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Tooth-billed Bowerbirds *Scenopoeetes dentirostris* select leaves of an introduced species as a novel court ornament following major habitat disturbance

J.D.A. Grant[1]*, C. Bailey[2] and C. Morris[3]

[1]Mailbag 71, Yungaburra QLD 4884, Australia
[2]P.O. Box 541, Hurley, New York 12443, United States of America
[3]1141 Colusa Avenue, Berkeley California 94707, United States of America
*Corresponding author. Email: jack.grant@sit.edu

Abstract. Following major forest disturbance by Cyclone Larry in 2006, Tooth-billed Bowerbirds *Scenopoeetes dentirostris* commonly used leaves of the introduced Wild Tobacco *Solanum mauritianum* as court ornaments, whereas these leaves were very rarely used beforehand. Their use continued for up to 12 years, declining in parallel with their availability. Leaf traits considered likely to influence ornament choice (e.g. size, brightness, retention of colour) were investigated for tobacco and other commonly used plant species, but none of these traits clearly accounted for the patterns of leaf choice. Nor did observations support a cultural basis for leaf choice, with birds in widely separated groups using tobacco leaves. Observed longer-term shifts in leaf choice and the availability/use data lead to the suggestion that the increased abundance of tobacco plants after the cyclone may have triggered the use of its leaves as a 'novel' resource.

Introduction

The Tooth-billed Bowerbird *Scenopoeetes dentirostris*, endemic to the Wet Tropics bioregion of north-eastern Queensland, is one of the more primitive members of the bowerbird family (Ptilonorhynchidae). Molecular studies place it near the base of the family's phylogenetic tree (Kusmierski *et al.* 1997; Endler *et al.* 2005), and its behaviour accords with that position: it is the only 'true' bowerbird (i.e. polygynous, court- or bower-attending members of the family) whose males do not construct a bower (see Frith & Frith 2004). During the breeding season, males of this species maintain a display court (cf. Frith 2016), an area of forest floor cleared of litter and decorated with upturned leaves. Court decorations are often consistently dominated by leaves of the same plant species (herein 'leaf species') within clusters of courts recently termed 'exploded leks' since males are in aural but not visual contact while singing over their courts, but hereafter referred to simply as 'groups' because lekking has not been convincingly demonstrated (Frith 2016). However, the leaf species used vary greatly between localities, and this is sometimes regarded as being indicative of local cultural influences (Frith & Frith 2004), such as are at play in the complex behaviours of some other bowerbirds (see Madden 2008).

The impetus for this study came from the observation that many males from several groups displayed novel leaf choices following intense disturbance by severe tropical Cyclone Larry, which crossed northern Queensland on 20 March 2006. The cyclone tracked across the Atherton Tablelands, where the Tooth-billed Bowerbird is a common rainforest species above ~600 m above sea level (asl). Widespread disturbance resulted in pronounced vegetation change, particularly canopy opening (Catterall *et al.* 2008; Kanowski *et al.* 2008), leading in turn to proliferation of early successional plants including many introduced species (Murphy *et al.* 2008). Wild Tobacco *Solanum mauritianum* (hereafter referred to as 'tobacco'), naturalised in Australia since *c.* 1883 (Symon 1981), was one of the species that flourished in the wake of the cyclone, and the following year this species was noticed as a common court ornament of several groups (see Figure 1). Previous surveys (2002 and 2005) on the eastern Tablelands had shown it to be rarely used, with a single leaf recorded in one season across 42 courts (JDAG unpubl. data). This dramatic shift in leaf preferences raises intriguing questions about the basis on which leaf species are chosen, for example whether environmental influences (such as availability) are as important as putative cultural effects, and what role is played by the characteristics of the leaves themselves. To date, the only systematic examination of the basis on which leaf species are chosen was by Panayi (2016), who found that leaf size, brightness and decay rate are among the most important factors.

Relevant sexual selection theory might predict that (i) size and colour of leaf ornaments, as proxies for their conspicuousness, should be important given pre-existing sensory bias in females (see review by Fuller *et al.* 2005); and (ii) leaf characteristics that affect time taken to collect

Figure 1. A male Tooth-billed Bowerbird (lower right) approaches his court with a leaf of Wild Tobacco. Photo: J.D.A. Grant

and maintain ornament displays could function as proxies for male effort, and thus as a basis for female selection under the 'good genes' scenario (see Andersson 1994).

The aim of this study was to describe the use of tobacco leaves as a court ornament over the years following this major disturbance, and more broadly to assess how the use of this species illuminated the factors influencing leaf choice.

Study area and methods

Study area

This study was conducted on the eastern Atherton Tablelands, on private properties in the Lake Eacham area (17.286°S, 145.635°E). Some of these properties are within a 449-ha remnant of the original forest cover, which also includes the adjacent Crater Lakes National Park, and some are in smaller forest fragments within 1.5 km of that larger remnant. This area is at an elevation of 750–800 m asl, with a mean annual rainfall of ~1580 mm. The sites used were on basaltic soil, supporting Complex Mesophyll Vine Forest (Type 1b of Tracey 1982). The terrain is copiously dissected by mostly perennial watercourses, forming a network of ridges and gullies. Most Tooth-billed Bowerbird courts were sited on ridges, hill-tops and upper slopes, as is typical of the species (Frith & Frith 1994).

Court surveys

Courts were surveyed in the breeding seasons of 2002, 2005, 2007–2013, 2015, 2017 and 2018. Data were not collected in the 2006 season, which was truncated and had fewer birds than usual decorating courts, presumably because of the highly disturbed conditions and shortage of fruit following the cyclone (Freeman & Vinson 2008). In most years, some courts were active as early as mid July and as late as late January, but surveys began in September and finished in December each season, capturing the months when most males were attending their courts. Each court was surveyed a minimum of six times per season. The number of groups included was consistently five (with a total of 42 courts) between 2002 and 2007, but varied afterwards as (i) the sample size was increased to seven groups (51 courts) in 2008 and (ii) the number of occupied courts in the same seven groups declined to between 34 and 38 over the ensuing years (see Freeman & Vinson 2008; Freeman *et al.* 2018). Courts were located each season by listening for singing birds, allowing any new courts to be included in the study. It was assumed that all the birds in each group were audible from at least some of the other courts, since the song carries at least 100 m through the forest (JDAG unpubl. data). All courts were plotted by GPS. Leaves on each court were identified and counted during November each year, part of the 'peak' season as noted by Frith & Frith (1994), including only those on the cleared area, i.e. the court proper, and excluding leaves discarded to the sides of the clearing. Any decayed leaves found on the court were assumed to have fallen from above and were not counted.

Leaf characteristics

The six most commonly used leaf species—Needlebark *Macaranga subdentata* (comprising 62.3% of all leaves used in the study), Red Tulip Oak *Argyrodendon peralatum* (11.9%), Rusty Laurel *Cryptocarya mackinnoniana* (9.7%), Tobacco (6.9%), Brown Tamarind *Castanospora alphandii* (3.9%) and Northern Red Ash *Alphitonia whitei* (3.8%)—were examined to compare a range of characteristics hypothesised to be involved in leaf selection: size, reflectance, petiole strength, and durability on the court.

Size (area) of leaves used as court ornaments was measured using image analysis software (Digimizer, version 5.1.2, Medcalc Software): three samples of each leaf species from each of five courts (selected by presence of all six leaf species) were photographed on the courts with a scale measure placed alongside. The 15 area measurements for each species were averaged. Size was assumed to be related to conspicuousness of the ornaments on a court, and thus representative of ornament quality.

Fresh samples (picked from the trees rather than collected from courts) were measured for reflectance to assess brightness, another measure of how visually conspicuous the leaves are on the court (all courts studied were on the same basaltic soil type, so the contrast with the ground varied mainly in accordance with leaf brightness). Two samples of each species were assessed individually. Each leaf was placed upper surface down on a piece of black velvet and all outside light blocked by covering the setup with more black velvet. An illumination source (200–1050 nm) was shone on them and moved to five different locations on each leaf. An Ocean Optics USB 2000 spectrophotometer was used to measure reflected wavelength intensities. The spectral data from these locations were averaged, and brightness was then calculated by summing each species' reflectance from 370 to 700 nm (the approximate visual spectrum for birds).

Next, the strength of the petiole was assessed to gauge the relative difficulty or time taken to collect leaves of each species by the bird, which bites through the petioles to gather leaves for his court (see Frith & Frith 2004). Petiole strength was measured with a weighted blade apparatus consisting of a commercially available (Stanley knife) blade mounted perpendicular to a small spring-mounted piece of plywood. The leaf petiole was positioned beneath the blade, and weight was applied to the apparatus by means of a plastic container sitting on the plywood, which was filled with water until the leaf petiole was fully severed. The weight of water added to the empty container was recorded as an index of the force required to sever the petiole. Five petiole samples for each species were tested and the results averaged.

Leaves were assessed for durability on the court by investigating how long the original leaf colour and shape were retained, since leaves are typically removed from the court as they become discoloured and/or curled because of desiccation (Grant & Laurance 1991). Five samples of each leaf species, freshly collected, were placed upper surface down on an artificial 'court', a cleared area of forest floor near one of the study groups, so exposed to similar conditions of temperature, humidity and shade. The samples were checked twice daily for changes in colour and shape (compared with fresh specimens).

In November of the 2012 season, a series of marking experiments was conducted to gather more detailed information on the turnover of leaves of four groups (20 courts). Leaves were individually marked on the groundward surface (upper surface when on the tree), each with a code that also included court number. Checks at intervals of 2–3 days enabled tracking of leaf longevity and the rate at which new leaves were added.

Availability of tobacco

From 2008 onwards, sources of tobacco leaves were surveyed in the vicinity of each group that was studied. Most of the plants were distributed along roadsides and other forest edges and were easily located, but intensive searches were also conducted within forest to find any plants growing closer to courts than the nearest known forest-edge specimens. All tobacco locations were plotted by GPS, and distances from each plant to the courts in the closest group were calculated on ArcGIS. The known plants were monitored each season and any new plants noted, to determine changes in availability over time. All tobacco plants within 100 m of any court were recorded; sampling this limited area was considered adequate since male Tooth-billed Bowerbirds remain within a relatively short distance of their courts (median movement 40–86 m) during the breeding season (Frith *et al*. 1994).

Results

Tobacco use and availability

Before Cyclone Larry, court surveys in 2002 and 2005 recorded one tobacco leaf (of 3709 leaves counted) on 42 surveyed courts. Tobacco use increased dramatically after the cyclone, and it was used as a court ornament on 40% of courts in the study area in 2007, occurring in four of six groups surveyed (Figure 2). Three of these four groups were in the main forest remnant, up to 800 m apart, and the fourth was in a separate remnant, 1.6 km from the nearest group. The remaining 60% of courts (including many in groups where tobacco was used) featured only leaves of the same species as used before the cyclone, indicating that the previously favoured leaf species were still readily available. Tobacco use increased in frequency over subsequent years to a peak in 2012, when it was used on 53% of courts, and gradually declined in use thereafter until only a single male was using it in 2017. This bird collected leaves from two tobacco bushes on the forest edge within 25 m of its court, but use of tobacco leaves on this court ceased early in the 2018 season. The numbers of leaves used on courts showed a similar pattern but peaked earlier, with tobacco comprising a mean of 52% of leaves on courts where it was used in 2008 (Figure 3). The maximum numbers per court were also seen in 2008, with four courts showing >90% tobacco leaves, including two at 96%. Between 2008 and 2013, tobacco ranked as the third most used court ornament overall (Table 1), comprising 11% of all leaves at the height of its use in 2012, and 19% of leaves on the courts where it was used.

Availability of tobacco changed over time also: the plants growing in forest gaps, and some of those on forest edges, were clearly recent colonists when first censused

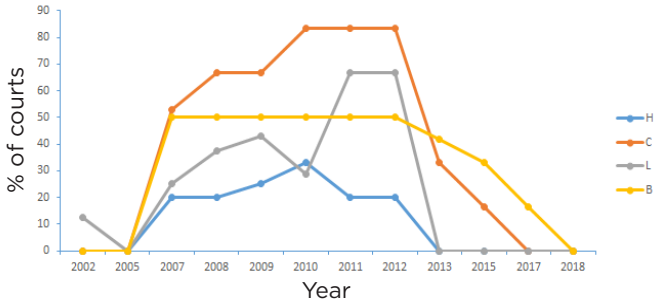

Figure 2. Percentage of courts with Wild Tobacco leaves used as court ornaments, from four groups (H, C, L, B) of Tooth-billed Bowerbirds, Lake Eacham area, Atherton Tablelands, Queensland, in 2002–2018. The number of courts in each group changed over time (see text) but modal numbers were H: 6, C: 9, L: 5, and B: 8.

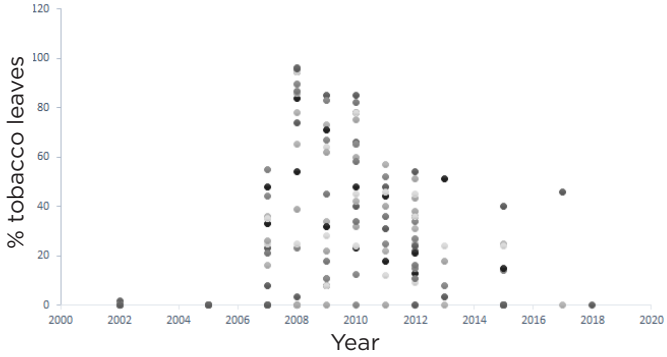

Figure 3. Percentage of Wild Tobacco leaves on Tooth-billed Bowerbird courts, 2002–2018. Data are for court surveys in November of each year. Each point represents tobacco leaves as a percentage of all leaves on a single court; variation in shading of points is simply to assist viewing. Sample sizes of courts were: 42 (2002–2007, 2009), 51 (2008), 38 (2010), 34 (2011), 36 (2012), 37 (2013, 2015) and 35 (2017, 2018).

in 2008, as judged from their small size and limited woody development. Between 2008 and 2018, there was a gradual decline in the number of tobacco plants recorded (Figure 4); this was mainly because of the death of plants in forest gaps and edges as the canopy regenerated and shaded them out. The use of tobacco leaves as ornaments ceased in 2018, at a time when the last plants used had declined markedly in health and were producing fewer and smaller leaves than previously.

Distance to the nearest tobacco plant was strongly implicated as a determinant of its use as a court decoration: of 19 males using tobacco in 2008, 60% had courts within 50 m of a tobacco plant, and 90% were within 100 m of a plant. Although some non-using males were within 50–100 m of the nearest tobacco plant, the majority (72%, n = 21) were >100 m away. Overall, the courts of tobacco users were significantly closer to tobacco plants than those of non-users (t-test, P = 4.20E–07). Among tobacco-using males, in November 2008 there was a strong correlation between the mean number of tobacco leaves on a given court and distance of the court from the nearest tobacco plant (R^2 = –0.79, P <0.001) (Figure 5). In November 2012, no significant relationship between these variables was evident (R^2 = –0.24, P >0.05).

Table 1. Use of the six leaf species most commonly included as court ornaments, as monitored during intensive surveys of 20 Tooth-billed Bowerbird courts in November 2012: percentage of courts on which each species was used, mean number of leaves of each species per court and mean number of leaves added per court per day. Figures in parentheses are leaf numbers added as a percentage of mean number of that species on the court.

Leaf species	*% courts*	*Mean no. leaves/court*	*Mean no. leaves added/day*
Needlebark *Macaranga subdentata*	100	31.25	3.15 (11.2)
Red Tulip Oak *Argyrodendron peralatum*	40	17.75	0.99 (7.4)
Wild Tobacco *Solanum mauritianum*	55	11.00	1.10 (11.09)
Rusty Laurel *Cryptocarya mackinnoniana*	60	9.38	0.93 (11.72)
Brown Tamarind *Castanospora alphandii*	55	5.00	0.22 (5.6)
Northern Red Ash *Alphitonia whitei*	75	3.60	0.31 (11.86)

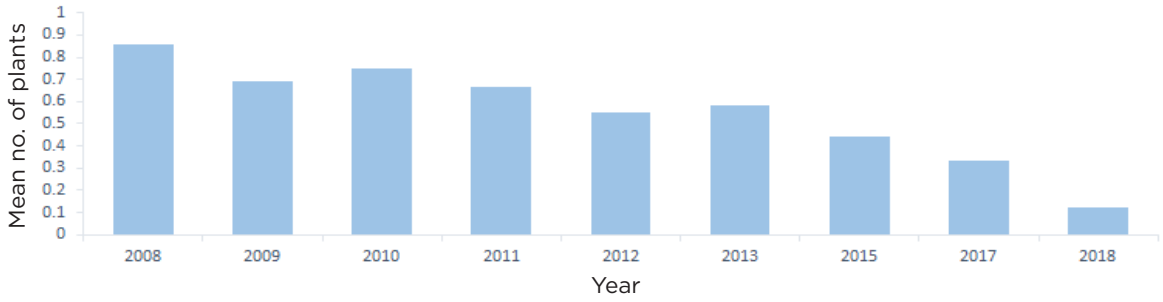

Figure 4. Abundance of Wild Tobacco plants within 100 m of Tooth-billed Bowerbird courts, 2008–2018. See Figure 3 for sample sizes of courts for each year.

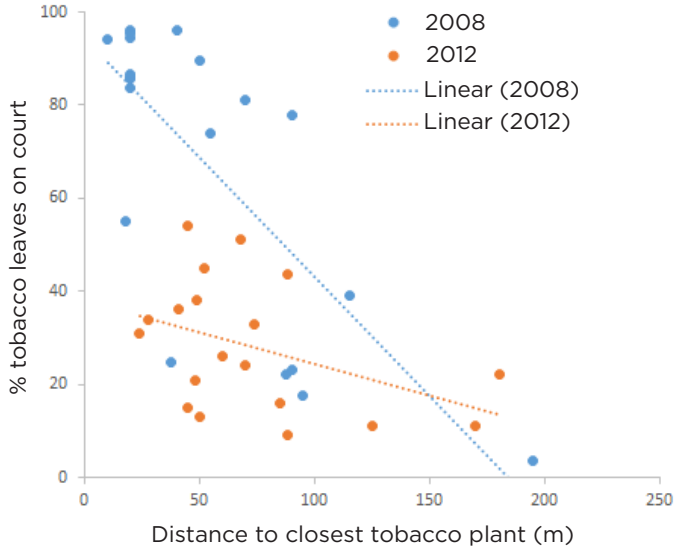

Figure 5. Wild Tobacco leaves as a percentage of all leaves on Tooth-billed Bowerbird courts, in relation to distance of nearest tobacco plant, in 2008 (n = 20 courts, R^2=–0.79, P <0.001) and 2012 (n = 19 courts, R^2=–0.24, P >0.05).

Leaf characteristics

The comparison of leaf characteristics showed that tobacco leaves ranked highly in terms of attributes that might make them superior court ornaments: they were on average larger than leaves of all other species used (Figure 6a), up to three times larger than the most commonly used species overall (Needlebark). Tobacco leaves also retained their original colour longest (Figure 6b) and their shape longer than any species except Red Tulip Oak (Figure 6c); leaves of most other species discoloured within 2–3 days and began to curl within 1–3 days. Tobacco leaves retained original colour for up to 1 week and never curled, instead becoming limp as they aged and remaining flat on the court. Leaves of Red Tulip Oak also performed well in this regard, retaining their original colour for up to 10 days, and remaining flat for 4 days. In addition, petiole strength was the lowest for tobacco, with other species ranging from 40 to 600% stronger (Figure 6d). Reflectance measurements showed that tobacco ranked third highest, with Red Tulip Oak and Northern Red Ash having brighter undersurfaces (Figure 6e).

Leaf-marking in 2012 revealed that the three most commonly used species were replaced on courts

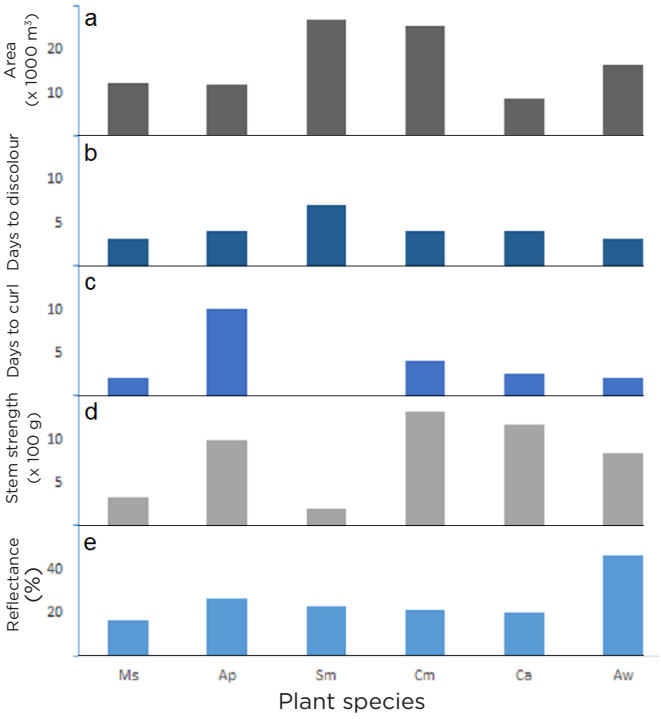

Figure 6. Characteristics of the six most commonly used leaf species on Tooth-billed Bowerbird courts: (a) leaf surface area; (b) number of days until leaf colour change; (c) number of days until leaf begins to curl (tobacco is excluded here because its leaves were never seen to curl); (d) stem strength as measured by weight required to sever stem (see methods); and (e) reflectance, shown as percentage of total. Leaf species are arranged from left to right by rate of overall use: Ms = Needlebark *Macaranga subdentata*, Ap = Red Tulip Oak *Argyrodendron peralatum*, Sm = Wild Tobacco *Solanum mauritianum*, Cm = Rusty Laurel *Cryptocarya mackinnoniana*, Ca = Brown Tamarind *Castanospora alphandii* and Aw = Northern Red Ash *Alphitonia whitei*.

(proportion of leaves of a given species on the court replaced per day) at rates that were not significantly different (ANOVA: F= 4.453, d.f.= 2,30, P >0.05) and in overall comparisons tobacco leaves were replaced at a similar rate to most other species (Table 1). Overall, the rate at which leaves of each species were added was not correlated with the mean number of that species found on the court (R^2 = 0.10, P >0.05).

Discussion

The use of tobacco leaves as a court ornament by Tooth-billed Bowerbirds, a rare occurrence in this study before Cyclone Larry, became commonplace and persisted for up to 12 years. Its use declined as the availability of the plant decreased, until in 2018 a single male used tobacco for just part of the season. Harrington (2011) described a change in ornament species in a group of Tooth-billed Bowerbirds, but the abrupt and transient change in court ornaments seen in our study in multiple groups is the first documented observation of its kind.

The most important influence promoting the sudden popularity of tobacco appears to have been the equally rapid change in its abundance in the study area following Cyclone Larry in 2006. Although no pre-cyclone estimates of tobacco abundance are available, many of the plants close to courts afterwards were young and occurred in newly created light gaps within the forest. The decline of tobacco documented between 2008 and 2018 is likely to reflect a return to pre-cyclone levels as the disturbed forest slowly regenerated (see Thompson *et al.* 2007). The local upsurge and subsequent decline of tobacco parallel the temporal pattern of its use as an ornament. Yet it seems likely that its use was not driven simply by availability, as leaf choice is also influenced by size, brightness and decay rate (Panayi 2016). Tobacco leaves are in a broadly similar size and colour range as the leaves of other ornament species, and these combined characteristics are undoubtedly important factors in its adoption. However, the extent to which it was used during this study period demands a fuller investigation.

Leaves of at least 38 species of plants have been recorded as court ornaments of Tooth-billed Bowerbirds (Frith & Frith 2004; Quill 2004; JDAG unpubl. data), but many questions remain about the basis on which leaves are chosen (Panayi 2016). Size and colour seem clearly related to conspicuousness, and as such are likely to attract the attention of females. The importance of size in selection of tobacco leaves is supported by the observation that the leaves chosen were at the top of the size range for that species whereas readily available smaller leaves were ignored. Panayi (2016) also demonstrated that male Tooth-billed Bowerbirds selected larger over smaller leaves of a species provided experimentally. It seems likely that the change in frequency of tobacco leaves on courts between 2008 and 2012 (see Figure 5), despite the presence of tobacco plants close to courts, was because of a decline in leaf size as the plants were shaded out by regenerating canopy. However, size was overall a poor predictor of the frequency with which leaves were used, as the two most commonly used species (Needlebark and Red Tulip Oak) ranked fourth and fifth respectively in terms of surface area. Panayi (2016) likewise found that size was not a good predictor of leaf species chosen, with no significant difference in leaf size of species used compared with those unused but also available in the vicinity of courts. In terms of leaf colour, the court presents as a show of pale leaves contrasting with the darker soil, but the leaf species used did not seem to be chosen mainly for their paleness. Of the six most commonly used species, Northern Red Ash had the highest reflectance yet was used the least. Conversely, Needlebark had the lowest reflectance, yet was the most frequently used decoration overall. An examination by Quill (2004) of black-light properties of a variety of leaf species used on courts found no obvious differences between species in ultraviolet reflectance, suggesting that cryptic visual cues are not significant. Nor was Needlebark favoured for its durability on the court, as its leaves were among the quickest to discolour and curl. The only characteristic for which Needlebark ranked highly was stem strength, for which it was the softest of the five native species tested, with only tobacco having a softer petiole.

Given the mismatch between most leaf characteristics and rate of use, it is possible that either (i) a combination of characteristics might influence the choice of leaf species or (ii) preference is determined by factors other than the leaf characteristics. Although no notable character combinations are intuitively obvious for the native species

examined, the combination in tobacco leaves of largest size, softest stem and relatively bright appearance might have influenced the extensive adoption of leaves of this plant as a decoration. However, no straightforward index of ornament quality is apparent. A reasonable proxy for quality may be the longevity of ornaments on the court (see Frith & Frith 2004), and initially it seemed possible that any preference for tobacco could be partially explained this way since the superior colour and shape retention might suggest that its leaves would need to be replaced less often; however, any advantage conferred was not detectable as tobacco leaves were added at a similar rate to those of other species. Another under-appreciated factor influencing leaf choice was indicated by Quill (2004), who found that ornaments of certain species (most notably Umbrella Tree *Schefflera actinophylla*) were regularly eaten by unidentified nocturnal folivores.

Leaf species used as ornaments vary greatly between and within localities, further obscuring our understanding of a hypothetical index of leaf quality. In the most extreme variation seen within a single forest patch in this study, one 2008 group used almost exclusively (92%) Red Tulip Oak, whereas three neighbouring groups (within a radius of 1 km) used only 6.5% Red Tulip Oak (on average) and heavily favoured Needlebark. In this case, the variation simply involved a difference in proportions of the two most widely used species in the area, whose relative use was also observed to change within seasons on individual courts, and moreover varied greatly between seasons. Although distinctly different ornament choices have been recorded between groups separated by longer distances, leading to the suggestion of local cultures (Frith & Frith 2004), long-term flux in patterns of leaf choice also occurs, whereby distinctive choices of ornaments have changed and appear to have stabilised at new selections. One instance of changing leaf choice was documented by Harrington (2011), who monitored a group of 10 banded birds. An unknown bird appeared in this study area, using a leaf species (Hard Alder *Pullea stutzeri*) new to the established local birds; following the interloper's 5-year tenure at this group, several of the local birds had adopted the new ornament and continued to use it for at least another decade. As noted by Harrington (2011), this could represent an example of social learning, presumably following the inspection of the new bird's court by the other residents. Another example of changing leaf choice occurred in group B in the present study, where Red Tulip Oak comprised 69% of ornaments when first recorded in 2002, but there was a gradual change to 75–78% Needlebark between 2013 and 2017. Similarly, the predominantly (>90%) Umbrella Tree ornaments of a 1988–1989 group documented by Grant & Laurance (1991) on the eastern Tablelands (6 km from the present study site) changed to a majority (~63%) of Ivory Basswood *Polyscias australiana* by 2005 (A. Freeman pers. comm.), and a group adjacent to our study area using mainly Hard Alder from at least 1999 to 2012 shifted to the more widely used Ivory Basswood by 2014 (JDAG unpubl. data). The latter two examples demonstrate that groups with distinct ornament choices may converge over time, and it is noteworthy that leaf use in both has converged with the very distant (~200 km south) Paluma Range groups studied by Frith & Frith (1994). Another relevant observation is that of Jackson (1909), who found that the Tooth-billed Bowerbirds of the Lake Eacham area in 1908 used mainly leaves of Grey Bollywood *Neolitsea dealbata*, a species never seen on courts during our study. Grey Bollywood is an early successional species that occurs commonly in forest gaps following disturbance (Goosem & Tucker 2013) and might have been readily available to bowerbirds in the unlogged forest of 1908 because of a recent (1906) cyclone that caused widespread disturbance in the region (Anon. 1906). Several of the leaf species most commonly used by Tooth-billed Bowerbirds, such as Ivory Basswood (Frith & Frith 2004), Umbrella Tree (Grant & Laurance 1991), Hard Alder and Northern Red Ash (our study) are likewise favoured by disturbance and must have greatly and permanently increased in abundance since logging and fragmentation of rainforests became widespread in northern Queensland over the past 100 years (Winter *et al*. 1987). These leaf choices suggest a broader relationship between availability and use, like that shown for tobacco in the present study.

The role of cultural mechanisms in determining variations in leaf choice is unclear. In a review of cultural aspects of bowerbird behaviour, Madden (2008) followed the lead of McGrew (2004) in proposing that culture is characterised by a suite of four behaviours: (i) learned (e.g. behaviours that are refined as individuals mature), (ii) socially transmitted (learned from conspecifics), (iii) normative (conservative, or varying within prescribed limits), and (iv) collective (varying more between than within subpopulations). The available evidence suggests that learning of leaf preference occurs in Tooth-billed Bowerbirds, since immature males initially decorate courts with a wider selection of leaves than do adults, and later refine their choices to match those of nearby males (Frith & Frith 1994; JDAG unpubl. data). Social transmission of ornament choices is also suggested by spatial variation in leaf species used (Frith & Frith 2004) as well as by the synchronous temporal variation within groups described above. As noted by Madden (2008), experimental examination of the processes involved is needed to clarify the role of social learning in these behaviours. The temporal shifts in ornament use reported in our study undermine the consistency expected in the normative and collective criteria for cultured behaviour; in particular, the selection of an introduced species' leaves suggests non-normative behaviour, especially in an evolutionary context. A cultural hypothesis would also predict that tobacco use, if spread as a result of social learning, should potentially lead to greater similarities within social groups than between groups (Madden *et al*. 2004; McGrew 2004). In the present study, the adoption of tobacco occurred across multiple groups, resulting in broad similarities between groups, the opposite of what might be predicted. Two of the tobacco-using groups were well separated from the others (800 m and 1.6 km), suggesting that the court owners at those groups began to use tobacco independently; Frith *et al*. (1994) recorded maximum movements of <400 m from their courts by males in the peak display season, so there seems to be little potential for transmission of this behaviour over the distances observed here. In addition, the use of tobacco was strongly related to its availability in the environment, a correlation that undermines one of the key criteria for assigning a cultural basis to bowerbird behaviour. Madden *et al*. (2004), for example, demonstrated a cultural influence by showing that Spotted Bowerbird *Chlamydera maculata* groups had distinct ornament preferences that were unrelated to their local availability.

It is possible that some of the Tooth-billed Bowerbird courts monitored in the present study were occupied by young males that had recently taken over courts. Vacant court sites might have become available because of the intense disturbance of the cyclone, or because of the fruit shortage following in its wake (see Freeman & Vinson 2008). A different set of court ornaments might be expected if young males were taking over sites (see above). However, of the court-holders that were aged (eight individuals) in the first season after the cyclone, all were adults as indicated by the black interior of the mouth (Frith & Frith 2004). This included four males that were decorating with tobacco leaves, one of whom was an adult banded in 1999. Thus, it seems less likely that the change in ornaments was because of a major demographic change in the population.

A new hypothesis may explain the above examples of changes in ornament choice, as well as the adoption of tobacco. This is a 'novelty' hypothesis, whereby periodic changes in ornaments occur in an attempt to engage female preferences. Female preference for novelty is a concept familiar in studies on sexual selection (Andersson 1994) and has been explored in relation to selection of rare objects as ornaments by bowerbirds (e.g. Frith & Frith 1990; Hunter & Dwyer 1997; Madden & Tanner 2003). Novel ornaments can be envisaged as influencing female assessment of courts—males presenting a novel selection of leaves would be rewarded with increased mating success in this scenario, leading to selection for further switching of ornament species. With a limited array of appropriate leaf species in any given locality, any advantage conferred by novel ornaments could be pursued by males periodically changing the species presented. Under average circumstances, this could be achieved by substitution of suitable species (those with appropriate display characteristics) from the selection available in the forest, but following major environmental change (such as after a cyclone or other large-scale disturbance) previously rare species could also be used for as long as they remain sufficiently abundant. Seen in this context, the flourishing of tobacco after the cyclone presented a ready-made novel resource that male bowerbirds could use to attract the attention of females. The spreading use of a novel ornament could occur through social learning. However, the observed pattern of variation in ornament choices seems difficult to reconcile fully with current ideas of 'culture' (Madden 2008), since it may involve loss of locally distinct preferences. Given the temporal shifts in leaf preferences reported here, the evidence for cultural transmission of leaf preferences is ambiguous. However, the behavioural complexities of decorating a court with multiple leaf species remain poorly understood, and deserve further investigation. In particular, a future study where mating success can be measured would greatly add to our understanding of this system.

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