Union 1998). The two opportunists accounted for the fewest number of visits and, although all records of mistletoe fruit consumption were restricted to the large tree in the laboratory clearing during early September, both species frequently visited the other seven focal trees throughout the study period. The two opportunists exhibited different feeding behavior, with Social Flycatchers having longer foraging bouts (mean of 102 sec compared with 53 sec) and visiting more mistletoe clumps per bout (3.2 compared to 1.6) than congeneric Rusty-margined Flycatchers. Both birds exhibited similar foraging techniques, alighting on the host branch near the haustorial connection with the mistletoe and systematically picking off individual fruit from the projecting axillary spikes.

Of the two specialists, the Yellow-crowned Tyrannulet accounted for many more records than the Paltry Tyrannulet, in terms of both total number of visits (312 vs. 54) and number of watches in which it was recorded visiting mistletoe clumps (96 vs. 33). The two species were similar in the duration of feeding bouts (61 vs. 67 sec), feeding rate (10 vs. 9 fruits per min) and number of clumps visited per foraging bout (both 2.6; Table 1), but differed in the frequency of visits (mean of 7.5 per h vs. 3.3). All foraging observations of both species were within mistletoe clumps and the birds were very regular in their movements: consistently coming from one direction, moving through the host tree from one mistletoe to the next, then flying off in the opposite direction (recalling the 'trap-lining' strategy of many hummingbirds). As well as consuming fruits, Yellow-crowned Tyrannulets appeared to 'check' the ripeness of fruit, frequently squeezing berries but not removing them from the axillary spikes. Between foraging bouts, both tyrannulets perched on narrow branches (of both host trees and mistletoe plants, but not adjacent trees), periodically regurgitating mistletoe seeds in groups of three or four, occasionally wiping their bill to remove adhering seeds.

The sole generalist frugivore (Ochre-bellied Flycatcher *Mionectes oleagineus*) was observed undertaking 88 foraging bouts during 25 timed watches. It spent longer foraging for mistletoe fruits than the two specialists (mean of 89 sec per feeding bout) and had a lower feeding rate (mean of 7.2 fruits per min) but visited a comparable number of clumps per bout (mean of 2.7; Table 1).

The two specialists and single generalist did not show any marked diel variation in visitation, with records coming from all parts of the day. Rather than comparing these mean feeding rates or visitation frequencies directly, the raw numbers were combined to allow their relative consumption of fruit to be compared. By multiplying the feeding rate by the total time observed foraging for mistletoe fruit, the relative importance of these five species can be estimated in terms of number of fruits removed (absolute numbers converted to proportions; Table 1). The two specialists accounted for 73 percent of fruit removed, with 20 percent taken by the generalist Ochre-bellied Flycatcher and the remaining 7 percent by the two opportunists (Table 2).

The three other species observed visiting mistletoe clumps were insectivores, foraging for insects within host foliage and moving into mistletoe foliage but not consuming mistletoe fruit. Slaty-tailed Trogons *Trogon massena* were recorded visiting the host tree during seven 30-min watches, plus one additional record in which a bird flew from the host tree into one of the mistletoe clumps to snatch a large phasmid. Chestnut-sided Warblers *Dendroica pensylvanica* were recorded during two consecutive watches, on both occasions gleaning from the foliage of both host tree and mistletoe. Common Tody-Flycatchers *Todirostrum cinereum* were recorded visiting focal trees during 11 separate watches, seven of which included visits to mistletoe clumps. Both the Tody-flycatcher and Warbler appeared to be foraging intentionally within mistletoe foliage, with individual birds observed systematically searching for small insects in mistletoe foliage, flying from one mistletoe clump directly to another. No birds visited mistletoe clumps during 78 of the 201 watches, typically associated with sudden showers or high wind. 15 other species used the trees as foraging substrates or perches but were not observed visiting mistletoe clumps (see Table S1) and no nocturnal animals were observed visiting mistletoe clumps, either during the 5 h of observation or detected using motion-triggered infra-red cameras.

To contextualize these findings, proportions of mistletoe fruit removed by specialists, generalists and opportunists were calculated from four previous studies involving six other species of loranthaceous mistletoe, eight species of viscaceous mistletoes and *Antidaphne viscoidea* from the Santalaceae (ex Eremolepidaceae; Der & Nickrent 2008). With the exception of *Cladocolea lenticellata* and *Struthanthus concinnus*, in which the great majority of fruit were consumed by generalist frugivores (83% and 97.5%, respectively), the four other loranthaceous species exhibited similar patterns to that data presented herein, with 60–80 percent of fruit consumed by specialists, 11–18 percent by generalists and 9–22 percent by opportunists (Table 2). Proportions for Viscaceous species were quite different. Excepting *Phoradendron robustissimum* and *Viscum*

TABLE 2. *Proportion of mistletoe fruit consumed by mistletoe specialist frugivores, generalist frugivores, and occasional fruit eaters that consume mistletoe fruit opportunistically, derived from previous studies of bird visitation to mistletoe plants. The horizontal divisions distinguish those findings reported herein from previous studies of mistletoe in the Loranthaceae, Viscaceae and Santalaceae (from top to bottom). Using mean feeding rates of birds feeding in high density hosts for Sargent's (1994) data, assuming Euphonia luteicapilla has comparable feeding rate to the congeneric E. elegantissima. For Restrepo's (1987) data, the only specialist member of the genus is E. laniirostris: the other two species and both Chlorophonia species are considered generalist frugivores (after Restrepo 1987). Mistletoe nomenclature follows Restrepo* et al. *2002.*

Mistletoe species	Specialists (%)	Generalists (%)	Opportunists (%)	Source
Oryctanthus occidentalis	73	20	7	This study
Cladocolea lenticellata	17	83	0	Restrepo 1987,
*Struthanthus concinnus***	0	97.5	2.5	Guerra & Marini 2002,
*Struthanthus oerstedii**	60.0	18	22	Sargent 1994,
*Oryctanthus spicatus**	71	14	15	Sargent 1994,
*Tapinanthus leendertziae**	64	15	20	Godschalk 1983,
*Tapinanthus natalitius**	80	11	9	Godschalk 1983,
Phoradendron robustissimum	60	40	0	Sargent 1994,
Phoradendon chrysocladon	34	66	0	Sargent 1994,
Phoradendron robaloense	21	79	0	Sargent 1994,
Phoradendron corynarthrum	0	100	0	Sargent 1994,
Phoradendron colombianum	0	100	0	Restrepo 1987,
*Phoradendron inaequidentatum**	11	89	0	Restrepo 1987,
*Antidaphne viscoidea**	93	7	0	Sargent 1994,
*Antidaphne viscoidea**	56	0	44	Restrepo 1987

*Estimated from visitation rate alone, except for *P. inaequidentatum* and *A. viscoidea* (Restrepo 1987) where proportions calculated from visitation frequency and foraging bout duration.

**Note that for Guerra and Marini's (2002) *Struthanthus concinnus* data, no specialists were recorded visiting the plants (*Phaeomyias murina* was scored as a generalist but further autecological work may demonstrate this poorly-known species is better considered a mistletoe specialist).

combreticola where specialists were the dominant consumers (60% and 94%, respectively), generalists were the dominant consumers for six mistletoe species, taking 100 percent for three species. Interestingly only one mistletoe species in this family had fruits consumed by opportunists (*Parus niger* an occasional consumer of *V. combreticola* fruit in South Africa; Table 2). Finally, proportions from the two studies of *A. viscoidea* were surprisingly different—while *Zimmerius* spp. flycatchers were the sole specialists in both studies, the proportion of fruit removed was 93 percent in Costa Rica compared with 56 percent in Colombia, with the remaining 44 percent consumed by the opportunistic granivore *Carduelis xanthogastra* (Table 2).

DISCUSSION

The observations from Barro Colorado Island indicated that mistletoe specialist frugivores consumed the majority of mistletoe fruit, though more than a quarter of all fruit removed was taken by non-specialists with broader diets. In addition to evaluating the different roles of specialists, generalists and opportunists, a fourth group (insectivores that forage within mistletoe clumps) was identified as occasional mistletoe dispersers. These findings indicate that the importance of mistletoe specialists as seed dispersers varies considerably, and may not be as great or uniform as assumed.

GENERALISTS VERSUS SPECIALISTS.—The sole generalist frugivore recorded consuming mistletoe fruit—the Ochre-bellied Flycatcher—removed an estimated 20 percent of all mistletoe fruits; almost twice the contribution of one of the specialists. Ochre-bellied flycatchers have been recorded taking a wide range of small fruits supplemented by spiders gleaned from beneath leaves (Westcott & Graham 2000 and references therein). Gut-passage times range from 13 to 26 min depending on the plant being consumed. Movement data derived from radio-tracked individuals found median distance moved in single flights of 64 m, but most flights were short distances (modal distance of 26 m; Westcott & Graham 2000).

This information, coupled with the bird's behavior of sitting for extended periods in heavily shaded perches within the subcanopy and understory (Westcott & Smith 1994), suggests that the Ochre-bellied Flycatcher offers a low quality dispersal service for mistletoes, comparable with congeners *Mionectes olivaceus* and *M. striaticollis* (Wheelwright *et al.* 1984, Restrepo 1987, Restrepo *et al.* 2002). Lacking a testa, mistletoe seeds are photosynthetically active, and need to be deposited in well-lit sites for successful establishment (Watson 2001, Mathiasen *et al.* 2008). While this may occasionally occur if seeds are voided during flight, all observations during this study related to seeds being regurgitated then wiped on shaded branches of the host tree, mistletoe or, more rarely, adjacent trees. A generalist frugivore is unlikely to be an important disperser, as there is a low likelihood of moving seeds to suitable safe sites on uninfected trees. Indeed, if fruit were limiting, this species may have a detrimental impact on mistletoe recruitment by competing with other birds offering higher quality dispersal services.

The Yellow-crowned Tyrannulet was the more frequently recorded mistletoe specialist. This study adds to previous observations (Leck 1972, Davidar 1987, Hosner 2005) and supports designating this monotypic genus as a mistletoe specialist frugivore (*contra* Gotelli & Graves 1990, Reid 1991). The Paltry Tyrannulet had similar behavior, visiting clumps both singly and in pairs, and regurgitating seeds upon narrow branches (Table 1). These findings concur with previous work (Leck 1972, Davidar 1987, Restrepo *et al.* 2002) and are consistent with Sargent's (1994) estimate that it derives more than 80 percent of its nutrition from mistletoe fruit (justifying the alternative English name of Mistletoe Tyrannulet).

In terms of dispersal quality, this study reinforces the view that the narrow diet of mistletoe specialists might decrease the quality of dispersal services (Rawsthorne *et al.* 2012): by moving from mistletoe clump to mistletoe clump, these birds offer little opportunity to disperse seeds to uninfected hosts or stands, but rather promote aggregation of mistletoes within and among trees (Aukema 2004, Rist *et al.* 2011). Seeds might occasionally be voided during flight (as with Ochre-bellied Flycatchers), but this is unlikely to result in seedling establishment. Such restricted seed dispersal could increase the parasite load of infected hosts, lowering individual fitness of parasite and host (Rawsthorne *et al.* 2012).

To evaluate the generality of the relative roles of specialists and generalists in dispersing Neotropical mistletoes, direct comparisons can be made with three studies that measured visitation to four mistletoe species (Table 2). Specialists accounted for 17, 0, 60 and 71 percent of fruit removed, with generalists removing 83, 97.5, 18 and 14 percent. While the results for *S. oerstedii* and *O. spicatus* were strikingly congruent with this study, the other two species differed markedly, the great majority of their fruits removed by generalists. For *Cladocolea lenticellata*, most visits (48 of 74) were by the Streak-necked Flycatcher *Mionectes striaticollis*, a generalist frugivore with a variable fraction of insects in its diet (two studies of foraging behaviour behavior found 42 and 6 percent of foraging records related to insects: Remsen 1985, Greeney *et al.* 2006, respectively). For *S. concinnus* in Southeastern Brazil, three generalist frugivores were responsible for removing most of the fruit: Swallow Tanager *Tersina viridis* (26%), Pin-tailed Manakin *Ilicura militaris* (21%) and Grey-eyed Greenlet *Hylophilus amauricephalus* (28%). No known mistletoe specialists were detected by Guerra and Marini (2002), but preliminary dietary data presented on the poorly known Mouse-coloured Tyrannulet *Phaeomyias murina* (which accounted for 10% of all fruit removed) indicate that this species may represent another mistletoe specialist tyrannid (see also Fitzpatrick 1980).

Two studies also included mistletoes from other families, but these plants are quite different to mistletoes in the Loranthaceae (in both ecological and evolutionary terms), their consistently smaller fruits often attracting a complementary set of frugivores (Godschalk 1983, Restrepo *et al.* 2002). Principal dispersers for Viscaceae mistletoes in the Neotropics are the morphologically uniform group of Cardueline finches in the genus *Euphonia*—a group often considered to be uniformly mistletoe specialist frugivores, though several species have a wider diet and are better considered generalist frugivores (Sargent 2000). While a specialist accounted for most fruit removed for one species (*Euphonia elegantissima* for *Phoradendron robustissimum*), generalist frugivores were more important for the other five species, in two cases accounting for all fruits consumed.

This marked difference between mistletoe families are consistent with Howe and Estabrook's (1977) predictions for high and low 'investment systems', whereby specialists are the dominant dispersers of large fruited Loranthaceae and generalists account for the majority of small fruits removed from Viscacaceae mistletoes. Switching to completely different avifauna, Godschalk's work in South Africa reported 64 and 80 percent of all visits to two *Tapinanthus* species (Loranthaceae) were by the specialist *Pogoniulus chrysoconus*, indicating that the non-exclusive role of mistletoe specialists is not purely a Neotropical phenomenon (see also Rawsthorne *et al.* 2011, 2012).

In terms of overall patterns, generalists exhibited the greatest variation—dominating estimated fruit consumption when specialists were absent, but not necessarily playing a subordinate role in the presence of specialists. Thus, some species like Grey-eyed Greenlet and Streak-necked Flycatcher may specialize on mistletoe seasonally (often defending infected hosts), while others such as Hepatic Tanager *Piranga flava* and Ruddy Pigeon *Patagioenas subvinacea* are more mobile species that eat mistletoe fruit as part of a wider diet. In terms of post-consumption behavior, specialists are more likely to perch in infected trees, but are no more likely to perch in suitable host plants (Sargent 1994, but see Calder 1983). Hence, neither group of birds necessarily offers superior seed dispersal services—what happens after removing the fruit is more important than dietary breadth. In systems where generalists dominate, visitation, consumption and eventual dispersal would be lower when other fleshy fruits are available (Snow & Snow 1988). If specialists predominate, there is a lower likelihood of seeds reaching uninfected hosts and increasing risk of small mistletoe populations becoming locally extinct, as specialists move elsewhere and the remaining mistletoes are dependent on a small number of progressively less vigorous hosts.

THE NEGLECTED ROLE OF OPPORTUNISTS AND NON-FEEDING VISITORS.—Despite accounting for 7 percent of the fruit removed in the Barro Colorado Island dataset, the post-consumption behavior of the two opportunists makes successful dispersal more likely. The foraging ecology of both species has been studied previously, their predominantly insectivorous diet complemented with a wide range of fruit and seeds, representing 34.3 percent of items in faeces for Rusty-margined Flycatcher, 22 percent for Social Flycatcher (data from Barro Colorado Island; Dyrcz & Flinks 2003). Between foraging bouts, both species routinely perched on exposed branches atop trees beside clearings and in vegetation fringing the island (both infected and infected trees), using these perches to regurgitate seeds and hawk for flying insects. Hence, although long distance dispersal is unlikely, both species probably disperse mistletoe seed to uninfected trees nearby, a form of contagious dispersal usually ascribed to mistletoe specialist frugivores (Aukema & Martínez del Rio 2004).

Examining other studies of mistletoe visitation, opportunists accounted for up to 22 percent of visits to the six other species of Loranthaceae, represented primarily by small insectivores. Generally considered fruit predation rather than seed dispersal, post consumption behavior was rarely noted, many species were observed regurgitating seeds once the fleshy pulp had been removed, generally considered to be more likely to achieve successful dispersal than defecation (Godschalk 1983, Roxburgh 2007). Interestingly, opportunists were not observed visiting any of the six Viscaceae mistletoes, which may be due to the smaller size and lower nutritional value of their fruits compared with Loranthaceae species (Godschalk 1983). The highest value relates to Restrepo's (1987) data for *A. viscoidea* (Santalaceae) in Colombia: 44 percent of visits to fruiting plants were by an opportunistic granivore (Yellow-bellied Siskin *Carduelis xanthogastra*). Although not necessarily representative, this value illustrates the potential role of opportunists as effective dispersers of mistletoe, expanding the list of potential vectors to include a wide range of non-frugivorous taxa (Watson 2001).

As with opportunists, few studies of mistletoe-bird interactions have considered species visiting mistletoe clumps while foraging for resources other than fruit or nectar. Rather than merely a subset of the canopy, foliage-gleaning insectivores may actively choose to forage in mistletoe (Turner 1991, Watson 2001), and mistletoe clumps have been found to support high abundances of favored prey including Lepidoptera larvae (Anderson & Braby 2009) and spiders (Burns *et al.* 2011). Although these insectivorous birds rarely, if ever, consume mistletoe fruit, this need not occur to effect successful dispersal—birds may inadvertently act as seed dispersers when the sticky seeds adhere to their feathers (epizoochory). Although best known in the dwarf mistletoes (Arceuthobium: Viscaceae; Punter & Gilbert 1989, Hawksworth & Wiens 1996), this mode of dispersal has been reported for other mistletoe groups (Liddy 1983), and allows seeds to be dispersed far greater distances than via internal dispersal. This mode of dispersal is presumed to be the process that led to initial mistletoe colonization of remote oceanic islands (Restrepo *et al.* 2002), and occasional dispersal of mistletoes well beyond their distributional range (Kuijt 1963, Watson 2011).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *Other species recorded visiting the eight focal trees, but not visiting mistletoes.*

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