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A simple method to collect viable rainforest tree seeds and study the frugivorous diet of satin bowerbirds (*Ptilonorhynchus violaceus*)

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Abstract: For more than 100 years, behavioural biologists have extensively studied satin bowerbirds (*Ptilonorhynchus violaceus*) to understand the complexities of bower construction and courtship, but this research has not accounted for the ecologically important role the species plays as a seed disperser in eastern Australia. In this study, we have used a simple method involving pans of water and mirrors to collect scats from male satin bowerbirds on the Dorrigo Plateau of northeastern New South Wales. Based on seeds identified from scats collected using this method, we identify the fruits of 37 plant species in 22 families that are eaten by satin bowerbirds and show that 35 of these species germinated after passage through the digestive system of bowerbirds. This method was developed for bush regenerators to collect rainforest tree seeds that are otherwise inaccessible and/or difficult to germinate; it is applicable throughout the range of satin bowerbirds. We hope the method will be adopted by bush regenerators for harvesting seeds otherwise difficult to source, and by ornithologists studying the diets and seed dispersal of these ecologically significant birds.

Keywords: Avian seed dispersal, frugivore, rainforest trees, bowerbirds, bush regeneration

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Introduction and Methods

Bowerbirds are only found in Australia and New Guinea, and for more than a century, they have been the subject of many studies of sexual selection (Darwin, 1888; Chisholm, 1924; Gilliard, 1969; Borgia, 1986, 1995; Frith & Frith, 2004; Hansell, 2007). Most species feed heavily on fruit and other plant material (leaves, flowers and/or buds) and will also include insects in their diet (Gilliard, 1969; Pruett-Jones & Pruett-Jones 1982; Pratt & Stiles, 1983; Diamond, 1986; Moore, 1991; Frith, 1995; Eddie, 2001; Borgia & Keagy 2006; Frith & Frith, 2016). These species may in turn be acting as seed dispersers. Some bowerbirds also incidentally disperse and/or cultivate plants or fungi that they use as bower decorations (Madden et al., 2012; Elliott & Marshall, 2016; Elliott et al., 2019).

Satin bowerbirds (*Ptilonorhynchus violaceus*) have a nearly 3,000 km range from northern Queensland to southern Victoria, and are among the most common, adaptable and best studied bowerbird species (Gilliard, 1969). They are noted to steal fruit from orchards, as well as eat a diversity of insects, wild fruits and leaves (Cole, 1910; Marshall, 1932; Chaffer, 1945; Gilliard, 1969; Diamond, 1986; Green, 1993). Despite their large range and abundance, there has been limited research into their diets, their role as seed dispersers, what species they actually ingest and whether or not the seeds of these species remain viable. Apart from a study reporting 11 fruit species eaten by satin bowerbirds in and around Lamington and Border Ranges National Parks in northeastern NSW (Green, 1993) and the chance observations by Marshall (1932) of satin bowerbirds eating four fruit species in the Sydney region, we were unable to locate previous research that directly studied the diversity of species eaten and/or tested the viability of seeds post-ingestion.

The objective of this study was to find a practical way to collect viable rainforest tree seeds for bush regeneration efforts; it was not designed as an ecological study, but it represents two decades of careful observation of satin bowerbirds and experimentation with methods of seed collection by the first author. Through trial and error, it became apparent that the technique we outline is simple yet highly effective for seed collection and provides data that we hope will be useful to bush regenerators, botanists and ecologists. We think this method could also be used more systematically by ornithologists to study the ecological significance of frugivory by satin bowerbirds and their role in seed dispersal.

To collect scats for this study, shallow tubs containing 30-100 mm water were placed at the edges of small clearings adjacent to undisturbed subtropical rainforest in areas known to be visited by satin bowerbirds (Figure 1). Two sites were used for this study; both were located on private property off of Blue Rock Road and Chaelundi Road near Dundurrabin, NSW. These areas were known to be used by bowerbirds but were not necessarily close to bowers or nest sites. For approximately 20 years, two tubs were put out at two different locations and left to collect scats during the spring, summer and autumn fruiting periods. A handheld or vanity mirror was placed vertically at one end of each tub of water (approximately 200 mm away from the edge of the tub). We observed male satin bowerbirds regularly visiting these stations, perching and 'dancing' in front of the mirror and depositing scats in the water in the process. Scats were removed from the tubs of water within three days of being deposited by birds. The scats were identified as bowerbird scats by close observation of which birds were visiting these stations. It is important to point out that this approach only attracts mature and nearly mature male satin bowerbirds (Figure 1). It is much harder to attract females or juvenile males, but they are more likely to visit a baited location. An effective way to collect their scats is to lay a flat piece of cardboard down (to make it easier to find scats) and stake an apple in the middle. The bowerbird will eat the apple and deposit scats on the cardboard while it eats, but the scats dry out quickly and this set-up has to be checked more regularly than using a tub of water. The data in this study is based on male satin bowerbirds. Though we have frequently observed satin bowerbirds foraging in mixed sex flocks and suspect that females and juvenile males are equally important seed dispersers, we do not have scat data to support this hypothesis.

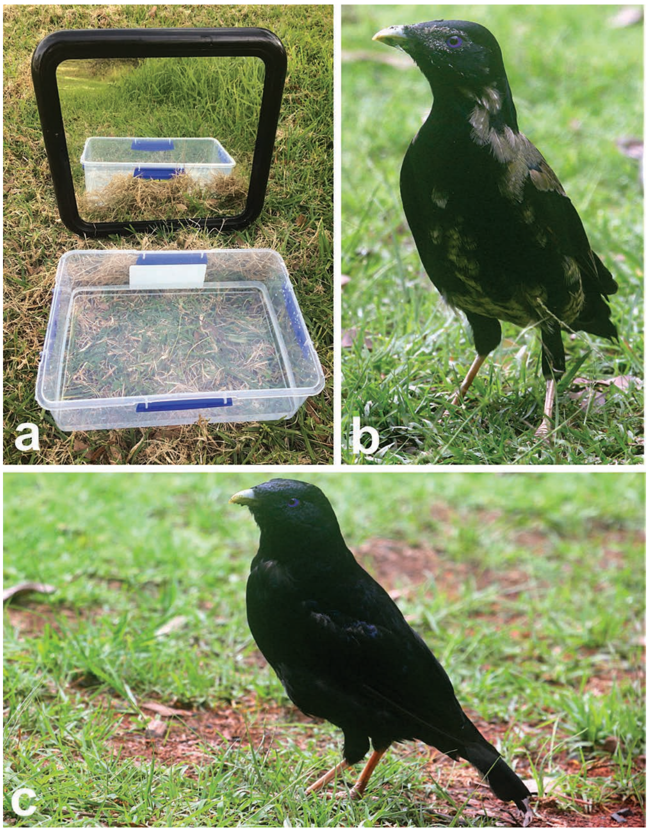

Figure 1: a An example of the simple set-up used in this study to collect scats. It requires a mirror to be placed in front of a shallow tub of water with enough room for the male bowerbird to perch and interact with his reflection while depositing scats in the tub of water. These scats were later collected, washed and sown into potting mix. **b** A nearly mature male with the mottled pattern that develops as he moults into his adult male plumage. Nearly mature males such as this one occasionally visited our stations, but not as frequently as adult males. **c** An adult male in full adult plumage. These males were the primary users of these stations.

The scats were removed from the tubs and the seeds cleaned with water and identified to species before being sown in potting mix. We have been unable to find a comprehensive identification reference for seeds of our region; seeds were identified based on previous experience with seeds found in the surrounding area, and any ambiguous identifications were confirmed once the seedlings germinated and began to grow. Several potting mixes were used, and the composition of the mix varied substantially depending on what was available (all mixes had previously proven successful in germinating and growing rainforest trees from the same area). Seeds were sown in a range of pot sizes placed in shade houses, and all pots were watered as needed. Notes were taken on which species successfully germinated. All successfully germinated trees were eventually planted as part of forest regeneration efforts in the surrounding area.

Results and Discussion

Based on approximately 2,500 scats, we found the fruits of 37 plant species representing 22 families to be eaten by satin bowerbirds (Table 1). Both sites where tubs were placed are adjacent to large intact areas of native bush with very few weed species, so we did not determine if satin bowerbirds might disperse weeds. It is possible that they may eat and disperse common non-natives such as *Cinnamomum camphora* or *Ligustrum lucidum*, but these species were absent from the locations we sampled. Bush regenerators who might try to apply this method should be aware of the areas where bowerbird scats are sourced, since the species composition of their habitat directly impacts the species that occur in their diets and scats. Only once during the course of this study were seeds of a non-native plant encountered in a scat; these were *Asparagus officinalis* seeds that were being cultivated in the first author's nearby vegetable garden. This instance was not included in the study.

Of the 37 species detected in scats in this study, all but two taxa (*Persoonia media* and *Trochocarpa laurina*) germinated. We have been unable to successfully germinate these two species regardless of seed source (even when ripe fruit was collected directly from the plant). These two genera are known to have dormant seed that can be difficult and/or slow to germinate (Campbell et al. 2012; Emery & Offord 2018; Emery & Offord 2019), so the lack of germination may just indicate that dormancy was not relieved by passage through the bowerbird gut. We were primarily focused on woody plants for regeneration efforts, so we have possibly overlooked herbaceous plants that might be ingested and dispersed by satin bowerbirds.

Since this study was focused on developing a method to collect viable seeds, we were interested in determining which plant species were being eaten by the birds and which species were viable after passage through the gut. We did not collect data to compare germination rates or percentages of seeds that were ingested versus seeds that were hand-collected. Based on experience of germinating these species from hand-collected seeds, we can highlight four tree species that appear to germinate more readily after being consumed by satin bowerbirds; however, additional study is still needed for further confirmation. *Elaeocarpus reticulatus* and the three *Polyscias* species, *Polyscias elegans*, *Polyscias murrayi* and *Polyscias sambucifolia* (Table 1), generally have comparatively low germination rates when seeds are harvested directly from the plant, but germination success is much higher when seeds are collected from satin bowerbird scats. *Dysoxylum fraserianum* and *Synoum glandulosum* also appear to have better germination rates when seeds are collected from satin bowerbird scats compared to seeds collected and cleaned by hand. For successful germination of many plants, it is important to clean off the fleshy coatings around the seeds (Mirov & Kraebel, 1939; Broschat & Donselman, 1987). Cleaning seeds of some rainforest trees can lead to accidental damage of seed coats (particularly in these two species), which reduces their viability. The difference we noticed in their germination from scats may be a result of collecting and processing methods rather than gut scarification.

Satin bowerbirds appear to primarily collect ripe fruit; scats therefore tend to have good material for propagation. When collecting seeds from *Myrsine howittiana* and *Myrsine variabilis* plants, it is difficult to determine which individual fruits are actually ripe, and germination rates tend to be low. Seeds collected from scats generally appear to have better germination rates, perhaps due to the fact that satin bowerbirds seem to choose the ripest fruit, and/or the seeds may benefit from scarification.

Schizomeria ovata is notoriously slow and difficult to germinate; Floyd (2008) reports its germination to be very erratic, sometimes taking up to nine years. It seems possible that this lengthy period of germination could be due to a lack of scarification by a frugivore, but in this study it took up to 18 months to germinate regardless of where the seeds were sourced (after 18 months, pots with ungerminated seeds were discarded due to limited shade house space). Based on our observations, it seems unlikely that bowerbirds improve *Schizomeria* germination rates. Floyd (2008) recommends cuttings as a more successful method to grow this species.

The seeds of many plants eaten by satin bowerbirds are easy to harvest and germinate without collecting them from bowerbird scats, but it can be difficult to collect fruit or seeds from the larger rainforest trees that fruit high up in the canopy, like *Citronella moorei*, *Diospyros pentamera* and *Sarcopteryx stipata*. Since satin bowerbirds feed on the ripe fruit and inadvertently carry seeds, their scats are an ideal source of viable seeds for these and other tall rainforest trees. We would struggle to source seeds from these species without the help of bowerbirds.

Based on observations of satin bowerbird feeding behaviour, Green (1993) reported 11 species of fruit in eight families as food sources, including four that we observed and seven species that we did not (Table 1); she did not test seed viability. Marshall (1932) observed satin bowerbirds feeding on four species in three families that were not recorded elsewhere, but he did not test germination. Without attempting to germinate the seeds, we can only speculate about the viability of these additional 11 species. But based on the combined data in these three studies, it is apparent that fruit of at least 48 plant species in 27 families are food sources for satin bowerbirds; some benefit from enhanced germination, and most species—or possibly all—benefit from seed dispersal.

Table 1: The 48 plant species in 27 families known to be eaten by satin bowerbirds (*Ptilonorhynchus violaceus*) and their viability from scats.

Viable column: **Yes** = viable in germination tests performed in this study; **No** = failed to germinate in this study; **Not found =** not found in the scats of birds sampled in this study.

Other Records: Marshall = observed by A. J. Marshall to be eaten in the Sydney region. **Green =** observed by R. J. Green to be eaten in and around Lamington and Border Ranges National Parks in northeastern New South Wales.

**Ficus muelleriana* (South Coast Fig) is a name used in Marshall (1932) for a fig supposedly eaten in the Kiama District of NSW. To the best of our knowledge, this species name is misapplied unless Marshall is reporting consumption of the fruit of an introduced African species.

Family	Species (common name)	Viable	Other Records
Araliaceae	*Polyscias elegans* (Celery Wood)	Yes	
	Polyscias murrayi (Pencil Cedar)	Yes	
	Polyscias sambucifolia (Elderberry Panax)	Yes	
Arecaceae	*Linospadix monostachyos* (Walking Stick Palm)	Yes	
Asteliaceae	*Cordyline stricta* (Narrow-leaved Palm Lily)	Yes	
Boraginaceae	*Ehretia acuminata* (Koda)	Not found	Green
Cardiopteridaceae	*Citronella moorei* (Churnwood/Soapy Box)	Yes	
Cunoniaceae	*Schizomeria ovata* (Crabapple)	Yes	
Dilleniaceae	*Hibbertia scandens* (Yellow Guinea Flower)	Yes	
Ebenaceae	*Diospyros australis* (Black Plum)	Yes	
	Diospyros pentamera (Myrtle Ebony)	Yes	Green
Elaeocarpaceae	*Elaeocarpus obovatus* (Hard Quandong)	Not found	Green
	Elaeocarpus reticulatus (Blueberry Ash)	Yes	
	Sloanea woollsii (Yellow Carabeen)	Yes	
Ericaceae	*Trochocarpa laurina*	No	
Eupomatiaceae	*Eupomatia laurina* (Bolwarra)	Yes	
Fabaceae	*Acacia binervata* (Two-veined Hickory)	Yes	
	Acacia melanoxylon (Blackwood)	Yes	
Lamiaceae	*Vitex lignum-vitae* (Yellow Hollywood)	Not found	Green
Lauraceae	*Cryptocarya foveolata* (Mountain Walnut)	Yes	
	Cryptocarya glaucescens (Jackwood)	Yes	
	Cryptocarya meisneriana (Thick-leaved Laurel)	Yes	
	Cryptocarya rigida (Forest Maple)	Yes	
Meliaceae	*Dysoxylum fraserianum* (Rosewood)	Yes	
	Synoum glandulosum (Scentless Rosewood)	Yes	
Moraceae	*Ficus macrophylla* (Moreton Bay Fig)	Not found	Green
	**Ficus muelleriana* (South Coast Fig)	Not found	Marshall
	Ficus rubiginosa (Port Jackson Fig)	Not found	Marshall
	Ficus superba (Deciduous Fig)	Not found	Green
	Ficus watkinsiana (Strangling Fig)	Not found	Green
Myrtaceae	*Acmena ingens* (Red Apple)	Not found	Green
	Acmena smithii (Creek Lilly Pilly)	Yes	Green
	Archirhodomyrtus beckleri (Rose Myrtle)	Yes	
	Syzygium australe (Brush Cherry)	Yes	
Primulaceae	*Myrsine howittiana* (Brush Muttonwood)	Yes	
	Myrsine variabilis (Muttonwood)	Yes	
Proteaceae	*Persoonia media*	No	
Ripogonaceae	*Ripogonum discolor* (Prickly Supplejack)	Yes	
Rosaceae	*Rubus* sp. (Wild Raspberry)	Not found	Marshall
Rubiaceae	*Psychotria loniceroides* (Hairy Psychotria)	Yes	
Rutaceae	*Acronychia oblongifolia* (White Aspen)	Yes	Green

Family	Species (common name)	Viable	Other Records
Sapindaceae	*Alectryon subcinereus* (Bird's Eye)	Yes	
	Diploglottis australis (Native Tamarind)	Yes	Green
	Guioa semiglauca (Guioa)	Yes	
	Sarcopteryx stipata (Steelwood/Corduroy)	Yes	
Sapotaceae	*Planchonella australis* (Black Apple)	Not found	Marshall
Trimeniaceae	*Trimenia moorei* (Bitter Vine)	Yes	
Vitaceae	*Cissus hypoglauca* (Five-leaved Water Vine)	Yes	

Though we did not systematically observe what plant species were predominant in the satin bowerbird diets, this study highlights the reliance of this bird on a diverse fruit-bearing plant community. On the Dorrigo Plateau, in years of heavy fruit set by *Elaeocarpus reticulatus*, it was apparent that this fruit was a preferred food and often formed a high percentage of satin bowerbird diets. We have observed topknot pigeons (*Lopholaimus antarcticus*) eating the fruit and possibly dispersing the seeds of *Acronychia oblongifolia*, *Cissus hypoglauca* and *Schizomeria ovata*; however, we have not tested seed viability after consumption by topknot pigeons. We have also observed brown cuckoo-doves (*Macropygia phasianella*) and Lewin's honeyeaters (*Meliphaga lewinii*) regularly eating the fruit of *Archirhodomyrtus beckleri,* but we have yet to test the viability of these seeds. Other frugivorous bird species are undoubtedly important seed dispersers in the region, but we have been unable to develop a way to attract them and consistently collect their scats.

We suspect that other members of the Ptilonorhynchidae may also be important seed dispersers in Australia and New Guinea. In far north Queensland, for example, 51 species of seeds were found in the scats of the tooth-billed bowerbird (*Scenopoeetes dentirostris*), many of which germinated from the scats (Moore, 1991). According to Moore, tooth-billed bowerbirds frequently visited and deposited seeds in areas that had been logged. We have observed that satin bowerbirds frequently flock in or around small clearings or disturbed sites; they are likely functioning similarly to tooth-billed bowerbirds by bringing seeds of many rainforest species into these disturbed areas, helping to reforest disturbed landscapes.

This study focused on a relatively small region, but many of the plant species and/or genera consumed and dispersed by satin bowerbirds are more widely distributed. Approximately two thirds of the trees in northeastern New South Wales and southeastern Queensland produce fleshy fruit (Williams et al., 1984). These fleshy fruits are ideally adapted for avian dispersal, and although many of them have not been studied, we suspect satin bowerbirds are playing an important role in their dispersal. There is incomplete data on the movement patterns and passage rates of seeds among satin bowerbirds, so we can only speculate about the possible distance they may be dispersing seeds. One study showed that immature males can have home ranges of up to 28.67 ha (Maxwell et al. 2004). We suspect the 48 species recorded (Table 1) are only a fraction of the diversity that is ingested and dispersed.

We hope this study will generate interest for more detailed and systematic studies throughout the range of the satin bowerbird in eastern Australia.

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